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Abstract: Both the behavioural and the morphological analyses confirm the special role of the dewclaw in the cheetah: a strong hook to stop running animals by using the energy of the victim itself. However, this would hardly be an explanation for the rather large dewclaw in the puma. The present finding of the puma as an intermediate between the cheetah and other large felids for dewclaw size, supports the idea that, despite some later reversal to a more primitive, typically feline structure, the puma originated from felids like the fossil cheetah-like cat *Miracinonyx inexpectatus* of North America, which had longer, more cursorial limbs (though maintaining fully retractile claws) and, as far as one can judge from phalanx size, larger dewclaws than the extant puma.

Short communications

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The cheetah (*Acinonyx jubatus*) dewclaw: specialization overlooked

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INTRODUCTION

The cheetah *Acinonyx jubatus* is an atypical felid, well known for having blunt, only slightly curved, and only partly retractile claws, clearly an adaptation for high-speed locomotion in the pursuit of swift mammals. However, saying that prey 'is usually knocked down by the force of the cheetah's charge' (Nowak, 1999) is incorrect, because this predator actually relies on the claw of the first digit of the forepaw, the so-called dewclaw, to hook the fleeing prey off balance. Although (1) this was understood by Indian hunters through their use of tame cheetahs and published (Burton, 1950) in a natural history journal circulating well outside India, (2) wounds attributable to the dewclaws of cheetahs were later observed (Schaller, 1972) on prey animals in Africa, the area of most research on this felid, and (3) the information from India was finally reported (though with the wrong year in the citation) in an authoritative book on African mammals (Kingdon, 1977), no systematic study of the dewclaw itself, or of explicitly related questions, has been made. Perhaps the general connotation of the term 'dewclaw', as intended for a non-functional claw on a rudimentary digit as in the case of dogs, has masked the importance of what is not only a strongly curved and sharply pointed, but also a very large claw in the cheetah. In fact, this specialization of the cheetah has escaped the attention of behaviourists (Eaton, 1970), anatomists (Gonyea & Ashworth, 1975), and palaeontologists (Adams, 1979).

METHODS

The present investigation developed along 2 lines.

(1) Frame-by-frame analysis of filmed sequences of the predatory behaviour of large felids, videotaped from television. This involved 3 instances of tiger *Panthera tigris* preying on sambar *Cervus unicolor*, spotted deer *Axis axis* and Hanuman langur *Semnopithecus entellus*; 4 instances of lion *Panthera leo* preying on Burchell's zebra *Equus burchelli* and the blue wildebeest *Connochaetes taurinus*; 2 instances of leopard *Panthera pardus* preying on Thompson's gazelle *Gazella thompsonii* and hare *Lepus* sp.; 1 instance of puma *Felis concolor*

preying on the wapiti *Cervus canadensis*; 9 instances of cheetah preying on the blue wildebeest, the topi *Damaliscus lunatus*, gazelle *Gazella granti* and *G. thompsonii*, and hare.

(2) Measurement of the dewclaw and, for comparison, the claw of the second digit of the forepaw in museum specimens, pelts or skeletons. Dorso-ventral height at the ungual base was considered as a good indicator of the size of the claws with special reference to their hooking power, and a convenient measure because of frequently worn, broken or, for skeletons, missing horny claws. The measure was taken as height of the horny claws that were accessible up to base for pelts, whereas height of the ungual crest of the distal phalanx was measured for skeletons. Although some slight effect of the different methods could not be excluded for the absolute values obtained, within-specimen (pelt or skeleton) relative values were used to compare the species. One-way ANOVA with Tukey multiple comparison of the means was performed on the measure of the dewclaw with the measure of the second-digit claw covariant. This procedure met the requirement of a parametric variable for ANOVA better than using the claw ratio, though claw ratios are presented additionally for easier reference (Table 1).

RESULTS

The predatory sequences showed that tigers, lions and leopards all relied on a strong impact to strike the prey to the ground, though depending on the prey's size the action varied from a blow with one forepaw to the collision of the predator's entire body. All the claws of the forepaws and, in the case of large prey, even of the hindpaws too, were used by the predator as hooking tools to progress with the mouth towards the prey's neck, this being reached very quickly, often before the prey fell down. In the one sequence with a puma the predator's jaws seemed less important initially (for prey grasping), but the body impact seemed even stronger, as the puma leaped to the forequarters of the still deer after an accelerative dash and struck it with both forearms while taking full grasp with the forepaws. On the contrary, the relative speed of the cheetahs to their

Table 1. Comparison of large felids for dewclaw size^a

Species	Dewclaw	Second-digit claw	Claw ratio	Dewclaw corrected ^b	Tukey ^c
Tiger	28 ± 2.0	26 ± 2.0	1.1 ± 0.006	21 ± 0.47	*
Lion	30 ± 0.6	28 ± 0.5	1.1 ± 0.008	21 ± 0.61	*
Leopard	17 ± 1.3	16 ± 1.1	1.1 ± 0.010	21 ± 0.35	*
Puma	19 ± 0.5	15 ± 0.3	1.3 ± 0.014	24 ± 0.42	*
Cheetah	20 ± 0.7	14 ± 0.4	1.4 ± 0.025	26 ± 0.45	*

^a Measures of dorso-ventral height at ungual base, in mm. Mean ± SE from four specimens of each species.

^b By second-digit claw covariant.

^c Multiple comparison of means on dewclaw corrected. Asterisks in same column for homogeneous means at 95% confidence level.

fleeing victims was always low, which made the impact rather weak. All the nine sequences showed that only when the prey was on its back had the cheetah's jaws a main role, the well-known strangling action. Although four inexperienced cheetahs bit a standing wildebeest in various parts of the body during conjunct attacks, the prey escaped eventually. Also with small prey (hare) a cheetah seemed more reluctant than a leopard to use the mouth, initially. Irrespective of the prey's size the cheetah forced it down through a hampering action, trying to anchor one forelimb or both to the prey's body. Cheetahs 'hanging' on large animals (wildebeest) clearly showed dewclaws being their only hooking tools.

The analysis of dewclaw relative size (Table 1) met, in part, the behavioural observation. In the tiger, lion and leopard, the dewclaw is only slightly larger than the claw of the second digit, which matches the joint action of these (and the other) forepaw claws in predation. The cheetah clearly shows an enlarged dewclaw, as expected from the separate role of this claw. The intermediate size of the dewclaw of the puma is an unexpected result, however.

DISCUSSION

Both the behavioural and the morphological analyses confirm the special role of the dewclaw in the cheetah: a strong hook to stop running animals by using the energy of the victim itself. However, this would hardly be an explanation for the rather large dewclaw in the puma. The one behavioural sequence analysed in this study is in line with the habit of the puma making short-distance, surprise attacks (Nowak, 1999). For the massive action of limbs to strike the prey this felid seems closer to representatives of the genus *Panthera*, these showing no special size or use of their dewclaws.

When the novel idea of a close relationship between the cheetah and puma was proposed, their dewclaws were not taken into consideration: Adam's (1979) statement that the Old World cheetah lineage had the limbs specialized as 'strictly propulsive structures', is inaccurate because of the predatory dewclaw of the extant cheetah. The present finding of the puma as an intermediate between the cheetah and other large felids for dewclaw size, supports the idea (van Valkenburgh,

Grady & Kurtén, 1990) that, despite some later reversal to a more primitive, typically feline structure, the puma originated from felids like the fossil cheetah-like cat *Miracinonyx inexpectatus* of North America, which had longer, more cursorial limbs (though maintaining fully retractile claws) and, as far as one can judge from phalanx size, larger dewclaws than the extant puma. Therefore, although a more behavioural study may suggest some special adaptation of the puma's dewclaw, its rather large size may be a leftover character, instead.

Although the dewclaw seems to have an important role in the predatory function of the forepaw in all felids, and thus it is properly not a 'dewclaw', in the cheetah it seems to have taken on the predatory function of the entire forepaw, as the other claws lost this function because of locomotory adaptation. A special study of fossil felids with robust first digits, as well as of extant felids with large dewclaws, would help to understand the progress towards cheetah dewclaw specialization, which has perhaps occurred with less extreme outcomes along other lines of felid evolution.

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Between-litter siblicide in captive Indian false vampire bats (*Megaderma lyra*)

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INTRODUCTION

Sibling rivalry seems to contradict Hamilton's rule of maximizing inclusive fitness (Hamilton, 1964). However, when critical resources are scarce and the competitors are close kin the individual must weigh the direct versus the indirect components of its inclusive fitness (Mock & Parker, 1997). In facultatively siblicidal species, conflicts arise mainly because of the phenomenon of 'parental optimism', in which the parents attempt to raise a larger brood than the average amount of expected resources allow (Lack, 1954; Temme & Charnov, 1987; Mock & Forbes, 1995). If critical resources are low, weaker or subordinate offspring may be killed by a stronger or dominant sibling. Sibling mortality may result from direct physical damage and/or socially enforced starvation (Mock, 1984).

Facultative siblicide (aggression between siblings is sometimes so severe that one or more of them are killed; Mock & Parker, 1997) has been described in many avian species (reviewed in O'Connor, 1978; Mock, 1984, 1987; Mock & Parker, 1997) but rarely in mammals. Fatal sibling aggression in mammals has been documented in domestic pigs (Fraser, 1990), arctic foxes *Alopex lagopus* (Macpherson, 1969), red foxes *Vulpes vulpes* (Henry, 1985), spotted hyenas *Crocuta crocuta* (Frank, Glickman & Licht, 1991; Hofer & East, 1997) and Galapagos fur seals *Arctocephalus galapagoensis* (Trillmich, 1986, 1990). Siblicide in Galapagos fur seals is currently the only known example where the siblings were from different cohorts. Milk production in Galapagos fur seals is probably limited by maternal condition, and maternal condition may vary dramatically from year to year as a result of unpredictable changes in food resources (El Niño). As a result pups may be weaned between 1 and 3 years of age, and

mothers may simultaneously nurse offspring from different cohorts (Trillmich, 1986, 1990; pers. comm. in Mock & Parker, 1997).

Fatal sibling aggression in captive false vampire bats

During routine observations of a captive colony of Indian false vampire bats *Megaderma lyra*, housed in a room of c. 15 m² at the University of Munich (see Leippert, 1994), we observed a probable case of fatal sibling aggression. To our knowledge, this is the first observation of fatal sibling rivalry in a bat, and only the second observation of fatal between-litter sibling aggression.

Indian false vampire bats give birth to a single pup once a year between January and April (Balasingh, Subbaraj & Suthakar Isaac, 1994; Goymann, Leippert & Hofer, 1999), weaning in captivity occurs after c. 3 months and sexual maturity is reached after 15 months in males and 19 months in females (Tuttle & Stevenson, 1982).

False vampire bats were kept for breeding purposes and fed *ad libitum* with mice, a natural prey in their original habitat. The group consisted of three adult females (M-010, M-017, and M-009) and one adult male (M-016), all caught in caves around Madurai, Southern India, in 1991. Except for weekends, bats were routinely observed during their active period through a glass screen for 2–3 h/day.

Additional evidence came from a field study on a colony of free-ranging false vampire bats in Tirunelveli, India, where individually marked false vampire bats were observed during the breeding season in 1995 (for details see Goymann *et al.*, 1999).

On, 26 January 1993, M-010 gave birth to M-029, a female pup, and nursed it until the middle of May 1993. False vampire teats change colour from red to white when lactation stops (D. Leippert, pers. obs.). M-010's teats began to change colour on 10 May 1993, and were

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