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 huntsmen 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 thomsonii* 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 *Damastriscus lunatus*, gazelle *Gazella granti* and *G. thomsonii*, 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
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 retractive 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. 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.

### Acknowledgements

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### REFERENCES


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 m$^2$ 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
completely white on 17 May 1993. Even after weaning, M-010 and M-029 frequently roosted together, and participated in physical contact that involved touching each other’s belly and one embracing the other with its wing membranes (body-contact, Goymann et al., in press). In the captive colony this behaviour was only observed between mothers and their offspring, and in free-ranging false vampire bats the number of body-contacts per hour significantly dropped as the number of newborn pups increased during the breeding season (Spearman rank correlation: \( r_s = -0.54, n = 48, P < 0.001 \), suggesting that mothers with dependent pups engage less in body-contacts with other false vampire bats. M-029 also continued to suck from her mother’s teats after weaning, although during weekly routine examinations no milk could be detected in M-010’s milk ducts. Suckling after weaning was also observed in the other mother–daughter pair of the same year, M-017 and M-030.

A year later (the colony consisted of the same adults and the two yearlings), M-010 gave birth to another female pup, M-031, on 15 or 16 January 1994. M-029 was observed to suckle from her mother’s teats until 2 weeks before the birth of M-031. We observed M-029 repeatedly attacking M-031 on 10 different days during the first 2 weeks after M-031 was born. During these attacks M-029 opened her mouth, bared her teeth and emitted a broadband vocalization commonly uttered during aggressions (W. Goymann & D. Leippert, pers. obs.), and then tried to bite her younger sister who was hanging from the neck of her mother (Fig. 1). M-031 always retreated from these attacks, and thus M-029 was not observed to bite M-031 during observation periods. On 27 January 1994, however, M-031 was found dead on the floor of the roost with bite wounds in an eye and ear. When hunting, M-029 typically attacked the head of mice, biting at their eyes and ears, a killing tactic not employed by other members of the colony. This, and the fact that no other false vampire had behaved aggressively towards M-031 during the previous observation sessions suggested that M-031 was killed by her sister M-029.

**DISCUSSION**

Although M-031’s death was not directly observed the evidence suggests that she was killed by her sister M-029 because: (1) for the first 10 days after the birth of M-031, M-029 repeatedly tried to attack and bite her sister, and (2) the wounds on M-031’s head were consistent with those observed in prey killed by M-029, but atypical for wounds inflicted on prey by other members of the colony.

We consider it unlikely that this probable case of siblicide was an artefact created by increased aggression resulting from captivity. Indian false vampire bats in the Munich colony live in a relatively large and structured environment with crevices and other places to retreat. In general, aggression between false vampire bats in the colony was very low and did not include attacks that led to injuries. It is thus unlikely that housing conditions increased levels of aggression among members of the colony.

Is fatal sibling rivalry likely to occur in free-ranging false vampire bats? Detailed observations of individually recognized free-ranging mothers and their weaned offspring about the time of subsequent parturition have not been undertaken. It is possible, however, that mothers minimize the opportunity for between-litter sibling aggression by separating vulnerable young from older siblings, as has been proposed for various ground-nesting siblicidal birds (Ingram, 1959; Parmelee, Stephens & Schmidt, 1967; Harvey et al., 1968). Some mothers ‘park’ their young pups in special night roosts away from both the day roost and nocturnal foraging areas (Audet et al., 1991; Goymann et al., 1999), as individually marked pups were consistently found either in these night roosts or in the day roost (Goymann et al., 1999). ‘Parking’ pups in a night roost is likely to be energetically more costly to mothers than leaving pups in day roosts because of additional travel time and the weight of the pup. Pups may also incur additional energetic costs because temperatures at night in night roosts were similar to outside temperatures (25.8 ± 1.5°C, mean (SD), \( n = 30 \)) and significantly lower than temperatures at night in day roosts (30.6 ± 0.8°C, \( n = 24 \), Mann–Whitney U-test: \( U = 720, P < 0.0001 \)). We suggest that mothers with both a newborn pup and a sub-adult offspring from the previous year could minimize the risk of siblicide by ‘parking’ their pups in a night roost unknown to the sub-adult, instead of leaving them in the day roost, whereas mothers without sub-adults might be more likely to leave pups in day roosts. Leaving pups in night roosts may thus be a maternal adaptation to the conflict (Trivers, 1974) between parent and offspring about the allocation of maternal resources to different litters. If this is the case, mothers in captivity may not be able to separate cohorts effectively, since there is insufficient space to hide pups from sub-adult offspring.

In siblicidal species, monopolization of parental resources mainly occurs when these resources represent a major contribution to offspring growth and survival. Monopolization of parental resources is thus common in species with small litter sizes (O’Connor, 1978), prolonged intensive care, and/or unpredictable food resources, such as spotted hyenas (Hofer & East, 1993, 1996) and Galapagos fur seals (Trillmich, 1986, 1990; Mock & Parker, 1997). Litter size in Indian false vampire bats is usually one and lactation lasts for about 3 months, an unusually long period for non-fruit eating bats (Neuweiler, 1993). In the captive false vampire colony, mother and offspring maintained close contact and searched for each other using squeaking sounds (Habersetzer, 1983; Goymann et al., 1999) long after weaning, suggesting an extended period of parental investment.
Feeding ecology varies seasonally in an Indian false vampire population in Rajastan (Advani, 1981), where individuals tend to take a higher proportion of vertebrate prey (78%) during the cool season (December–February) and a higher proportion of insects (70%) during the rainy season (July–September). However, it is unknown whether food resources were limited or unpredictable at some time of the year and how foraging economics were influenced by variable proportions of vertebrate and invertebrate prey.

The possible benefits for a sub-adult false vampire of killing its newborn sibling may be:
(1) Direct gain by renewed access to maternal milk; unfortunately we could not ascertain this as M-029 was removed from the colony immediately after the death of M-031.
(2) Dependence on their mother to improve hunting skills, as hunting skills of sub-adult false vampire bats are poor compared to those of adults (D. Leippert, pers. obs.). In free-ranging Indian false vampire bats some individuals form small groups when emerging from day roosts (W. Goymann & D. Leippert, pers. obs.) and the same individuals repeatedly share hunting perches during the night. However, it is unknown whether these associated individuals are related and include sub-adults. We suggest that it is possible that the absence of a younger sibling may improve the survival of sub-adults if this extends the tutoring of sub-adult hunting by mothers, or if mothers share kills with sub-adults.
(3) If close relatives share the same feeding area then sub-adults may seek to eliminate future competitors, particularly those of the non-dispersing sex (Gowaty, 1993; Smale et al., 1995; Golla, Hofer & East, 1999). If false vampire bats follow the general mammalian pattern of males dispersing further than females (Greenwood, 1980; Stearns, 1992) then competition between sisters should be intense, consistent with our observation of sibling rivalry and probable siblicide.

In conclusion, Indian false vampire bats have life-history features compatible with the expectations of current theory on fatal sibling rivalry. However, we cannot rule out the possibility that the sibling aggression we observed was an artefact of captivity and thus may not be a sufficiently general phenomenon to require a

Fig. 1. Indian false vampire pup hanging from the neck of its mother. In this position M-031 was frequently attacked by its older sister M-029.
selectionist explanation. Further studies of false vampire bats are required to quantify the levels of competition between siblings, and to ascertain whether fatal sibling rivalry occurs in free-ranging populations.

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REFERENCES

Tooth succession in the greater cane rat *Thryonomys swinderianus* (Temminck, 1827)

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**Abstract**

Tooth succession was followed in captive greater cane rats *Thryonomys swinderianus* of known ages with the aid of regular radiographs. The incisors and single premolar tooth (dP 4/4) in each quadrant are persistent deciduous teeth that are not replaced by permanent teeth. Tooth succession is relatively slow, with eruption of the lower cheek teeth in advance of the upper ones. During the first 5 months of post-natal development, three cheek teeth per quadrant become functional. Another 5 months elapse before the fourth cheek tooth erupts. The same slow growth can be seen in the increase in mass, which only doubles 5 months after puberty (5 months).

**Key words:** tooth succession, tooth eruption, greater cane rat, *Thryonomys swinderianus*

**INTRODUCTION**

Cane rats, or ‘grass cutters’ occur throughout Africa south of the Sahara Desert, where the greater cane rat *Thryonomys swinderianus* is a semi-aquatic inhabitant of marshy areas (Feldhamer *et al*., 1999). It may reach high densities and cause significant damage to cultivated crops and plantations. Cane rats are important as a food source for many African cultures. The cane rats are hunted and used as bushmeat, or farmed, and large quantities of the meat are sold at markets (Ajayi, 1971; Asibey, 1974a,b; Martin, 1983; National Research Council, 1991; Feldhamer *et al*., 1999). They are the second largest rodents in Africa and have an average mass of 4.5 kg and 3.6 kg for males and females, respectively (Skinner & Smithers, 1990). Their dental formula is 1/1, 0/0, 1/1, 3/3 (Woods, 1984; present study) but little is known about the sequence of eruption in relation to age. The only known record where tooth eruption is correlated with age in the cane rat, is that of Asibey (1974a) who divided cane rats into three age groups according to the number of cheek teeth that have erupted.

The purpose of the study is to determine the age at which tooth eruption occurs in the greater cane rat in South Africa in captivity. This will not only be useful zoological information, but also will help cane rat farmers to determine the most suitable age for marketing.

**MATERIAL AND METHODS**

The jaws of 4 pups (2 males and 2 females) from 1 of the litters of the breeding colony of cane rats kept at the Agricultural Experimental Farm of the University of Pretoria (Van der Merwe, 1997), were radiographed every 2 weeks through to adulthood. The radiographs were taken by personnel of the Radiology Department at the Faculty of Veterinary Sciences, Onderstepoort, Pretoria. During each visit the pups were immobilized with ketamine hydrochloride by the anaesthetist of the Veterinary Science Faculty, Professor G. F. Stegmann. During each visit the animals were also weighed on an electronic balance and examined for good health. Additional information was obtained from other pups born in the breeding colony. The ages of all the pups used for this study were known from recorded birth dates, and individual animals were identifiable by marking, which was done by inserting injectable electronic transponders (small, model TX1400L) just beneath the skin of the neck. A mini Portable Reader MPR (Model HS5900; Destron-Fearing Corporation) was then used to read the transponders.

The sizes of the skulls at the various ages (Fig. 2a–f) are measurements taken of similar age skulls from the departmental skull collection (n = 112). The measurement used is defined as the condylobasal length of the skull (CBL) from the anteromost point to the back of the occipital condyles. Because there was no significant difference in the eruption pattern of the cheek teeth between males and females at ages up to the 4 cheek teeth stage, it was not necessary to treat them separately. The average size of 9 adult skulls (4 functional cheek teeth in each quadrant) was 92 mm (range 85–106).

In this study an erupted tooth is defined as one which has pierced the gum.

**RESULTS**

Table 1 illustrates the sequence of tooth succession in the greater cane rat. At birth the incisors have erupted.
Still level with that of the jaw bone. CBL = 38 mm.

Fig. 1. Skull of a greater cane rat pup that had died. In this pup the first cheek tooth (dP 4/4) was visible above the gum line, but not the second (M 1/1). In the cleaned skull it can be seen that the surface of the first cheek tooth in each quadrant is well above that of the second cheek tooth whose surface is still level with that of the jaw bone. CBL = 38 mm.

The premolars (dP 4/4) and first molars (M 1/1) are not yet visible above the gumline. Within a few days after birth the premolars become visible above the gumline (Fig. 1). At an age of 21 days the first cheek teeth (dP 4/4) are well established, with the lower M₁ visible above the gumline but not the upper M₁ (Table 1). Erupion of the lower teeth occurs in advance of the upper ones, as can be seen in 21 day old pups where the lower first molar (M₁) has erupted, while the upper first molar (M₁) has not yet pierced the gumline (Table 1; Fig. 2a). The same was found at the age of 122 days, when the lower second molar (M₂) was visible above the gumline, but not the upper second molar (M₂) (Table 1; Fig. 2d). At an age of 236 days the lower third molar (M₃) was visible above the gumline but not the upper third molar (M₃) (Table 1; Fig. 2f). From an age of c. 53 days to 110 days, two cheek teeth in both the upper and lower tooth-rows were functional (dP 4/4 + M 1/1). At the age of 53 days the position where the second molar is starting to develop in both the upper and lower jaws is clearly visible (see Fig. 2e for explanation). From an age of c.151 days to 214 days, three cheek teeth were functional in both the upper and lower tooth-rows (dP 4/4 + M 1/1 + M 2/2). At the age of 187 days the position in the upper and lower jaws where the third molars are beginning to develop was clearly visible (Fig. 2e). Only from an age of c. 278 days were all four cheek teeth functional in both toothrows (dP 4/4 + M 1/1 + M 2/2 + M 3/3). Although the lower teeth erupt in advance of the upper ones, thus leading to stages in the life cycle where there are more functional cheek teeth in the lower tooth-row than in the upper one, it is nevertheless possible to identify four age classes (Table 2).

Post-natal growth in the greater cane rat is slow. At 5 months old (151 days; three cheek teeth) the average mass of males and females is 1.5 ± 0.4 kg (average hindfoot length: 70.7 ± 3.5 mm) and 1.3 ± 0.3 kg (average hindfoot length: 65.5 ± 3.3 mm), respectively (see Table 1). It takes approximately another 5 months for the mass to double. At an age of c. 9 months (278 days) the mass of males and females is 2.5 ± 0.6 kg (average hindfoot length: 75.4 ± 1.7 mm) and 2.2 ± 0.3 kg (average hindfoot length 71.3 ± 1.4 mm), respectively.

Table 1. Tooth succession in the greater cane rat *Thryonomys swinderianus* (dental formula of adults: 1/1, 0/0, 1/1, 3/3). Sample sizes in parentheses

<table>
<thead>
<tr>
<th>Age (days)</th>
<th>Tooth succession</th>
<th>Average male mass (g) + sd</th>
<th>Male hindfoot length (mm) + sd</th>
<th>Average female mass (g) + sd</th>
<th>Female hindfoot length + sd (mm) + sd</th>
</tr>
</thead>
<tbody>
<tr>
<td>Newborn</td>
<td>I 1/1 C 0/0 dP +/+ M +/+ , <em>+/+</em></td>
<td>166.4 ± 20.7 (9)</td>
<td>38.6 ± 1.0 (2)</td>
<td>158.1 ± 22.7 (11)</td>
<td>38.9 ± 3.4 (4)</td>
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<tr>
<td>21</td>
<td>I 1/1 C 0/0 dP 1/1 M +/+ , <em>+/+</em></td>
<td>342.6 ± 44.9 (12)</td>
<td>48.2 ± 2.2 (11)</td>
<td>330.4 ± 45.2 (10)</td>
<td>46.9 ± 2.0 (7)</td>
</tr>
<tr>
<td>39</td>
<td>I 1/1 C 0/0 dP 1/1 M 1/1 , <em>+/+</em></td>
<td>510.4 ± 91.1 (13)</td>
<td>53.3 ± 2.7 (11)</td>
<td>504.0 ± 94.1 (13)</td>
<td>52.0 ± 3.4 (8)</td>
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<tr>
<td>53</td>
<td>I 1/1 C 0/0 dP 1/1 M 1/1 , <em>+/+</em></td>
<td>614.2 ± 111.2 (14)</td>
<td>56.5 ± 2.9 (11)</td>
<td>632.5 ± 132.7 (13)</td>
<td>54.7 ± 3.1 (8)</td>
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<tr>
<td>66</td>
<td>I 1/1 C 0/0 dP 1/1 M 1/1 , <em>+/+</em></td>
<td>672.9 ± 139.2 (14)</td>
<td>58.7 ± 3.5 (11)</td>
<td>689.5 ± 141.0 (13)</td>
<td>56.4 ± 3.5 (8)</td>
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<tr>
<td>81</td>
<td>I 1/1 C 0/0 dP 1/1 M 1/1 , <em>+/+</em></td>
<td>784.4 ± 185.8 (14)</td>
<td>60.5 ± 4.0 (11)</td>
<td>811.5 ± 199.6 (13)</td>
<td>58.0 ± 4.3 (8)</td>
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<tr>
<td>98</td>
<td>I 1/1 C 0/0 dP 1/1 M 1/1 , <em>+/+</em></td>
<td>886.2 ± 252.6 (14)</td>
<td>63.2 ± 4.4 (11)</td>
<td>895.9 ± 509.5 (13)</td>
<td>60.3 ± 3.6 (8)</td>
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<tr>
<td>110</td>
<td>I 1/1 C 0/0 dP 1/1 M 1/1 , <em>+/+</em></td>
<td>1067.1 ± 248.2 (13)</td>
<td>66.4 ± 3.0 (8)</td>
<td>1015.2 ± 243.3 (13)</td>
<td>62.9 ± 4.0 (5)</td>
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<td>I 1/1 C 0/0 dP 1/1 M 1/1 , <em>+/+</em></td>
<td>1166.8 ± 266.2 (13)</td>
<td>68.2 ± 4.0 (6)</td>
<td>1023.6 ± 353.7 (13)</td>
<td>57.5 ± 3.2 (8)</td>
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<td>I 1/1 C 0/0 dP 1/1 M 1/1 , <em>+/+</em></td>
<td>1340.2 ± 319.5 (13)</td>
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<td>1230.0 ± 248.3 (13)</td>
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<td>1484 ± 358.1 (13)</td>
<td>70.7 ± 3.5 (11)</td>
<td>1330 ± 266.7 (13)</td>
<td>65.1 ± 2.9 (9)</td>
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<td>167</td>
<td>I 1/1 C 0/0 dP 1/1 M 1/1 , 1/1</td>
<td>1647 ± 436.2 (13)</td>
<td>73.9 ± 3.3 (6)</td>
<td>1333 ± 413.2 (13)</td>
<td>67.2 ± 2.6 (11)</td>
</tr>
<tr>
<td>187</td>
<td>I 1/1 C 0/0 dP 1/1 M 1/1 , 1/1</td>
<td>1777 ± 497.1 (12)</td>
<td>72.1 ± 3.4 (8)</td>
<td>1592 ± 263.4 (13)</td>
<td>68.8 ± 2.1 (9)</td>
</tr>
<tr>
<td>201</td>
<td>I 1/1 C 0/0 dP 1/1 M 1/1 , 1/1</td>
<td>1890 ± 594.7 (12)</td>
<td>75.9 ± 2.8 (4)</td>
<td>1694 ± 277.5 (13)</td>
<td>69.1 ± 1.9 (11)</td>
</tr>
<tr>
<td>214</td>
<td>I 1/1 C 0/0 dP 1/1 M 1/1 , 1/1</td>
<td>2014 ± 590.2 (12)</td>
<td>73 ± 3.7 (12)</td>
<td>1781 ± 282.5 (13)</td>
<td>70.0 ± 1.7 (9)</td>
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<tr>
<td>236</td>
<td>I 1/1 C 0/0 dP 1/1 M 1/1 , 1/1</td>
<td>2199 ± 614.1 (11)</td>
<td>75.9 ± 4.5 (6)</td>
<td>1937 ± 283.6 (13)</td>
<td>69.9 ± 1.4 (11)</td>
</tr>
<tr>
<td>264</td>
<td>I 1/1 C 0/0 dP 1/1 M 1/1 , 1/1</td>
<td>2385.8 ± 601.1 (11)</td>
<td>76.2 ± 3.1 (9)</td>
<td>2084 ± 268.6 (13)</td>
<td>70.3 ± 1.4 (9)</td>
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<tr>
<td>278</td>
<td>I 1/1 C 0/0 dP 1/1 M 1/1 , 1/1</td>
<td>2544 ± 628.6 (11)</td>
<td>75.4 ± 1.7 (4)</td>
<td>2185 ± 251.6 (13)</td>
<td>71.3 ± 1.4 (6)</td>
</tr>
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</table>

• Tooth not visible in radiograph; + tooth visible but not erupted (i.e. not piercing the gumline).

Hindfoot length does not include the claw.

Post-natal growth in the greater cane rat is slow. At 5 months old (151 days; three cheek teeth) the average mass of males and females is 1.5 ± 0.4 kg (average hindfoot length: 70.7 ± 3.5 mm) and 1.3 ± 0.3 kg (average hindfoot length: 65.5 ± 3.3 mm), respectively (see Table 1). It takes approximately another 5 months for the mass to double. At an age of c. 9 months (278 days) the mass of males and females is 2.5 ± 0.6 kg (average hindfoot length: 75.4 ± 1.7 mm) and 2.2 ± 0.3 kg (average hindfoot length 71.3 ± 1.4 mm), respectively.
Fig. 2. Radiographs of the dentition of a greater cane rat: (a) 21 days old: the first cheek tooth in each quadrant has erupted and is functional, while the second cheek tooth in the lower jaw has just erupted, but not yet in the upper jaw (CBL = 47 mm); (b) 39 days old: two functional cheek teeth in each quadrant; the surface areas of both are at the same level above the gumline (CBL = 56 mm); (c) 81 days old: two functional cheek teeth in each quadrant; the third cheek tooth in both jaws is visible, but has not yet erupted (CBL = 65 mm); (d) 122 days old: two functional cheek teeth in the upper jaw and three in the lower jaw; the third upper cheek tooth is visible but has not yet erupted (CBL = 69 mm); (e) 187 days old: three functional cheek teeth in both upper and lower jaws; the position in both the upper and lower jaws where the fourth cheek tooth is developing is clearly visible and is indicated with arrows (CBL = 73 mm); (f) 236 days old: three functional cheek teeth in the upper and four in the lower jaw; the fourth upper cheek tooth is clearly visible but has not yet erupted (CBL = 82 mm).
in both tooth-rows. row, two to three in the lower tooth-row; (3/3±3/4), three in the upper tooth-row, three to four in the lower tooth-row; (4/4), four

Class Age of animal (months) Remarks regarding the cheek teeth

<table>
<thead>
<tr>
<th>Class</th>
<th>Age of animal (months)</th>
<th>Remarks regarding the cheek teetha</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Newborn–1 month</td>
<td>One functional tooth predominates (0/0–1/2)</td>
</tr>
<tr>
<td>2</td>
<td>1–5 months</td>
<td>Two functional teeth predominate (2/2–2/3)</td>
</tr>
<tr>
<td>3</td>
<td>5–9 months</td>
<td>Three functional teeth predominate (3/3–3/4)</td>
</tr>
<tr>
<td>4</td>
<td>9 months and older</td>
<td>Four functional teeth (4/4)</td>
</tr>
</tbody>
</table>

aCheek teeth: (0/0–1/2), zero to one in the upper tooth-row, zero to two in the lower tooth-row; (2/2–2/3), two in the upper tooth-row, two to three in the lower tooth-row; (3/3–3/4), three in the upper tooth-row, three to four in the lower tooth-row; (4/4), four in both tooth-rows.

(see Table 1). The three-cheek-teeth stage was reached in 5 months and a further 5 months elapsed before the fourth cheek tooth erupted.

**DISCUSSION**

Milk dentition is not normally seen in rodents (Rosevear, 1969). However, Luckett (1985) and Moss-Salentijn (1978) mention that for lagomorphs and rodents the large, evergrowing incisors are dI 2/2 (deciduous incisors 2/2). My studies on the greater cane rat support this view, because I could not find any evidence that the incisors and premolars are replaced, and it would appear that they are persistent deciduous teeth. Even in small foetuses (45 g), the unerupted incisors are strongly built, deeply rooted and very prominent, giving an impression of permanency. These incisors have the same appearance as the incisors of a newborn pup, with the upper ones rooted above the premolar and first molar tooth, and the lower ones spanning the total distance of the lower jaw (Fig. 2a–f). The premolar is also not replaced and remains deciduous throughout life (Friant, 1945; Wood, 1962; Woods, 1976). My studies also did not reveal any signs of a replacement premolar in foetuses of 45 g and 56 g in mass (average mass 2 days after birth; males 166 g and females 158 g), or at any stage during post-natal life. Woods (1976) examined three foetal cane rats and found no indication of permanent premolars, and stated that the cusp patterns of the upper and lower premolars were similar to those of juvenile cane rats described by Wood (1962). Woods (1976) concluded that Friant (1945) was correct in her assertion that the deciduous premolars of cane rats are retained throughout life, i.e. there is no replacement of dP4/4 by P4/4. The dental formula therefore is dP4/4, M1.2.3/1.2.3. She found that the premolars in all her specimens of *Choeromys harrisoni (= Thryonomys gregorianus)* had more wear than any of the molars, indicating that they were not replaced. Wood (1962) supported this finding. This would then suggest that premolars erupt before any of the molars in rodents. I was unable to find signs of replacement even in relatively small cane rat foetuses (age unknown; about 1/4 the size of full-term foetuses and still completely naked). Small incisors and the first and second cheek teeth in the upper and lower jaw were already present. However, they were not visible and the jaws had to be dissected to see them. In this species the precocial young are born with hair and open eyes, and are capable of following their mothers an hour after birth (Skinner & Smithers, 1990). At this stage it would seem that there is no replacement of the incisors and the premolars, and that they remain as persistent deciduous teeth throughout life.

The upper incisors of the greater cane rat are described as curved, rooting above m1 and m2 (Rosevear, 1969). Fig. 2a–f, however, clearly show that they root above the premolars and first molars (dP4 and M1). The cheek teeth are described as 4/4 with the posterior one erupting well after the others (Rosevear, 1969; De Graaff, 1981). The same was found in the present study where the lower M3 became visible for the first time c. 3.8 months after M2 became visible (see Table 1). The upper M3 became visible only c. 4.2 months after M2 became visible. The eruption of the lower teeth before the upper ones in the greater cane rat is consistent with the normal eutherian dental development (see Luckett, 1985). The sequence of eruption of teeth in the greater cane rat is expected to be similar irrespective of the environment in which the animals are raised, however, the time interval between eruptions of the successive teeth is likely to vary with the environmental conditions.

Asibey (1974a) reports that greater cane rats in Ghana mature at an age of c. 5 months (three cheek stage), and that the mass of the heaviest animals in captivity at that age was 1.0 kg (males) and 0.9 kg (females). In the present study the animals were slightly heavier at the same age (Table 1). This nevertheless emphasizes the slow growth in the greater cane rat, especially as they only double their mass about 5 months after maturity, and then need a further 7.5 months to reach the average mass of 4.5 kg and 3.6 kg for males and females, respectively (Skinner & Smithers, 1990). Only at an age of 17.5 months (527 days) did one of the faster growing males in the breeding colony reach a mass of 4.5 kg. At an age of 17.2 months (516 days) the heaviest female weighed only 3.0 kg.

**Acknowledgements**

I thank the University of Pretoria for financial aid and Mr N. S. H. Wilson for critically reading this report.
In a recent paper, Dawson et al. (1999) investigated how the morphology of the contour and downy afterfeathers of gentoo penguins *Pygoscelis papua* function as thermal insulators. Their model considered how the morphology of individual down feather barbs interact to create an efficient insulatory barrier. They noted that, during diving, the feathers must be compressed and return to their original configuration due to stored strain energy. In addition, the downy feathers of penguins have to withstand significant wind loading whilst the birds are on land (Taylor, 1986). Despite the obvious necessity for mechanical competence and resilience of down feathers, we still know little about their mechanical performance.

The mechanical performance of feathers is controlled by two factors; the geometry of the feather and the basic mechanical properties of the materials from which it is composed. Purslow & Vincent (1978) demonstrated that it is possible to accurately model the mechanical behaviour of whole feathers using an estimate of the stiffness (Young’s modulus) of feather material and the geometric properties (second moment of area) of feather shafts. Recently, we have started to learn more about the mechanical behaviour of birds’ feathers. Bonser & Purslow (1995) examined the elastic properties of sections of keratin from primary flight feathers of birds and argued that the material itself was mechanically conservative as they found little evidence of interspecific variability across a range of phylogenetically diverse species. They concluded that the shape of feathers must be the principal way in which performance can be modulated. More recently, Bonser & Dawson (1999) measured the tensile properties of commercially treated duck and goose down. As this material is aggressively cleaned and de-greased by using abrasives and detergent it is likely that the properties of commercially prepared down differ from those in its natural state.

Penguins’ feathers are not laid down in tracts, as in other birds, and are evenly spaced over the whole skin (30–40 cm⁻²). All the feathers are of similar species, being a modified lance-shaped contour feather. Insulation is provided by a long downy afterfeather rather than the more familiar down plumules of domesticated fowl. The morphology of down feathers makes them amenable to testing as individual fibres. Each barb is composed of two principal structures, the ramus and barbules. The ramus is the principal feather shaft and the barbules are orientated perpendicular to the ramus along its length (nomenclature follows Lucas & Stettenheim, 1972). The morphology of a penguin feather is shown in Fig. 1.
In this paper, we describe the mechanical behaviour of whole rami of untreated barbs from the plumulaceous afterfeathers of gentoo penguins *Pygoscelis papua* (Forster).

**MATERIALS AND METHODS**

Individual barbs of down were taken from the bases of gentoo penguin feathers. The midlength of each barb was glued, by using cyanoacrylate adhesive, to a rectangular card frame. The same relative position on each barb was used to reduce the possible influence of positional differences in properties (see Bonser & Purslow, 1995). The diameter of each barb was measured using a microscope with calibrated graticule. The mean gauge length of the specimens was 3.21 mm (sd 0.12) and their mean radius was 16.6 μm (sd 1.67). Cross-sectional area of the specimens was calculated assuming that they are circular and solid. There did not seem to be any evidence of significant voids within the rami when viewed through the microscope; the translucency of the barbs would allow the presence of a foam or medullary void to be seen. The specimens were tested in a single fibre test machine, using the same method as adopted by Bonser & Dawson (in press). Briefly, the machine comprises an inclined beam with a saddle supported by an air bearing. One end of the specimen is clamped to this and the other to a fixed clamp. The beam is elevated and the fibre extension measured directly by an LVDT whose core is fixed to the saddle. The rectangular card frames are clamped with the beam horizontal and their sides cut to allow the fibre to extend once loaded. Each specimen was taken to ultimate failure and the initial Young’s modulus and stress at failure of the fibre calculated. In total, results were obtained from 29 rami. All tests were performed at ambient room temperature and humidity (23 °C, 73%).

**RESULTS**

The mean structural Young’s modulus of the barbs was 1.74 GPa (SEM 0.09, n = 29) and stress at failure was 219.5 MPa (SEM 11.10, n = 29). There was a significant linear relationship between Young’s modulus and stress at failure ($r^2 = 43.7\%$, 27 d.f., $P < 0.001$) (Fig. 2). Best fit for the data was given by:

$$\sigma_{ult} = 81.364 E + 78.213,$$

where $\sigma_{ult}$ is the ultimate failure stress (MPa) and $E$ is initial Young’s modulus (GPa).

**DISCUSSION**

The mean structural Young’s modulus of the rami of penguin feathers, 1.74 GPa, falls well within the published estimates of compact feather keratin modulus from the literature (see Bonser, 1996) but is roughly 30% lower than the mean of 2.5GPa reported for primary flight feathers by Bonser & Purslow (1995). It must be noted, however, that the range of Young’s modulus they reported did extend to the value for down feathers we report here. In the context of keratinous materials in general, these differences are small. In mammals, the moduli $\alpha$-keratin materials (hair, hoof, horn) varies between 0.19 and 5.8 GPa when tested under similar conditions (see Fraser & MacRae, 1980). Despite the downy feathers of penguins being highly specialized and penguins having been flightless since at
least the Eocene, the properties of their feathers are quite similar to those of flight feathers in carinate birds. It may be that the amount by which a bird can alter the properties of the β-keratin composite is small. Alternatively, retention of mechanical competence may be just as important for down feathers as flight feathers; even in ratites and penguins, many feathers retain the interlocking barbules associated with aerodynamically functional feathers (McGowan, 1989), so it may be predicted that the mechanical properties of keratin would differ little as well.

There is considerably less known about the failure properties of the feather keratin composite than there is about its elastic properties. Only two authors have considered the ultimate failure properties of feather keratin; Crenshaw (1980) reported an ultimate stress of 226 MPa in pigeon feathers and Hertel (1966) found it to be 353 MPa in pheasants. The stress at failure of penguin down (≈ 220 MPa) is marginally lower than that reported for contour and flight feathers, although the difference is small. Again, it seems that there is little difference between the properties of basic flight and contour feathers and the highly derived and specialized insulatory plumage of the flightless penguin.

The significant correlation between elastic and ultimate properties of the rami is not surprising. Factors affecting the stiffness of biological materials often have a concomitant effect on their strength. An important question for future research must be to determine which structural factors are responsible for determining the stiffness and strength of feather keratins. There is considerable evidence from amino acid analyses that the morphological parts of feathers differ in composition. It is known that the barbs of penguin down feathers have a higher water content than other feather parts (Murphy, King & Taruscio, 1990) and this may be a factor in modulating properties. Bertram & Gosline (1987) demonstrated that the modulus of keratin from the hooves of horses showed a decrease in stiffness of two orders of magnitude between zero and full hydration. It is quite plausible that increased hydration acts to marginally decrease the measured modulus of down barbs when compared with keratin from the rachis of flight feathers. Further, Murphy et al. (1990) found that in P. papua there were noticeable differences in amino acid composition of feather rachis and barbs and, additionally, the total nitrogen content of barbs was c. 70% higher and the water content was c. 16% higher in the barbs than the rachis. To put these differences in context, however, we need to know how they are manifest in either the crystalline or amorphous matrix of the β-keratin assembly.

There are numerous factors that may have a role in determining the measured moduli of feather keratin composite. Only by understanding more about how the biochemical composition and ultrastructure of the keratin composite interact with the environment will we understand how the mechanical properties of feathers are modulated. The results we have presented here do demonstrate that, despite profound differences in function, the mechanical properties of specialized insulatory feathers are remarkably similar to those used as aerodynamic surfaces. This similarity suggests that either birds are not capable of modulating the mechanical performance of feather keratin as a feather develops or that maintenance of mechanical competence is just as important for insulatory feathers to function well as it is for flight feathers.

Acknowledgements

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REFERENCES


