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STRUCTURE AND FUNCTION OF HAIR CRESTS AND CAPES IN AFRICAN CARNIVORA

CHRISTEN WEMMER AND DON E. WILSON

Abstract

THIS study examines ecological correlates of specialized hair tracts in 55 of the 64 species of African Carnivora. Seventy-five percent of the species have torso hair of more or less uniform length. The remainder have hair that is elongated as narrow middorsal crests or broad dorsal capes. Threat displays that increase apparent body size are widespread in carnivores, but piloerection of crests and capes produces disproportionate increases in body size. The occurrence of crests and capes among taxa refutes the hypothesis that these structures have evolved primarily for intimidation in species capable of inflicting fatal wounds. Crests and capes are attributes of many relatively defenseless species, as well as those specialized for killing large vertebrates. More evidence supports the hypothesis that long dorsal hair is primarily an antipredator adaptation. A significant number of long-haired species are poor climbers unable to seek arboreal refuge from predators. Among viverrids long-haired species occur in open habitats and short-haired species occur in forests and woodlands. Herpestids are generally poor climbers and exhibit no correlation between hair length and habitat. However, larger and perhaps more conspicuous species tend to have long dorsal hair. The relative dorsal hair length of the torso in canids and herpestids was significantly correlated with number of sympatric carnivores not exceeding by 50% the head and body length of each species being evaluated. Inability to climb trees, intermediate body size, and occurrence in open habitats may increase vulnerability to predators, and place a selective premium on hair patterns that maximize the illusion of a larger body.

"Hardly any expressive movement is so general as the involuntary erection of the hairs, feathers and other dermal appendages; The action serves to make the animal appear larger and more frightful to its enemies or rivals, and is generally accompanied by various voluntary movements adapted for the same purpose, and by the utterance of savage sounds."

Charles Darwin, 1872

Introduction

Elements of the mammalian integument have been important in the evolution of visual, olfactory, and auditory modes of communication. Social functions of the skin emerged by modifications of the widespread and probably primitive association of follicle, hair(s), arrector pili muscle, and apocrine gland. The diversity of dermal scent glands (Schaffer, 1940), richness of hair color and length patterns (Cott, 1940; Miller, 1931), and bizarre adaptations such as sound-producing quills (Darwin, 1872; Ewer, 1968; Gould, 1965), attest to the evolutionary significance of the integument.

Color, length, and density characteristics of the pelage, collectively termed hair patterning (Miller, 1931), have been the focus of numerous taxonomic studies, but have stimulated fewer investigations of their adaptive significance. Thermal properties of insulation and color are well known (Herrington, 1951; Hutchinson and Brown, 1969; Scholander, 1950; Tregear, 1965). Social and antipredator functions were summarized in 1940 by Cott, but little research was done on these topics for the next three decades. Renewed interest and controversy have been stimulated by recent work on mimicry (Gingerich, 1975; Goodhart, 1975; Greene, 1977) and pursuit invitation signals (Coblentz, 1980; Hirth and McCullough, 1977; Smythe, 1970). The present study deals with visual communication mediated by erection of specialized zones of hair, in Darwin's words, "generalized expressive movement." Elongation of dorsal pelage to enhance the illusion of larger body size is a recurrent adaptation of terrestrial mammalian predators and omnivores in Africa, Asia, South America, and probably Australia. The objectives of this study are to describe some design features of specialized pilomotor tracts within sub-Saharan carnivores, and to examine ecological correlates of such characteristics.

Methods

Hair-length measurements were taken from flat or stuffed museum specimens in adult pelage. A middorsal and lateral series of guard hair measurements was taken at shoulder, midback, and rump. Dorsal and lateral hair length was then calculated by averaging the three measures. The length of hair of the tail was measured at two places, one third the total length from both the base and the tip. A ruler was placed perpendicular to the skin, and the length of the majority of guard hairs was measured. With one exception (*Civettictis civetta*), no consistent or significant difference could be found between the length of dorsal and lateral tail hair. We averaged tail hair length, therefore, using only the two dorsal measures. Although these are somewhat crude estimates, they give a fair appraisal of species differences. Specimens in molting condition or missing hair were avoided or the hair in the molting section of the skin was not measured if samples were small. Fifty-five species were examined, and an average of 10 specimens per species was measured (range 1 to 24). Head and body length measurements were obtained for all species. We calculated nearly all indices using body measurements taken from the tags of those specimens used for hair-length measurements. Dorst and Dandelot (1970) was used as the source for head and body length of five additional species (Fig. 1). Taxonomic usage follows Ellerman et al. (1953) and Meester and Setzer (1971). Cross-sectional profiles are based on seven hair-length measures taken in the midbody region. Hair length was measured on the spine, side, and ventrum on one half of the skin. Two other measurements were made at points equidistant between the lateral and dorsal, and lateral and ventral measurement points. Diagrams show the measured half of the skin and its mirror image. Circumferences were normalized to facilitate comparisons of hair-length profiles.

Information on threat displays was gathered from the sources listed in Table 1, including photographs of species for which descriptions are lacking or incomplete. Photographs by field workers and from the National Zoological Park photofiles were additional sources of information on displays. A polar planimeter was used to measure body surface areas from photographs of animals in normal and piloerected postures.

We excluded otters from analyses because of their aquatic habits,

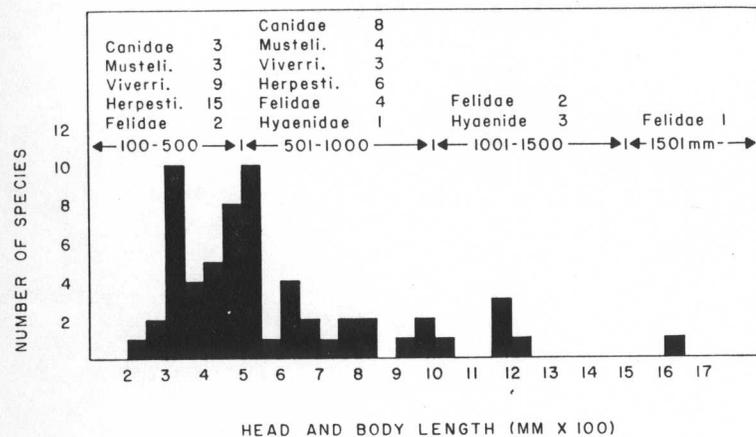


FIG. 1. Frequency histogram of body size (head and body length) in the sub-Saharan carnivore fauna (60 species).

but included the aquatic genet (*Osbornictis piscivora*) because its specializations for aquatic life are less developed. The mane of the male African lion differs from the hair structures we are concerned with; therefore, only measurements of a female lion were used.

Results

Sub-Saharan carnivore fauna.—There are about 64 species of living carnivores representing six families south of the Tropic of Cancer. These species range in size from the dwarf mongoose (*Helogale parvula*) (0.3 kg) to the lion (*Panthera leo*) (172 kg). One-half of the 64 species are less than 500 mm in head and body length, and 90% are less than 1 m long (Fig. 1). Two families, the Felidae and Hyaenidae, constitute the largest carnivores, but all families have representatives less than 1 m in body length.

Hair-length patterning.—We were able to examine 55 (90%) of the non-aquatic species (n = 61). Most short-haired species (lateral

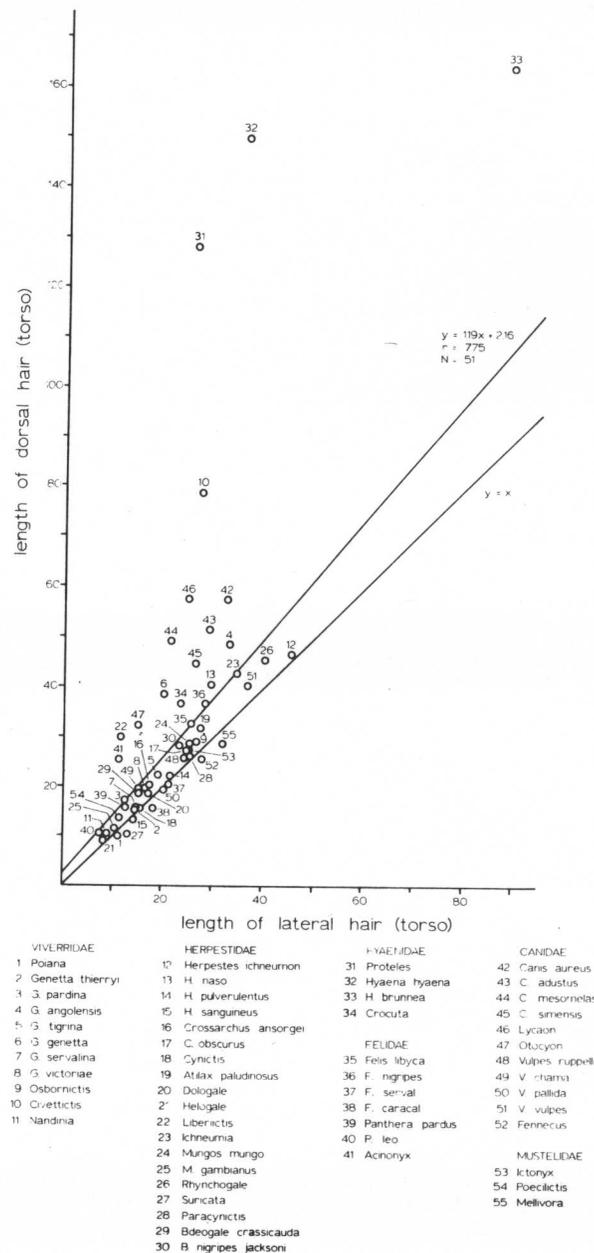


FIG. 2. Scatter diagram of lateral hair length plotted against dorsal hair length in 55 species of sub-Saharan carnivores.

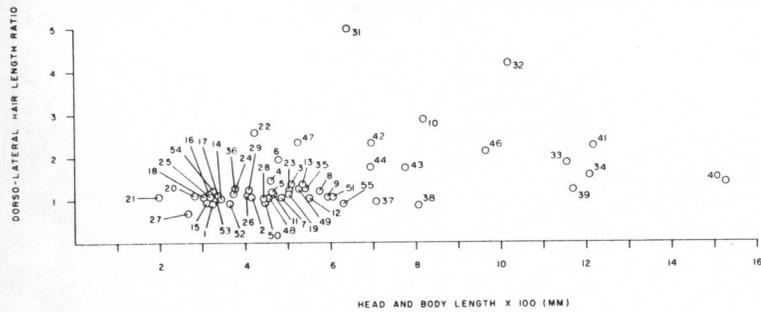


FIG. 3. Dorso-lateral length ratios of torso hair versus head and body length in sub-Saharan carnivores. Refer to Fig. 2 for species corresponding to numbers.

hair < 25 mm) show a one-to-one relationship between length of lateral and dorsal body hair (Fig. 2). However, many species have dorsal hair longer than lateral hair. To predict dorsal from lateral hair length, we calculated the formula $y = 1.19x + 2.16$ ($r = 0.775$, $n = 51$). We excluded the four most deviant species from this calculation (*Civettictis civetta*, *Proteles cristatus*, *Hyaena hyaena*, *H. brunnea*). When these species are included, $r = 0.74$ ($n = 55$) and the slope increases ($y = 1.854x + 7.75$). Most species show relatively slight differences in length of dorsal and lateral hair, but 25% of 55 species are exceptions (Fig. 3). *Proteles cristatus* and *Hyaena hyaena* exhibit extreme ratios (>4.0); six species show moderate ratios (2.0 to 3.0), and six other species show ratios between 1.5 and 2.0. Large ratios exist in both long- and short-haired species, but nearly all species with the greatest ratios have disproportionately long dorsal hair.

Length of lateral and dorsal hair increases as a function of head and body length (Fig. 4). However, relative length of dorsal body hair varies considerably. Thirty-five species (63%) have hair less than 7% of the head and body length, and 17 species (31%) have hair between 7 and 14% of the head and body length. Only three

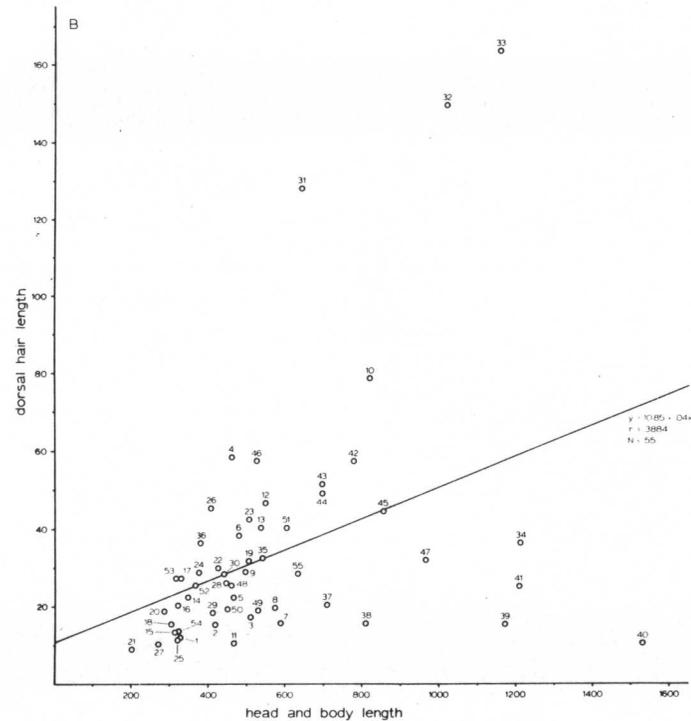
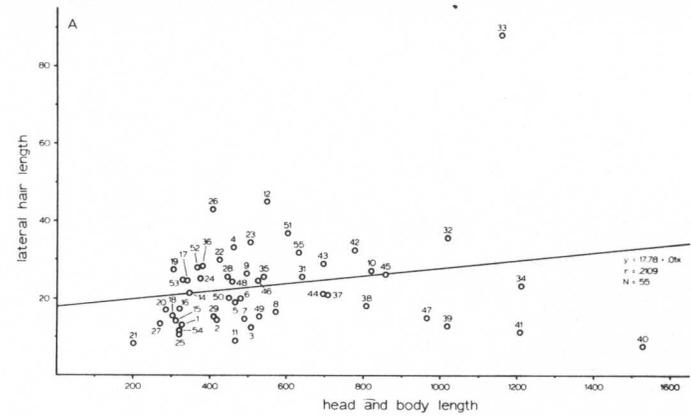


FIG. 4. Scatter diagrams of head and body length versus lateral hair length (A), and dorsal hair length (B) in 55 sub-Saharan carnivores. Refer to Fig. 2 for species corresponding to numbers.

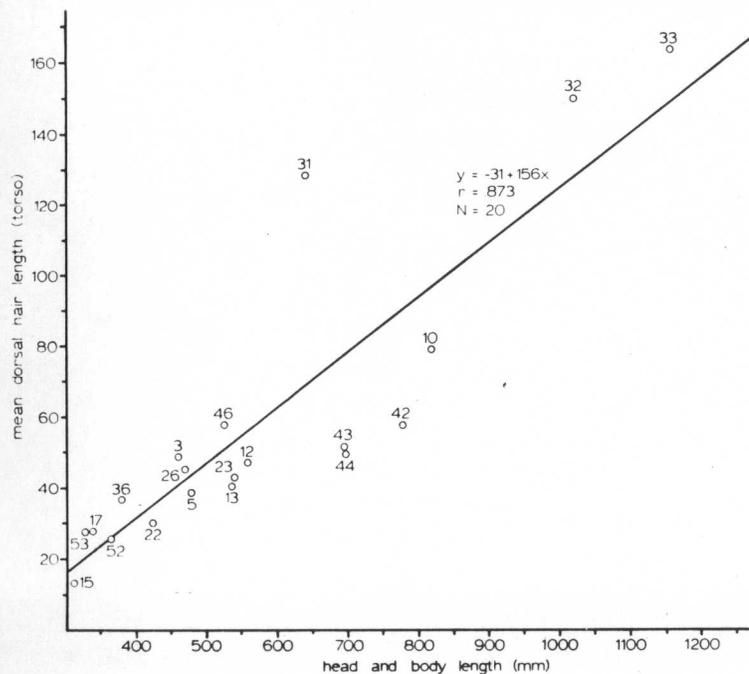


FIG. 5. Scatter diagram of head and body length versus dorsal hair length of the torso in 20 species of sub-Saharan carnivores having dorsal body hair exceeding 7% of head and body length. Refer to Fig. 2 for species corresponding to numbers.

species (5%) have hair exceeding 14% of the head and body length. When those 20 species having hair exceeding 7% of the head and body length are considered as a group, 76% of the variance in mean absolute dorsal hair length is predicted by length of head and body (Fig. 5). The correlation is still significant when the four largest species are deleted ($y = 4.96 + 0.72x$, $r = 0.806$, $n = 16$). Tail length and length of dorsal hair of the tail are not significantly correlated ($y = 45.65 + 0.02x$, $r = -0.144$, $n = 54$), but species with long dorsal pelage also have long-haired tails. Bushy tails occur in both short- and long-tailed species.

Variations in crest form.—Three categories of hair form are recognizable by viewing the torso in cross-section (Fig. 6). Long hair may be confined to a narrow middorsal zone forming a crest (*Prot-*

eles cristatus, *Civettictis civetta*, *Genetta tigrina*), or long hair may form a broad cape across the back (*Genetta genetta*, *Canis mesomelas*). The third category includes species in which there is no zone of pronounced elongation (*Herpestes sanguineus*, *Atilax paludinosus*).

Threat displays.—Intraspecific and interspecific threat behavior has been described in 25 sub-Saharan species representing all carnivore families (Table 1). The completeness of behavioral descriptions, however, is far from satisfactory. Although some differences are real, others undoubtedly are due to incomplete observation. Nearly all species show fundamental similarities. The shared elements include leg extension, spinal convexity, piloerection, and tail elevation. Differences between species in the expression of these components are probably a function of anatomy. Pronounced arching of the back occurs in species with long torsos and supple spines (for example, in species of *Felis* and *Genetta*). Species of *Canis* extend the hindlegs strongly, but often retain flexed forelimbs; both the forelegs and hindlegs are extended in *Proteles cristatus* and *Civettictis civetta*. The lion, leopard (*Panthera pardus*), and cheetah (*Acinonyx jubatus*) lack display elements that increase stature (leg extension, back-arching). The serval (*Felis serval*) feigns increased size like most other species, but also threatens like the larger felids.

Scant information on body orientation toward rivals during threat suggests this element of threat has been overlooked. The findings are also tentative because some species (*Civettictis civetta*) require very strong stimulation to elicit lateral orientation. Lateral orientation is absent in some small forms (*Herpestes* spp.), but present in another (*Ictonyx striatus*). Many medium-sized carnivores display laterally, but incomplete information prevents conclusions. We predict that lateral displays will be most common in species having strongly developed crests. To summarize, stature-enhancing displays are widespread in African carnivores, regardless of degree of crest development.

Piloerection.—Piloerection in social contexts is assumed to be an autonomic response to exciting stimuli, motivated by aggression, fear, or a combination thereof. It is also a non-specific reaction to many other circumstances, and can be regarded as an excitation indicator because of apparent correspondence between the intensity of stimulation and the degree and duration of the pilomotor response (Gould, 1971). Besides the illusion of increased body size, piloerec-

TABLE 1
AGGRESSIVE DISPLAYS IN SUB-SAHARAN CARNIVORA

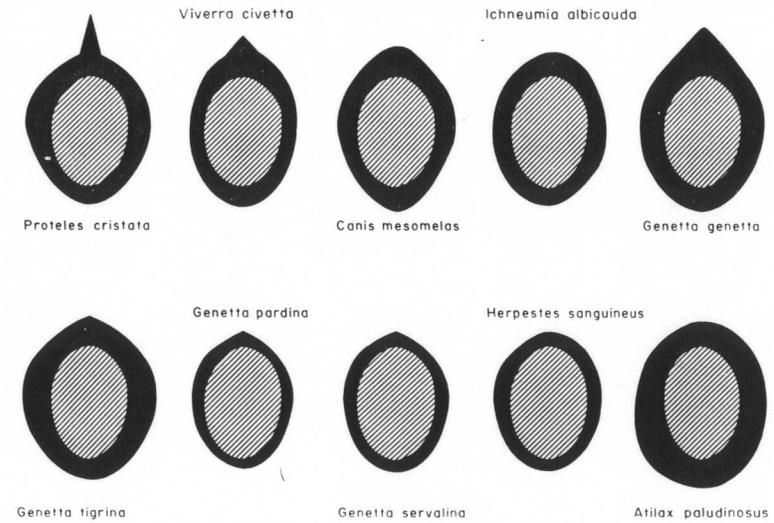
Species	Display elements								References	
	Leg spread	Stiff-legged gait	Spinal con-vexity	Head and shoulders	Tail position		Body orientation			
					Down	Up	Lateral-tangential	Pilo-erection		
Hyaenidae										
<i>Hyaena hyaena</i>	-	-	-	-	+	+	+	+	+	Kruuk (1976); Rieger (1979)
<i>Hyaena brunnea</i>	-	-	-	-	+	+	+	+	+	Mills (1978); Owens and Owens (1978)
<i>Proteles cristatus</i>	+	-	-	+	+	+	+	+	+	Dobroruka (1967); von Ketholdt (1966)
<i>Crocuta crocuta</i>	-	-	-	-	+	+	+	+	+	Kruuk (1972)
Felidae										
<i>Felis aurata</i>	+	+	+	+	+	-	+	+	+	Leyhausen (1979)
<i>Felis margarita</i>	+	+	+	+	+	-	+	+	+	Hemmer (1974, 1977)
<i>Felis libyca</i>	-	+	-	-	-	-	-	+	+	Armstrong (1977)
<i>Felis caracal</i>	+	-	+	+	+	-	+	+	+	Kingdon (1977); York (1973)
<i>Felis serval</i>	-	+	+	+	+	+	+	+	+	Leyhausen (1979)
<i>Acinonyx jubatus</i>	-	-	+	+	+	-	+	+	+	Leyhausen (1979)
<i>Panthera pardus</i>	-	-	+	+	+	-	+	+	+	Leyhausen (1979)

TABLE 1
CONTINUED

Species	Display elements								References	
	Leg spread	Stiff-legged gait	Spinal con-vexity	Head and shoulders	Tail position		Body orientation			
					Down	Up	Lateral-tangential	Pilo-erection		
Viverridae										
<i>Panthera leo</i>	+	+	-	-	-	+	+	+	+	Schaller (1972)
<i>Panthera leo</i>	+	+	-	+	+	-	-	+	+	Leyhausen (1979); Schaller (1972)
Viverridae										
<i>Genetta tigrina</i>	-	+	-	±	+	-	+	+	+	Wemmer (1977)
<i>Genetta genetta</i>	-	+	-	±	+	-	+	+	+	Gangloff and Ropartz (1972)
<i>Civettictis civetta</i>	-	-	-	+	+	-	+	+	+	Ewer and Wemmer (1974); Wemmer (1977)
<i>Nandinia binotata</i>	-	+	+	-	+	+	+	+	+	Wemmer (1977, pers. observ.)
Herpestidae										
<i>Suricata suricatta</i>	-	+	+	-	-	+	+	-	+	Ewer (1963); pers. observ.
<i>Crossarchus obscurus</i>	-	+	+	-	+	-	-	+	+	Ewer, in Kingdon (1977)
<i>Herpestes ichneuman</i>	-	+	+	-	+	-	+	-	+	Leyhausen (1979)

TABLE 1
CONTINUED

Species	Display elements										References	
	Legs spread	Leg extension	Stiff-legged gait	Spinal cavity	Spinal con-shoulders	Tail position		Body orientation		Piloerection		
						Down	Horizontal	Lateral-tangential	Frontal			
<i>Ichneumia albicauda</i>	-	+	-	+	+	+	+	+	+	+	+	Leyhausen (1979); Waser (pers. comm.)
Canidae												
<i>Canis aureus</i>	-	+	?	-	+	+	+	+	+	+	+	Estes and Goddard (1967); Fox (1971); Golani and Keller (1971); Golani and Mendelsohn (1975)
<i>Canis mesomelas</i>	+	+	-	-	+	+	+	+	+	+	+	Moehlman (pers. comm.)
<i>Vulpes vulpes</i>	+	+	-	-	+	+	+	+	+	+	+	Fox (1969); Tembrock (1957)
<i>Otocyon megalotis</i>	-	+	-	-	+	+	-	+	+	+	+	Kleiman (1967); Lamprecht (1979)
Mustelidae												
<i>Ictonyx striatus</i>	+	+	+	-	-	-	-	+	+	+	+	Rowe-Rowe (1978)
<i>Poecilogale albinucha</i>	+	+	+	-	-	-	-	+	+	+	+	Rowe-Rowe (1972, 1978)

FIG. 6. Cross-sectional profiles of guard hair at mid-body in 12 species of carnivores. *Viverra civetta* = *Civettictus civetta*.

tion almost always modifies body shape or profile, and sometimes is accompanied by changes in color pattern (Wemmer, 1977).

The illusion of increased body size during piloerection depends on the hair pattern of the displaying animal and its body orientation to the rival (Fig. 7). The erectile crest of *Proteles cristatus* can increase its lateral aspect by as much as 74%, but it is obvious that a frontal perspective is much less enhanced. Piloerection in *Civettictus civetta* increases lateral aspect at least 30%, and the white spinal stripe formed by the base of the crest undergoes a six-fold increase in size. The presence of this white area appears to vary geographically, and is more prominent in forested than in savanna populations. *Hyaena hyaena* increases lateral aspect by 38%. These measures, based on photographs of single animals, confirm the magnitude of the illusion of increased body size.

Evolution of Long Dorsal Hair

Probably several factors have influenced the evolution of long dorsal hair, but likely only one played a primary role. In searching

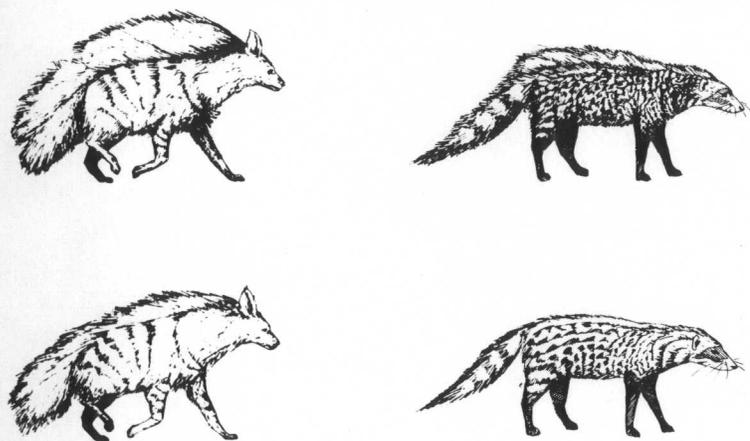


FIG. 7. Lateral views of *Proteles cristatus* (left) and *Civettictis civetta* (right) with dorsal hair relaxed (bottom) and erected (above).

for relations we divided the 55 species into long-haired and short-haired categories. This was an arbitrary choice because the relative lengths of dorsal body hair approximate a normal distribution (Fig. 8). Species exhibiting moderate to long dorsal crests and capes (relative hair lengths $> 7.0\%$) were classified as long-haired. No food habit predominates in this group, and no differences were found in mean head and body length ($t = 0.008$, d.f. = 53, $P = 0.9$), or in nocturnal and diurnal activity ($\chi^2 = 0.514$, d.f. = 1, $P = 0.48$) between long- and short-haired groups. Hypotheses are discussed below.

Thermoregulation hypothesis.—Hair has important insulative properties. Therefore, could long dorsal body pelage be an adaptation to conserve heat? Measures of hair density and insulation quality are necessary to answer this question conclusively. The undercoat of the pelage is specialized to create dead air space, and guard hairs, the components of crests and capes, contribute little to

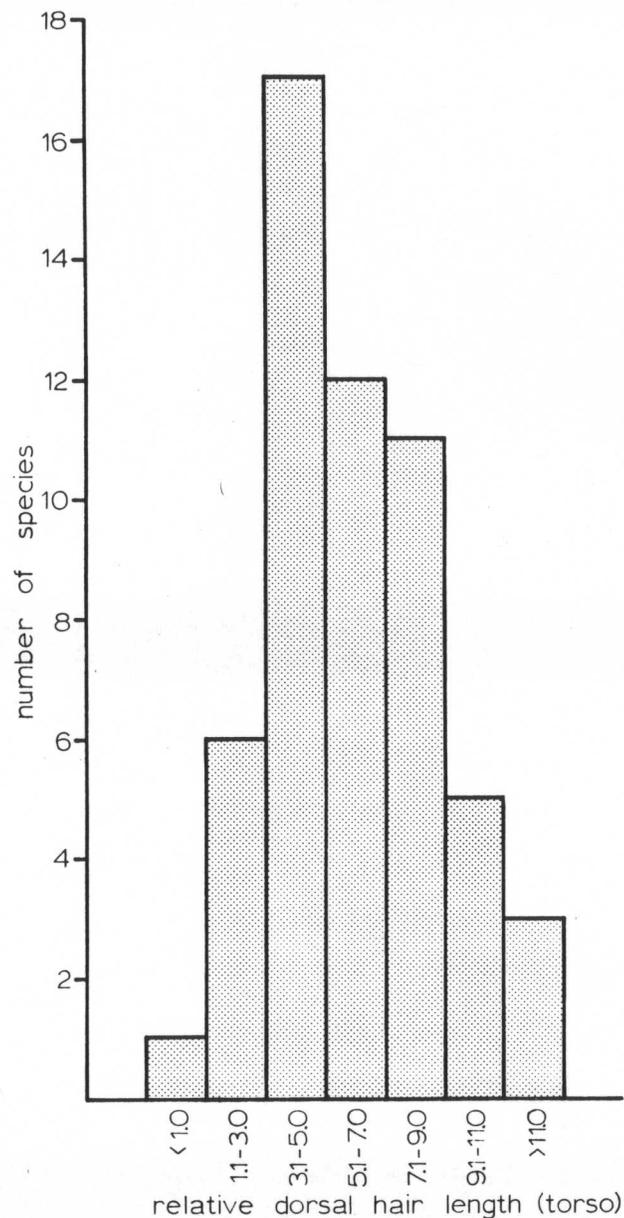


FIG. 8. Frequency distribution of dorsal hair length in species of sub-Saharan carnivores.

insulation (Herrington, 1951; Scholander, 1955). A range of thermoregulatory adaptations may be inferred from differences in the undercoat and the microenvironments of tropical carnivores. Diurnal *Mungos* spp., for example, lack undercoats (Rosevear, 1974), and this probably is true for *Suricata suricatta*. On the other hand, nocturnal desert foxes (*Vulpes pallida*, *V. ruppelli*, and *Fennecus zerda*) have well-developed insulation layers. In general, however, long dorsal hair consists of bristles and awns dense enough to create an illusion of substance when erect, but are probably insufficiently packed to impede convection and aid thermal resistance. We doubt that differences in dorsal pelage length and conformation are related to thermoregulation patterns.

Intraspecific conflict hypothesis.—Effecting larger body size may serve primarily to resolve intraspecific conflict. Interspecific similarities in pilomotor threat displays may have resulted from convergent or parallel evolution, and differences in length of dorsal hair may be related to social organization. We tested the prediction that the number of short- and long-haired species would differ when sorted into solitary versus group-living categories. The latter category included all monogamous and clan-living species, and species reported in anecdotal sources to forage, den, or travel communally (Kingdon, 1977; Roberts, 1951). There was no significant difference between groups ($\chi^2 = 0.189$, d.f. = 1, $P = 0.667$).

There are two corollaries of this hypothesis. Intimidation structures (that is, crests or capes) should be largest in species able to inflict fatal wounds. Piloerection almost always accompanies fighting. Owens and Owens (1978) reported that *Hyaena brunnea* raised their hackles during competitive interactions around food and during fights involving neck-biting and chasing. Rieger (1978) made similar observations of *Hyaena hyaena*. *Proteles cristatus* has weak jaws and reduced dentition, but has the largest crest of all carnivores. Cats are among the most effective killers, but only one of the six African species examined has dorsal hair exceeding 7% of head and body length.

The second corollary is that polygynous carnivores should exhibit sexual dimorphism in crest size. No species examined except the African lion shows such differences. Schaller (1972) described the mane of *Panthera leo* as a secondary sexual characteristic permitting recognition at a distance of sex and possibly of individuals. The mane's ancillary function is probably to decrease chance of injury

during fights by shielding the head and neck. Schaller gave no evidence that the mane is erected; thus the mane of the lion differs in several ways from carnivore crests and capes.

There is insufficient evidence to support the intraspecific conflict hypothesis. Many relatively defenseless species have long dorsal hair, and crests and capes are not a common attribute of taxa with strong jaws and teeth or other specializations for killing large vertebrate prey. On the contrary, there is now evidence that dermal shields evolved in some species to protect body parts frequently bitten during intraspecific conflict (Kruuk, 1972; Owens and Owens, 1979).

Interspecific conflict hypothesis.—Is long dorsal body hair primarily an antipredator adaptation? Long-haired species share one feature which might predispose them to predation. Eighty-five percent of the 20 species lack adept climbing ability; only 31% are non-climbers in the short-haired group. The difference is significant ($\chi^2 = 13.72$, d.f. = 1, $P < 0.001$). Many species depend on the ability to climb trees to escape ground predators. If this is true of African carnivores, climbing species living in open habitats should have longer dorsal hair than forest species. This prediction is based on the assumption that forest species have ready access to an arboreal refuge, and that the chance of being close to a tree is much less in savanna.

In the Viverridae the prediction generally holds. *Civettictis civetta* is the only African species that cannot climb. *Osbornictis piscivora*, a genet with incipient aquatic adaptations, is probably a less skillful climber than other genets. Forest viverrids have short to medium-length hair, whereas desert and savanna species have longer dorsal hair (Fig. 9).

Most African mongooses are terrestrial and are poor climbers. *Herpestes sanguineus* is the only known exception; it forages in bushes and small trees (Rood, pers. comm.; Taylor, 1975). Fifteen of the 20 herpestid species are diurnal, and an equal number occur in savanna or desert habitats. Five species are restricted to primary or secondary forest. There is no trend within the family for longer-haired species to occur in more open habitats (Fig. 10). On the contrary, *Suricata suricatta* and *Cynictis penicillata* from arid southern Africa have very short pelage.

The 18 species of African herpestids average 279 mm in head and body length (range 200 to 547), 25% smaller than the average

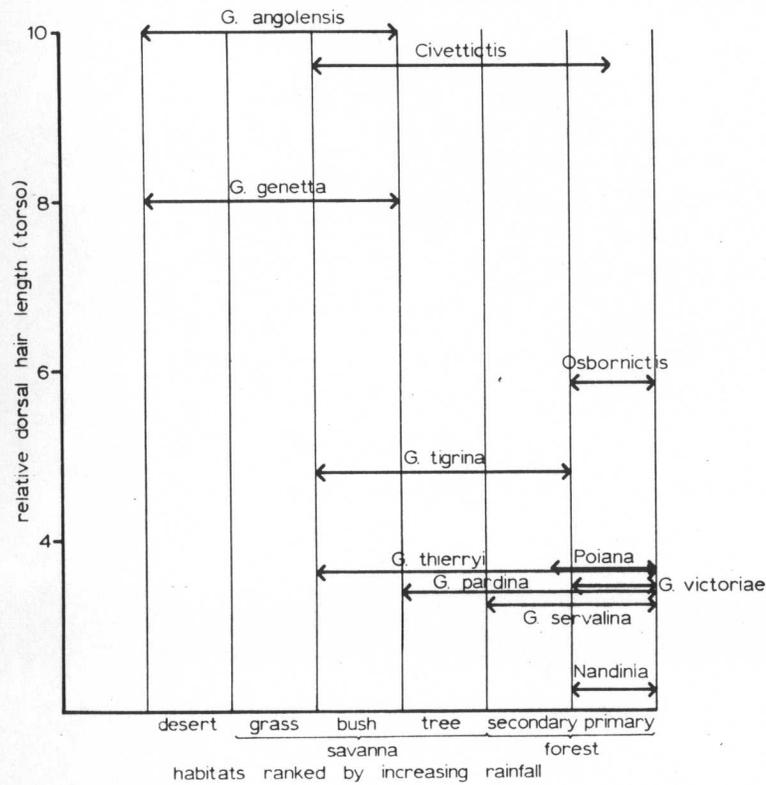


FIG. 9. The relationship of habitat selection and dorsal hair length of the torso in sub-Saharan Viverridae.

viverrid (\bar{X} = 499 mm, range 326 to 819). It could be argued that smaller, open-habitat herpestids evade predators more effectively than larger species by hiding in ground vegetation. The "tweed" coat pattern of most species is clearly cryptic in well-lit grassy and scrub habitats, and grassland can be regarded as a closed or three-dimensional habitat for small-bodied mongooses. Indeed, the seven long-haired mongooses have significantly larger bodies (\bar{X} = 437.8 mm, range 311 to 547) than short-haired species (\bar{X} = 350.4 mm, range 200 to 504, t = 1.98, d.f. = 15, P < 0.05, one sided). How-

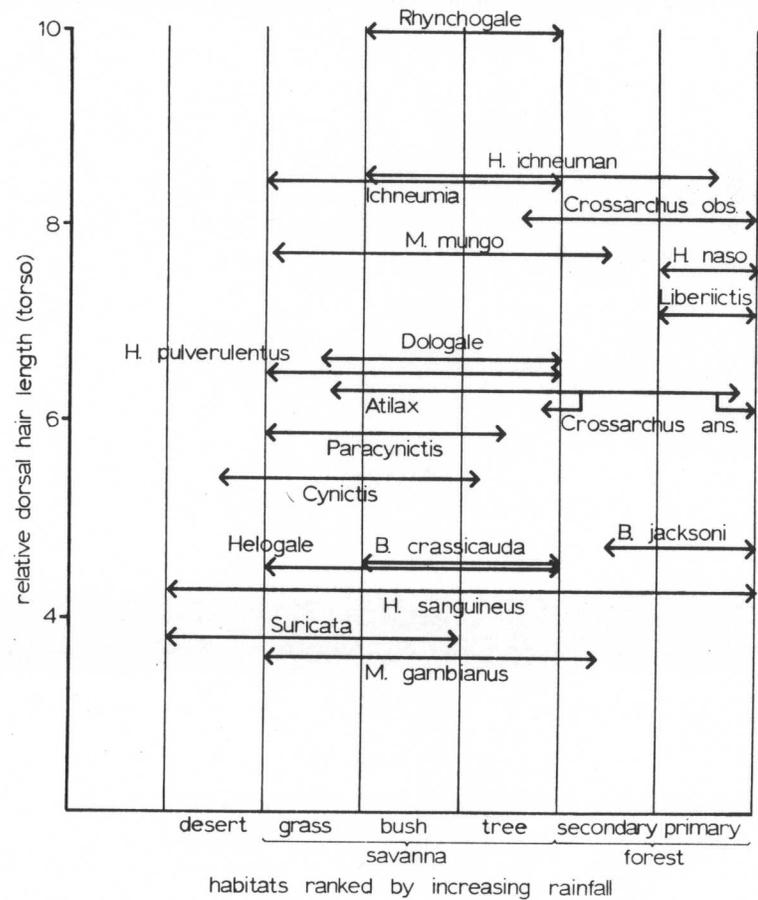


FIG. 10. The relationship of habitat selection and dorsal hair length of the torso in sub-Saharan Herpestidae.

ever, we question whether this slight size difference between the two groups appreciably affects vulnerability.

Vulnerability to interspecific conflict.—If hair length has anti-predator function, a correlation might exist between dorsal hair length and number of sympatric carnivores. This hypothesis was tested by plotting relative dorsal hair length against the number of

carnivores that 1) overlapped the range of the species by >25%, 2) were equal to or larger than the species, and 3) had similar activity periods. No significant relationship was found ($y = 4.9x + 0.12$, $r = 0.139$, $n = 51$). Two further refinements were made on the sympatric carnivores variable. The potential to visually intimidate a larger rival probably decreases with increasing size difference between two contenders. Therefore, two size ranges of sympatric carnivores were specified. The smaller range included all sympatric species no smaller than 20%, nor larger than 30% of the head and body length of each species being evaluated. The larger range included sympatric carnivores with the same lower limits in body size, but not exceeding 50% of the head and body length of each species being evaluated. A small percentage of variance in relative dorsal hair length is predicted by number of sympatric species ($y = 4.18 + 0.11x$, $r = 0.204$, $n = 51$ for sympatric carnivores <50% larger; $y = 3.41 + 0.129x$, $r = 0.191$, $n = 49$ for sympatric carnivores <30% larger). The results are not surprising because there are fewer large than small carnivores. However, when the effects of large size were removed by considering only carnivores between 300 and 600 mm in head and body length, there was no improvement in fit ($y = 3.76 + 0.25x$, $r = 0.184$, $n = 34$ for sympatric carnivores <50% larger; $y = 3.87 + 0.02x$, $r = 0.016$, $n = 31$ for sympatric carnivores <30% larger).

Finally, each family having an adequate number of species was treated separately. In the Canidae and Herpestidae, relative dorsal hair length of the torso was significantly correlated with number of sympatric carnivores not exceeding head and body length by 50% ($P < 0.05$) (Fig. 11). When the four hyaenids were included with the canids on the basis of similar body form and ecology, the correlation was not significant ($y = 4.51 + 0.177x$, $r = 0.288$, $n = 15$, $P > 0.05$).

Discussion

Crests and capes of long dorsal hair occur in both sexes in a range of medium-sized African carnivores. Guard hair length is

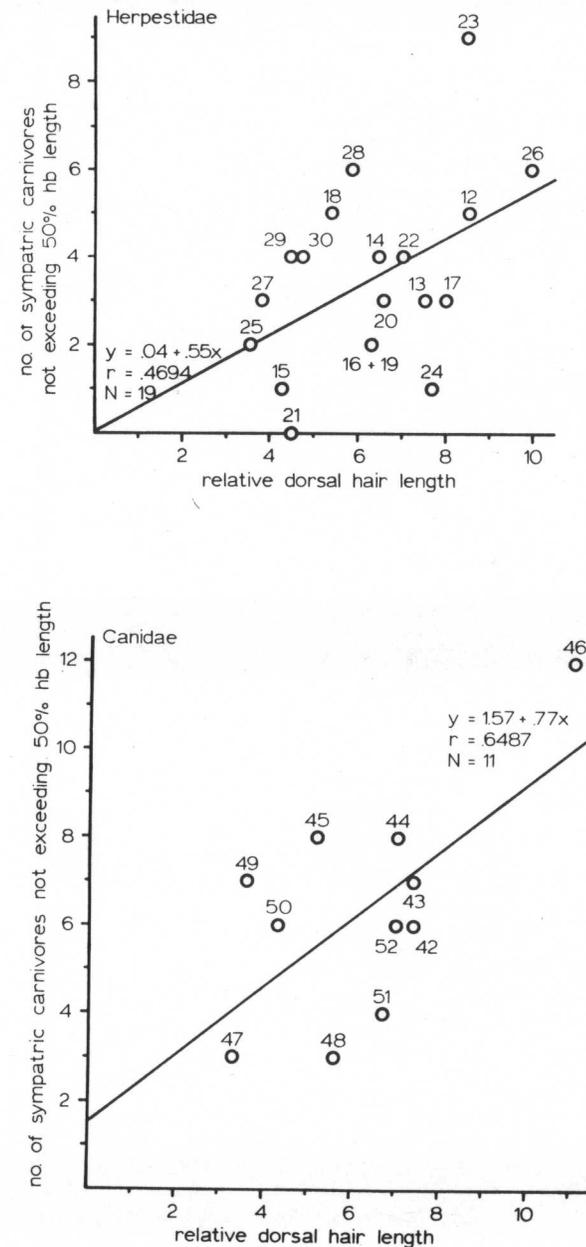


FIG. 11. Correlations between relative dorsal hair length of the torso and number of sympatric carnivores not exceeding 50% head and body length in the Herpestidae and Canidae. Refer to Fig. 2 for species corresponding to numbers.

probably related to underhair length, but the long guard hair probably lacks significant insulative properties. Erection of body hair commonly occurs in social contexts, and the illusion of increased stature and girth is appreciable in species having crests and capes. Estes and Goddard (1967:66) remarked that "A little 15 pound jackal, coat fluffed, head down, and snarling would stand its ground and snap ferociously if the hunting dog continued to advance . . . it proved a surprisingly effective intimidation display." Intraspecific rivalry for food and space undoubtedly selected for the intimidation value of long dorsal hair. However, long-haired species do not share behavioral or ecological features that reveal the adaptive character of these specialized hairs. Better understanding of natural history should clarify intraspecific factors favoring evolution of capes and crests.

We hypothesize that interspecific aggression also has selected for long dorsal hair. Widespread lack of climbing ability, intermediate body size, and occurrence in open habitats may increase an animal's vulnerability or reduce its escape options during interspecific conflict. These characteristics are often shared by species having well-developed crests and capes (that is, >7% head and body length). Carnivores usually avoid one another unless there are benefits of association. However, competitive associations often precipitate hostility, which sometimes leads to the death of the smaller or outnumbered species. Though flight is a prevalent first reaction in many species, it may also invite pursuit under certain circumstances (Smythe, 1970). Conduct diminishing the probability of attack probably is a more fit alternative if the defending species lacks speed.

The safest action for a weaker animal confronted at close range by an aggressor is probably threat rather than attack or flight. Subsequent escape is most likely to be successful when the attention of the aggressor is diverted. The ability to intimidate by feigning larger body size is undoubtedly a function of the size difference between rivals. In the preceding analyses, sympatric carnivores were considered to be potentially responsive to intimidation if they did not exceed the head and body length of the species by 50%. Only mongooses and canids, families of primarily terrestrial and open habitat species, showed a significant correlation between relative length of dorsal hair and number of sympatric carnivores as we have defined them. A refined analysis should focus on type and intensity of interspecific relationship, but this information is scant.

Dorsal hair length of hyaenids and viverrids could not be predicted by number of sympatric carnivores according to our definition. Three of the four hyaenids have exceptionally long dorsal body hair. All forage long distances for dispersed foods, but only *Crocuta crocuta* achieves high population densities and cooperatively kills large-bodied prey (Kruuk, 1972, 1976; Kruuk and Sands, 1972; Mills, 1978; Owens and Owens, 1978). Cooperative group behavior may have replaced the need of the individual for intimidation by piloerection. This reasoning, however, does not explain the existence of poorly developed capes in some social mongooses (for example, *Crossarchus obscurus* and *Mungos mungo*).

Neither viverrids nor felids show correlations between relative dorsal hair length and number of sympatric carnivores no larger than 50% of head and body length. However, nearly all of these species are fleet-footed, adept climbers, and have relatively short dorsal body hair (<7% of head and body length). The exceptions include the long-crested *Civettictis civetta*, which cannot climb, and the long-haired *Genetta genetta* and *G. angolensis*. Like all genets they are good climbers, but *G. genetta* lives in arid open habitats, and *G. angolensis* is a woodland savanna species. *Felis nigripes* is the only felid with dorsal body hair exceeding 7% of its head and body length. It is an able climber, but occupies barren wastelands of southern Africa. These species support the contention that climbing forms living in open habitats tend to have longer dorsal hair than those living in forests. However, several exceptions to the general trends require explanation, and underscore the fact that there is no universal set of characters predicting the occurrence of long crests and capes. Vulnerability to interspecific conflict for food and space is hypothesized to be a critical factor. Intermediate body size, poor climbing ability, or occurrence in open habitats are features that may increase vulnerability. Additional factors probably also play a role. There is limited evidence that the importance of individual intimidation incorporating crests and capes is reduced in group-living species. Explanation of exceptions to the general trends should clarify additional factors that have been critical in the evolution of crests and capes.

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