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Wounding, mortality and mane morphology in African lions, *Panthera leo*

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A protective role for the lion's mane has long been assumed but this assumption has never been tested. We compared patterns of injury, mane development and adult mane morphology in a population of African lions and found no compelling evidence that the mane conferred effective protection against wounding. The mane area was not a specific target of attacks, and injuries to the mane area were not associated with higher mortality than other injuries. Regions of the mane that were most frequently attacked did not show earlier onset of mane growth in subadult males or longer/darker mane hair in adult males. Adult males appeared to be wounded less frequently on the mane area than predicted by surface area, but it is unclear whether this trend was only caused by observer bias from decreased visibility. We conclude that, although the mane may have conferred protection during the early evolution of the trait, protection appears to be secondary to the strong sexually selected advantages of the mane as a condition-dependent ornament.

Competition between males for mates has led to the evolution of a wide variety of sexually dimorphic traits. These traits generally serve as weapons and/or signals advertising male quality to rivals (reviewed in Andersson 1994), and some also have protective value; for example, ungulate horns and antlers are used as offensive weapons, but their elaboration may serve a defensive purpose (Geist 1966; Clutton-Brock 1982). Traits whose function is purely protective have also been documented; some crustaceans have sexually dimorphic 'cephalothoracic shields' (e.g. Mantelatto & Martinelli 2001), and male mammalian herbivores often have 'dermal shields' consisting of thickened skin in areas that are targeted during attacks (Darwin 1871; Jarman 1972, 1985). Darwin (1871) considered the lion's mane to be a protective trait, but recent evidence demonstrates that the mane serves primarily as a condition-dependent signal (West & Packer 2002): males with darker manes show higher levels of testosterone, longer life expectancy and greater survival after wounding, and their cubs enjoy higher survival. West & Packer briefly examined the risk of injury to the mane area (and its associated mortality), but in this paper we present the results of a more comprehensive analysis to address the protection hypothesis in greater detail (Withgott 2002).

The lion's mane consists of hair up to 23 cm long (C. Packer & L. Herbst, unpublished data), in colour from almost white to black, and covering, to varying degrees, the heads, necks, shoulders and chests of male lions (West & Packer 2002). Schaller (1972) suggested that the mane protects the area of the body 'towards which most social contact is directed' (page 360) by absorbing blows and bites. Darker mane hairs are thicker than lighter hairs (West & Packer 2002), so it is possible that darker manes provide better protection. These ideas suggest that males with longer and darker manes will be wounded less frequently and/or with less severity on the area covered by the mane, but direct tests of this prediction are difficult. Individual males are seldom seen daily, and the mane itself introduces a bias by obscuring many wounds beneath it from view. Furthermore, even in the best-studied populations, serious fights between lions are rarely observed (Table 1).

The mane's hypothesized protective function depends on three basic assumptions: fights between lions are common or dangerous enough to warrant protection, the mane area is a frequent and/or vulnerable target, and the mane confers significant protection, with more exaggerated phenotypes providing better protection. We addressed the hypothesis with a series of specific predictions. (1) Male

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Table 1. Attacks among Serengeti and Ngorongoro adult lions during 1966–2002 in which the observer noted the area of the body attacked

Date	Attacker	Attacked	General area	Exact area	Observer
4 Aug 1987	Male	Male	Body	Groin	C. Packer
10 Mar 1999	Male	Male	Body	Back	P. West
3 Oct 1999	Male	Male	Body, legs	Hip, groin, legs	B. Kissui
1966*†	Male	Female	Body	Back	R. Schenkel
1996*	Male	Male	Mane	Head	M. Iwago
16 Mar 1969†	Male	Female	Mane	Neck	G. Dove
21 Aug 1997	Female	Male	Legs	Legs	P. West
9 Aug 1996	Female	Female	Legs, body	Legs, hip	G. Hopcraft
24 Aug 1997	Female subadult	Male	Body	Hip	G. Hopcraft
24 Aug 1997	Male	Female subadult	Mane	Neck	G. Hopcraft

Attacks against cubs are excluded, but a fight between a male and a subadult female is included to show a potential effect of size on fighting style; the adult male attacked the subadult on the neck while she bit him on the hip.
*Publication date of observation.
†Reported by G. Schaller (1972).

lions should readily attack the areas of the forehead, neck, shoulders and chest that are covered by the mane. (2) Lion-inflicted wounds should be observed most frequently on these parts of the body, especially in adult females and subadults where the mane area is clearly visible. (3) Wounds on these areas should also result in more frequent mortality. (4) Longer and darker hairs should be either more densely packed or stronger. Hair density is difficult to measure in free-ranging animals, but hair strength is reliably indicated by breakage at the distal ends of individual hairs (Braida et al. 1994); broken ends should be less common among darker and longer hairs. (5) Mane darkness and length develop at different rates on the forehead, neck, shoulder and chest and often vary considerably within the manes of individual males; these variations should reflect the frequencies and mortality rates associated with wounds to each area.

METHODS

Study Population

Detailed field work was conducted in 1996–2001 on approximately 300 lions living in a 2000-km^2 area of the Serengeti National Park (Packer et al. 2005) and approximately 50 lions living in the Ngorongoro Crater, Tanzania (Kissui & Packer 2004). Long-term behavioural, demographic and photographic records on these populations date back to 1963 (West & Packer 2002). We located individual prides by sight and by radiotelemetry. All study lions were individually recognizable by natural markings and were habituated to vehicles. On average, each lion in the study area was seen once every 3–4 days. For the purposes of this study, we concentrated on adults ($\geq$4 years) and subadults (between 2 and 4 years).

Model Experiments

We experimented with a taxidermically mounted lion and life-sized toy 'model' lions to determine the circumstances under which male lions initiate attacks and to measure how these attacks are distributed across the body. Three replicates were performed in the late 1980s and consisted of broadcasting the roar of an unfamiliar male to resident males while presenting a mounted male with a dark brown sheepskin serving as a mane (Grinnell et al. 1995). In 17 additional tests on unique individuals between 1996 and 2001, we attracted resident males with playbacks of hyaenas feeding at a kill and presented them with two model lions with contrasting manes. When the lions approached, we recorded which model they came closest to as well as their behaviour towards the models. We used three identical models in rotation to ensure equal exposure to human handling and to real lions. Models were placed downwind from the lions to limit the influence of olfaction. Eight of these 17 experiments were performed on one resident male, five on two or three resident males where all approached, and the remaining four on one resident male that approached in the company of a female. In 2002, we twice performed an experiment in which we broadcast the roar of an unfamiliar male to resident males and simultaneously presented them with a 'maneless' model that had just enough mane to identify it as male.

Surface Area Measurements

If lions target a specific area of the body during aggressive encounters, then the distribution of lion-inflicted wounds should differ significantly from a random distribution based on surface area. We used measurements from 20 immobilized Serengeti lions (five adult females, five adult males, five subadult females and five subadult males) and a digital photograph of a male lion skin from the collection at the Bell Museum at the University of Minnesota, U.S.A., to obtain measurements of a lion's surface area. Data from immobilized lions consisted of body length, tail length, foreleg length, heart girth and neck girth. We first averaged the measurements of each age–sex class and used them to confirm that the general body proportions of all age–sex classes are the same. We then used IP Lab 3.5 Evaluation software (Rockville, Maryland, U.S.A.) to take linear measurements from the digital picture corresponding to the field measurements,

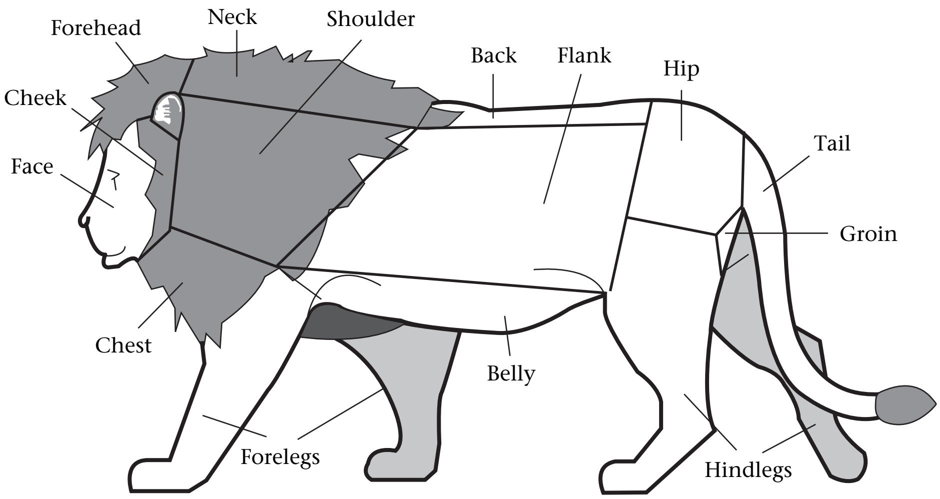

Figure 1. Mane and body categories. The forehead, neck, shoulder and chest are considered the 'mane area' and the back, belly, flank, hip and groin are considered the 'body area'. Front and hind legs were combined into one 'legs' category.

and we used a chi-square analysis to determine whether the digital measurements accurately represented a live lion. Finally, we divided the lion's body into 13 parts (Fig. 1), and we used Adobe Photoshop to count pixels on each part. Pixel counts were used to generate expected frequencies of wounds to each area.

Wound Counts

Wounds were recorded opportunistically from 1974 to 2001 as part of the general lion-monitoring programme. We categorized wounds according to body area (Fig. 1) and type (puncture, cut, bite, broken bone, abscess, limp, unspecified wound and unspecified injury). Our mane area categories (cheek, forehead, neck, chest and shoulder) were designed for evaluating mane variation rather than wounds; thus, wounds to the throat were categorized as 'chest' wounds and wounds to the side of the neck were categorized as 'shoulder' wounds. No wounds to the cheeks had been recorded, so we eliminated the cheek category.

We assumed that punctures, cuts, bites and unspecified wounds were inflicted by other lions, and we excluded broken bones, abscesses, limps and unspecified injuries because these could occur through a variety of circumstances. We examined the overall proportion of lion-inflicted wounds for each age–sex class and compared mortality rates of wounds that were and were not inflicted by lions. Dead lions are rarely found intact, so we used two approximate measures of mortality associated with wounding: whether lions were either found dead or disappeared (1) within 1 month and (2) within 1 year after the date their wound was recorded. Although deaths/disappearances that occurred within 1 year may be less clearly related to a specific wound, lions are commonly observed with wounds that fester for months before the animal disappears (Schaller 1972; West & Packer 2002).

We used surface area measurements to generate expected wound counts for each body part and compared these values to observed frequencies for each age–sex class. To determine whether the area covered by the mane is a special target, we combined wounds to the body (flank, back, hip, belly, groin) and compared them to combined wounds to the mane area (forehead, chest, neck, shoulder) for each age–sex class. To determine whether injury to the mane area was more dangerous, we calculated the proportions of wounds to the body, mane, legs and face that were associated with mortality within 1 month and 1 year of wounding for all age–sex classes. We also compared the frequencies of wounds to the body and wounds to the mane area that were fatal within 1 month and 1 year of wounding within age–sex classes.

'Multiple wounds' complicate the mortality analysis because they may be associated with higher mortality rates. To control for multiple wounds, we separately analysed 'unique' wounds (i.e. those that were not associated with other wounds within the previous or following year). We first compared the overall mortality rates of unique wounds with nonunique wounds. We then combined unique fatal wounds to the bodies and mane areas of adult females and subadults and compared their frequencies to those predicted by surface area. We excluded adult males because the mane probably prevents less severe wounds from being observed.

Finally, we compared frequencies of wounds to the chest, forehead, neck and shoulders according to surface area and measured their associated monthly and annual mortality rates. The results of these analyses were used to make predictions about variation in hair length and darkness between the four mane parts.

Mane Hair Analyses

We analysed 204 mane hairs from 35 male lions. Hairs were collected during routine immobilization of Serengeti lions and were cut from the forehead and chest. All hairs were washed with acetone, followed by three washes with distilled water and a final wash with acetone. Hairs were air-dried for 5–10 min and mounted onto microscope slides with a toluene-based mounting solution. When hairs were too long for one slide, the hairs were cut into approximately 3-cm segments and placed on multiple slides in proximal-to-distal orientation. Each slide was examined using bright field microscopy at 20× magnification (Olympus UPlanApo 20×\0.7), and the microscopic image of each hair was captured at 10× magnification using MetaMorph software (MetaMorph Imaging System, Sunnyvale, California, U.S.A.). We evaluated the distal end of each hair for signs of breakage, as evidenced by a jagged, horizontal surface as opposed to a healthy taper. Hair-length measurements were imprecise, because the hairs were cropped 0.5–2.5 mm from the body. We therefore grouped hairs into four categories based on the number of slides necessary to mount the full length of each hair. Hair colours followed a bimodal distribution and were mostly either very dark or very light (West & Packer 2002); we eliminated the few medium-coloured hairs to simplify the analysis and recorded each hair's length, darkness and whether its distal end was broken.

Mane Characteristics

Mane characteristics were evaluated using photographs taken of 568 males from 1964 to 2000 (West & Packer 2002). Most photographs taken from 1964 to 1990 were black and white; colour film was used from 1991. Each photograph was graded for length and colour by five undergraduate judges who had never seen the animals in the wild. Students graded both the overall colour and length of the mane as well as the colour and length of individual areas of the mane (chest, forehead, neck, shoulders). Multiple images of the same male were evaluated collectively if they were taken within 1 week. For each male, the judges' highest and lowest scores were discarded, and the remaining three were averaged. We found no statistically significant effect of picture quality or film type on the judges' scores (West & Packer 2002).

We used the mane darkness and length scores of 354 subadult males aged 1–4 years to generate patterns of mane development. We subdivided the data into 11 age classes and averaged the values within each class. We used the darkness and length scores of 313 adult males above age 4 to create colour and length profiles of adult manes. We tested for length and darkness differences between the four mane parts with repeated measures single factor ANOVAs followed by paired t tests. Data were tested for normality using the Shapiro–Wilk's test. Only chest colour scores varied significantly from a normal distribution ($P < 0.05$, skewness $= -0.013$, kurtosis $= -0.58$), but this deviance was too small to require the use of nonparametric statistics.

RESULTS

Model Experiments

The results of all model experiments are presented in Table 2. The number of males in a coalition has a strong effect on coalition success (Grinnell et al. 1995); thus, although resident males always approached the models when attracted by hyaena vocalizations, they were significantly more likely to get within sniffing distance (0 m) if they were accompanied by at least one other male (Fisher's exact test, one-tailed: $N = 13$, $P = 0.0435$). However, males attacked the models only when their pride females or territory was directly threatened. Hyaena vocalizations do not themselves represent a challenge to females or territory, but in all cases where hyaena calls were broadcast and a male approached with a female, the male attacked a model ($N = 4$). Although the presence of a female evened the numbers odds, this does not explain the attacks; males never attacked a model when two males approached the models after hearing hyaenas ($N = 4$; comparison between approaches with female and male: Fisher's exact test, two-tailed: $N = 8$, $P = 0.0286$). Males roar to advertise territory ownership; thus, the roar of a strange male within their territory is a serious threat to residents (Grinnell et al. 1995). Accordingly, resident males without females attacked a model in all experiments where a roar of a strange male was broadcast, but they never attacked when scavenging hyaenas were broadcast (Fisher's exact test, one-tailed: $N = 18$, $P = 0.0002$).

Experiments with model lions also indicated that the mane area was not the primary target during attacks. Although sample sizes were small, males bit the models on the hindquarters in all nine experiments involving an attack. In the three experiments using the mounted male with a sheepskin mane, males attacked the mount on its lower back (Grinnell et al. 1995). In the four experiments with two maned models, males attacked first on the back ($N = 2$), the base of the tail ($N = 1$) or the hindleg ($N = 1$). It is possible that males avoid attacking the mane area because the mane provides an effective shield. We could perform only two tests with a 'maneless' male model (where the mane area was fully exposed), but the males first attacked the model on the back in both cases.

Surface Area

Field measurements of immobilized lions revealed that body proportions were similar across all age–sex classes (chi-square test: $\chi^2_4 = 1.619$, $P = 0.9998$), and there were no significant differences between field measurements and those based on the digitized lion skin picture ($\chi^2_4 = 7.13$, $P = 0.1292$).

General Wounding Patterns

A total of 1332 wounds were recorded between 1974 and 2001. Seventy-eight of these were on juveniles less than 2 years of age and were eliminated. Of the remaining 1254 wounds, 991 (79%) were categorized as lion-inflicted. Of all lion-inflicted wounds, 336 were 'unique' and not associated with wounds to other areas of the body within the previous or following years. The proportion of wounds that were lion-inflicted was high in all age–sex classes (adult males: 310/398 (88%); adult females: 485/576 (84%); subadult males: 97/159 (61%); subadult

Table 2. Responses of free-ranging adult lions to life-sized lion models (maned, maneless) and to a taxidermic mount of an adult male (sheepskin mane) during broadcasts of hyaena vocalizations or roars from an unfamiliar male lion

Experiment	Audio	Visual	Number of Males	Number of Females	Attack	Response
1	Hyaenas	Two maned models	1	0	No	Approach to 10 m
2	Hyaenas	Two maned models	1	0	No	Approach to 20 m
3	Hyaenas	Two maned models	1	0	No	Approach to 5 m
4	Hyaenas	Two maned models	1	0	No	Approach to 5 m
5	Hyaenas	Two maned models	1	0	No	Approach to 20 m
6	Hyaenas	Two maned models	1	0	No	Sniff*
7	Hyaenas	Two maned models	1	0	No	Sniff
8	Hyaenas	Two maned models	1	0	No	Sniff
9	Hyaenas	Two maned models	2	0	No	Sniff
10	Hyaenas	Two maned models	2	0	No	Sniff
11	Hyaenas	Two maned models	2	0	No	Sniff
12	Hyaenas	Two maned models	2	0	No	Sniff
13	Hyaenas	Two maned models	4	0	No	Sniff
14	Hyaenas	Two maned models	1	1	Yes	Bite back then run away
15	Hyaenas	Two maned models	1	1	Yes	Bite hindleg then bite groin
16	Hyaenas	Two maned models	1	1	Yes	Bite base of tail then bite rear leg
17	Hyaenas	Two maned models	1	1	Yes	Bite back then bite groin
18†	Male roar	Sheepskin mount	2	0	Yes	Bite back; subsequent behaviour not recorded
19†	Male roar	Sheepskin mount	2	0	Yes	Bite back; subsequent behaviour not recorded
20†	Male roar	Sheepskin mount	2	0	Yes	Bite back; subsequent behaviour not recorded
21	Male roar	Maneless model	3	0	Yes	Bite back then bite throat
22	Male roar	Maneless model	3	0	Yes	Bite back then bite throat

*Sniff denotes an approach to 0 m.
†From Grinnell et al. (1995).

females: 107/121 (88%)), suggesting that intraspecific aggression is common. Lion-inflicted wounds were less severe than other wounds: 8% (84/991) of lion-inflicted wounds were associated with mortality within the following month compared to 14% (36/263) of non-lion-inflicted wounds (Fisher's exact test, two-tailed: $P = 0.0132$), although this was not true of mortality within the following year: 28% (274/991) of lion-inflicted wounds were associated with mortality within the following year compared to 31% (82/263) of non-lion-inflicted wounds (Fisher's exact test, two-tailed: $P = 0.2815$).

We examined all lion-inflicted wounds and determined that their general distribution was not predicted by surface area; foreheads, legs and faces were wounded more often than expected (chi-square test: $\chi^2_{11} = 2713.42$, $P < 0.0001$; Table 3). However, we also compared wounds on the combined mane area (forehead, chest, shoulders, neck) to wounds on the body (back, belly, flank, hip, groin) and found that wound frequencies of adult females, subadult females and subadult males did not differ significantly from those predicted by surface area ($\chi^2_1 = 0.004$, $P = 1$; $\chi^2_1 = 0.147$, $P = 0.6629$; $\chi^2_1 = 0.023$, $P = 0.9203$, respectively; Table 3), but adult males were wounded significantly less on the mane area ($\chi^2_1 = 13.197$, $P = 0.0003$; Table 3). These results suggest that the general mane area is not a target, but hint that attackers avoid the mane, or that the mane protects this area from attack. However, the mane also obscures some wounds from view, biasing our results. This bias is illustrated by the wounding pattern in subadult males, who have enough mane to provide some protection but not enough to obscure wounds from view.

Mortality Rates

Mortality rates suggest that wounds to the mane area were not more dangerous than wounds to other parts of the body. For combined age–sex classes, there was no difference in the rates of mortality within 1 month between the mane area, the body, the legs and the face (mane: 10/106 wounds; body: 23/233; legs: 9/186; face: 9/143; exact 2×4 test (Uitenbroek 2000), two-tailed: $P = 0.2036$). There was a significant difference between mortality rates after 1 year primarily because of higher-than-expected mortality rates in body wounds (mane: 30/106; body: 79/233; legs: 40/186; face: 29/143; $P = 0.0082$). Wounds to the legs and face were generally less dangerous than those to the body and mane, and they were excluded from further analyses. In each age–sex class, the proportions of mane area wounds that were fatal within either 1 month or 1 year were not significantly higher than those of body wounds (Table 4).

Disappearance is a reliable indicator of mortality in cubs and adult females, but adult males may have disappeared because they dispersed from our study area. Dispersal can be inferred from disappearance when all members of a male coalition disappear simultaneously; asynchronous disappearance occurs only from mortality. Our data set included only two cases where a coalition disappeared

Table 3. Observed and expected lion-inflicted wounds for each age–sex class and total observed and expected wound counts to all body and all mane areas for all age–sex classes combined

				Wounds					
Category	Body part	Area (pixels)	Proportion	Adult females	Adult males	Subadult females	Subadult males	Total wounds	Expected wounds
Mane	Chest	17 022	0.06	16	1	2	0	19	63.99
Mane	Forehead	4751	0.02	16	2	5	3	26	17.86
Mane	Neck	13 927	0.05	10	2	3	2	17	52.36
Mane	Shoulder	34 481	0.13	31	7	7	11	56	129.63
All mane				74	12	16	16		
Body	Back	26 840	0.10	42	24	7	18	91	100.90
Body	Belly	35 505	0.13	17	4	5	0	26	133.48
Body	Flank	49 333	0.19	44	23	8	10	85	185.46
Body	Groin	6817	0.03	8	2	2	1	13	25.63
Body	Hip	33 044	0.13	48	23	19	4	94	124.23
All body				160	76	41	32		
Face	Face	7000	0.03	99	143	16	28	286	26.32
Legs	Legs	26 867	0.10	140	71	28	18	257	101.00
NA	Tail	8017	0.03	8	8	4	1	21	30.14
	Totals:	263 604	1	479	310	106	96	991	991
All mane parts (observed)				74	12	16	16		
All mane parts (expected)				74.07	27.85	18.04	15.19		
All body parts (observed)				160	76	41	32		
All body parts (expected)				159.93	60.15	38.96	32.81		

simultaneously, and the results were unchanged when these were excluded.

These analyses did not control for multiple wounds, because no significant differences were found between the mortality rates of unique and nonunique wounds within 1 month (unique: 29/336; nonunique: 84/991; Fisher's exact test: two-tailed, $P = 0.9103$) or 1 year (unique: 89/336; nonunique: 275/991; $P = 0.6718$), and the observed distribution of fatal unique wounds inflicted on the body versus the mane area occurred in proportion to their respective surface areas (chi-square test: $\chi^2_1 = 0.005$, $N_{\text{mane}} = 9$, $N_{\text{body}} = 20$, $P = 0.9427$; these wounds were fatal within 1 year; too few wounds were fatal within 1 month to address statistically).

Wounds Within the Mane Area

Within the mane area itself, wounds were not distributed according to surface area. Combining data from adult females and subadults, only the observed number of wounds to the forehead was higher than that predicted by surface area (chi-square test: $\chi^2_3 = 41.2, P < 0.0001$; Table 5). Adult males were significantly more likely to die within a year if they were wounded on the forehead or the neck (Table 6), and adult females were marginally more likely to die within a month if they were wounded on the forehead (Table 6). The sample size of wounds to each mane area within age–sex class was small, so we combined all age–sex classes (with and without adult males), but found no significant differences in the mortality rates across mane parts (Table 6). We also compared wounds to forehead/neck to chest/shoulder for all age–sex classes, but found no difference in mortality (Table 6). However, when we excluded adult males, wounds to the forehead were associated with higher mortality within 1 month compared to wounds to the neck/chest/shoulders (Table 6).

Mane Hair Analyses

Longer mane hair does not necessarily provide better protection; analyses of individual mane hairs revealed that the distal end of longer hairs was more likely to have the jagged surface indicative of breakage (one slide: 11/53; two slides: 12/88; three slides: 13/49; four slides: 8/14; exact 2×4 test, two-tailed: $P = 0.0041$). This result is counterintuitive (one expects broken hair to be shorter), but probably results from the weakening of hair shafts from weathering and sun damage (Braida et al. 1994). In

Table 4. Mortality comparisons of mane and body wounds for each age–sex class*

		1 month		1 year	
		Die	Live	Die	Live
Adult males	Mane	2	10	5	7
	Body	11	65	34	42
		P=1.0		P=1.0	
Adult females	Mane	7	66	19	54
	Body	17	142	58	101
		P=1.0		P=0.1343	
Subadult males	Mane	1	15	6	10
	Body	3	30	13	20
		P=1.0		P=1.0	
Subadult females	Mane	2	15	5	12
	Body	3	38	8	33
		P=0.6243		P=0.4941	

*Fisher's exact tests, two-tailed.

Table 5. Expected and observed frequencies of mane area wounds for adult female, subadult female and subadult male lions combined

Mane part	Pixels	Proportions	Expected wounds	Observed wounds	χ^2
Chest	17 022	0.24	25.71	18	2.31
Forehead	4751	0.07	7.18	24	39.45
Neck	13 927	0.20	21.04	15	1.73
Shoulder	34 481	0.49	52.08	49	0.18

contrast, the distal ends of dark hairs were significantly less likely to show signs of breakage, suggesting that darker hairs may provide better protection (light hair: 34/94; dark hair: 10/110; Fisher's exact test, two-tailed: $P < 0.0001$). A logistic regression including both hair length (number of slides) and tip darkness confirmed that both variables were significant (tip colour: Wald $\chi^2_1 = 17.98$, $N = 204$, $P < 0.0001$; number of slides: $\chi^2_1 = 4.30$, $N = 204$, $P = 0.038$).

Mane Development and Morphology

Figure 2 shows patterns of mane development in subadult males up to age 4 years and typical length and

Table 6. Analysis of lion mortality within 1 month and 1 year of mane area wounding for each age–sex class and all age–sex classes combined (with and without adult males)

Comparison	Interval	Fate	Mane area				*P**
			Chest	**Forehead**	**Neck**	**Shoulder**	
Adult males	1 month	Die	0	0	1	1	0.6818
		Live	1	2	1	6	
	1 year	Die	0	2	2	1	0.0101
		Live	1	0	0	6	
Adult females	1 month	Die	2	4	0	1	0.0545
		Live	14	12	10	30	
	1 year	Die	5	5	1	8	0.6512
		Live	11	11	9	23	
Subadult males	1 month	Die	—	0	0	1	1
		Live	—	3	2	10	
	1 year	Die	—	0	0	6	0.1552
		Live	—	3	2	5	
Subadult females	1 month	Die	0	1	1	0	0.4338
		Live	2	4	2	7	
	1 year	Die	1	1	1	2	1
		Live	1	4	2	5	
All classes	1 month	Die	2	5	2	3	0.2368
		Live	17	21	15	53	
	1 year	Die	6	8	4	17	0.9627
		Live	13	18	13	39	
All but adult males	1 month	Die	2	5	1	2	0.1117
		Live	16	19	14	47	
	1 year	Die	6	6	2	16	0.4909
		Live	12	18	13	33	
			Forehead/neck		**Chest/shoulder**		
All classes	1 month	Die	7		5		0.1187
		Live	36		70		
	1 year	Die	12		23		0.8356
		Live	31		52		
All but adult males	1 month	Die	6		4		0.1665
		Live	33		63		
	1 year	Die	8		22		0.3479
		Live	31		45		
			Forehead		**Chest/shoulder/neck**		
All classes	1 month	Die	5		7		0.1337
		Live	21		85		
	1 year	Die	8		27		0.9999
		Live	18		65		
All but adult males	1 month	Die	5		5		0.0448
		Live	19		77		
	1 year	Die	6		24		0.7998
		Live	18		58		

*Exact 2 × 3 and 2 × 4 tests (from Uitenbroek 2000).

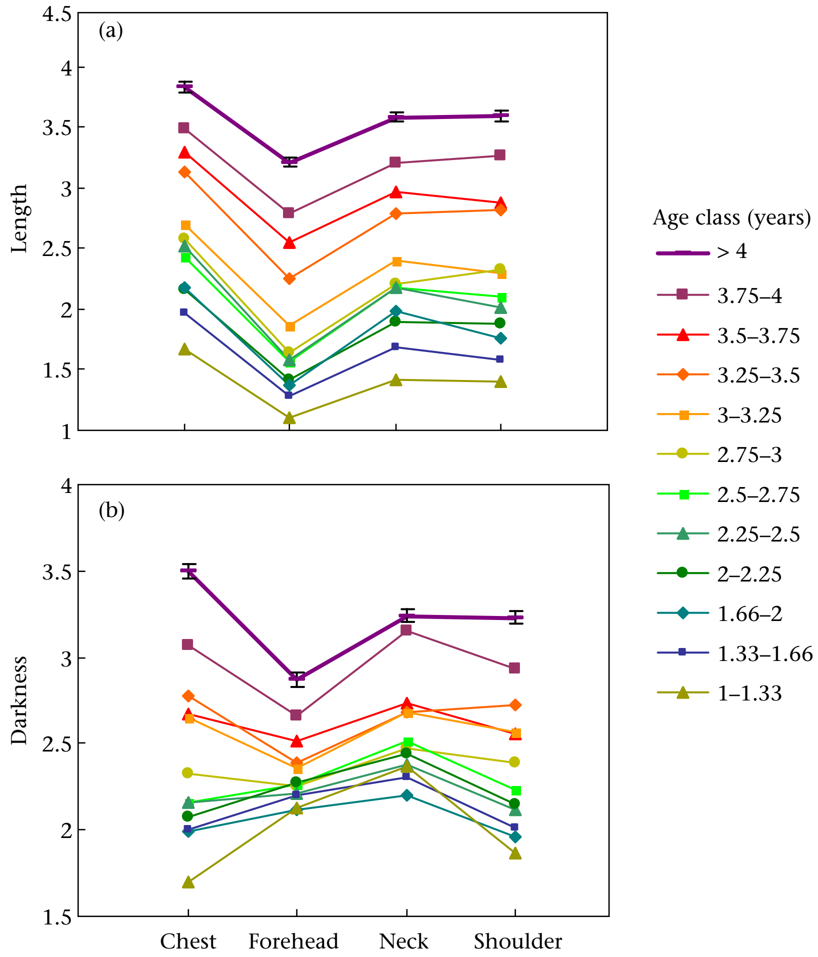

Figure 2. Average (a) length and (b) colour patterns of mane hair from the chest, forehead, neck and shoulder for 354 subadult males in 11 age classes and 313 individual adult males over 4 years of age. Graphs for each subadult category include multiple observations of each male.

darkness patterns in adult males. The data in Table 6 suggest that mane length should develop more quickly on the forehead and be greatest in adult males, but length actually develops earliest and fastest on the chest, while forehead mane development lags behind (Fig. 2a). In adult males, the difference in mane lengths between the four areas was significant (repeated measures ANOVA: $F_{3,\ 200} = 125.74$, $P < 0.0001$) and forehead manes were shortest. Chest manes were significantly longer than neck manes (paired *t* test, two-tailed: $t_{202} = 8.4534$, $N = 203$, $P < 0.0001$), necks and shoulders did not differ significantly ($t_{252} = 0.0117$, $N = 253$, $P = 0.9907$) and neck manes were significantly longer than forehead manes ($t_{266} = 13.3926$, $N = 267$, $P < 0.0001$).

Table 6 also suggests that the darkness of forehead manes should develop most quickly, but neck mane darkness developed at the same initial rate, and chest/shoulder manes become darker than both forehead and neck manes as subadult males approach adulthood (Fig. 2b). Differences in darkness between the four mane parts of adult males were also significant (repeated measures ANOVA: $F_{3,\ 210} = 112.19$, $P < 0.0001$). There was no significant difference between neck and shoulder darkness (paired *t* test, two-tailed: $t_{256} = 1.2055$, $N = 257$, $P = 0.2291$), but chests were darker than necks ($t_{213} = 5.1427$, $N = 214$, $P = 0.0001$) and foreheads were lighter than necks ($t_{269} = -13.8917$, $N = 270$, $P < 0.0001$).

DISCUSSION

Various behavioural tactics allow lions to avoid encounters that may escalate into aggression. Roaring advertises location and enables groups to avoid each other (McComb et al. 1994; Grinnell & McComb 1996). Lions can also assess group numbers and the roarer's identity, both of which assist them in avoiding dangerous encounters (McComb et al. 1992, 1994; Grinnell et al. 1995; Heinsohn & Packer 1995). The lion's mane contains information about age, injury and testosterone status, allowing male lions to use the mane to assess rivals and avoid superior competitors (West & Packer 2002). However, although fights between lions are seldom observed, our results suggest that a large proportion of injuries to lions are inflicted by other lions and that these injuries are a significant source of mortality.

The most severe injuries are probably inflicted during fights with lions outside of the pride. When coalition partners compete between themselves, they generally

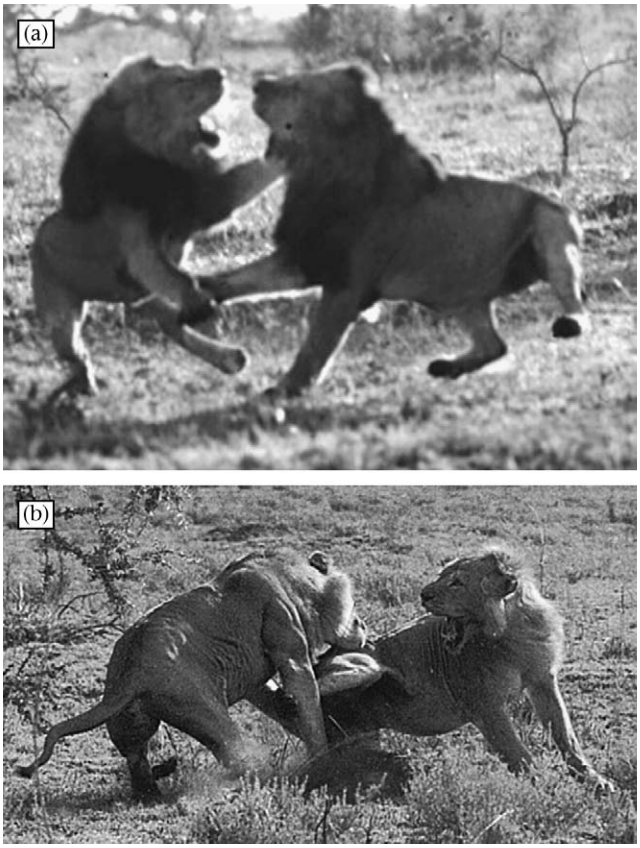

Figure 3. Fighting within and between male coalitions. (a) Two coalition males in a dispute over an oestrous female. Fighting consists of slaps and hits to the face. (Photo by C. Packer.) (b) Males from different coalitions in a dispute over a carcass and female. Fighting consists of serious attacks; note the attack is directed at the back/hips and away from the mane area. (Photo by P. M. West.)

swat and hit each other on the face (Fig. 3a) rather than engage in serious attacks. Coalition partners must cooperate to defend a pride against rivals and, given this mutual dependence, they cannot afford to severely injure a companion (Packer & Pusey 1982). In contrast, males fighting with strange males engage in more aggressive attacks and generally attempt to incapacitate their rivals (Fig. 3b). Tests with model lions provide additional information about when and why male lions fight. If there is no immediate danger to females or territory, resident males refrain from attacking rivals, but if females are present, or they are challenged by another male's roar, they attack with little hesitation, even when they are outnumbered. These observations conform both to previous studies of lion behaviour (Grinnell et al. 1995) and to general models of aggression; assessment permits lions to avoid fights when the odds of winning are low (Parker 1974; Maynard Smith 1982), but lions readily initiate aggression, regardless of the danger, when a valuable resource is threatened (Enquist & Leimar 1990).

Once fighting begins, the potential costs are high; recorded observations show that fights often end in quick death for at least one participant (Guggisberg 1963; Schaller 1972; Grinnell et al. 1995; Iwago 1996), and our results suggest that roughly one-third of lion-inflicted wounds result in mortality within the following year. These results confirm that lions would benefit not only from adaptations allowing them to avoid fights, but also from some form of protection from the teeth and claws of rivals. However, although a protective function of the lion's mane has long been assumed (Darwin 1871), our results provide little support for this hypothesis.

The morphology of sexually selected protective traits is generally tied to fighting strategy (Jarman 1985), but we found no sign of this relation in lions. Lions generally direct social contact towards the area covered by the mane (Schaller 1972), and hunting lions often bite prey at the head, neck and throat. Observations of infanticide reveal that lions tend to bite cubs on the head and neck (www.lionresearch.org), and in several instances where cheetahs were killed by lions in the Serengeti, the cheetah was bitten on the head (P. M. West, personal observation; M. Craft, personal communication). However, the mane area does not appear to be the primary target during fights between adult lions. Lions targeted the mane area in only two of eight observed fights (Table 1), and, in experiments with model lions, males always directed their primary attacks to the model's hindquarters even when the mane area was uncovered.

The results of our wound analyses should be treated with caution because they refer largely to wounds on live lions. We rarely observed mortally wounded lions, so the most serious wounds may often go unrecorded; we could compare only frequency and recovery from wounds that did not cause immediate death. Given these limitations, lion wounds are generally distributed according to surface area and provide no evidence that the general mane area is a target, nor are wounds to the general mane area associated with higher mortality. However, of the four mane areas, forehead wounds were more frequent than predicted by surface area, and were associated with higher mortality.

The high mortality rates of forehead wounds in maneless lions may be related to difficulties in licking and cleaning forehead wounds, but necks are equally difficult to clean and showed no similar trend. Furthermore, lions are often licked by their companions, and the foreheads/necks receive the most attention (Schaller 1972, page 89). A relationship between mortality and licking is suggested by the higher mortality rates of adult males from forehead and neck wounds because adult males are licked significantly less by companions than are females (Schaller 1972), and the results were significant in the death-within-1-year category, suggesting that death resulted from infection rather than wound severity. However, the sample size was so small for adult males that we are reluctant to draw firm conclusions from it. Regardless of the exact cause of death, the results suggest that males would benefit most from extra protection on their forehead, and that the length and darkness of forehead manes should develop earlier and more rapidly.

Our analysis of mane hair strength confirmed that darker hairs are stronger, but longer hairs were generally weaker, suggesting that the additive benefits of mane length are slight. Although it is still possible that some mane is better than no mane, we found no sign that mane length development reflects a need for protection on the head; forehead manes are actually the shortest throughout subadulthood. Forehead mane darkness develops before chest and shoulder darkness, supporting the protection hypothesis. However, neck manes are as dark as foreheads, and the necks, chests and shoulders all become darker than the forehead as subadults mature.

An alternative explanation for the initial darkness of foreheads and necks is the exaggeration of a pre-existing trait. Lions have various patches of dark hair that probably function in communication (Schaller 1972), and among these patches is a dark line running down the back of the head and the neck. Mane growth on the forehead and neck typically begins on this line, creating a 'mohawk' of elongated darker hair that gradually becomes obscured as the mane develops.

Although exaggerated manes are associated with significant heat-related costs, including decreased food intake and increased proportions of abnormal sperm (West & Packer 2002), it has been argued that the benefits of protection are sufficient to explain its evolution (Withgott 2002), and it is reasonable to assume at least some minimal protection by the mane. However, our results reveal only limited evidence of this protection. The best argument for the protection hypothesis is that we observed fewer wounds on the mane area of adult males, but it is difficult to say whether this was because of protection or observer bias resulting from masking by the mane. Other hints of protection are that the lion's forehead appears to be a frequent target, that wounds to the forehead are relatively dangerous, and that the forehead manes of young males are dark. Although these arguments support the need for added protection to the forehead, they fail to explain the evolution of chest, neck and shoulder manes. Furthermore, the forehead is already well guarded by its proximity to the lion's jaws and teeth (Fig. 3b); this proximity may explain why males direct their attacks to the hindquarters and argues against the need for additional protection.

Our results suggest that the current protective benefits of the mane are minimal, but they do not exclude the possibility of past protective benefits. Forehead manes may have initially evolved as protection and later taken on a signalling function that led to the mane's exaggeration. It is also possible that the entire mane evolved initially as protection, but that lion fighting behaviour subsequently changed. Studies of fighting behaviour in other felids, particularly the lion's closest relative, the tiger, *P. tigris*, may provide a better basis for comparison; if tigers target the shoulders, necks and chests along with the forehead, or if injuries to these areas also cause high mortality, the necessity for protection to these areas would be supported. Tigers and other maneless felids might also have protective dermal shields; if so, the location of these shields should provide clues about the areas most in need of protection. Regardless of the lion mane's original function, protective benefits are not sufficient to explain the maintenance of the trait; rather, the key benefit of the mane appears to derive from its function as a signal of male condition.

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