

Mane variation in African lions and its social correlates

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Abstract: Manes are generally thought to characterize all adult male lions (*Panthera leo*). Here we document a population of lions in Tsavo National Park, Kenya, that is largely maneless and describe aspects of their social organization. Because Tsavo's arid landscape supports sparse prey populations, we expected that surveys of lions there would document small social groups. We hypothesized that Tsavo lions would consequently experience reduced sexual selection pressures for mane development. Adult males from Tsavo typically have sparse blond hair forming a dorsal crest, beard, chest tufts, and (or) sideburns, but lack the large flowing manes reported from other lion populations. No fully maned lions were seen. Maneless males in Tsavo appear to be well integrated into pride life, and were observed copulating, hunting, and otherwise interacting with groups of females, playing with dependent cubs, and advertising territories with scent markings and roars. Only one adult male was observed in each of five prides, which differs surprisingly from the coalitions of 2–4 pride males noted in other lion groups. However, female group size was large (mean 7.4) and comparable with what has been documented in the Serengeti and elsewhere, refuting our "group size – mane size" hypothesis. Future research should focus on the effect of Tsavo's physical and physiological effects on mane condition, and the possible correlation of male hormone levels with both manelessness and small male-group size.

Résumé : On croit généralement que la crinière est une caractéristique de tous les lions (*Panthera leo*) mâles. Nous décrivons ici une population de lions du parc national du Tsavo au Kenya dont la plupart sont dépourvus de crinière et donnons certains aspects de leur organisation sociale. Parce que le paysage aride du Tsavo ne permet l'existence que de populations éparses de proies, nous pensons que les inventaires faits dans le parc décriraient de petits groupes sociaux et qu'en conséquence, il y aurait moins de pression de la sélection sexuelle en faveur de la crinière. Les mâles adultes du Tsavo possèdent typiquement des poils blonds épars formant une crête dorsale, une barbe, des touffes pectorales et (ou) des favoris, mais ils n'ont jamais la grande crinière ondulante décrite chez les autres populations de lions. Aucun lion n'a été observé avec une crinière complète. Les mâles sans crinière du Tsavo semblent bien intégrés à la vie en bande et ils peuvent être vus en train de s'accoupler, de chasser et d'interagir de diverses façons avec des groupes de femelles, de jouer avec des lionceaux dépendants et d'annoncer leur territoire à l'aide de marques odoriférantes ou de rugissements. Étonnamment, un seul mâle a été aperçu dans chacune de cinq bandes, alors que normalement dans les autres bandes de lions, il y a des coalitions de 2–4 mâles. Cependant, les groupes de femelles sont grands (moyenne 7,4), ce qui n'est pas ce qui prévaut dans le Serengeti et ailleurs; cela réfute donc notre hypothèse « taille du groupe – taille de la crinière ». Les études futures devraient examiner les effets physiques et physiologiques du Tsavo sur l'état de la crinière ainsi que la corrélation possible entre, d'une part, les hormones mâles et, d'autre part, l'absence de crinière et la taille réduite des groupes de mâles.

[Traduit par la Rédaction]

Introduction

Throughout history, manes of male lions (*Panthera leo*) have inspired admiration, fear, and legends in human societies. This adornment serves to make an already impressive 150–260 kg carnivore appear even larger. Despite widespread interest in the lion's mane, no consensus has been reached concerning its function. Some authors have suggested that manes serve to conserve heat (Swayne 1895), although this

seems unlikely given the large manes of African lions in extremely hot climates (e.g., Kalahari desert; Owens and Owens 1984), as well as the lack of manes in all temperate zone felids (e.g., *Lynx rufus*, *Puma concolor*), including Ice Age lions (Packer and Cliottes 2000). More credence is given to hypotheses that connect unique features of lion biology: manes and sociality.

Aside from the male coalitions sometimes found among cheetahs (*Acinonyx jubatus*) and the loose aggregations of domestic cats, lions are the only social cat species (Leyhausen 1979; Caro 1989; Caro 1994). For mammals, food abundance and distribution is widely believed to determine female sociality, while male social behavior is set by the distribution of females (Bradbury and Vehrencamp 1977; Emlen and Oring 1977; Wrangham 1980; Clutton-Brock 1989). In the case of felids, abundant large prey are required to offset the restrictive energetic costs of female grouping, thus allowing individuals to take advantage of the benefits of sociality, such as cooperative hunting and allonursing (Schaller 1972;

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Caro 1989; Stander and Albon 1993; Harvey and Kat 2000). This condition is best met in African lions, which regularly hunt prey larger than themselves and live in groups of 2–11 breeding females (“prides”) that are courted and defended by 2–4 males. Competition between male coalitions (and even within them; Packer and Pusey 1982) for access to prides is fierce and territorial fights are sometimes to the death (Iwago 1995). Both lion pride size and density are correlated with prey abundance (Van Orsdol et al. 1985).

Within this social organization, the mane might serve as intimidation, advertisement, and (or) physical protection. The manes of residents may deter trespassers and intimidate nomadic males contemplating a takeover attempt on a pride by serving as a visual signal of a territorial male’s control of a particular area. Females may be more likely to subordinate themselves to males with impressive manes and (or) might select males based on their mane condition. Finally, some have proposed that the mane offers physical protection to the vital head and neck areas against the teeth and claws of competing males (Schaller 1972; Ewer 1973; Bertram 1978; Myers 1987).

The principal, or overriding, function of the mane remains unclear, because some of these social hypotheses are nonexclusive and there are few data available to test them against each other. The selective pressures favoring manes must be strong, however, because numerous costs are apparent. In addition to the maintenance costs of growing the hair, the extra insulation may entail thermoregulatory costs for individuals in hot areas (Guggisberg 1961). Furthermore, by exaggerating its size, manes also make lions more conspicuous to potential prey and other territorial males (Schaller 1972). Finally, the long flowing mane hair may make it difficult for males to negotiate the thorns and brambles of thick bush habitat while pursuing prey (Pease 1914; Johnson 1924).

Not all modern African lions have full dark manes, and maneless males have periodically been reported (Selous 1908; Schaller 1973; Hunter 1999). Less is written about Asiatic lions (*Panthera leo persica*); although surviving animals in India have small manes compared with many African males, no modern specimens appear to be completely maneless, and extinct populations from Asia Minor apparently had large manes (Pocock 1930; Mazak 1964). Comparing the ecology and social life of maned and maneless lions may shed light on the evolutionary significance of the mane, yet little is known about maneless lions. Most reports of maneless lions have been from thick bush or arid habitat, while most long term lion research projects have focused on lions living in open grassland (Smuts et al. 1978; Packer et al. 1988; Mills and Shenk 1992). Furthermore, reports of maneless lions can easily be written off as aberrant (e.g., Elliot 1897). Studies of maned lion populations have documented maneless individuals that either were too young to have grown a full mane (Smuts et al. 1978) or had sustained an injury to their genitals that probably affected their hormone production (Pocock 1930; Denis 1964; Schaller 1973). Guggisberg (1961) describes a maned lion in Kenya losing its mane within months of being castrated.

However, recurring reports of maneless lions from the same location (e.g., Tsavo, Kenya; Lönnberg 1912; Patterson 1925; Schaller 1972) suggest that factors other than age and physical trauma must sometimes be involved, perhaps re-

lated to the differences in prey distribution between dry thorn scrub and fertile grasslands. Guthrie (1990) hypothesized that mane size should vary as a function of female group size, which in turn varies with prey abundance, creating a gradient of sexual selection pressure that grows with increasing abundance of large prey (attributing this hypothesis to studies by Clutton-Brock et al. (1982)). In contrast, less impressive mane condition, decreased size dimorphism, and smaller male coalition size should prevail in areas with smaller female groups. To test this hypothesis, we surveyed the lions of Tsavo National Park, to document the existence and frequency of maneless males and to compare the composition of their prides with those of “normal” populations. Maneless lions have been reported from Tsavo since Col. Patterson shot two infamous man-eaters in 1898 (Patterson 1914); both man-eaters were adult males and maneless. Tsavo encompasses a wide variety of arid and semi-arid savannas and bush and is thought to support low densities of major prey species (Leuthold and Leuthold 1976; Kahumbu et al. 1999). We predicted that low food abundance in Tsavo limits female lions to small groups. Male coalitions should consequently be smaller, or solitary males may dominate. Under these conditions, male lions may hunt more than typical pride males (Guthrie 1990; Funston et al. 1998), further increasing the costs of having a conspicuous mane. Additionally, the thick thorn scrub that blankets Tsavo may add to the costs of having a mane by restricting movement and (or) pulling hair out, while the hot dry climate may add to the thermoregulatory and water-balance costs. With waxing costs and waning social benefits, Tsavo males should have reduced or absent manes.

Methods

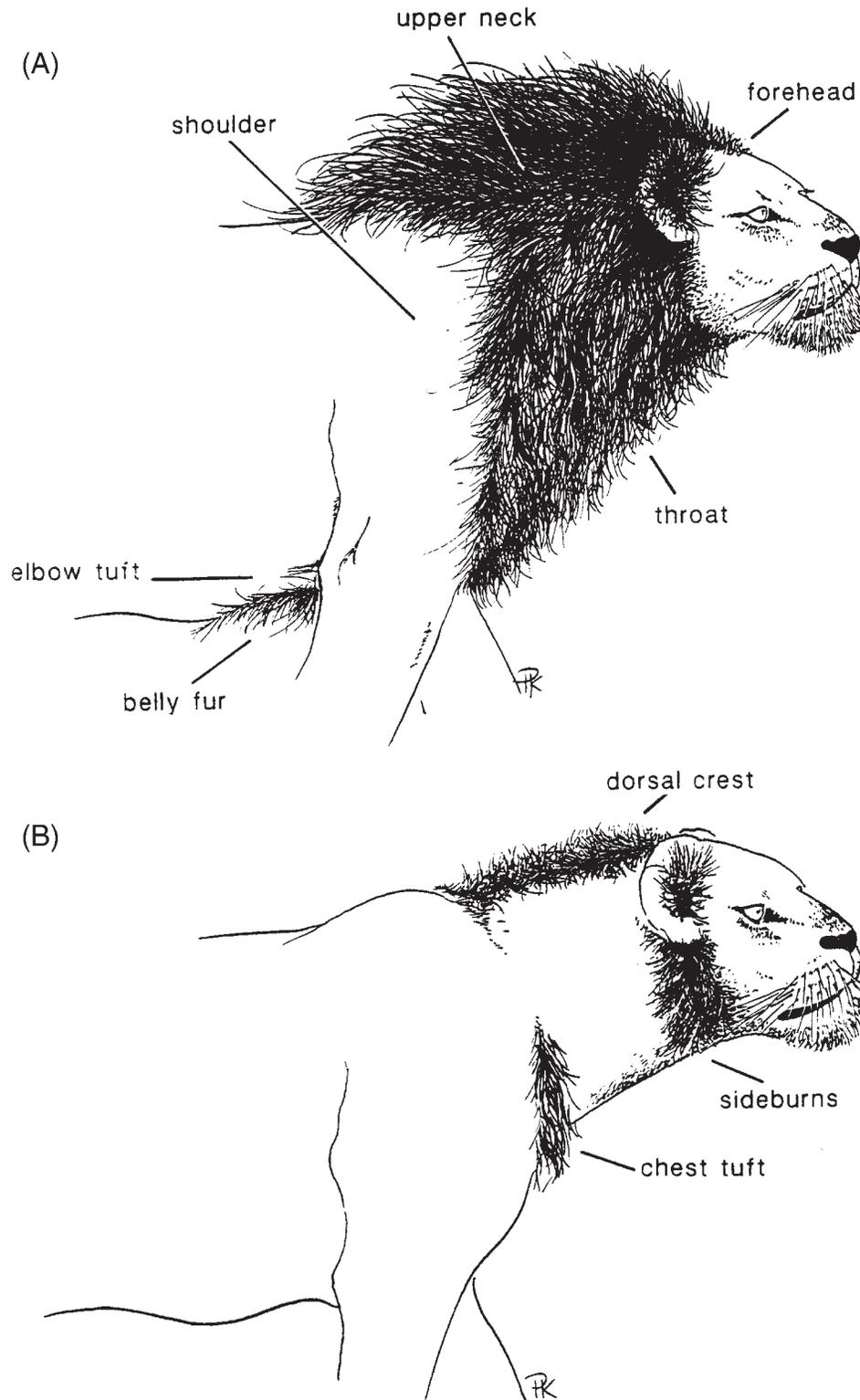
Study site

Lions were surveyed from September to December of 1999 in Tsavo East and Tsavo West National Parks, with a focus in an area of about 4150 km² in Tsavo East, south of the Galana River (ca. 3°15’S, 38°45’E). Surveys were focused around water sources, where prey and predators are most concentrated in the dry season. Mean annual rainfall varies locally between 250 and 500 mm, with most falling in one of two rainy seasons (March–May or November–December). The habitat is a dynamic mixture of *Acacia-Commiphora* woodland, open bush, and grassland that has changed over time in tune with changes in rainfall, fire frequency, and elephant populations, generally becoming more open savanna in recent decades (Leuthold 1996). During our field studies, areas south of the Voi River were predominantly grassland, while the land between the Voi and Galana rivers were dominated by thick thornbush. Woodlands were present along some rivers and in various parts of Tsavo West that we did not survey intensively.

Lion survey

Tsavo lions were surveyed with a number of different methods. Thirty lion groups were encountered at random while driving through the park. Tour vans are common in Tsavo, especially along the Voi River, and information from their ranks helped us find an additional four lion groups. One group was found by following spoor on foot with the

Fig. 1. (A) A fully maned adult male lion illustrating the shoulder, upper-neck, forehead, throat-hair, belly, and elbow components of a mane. (B) A typical Tsavo male lion illustrating the dorsal-crest, sideburns, and chest-tuft components of a mane. Drawing by P. Kernan.



aid of Kenyan Wildlife Service rangers and trackers from a local Waliengulu community. A call-in method was adapted to find lions and lure them out of the bush, so they could be photographed, sexed, and aged (Smuts et al. 1977; Mills 1985; Ogutu and Dublin 1998). For short-range (<200 m) work, an audiotape was broadcast through a 15-W amplified

speaker (SME PB-25 Mini-Vox, Mineroff Electronics, Elmont, N.Y.). To attract lions from farther away we used a more powerful but lower quality 35-W amplifier and speaker combination (speaker model BR-35, amplifier model SSA-60, Piyano, India). The play-back routine of Ogutu and Dublin (1998) was altered slightly to include three intervals of a

Table 1. Individual lions observed during the September–November dry season of 1999, including pride membership when known.

General location	Females	Males	Juveniles	Unknown	Total
Resident prides					
Aruba	8	1	2		11
Kanderi	6	1	3		10
Sala	10	1	2		13
Satao	9	1 ^a	0		10
Voi	4	1	8		13
Average	7.4	1.0	3.0		11.4
Nomadic groups or unknown status					
Ashaka	0	4	0		4
Ndara	3	0	1		4
Chapeyu	1	0	0		1
Sobo		1		2	3
Satarub	0	3	0		3
Balguda	1	1	0		2
Maungu	2	0	3		5
Manyani				6	6
Nomadaruba	1	1	0		2
Total	45	15	19	8	87

^aWe did not see the male of the Satao pride but have reliable reports from another biologist studying this pride that there was one male in the group (S. Andanje, personal communication).

Table 2. Number of sightings of the members of different prides and their attending males.

Pride	Total pride sightings	Sightings of pride male
Aruba	17	11
Kanderi	5	2
Sala	1	1
Satao	1	0 ^a
Voi	10	8

^aWe did not see the male of the Satao pride, but have reliable reports from another biologist studying this pride that there was one male in the group (S. Andanje, personal communication).

7-min broadcast followed by 3 min of silence. The tape was turned off once lions were sighted approaching the vehicle. Because lion densities were so low in most of the park, locations for call-ins were selected opportunistically, based on recent sightings by others or fresh footprints spotted in roadside dust.

Initially, a recording of lions squabbling over a kill (Cornell Library of Natural Sounds Catalogue No. 53435) and sounds of spotted hyenas (*Crocuta crocuta*) near a kill were used to attract lions. However, sounds from a competitive kill situation may intimidate some individuals, especially solitary females or females with young cubs (McComb 1992; McComb et al. 1993). Later, we obtained and used a more effective recording based on the vocalizations of a sick and dying young buffalo (*Syncerus caffer*) that attracted groups of all sizes and compositions and was apparently unbiased. Lions were photographed with a digital video camera (Sony TRV-900) and a SLR camera with a 300-mm lens. Using these images and field notes, we diagrammed facial whisker patterns and noted unique scars for individual identification (Pennycuik and Rudnai 1970).

To quantify the condition of a lion's mane, we divided the areas of a male lion's body into nine discrete areas where mane hair is known to grow (Fig. 1). We ranked each of these mane components on the hair length (1 = short, 3 = long), thickness (1 = thin, 3 = thick), and color (1 = blonde, 3 = black), and summed these ranks across components to get a total mane score for each individual. Absence of mane hair from a region scored a 0. Thus, a lion with a complete, long, thick, black mane would score 81, and a lion completely lacking a mane (e.g., most females) would score 0.

Results

The buffalo-calf tape was tested as a lion attractant in areas known to contain lions on eight occasions. Lions approached the vehicle in seven of these tests. The group that did not respond was apparently chasing a zebra herd through thick scrub when we spotted them crossing the road and initiated the test. However, a group of nine lions left a partially (~1/3) consumed buffalo carcass to approach the speakers. Six of the seven responding lion groups came close enough to the vehicle to allow photography and identification of individuals from scars and whisker patterns. One group stopped at the edge of cover 150 m from us, but did not flee when we approached them in the vehicle.

We identified 87 lions in Tsavo East National Park, including five well-defined prides near water sources (Table 1). The average number of females per pride was 7.4, but only one adult male was seen with each pride. The Aruba and Voi prides were seen most frequently (Table 2), and thus the group composition is probably most accurate in these cases. In addition, the Satao pride was being monitored by another biologist, who confirmed that our tally of nine females was accurate and that there was a single resident male. This male previously shared the pride with a second male that was subsequently gored and killed by a buffalo (S. Andanje, personal

Table 3. Summary and breakdown of mane condition for adult male lions recorded in the area of Tsavo National Park.

Lion ID	Age rank ^a	Forehead hair	Dorsal crest	Sideburns	Upper neck	Shoulder	Throat	Chest tufts	Elbow tufts	Belly fur	Total mane score	
Observed in 1999												
ArubaMonster	3	0	2–2–3	2–3–1	0	0	0	3–1–2	0	0	19	
Balduga	3	0	1–1–3	2–2–1	0	0	0	2–1–3	0	0	16	
Kanderi	3	0	3–3–3	3–3–1	0	0	0	3–3–2	0	0	24	
AshakBadEye	2	0	0	1–1–1	0	0	2–3–1	0	2–2–1	0	14	
AshakFluffh	2	0	?	2–2–1	0	0	2–2–1	0	0	0	10	
AshakaLeader	2	0	0	1–1–1	0	0	2–3–1	0	0	0	9	
AshakaOther	2	0	0	0	0	0	0	0	0	0	0	
Voi	2	0	2–1–1	2–1–1	0	0	2–2–1	2–3–1	0	0	19	
ArubNomad	2	0	2–2–3	3–2–1	0	0	2–3–2	2–2–2	0	0	24	
ArubSat1	1	0	0	0	0	0	0	0	0	0	0	
ArubSat2	1	0	0	0	0	0	0	0	0	0	0	
ArubSat3	1	0	1–1–2	0	0	0	2–1–1	0	0	0	8	
Sala	1	0	0	0	0	0	0	0	0	0	0	
Sobo	1	?	?	?	?	?	?	?	?	?	?	
Average											11.0	
Historic Tsavo specimens ^b												
ManEater1	3	0	0	2–2–1	0	0	0	2–1–3	0	0	11	
ManEater2	3	0	0	2–2–1	0	0	0	0	0	0	5	
Typical maned lions ^c												49

Note: The three characters scored for each mane components are length of hair (1, short; 2, medium; 3, long), thickness of hair (1, thin; 2, medium; 3, thick), and color of hair (1, blonde; 2, brown; 3, black). A score of 0 indicates no hair in the region in question. See Fig. 1 for definitions of mane components.

^aAn age rank of 1 indicates a young adult lion probably near the age that mane growth is first seen in typical lion populations (Smuts et al. 1978); an age rank of 2 indicates an adult; and an age rank of 3 indicates an older adult.

^bSee Fig. 2e.

^cSee Fig. 2a.

communication). None of the males observed had manes in the typical sense of that word. The average mane score was 11.0 ± 9.1 for all males, and 15.0 ± 7.8 when young adults were excluded (age rank 1 in Table 3). Tsavo males usually had some thin, short, blond hair forming dorsal crests, sideburns, throat hair, and (or) chest tufts, but lacked hair on the forehead, upper neck, shoulder, belly, and elbows (Table 3; Fig. 2). This manelessness was also observed in two historic lion specimens shot in Tsavo a century ago (Patterson 1914).

All behavioral observations suggested that these maneless lions behaved as normal reproductive males within the pride. One maneless male was observed copulating with a female on 9 October 1999. Furthermore, males in prides with cubs were observed to play and interact amiably with the young on numerous occasions. Males appeared to be territorial, as individuals were observed spraying on two occasions and roared on most nights.

Discussion

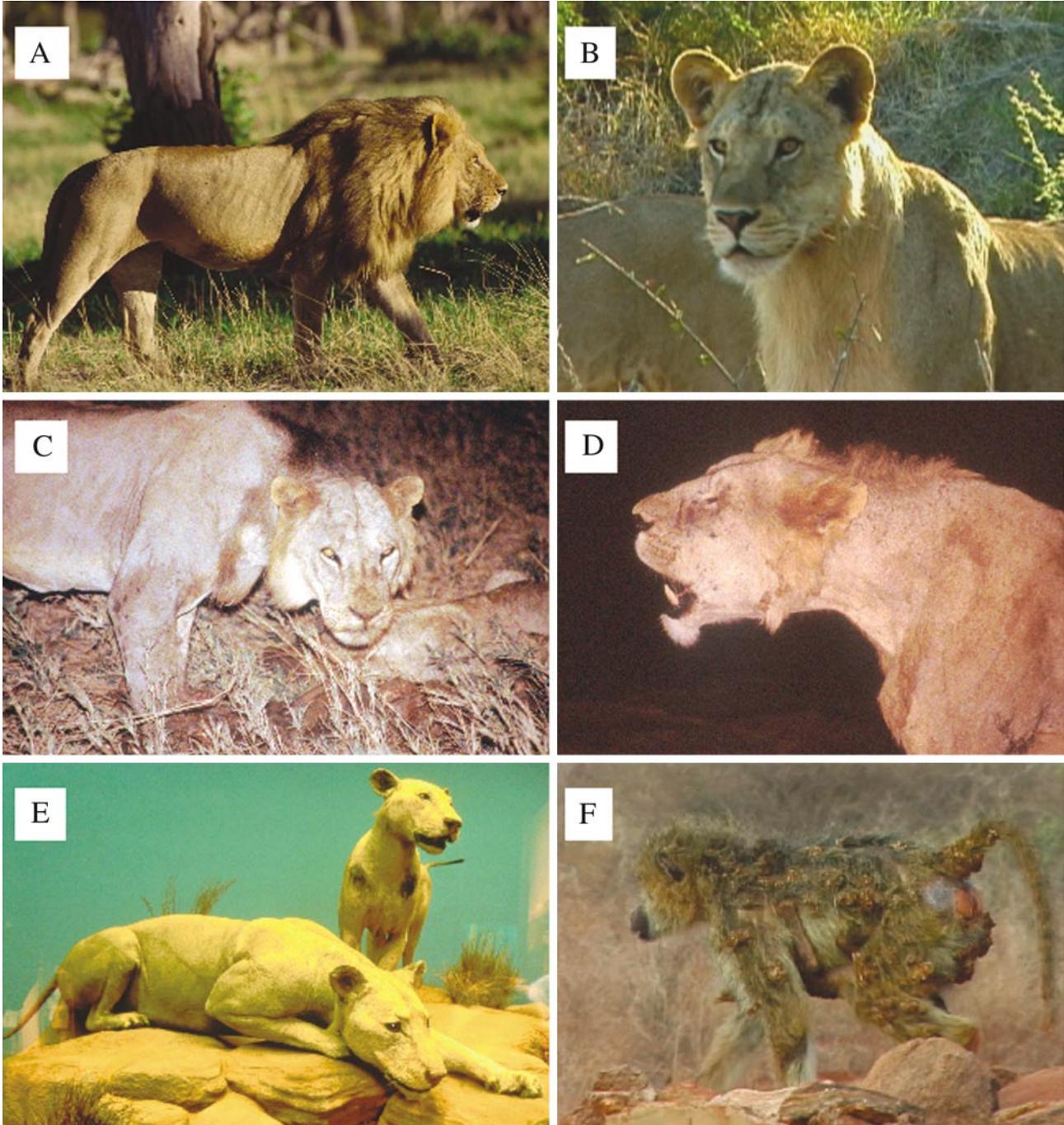
The lions of Tsavo give proof that manes are not a universal trait of adult male *P. leo*. Most Tsavo lions were completely maneless or maintained remnant tufts of hair on their head or neck. Behavioral and skeletal evidence shows that these maneless males are fully adult (Patterson et al. 1999) and that they are reproductively active within pride social systems. This leaves the obvious questions: why are Tsavo lions maneless and what are the behavioral and social consequences of this loss?

Our field data on female group size refute the hypothesis that males are poorly maned because small female group

size entails lower sexual selection (i.e., male–male competition and (or) female choice). Indeed, the average female group size for five Tsavo prides was large for the species (avg. = 7.4; Table 1) but within the range observed in studies of maned lions (reviewed in Van Orsdol et al. 1985). Average female group size in Tsavo is noticeably larger than in some other arid savannas in Africa (Rodgers 1974). Low male–male competition and lower sexual selection for manes could also result from a strongly female biased sex ratio. We found more females than males in our surveys (3:1; Table 1), but a female-biased sex ratio is commonly found in studies of maned lions (e.g., Schaller 1972). In addition, our surveys were more likely to overlook nonterritorial (“nomadic”) males that were avoiding the pride-controlled water sources. The number of adult male lions and male-coalition size in our study are comparable with those documented by Yamazaki (Yamazaki 1996) in a male-depopulated area of Zambia. In that case, however, this social variation was induced by high hunting harvest rates for males. Lions inside the Tsavo Parks have been strictly protected from hunting for more than half a century.

Without reason to expect that Tsavo lions experience lower sexual selection for manes, it seems more likely that they are maneless owing to higher environmental costs of possessing a mane. Specifically, we suspect that the hot, arid climate and thornbush habitat of Tsavo may combine to make it more costly to maintain a large mane in Tsavo than in more open, wetter, or cooler habitats. First, male lions in closed bushy habitat hunt more than males in open habitats (Funston et al. 1998). Conspicuous manes would make males more obvious to their potential prey, thereby making

Fig. 2. (A) A fully maned male lion from Botswana. Photograph by C. Harvey. (B–D) Adult male lions from Tsavo showing thin blonde sideburns and throat hair (AshakaLeader) (B), a large dorsal crest, sideburns, and chest tufts (Kanderi) (C), and a short dorsal crest, sideburns, and chest tufts with entangled burrs (ArubaMonster) (D). Photograph by R. Kays. (E) Two maneless man-eating lions shot near the Tsavo River by Col. Patterson in 1898. Reproduced with permission of the Field Museum, Chicago, Ill. (F) A yellow baboon (*Papio cynocephalus*) with entangled burrs. Photograph by R. Kays.



them less efficient hunters. Second, a large mane may get stuck on the abundant thorn bushes of Tsavo, thereby impairing travel, making noise, and ripping out hair. Third, we found the burr seed of a plant, *Pupalia lappacea*, to be abundant in many parts of the park in 1999. These burrs were incredibly sticky and were seen stuck to the long hairs of lions, baboons, and jackals (Fig. 2f). While they are easily

removed from short body hair, they become so entangled in longer hair that even dexterous baboons could not remove them without uprooting hair. We suspect that lions could tear out their own manes when attempting to remove mats of burrs. Last, but perhaps not least, the sweltering heat and extended drought of the coastal thorn scrub may exact an unsupportable cost from maned lions in terms of heat and

water budgets. In this climate, maned lions ought to have restricted activity periods (especially during daylight) and smaller hunting ranges around permanent water. Manes are known to vary in length and density with elevation (cf. Swayne 1895 for Somalia), and maneless populations in Tsavo lie 350 km from profusely maned lions atop the Aberdares moorlands.

It is not clear if manelessness has evolved as an adaptation to some aspect of the Tsavo environment (i.e., genetic cause) or if the thorns and burrs merely pull out the mane as it grows in adolescent males (i.e., environmental cause). If mane hair is pulled out in each generation of male lions, young males would be expected to have larger manes, and individuals in more open habitats would be expected to retain their manes longer. Rarely, fully maned lions are seen in Tsavo (S. Andanje, personal communication) but there is no known relationship with their age or habitat preferences. Furthermore, many of the maneless lions documented in our study used the more open, southern portion, of Tsavo East National Park. This suggests that either thorns are not an important cause of manelessness or that the evolutionary selection for manelessness is working on a landscape level rather than simply pulling the mane hair out locally. If manelessness is a newly evolved adaptation, the mechanism may involve testosterone (or its derivatives), which is linked to hair growth and hair loss in mammals (Randall 1993; Thornton et al. 1996).

In addition to being maneless, the pride males we observed in Tsavo were unusual by singly defending a group of females. Each of five prides documented had but a single male. It is possible that because our observations of several prides were rather limited (Table 2), we might have missed an additional pride male. However, for the two prides we know best (Aruba and Voi), there was clearly only one male present. Furthermore, the Satao pride was frequently observed by a biologist based in the area who regularly noted two male lions with the pride until one was killed by a buffalo in August of 1999 (S. Andanje, personal communication). After his companion's death, the surviving male remained alone with the pride. Obviously, male coalitions in Tsavo are far less common than has been reported elsewhere. In studies of maned lions, males left alone to defend a group of females are soon displaced by a coalition of males with superior fighting strength, which are much more likely to maintain tenure of a pride (Schaller 1972; Bygott et al. 1979).

How single maneless males are able to hold relatively large groups of females remains unknown. A common explanation for both the small manes in these males and their ability as singletons to retain tenure of and exist alongside large female groups is suggested by human male pattern baldness (i.e., androgenetic alopecia). Testosterone is thought to cause inhibition of hair growth and balding on the scalp in genetically disposed human males and stump-tailed macaques (*Macaca arctoides*) (Thornton et al. 1993; Randall et al. 1994; Obana et al. 1997). Testosterone is also higher in territorial males compared with nonterritorial individuals (Miller et al. 1987; Woodroffe et al. 1997; Rachlow et al. 1998) and is known to raise aggression levels (Hubert 1990; Lumia et al. 1994). Increased aggression by male lions may raise the stakes of male-male conflict and permit solitary males to fend off groups of challengers. This mechanism is testable

by assays of hormone titers of maned and maneless lions, a component of our on-going research.

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References

- Bertram, B.C.R. 1978. *Pride of lions*. Scribner, New York.
- Bradbury, J.W., and Vehrencamp, S.L. 1977. Social organisation and foraging in emballonurid bats. *Behav. Ecol. Sociobiol.* **2**: 1-17.
- Bygott, J.D., Bertram, B.C.R., and Hanby, J.P. 1979. Male lions in large coalitions gain reproductive advantages. *Nature (Lond.)*, **282**: 838-840.
- Caro, T.M. 1989. Determinants of asociality in felids. *In Comparative socioecology: the behavioral ecology of humans and other mammals. Edited by V. Staden and R.A. Foley*. Blackwell Press, Oxford, U.K. pp. 41-74.
- Caro, T.M. 1994. *Cheetahs of the Serengeti Plains: group living in an asocial species*. University of Chicago Press, Chicago.
- Clutton-Brock, T.H. 1989. Mammalian mating systems. *Proc. R. Soc. Lond. B Biol. Sci.* **236**: 339-372.
- Clutton-Brock, T.H., Guinness, F.E., and Albon S.D. 1982. *Red deer*. University of Chicago Press, Chicago.
- Denis, A. 1964. Cats of Africa: the African lion. *In Cats of the world. Edited by H. Loxton*. Houghton Mifflin Co., Boston. pp. 16-34.
- Elliot, D.G. 1897. Lists of mammals from Somali-land obtained by the museum's East African expedition. *Field Columbian Museum Zoological Series*, **1**: 109-155.
- Emlen, S.T., and Oring, L.W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science (Washington, D.C.)*, **197**: 215-223.
- Ewer, R.F. 1973. *The carnivores*. Comstock Publishing Associates, Ithaca, N.Y.
- Funston, P.J., Mills, M.G.L., Biggs, H.C., and Richardson, P.R.K. 1998. Hunting by male lions: ecological influences and socio-ecological implications. *Anim. Behav.* **56**: 1333-1345.
- Guggisberg, C.A.W. 1961. *Simba, the life of the lion*. Howard Timmins, Capetown.
- Guthrie, R.D. 1990. *Frozen fauna of the Mammoth Steppe: the story of Blue Babe*. University of Chicago Press, Chicago.

- Harvey, C., and Kat, P. 2000. Prides: the lions of Moremi. Smithsonian Institution Press, Washington, D.C.
- Hubert, W. 1990. Psychotropic effects of testosterone. In Testosterone: action, deficiency, substitution. *Edited by* E. Nieschlag and H.M. Behre. Springer-Verlag, New York. pp. 51–71.
- Hunter, L. 1999. No mane event. BBC Wildlife Magazine, August 1999 issue. p. 26.
- Iwago, M. 1995. In the lion's den. Shogakukan Inc., Singapore.
- Johnson, M. 1924. Camera trails in Africa. Grosset and Dunlop, New York.
- Kahumbu, P., Omond, P., Douglas-Hamilton, I., and King, J. 1999. Total aerial count of elephants in the Tsavo National Park and adjacent areas. Kenya Wildlife Service, Nairobi.
- Leuthold, W. 1996. Recovery of woody vegetation in Tsavo National Park, Kenya, 1970–94. *Afr. J. Ecol.* **34**: 101–112.
- Leuthold, W., and Leuthold, B.M. 1976. Density and biomass of ungulates in Tsavo East National Park. *East Afr. Wildl. J.* **14**: 49–58.
- Leyhausen, P. 1979. Cat behaviour: the predatory and social behavior of domestic and wild cats. Garland STPM Press, New York.
- Lönnberg, E. 1912. Mammals collected by the Swedish Zoological Expedition to British East Africa 1911. *K. Sven. Vetenskapsakad. Handl.* **48**: 1–188.
- Lumia, A.R., Thorner, K.M., and McGinnis, M.Y. 1994. Effects of chronically high doses of the anabolic androgenic steroid, testosterone, on intermale aggression and sexual behavior in male rats. *Physiol. Behav.* **55**: 331–335.
- Mazak, V. 1964. Note on the lion's mane. *Z. Saeugetierkd.* **29**: 124–127.
- McComb, K. 1992. Playback as a tool for studying contests between social groups. In Playback and studies of animal communication. *Edited by* P.K. McGregor. Plenum Publishing, New York. pp. 111–119.
- McComb, K., Pusey, A., Packer, C., and Grinnell, J. 1993. Female lions can identify potentially infanticidal males from their roars. *Proc. R. Soc. Lond. B Biol. Sci.* **252**: 59–64.
- Millar, K.V., Marchinton, R.L., Forand, K.J., and Johansen, K.L. 1987. Dominance, testosterone levels, and scraping activity in captive herd of white-tailed deer. *J. Mammal.* **68**: 812–817.
- Mills, M.G.L. 1985. Hyena survey of Kruger National Park, August–October 1984. In IUCN–SSC hyena specialist group newsletter. Vol. 2. International Union for Conservation of Nature and Natural Resources (IUCN), SSC pp. 15–25.
- Mills, M.G.L., and Shenk, T.M. 1992. Predator–prey relationships: the impact of lion predation on wildebeest and zebra populations. *J. Anim. Ecol.* **61**: 693–702.
- Myers, N. 1987. Africa. In Kingdom of cats. *Edited by* National Wildlife Federation. National Wildlife Federation, Washington, D.C. pp. 126–179.
- Obana, N., Chang, C., and Uno, H. 1997. Inhibition of hair growth by testosterone in the presence of dermal papilla cells from the frontal bald scalp of the postpubertal stump-tailed macaque. *Endocrinology*, **138**: 356–361.
- Ogutu, J.O., and Dublin, H.T. 1998. The response of lions and spotted hyaenas to sound playbacks as a technique for estimating population size. *Afr. J. Ecol.* **36**: 83–95.
- Owens, M., and Owens, D. 1984. Cry of the Kalahari. Houghton Mifflin Co., Boston.
- Packer, C., and Pusey, A.E. 1982. Cooperation and competition within coalitions of male lions: kin selection or game theory. *Nature (Lond.)*, **296**: 740–742.
- Packer, C., and Cliottes, J. 2000. When lions ruled France. *Nat. Hist.* **109**: 52–57.
- Packer, C., Herbst, L., Pusey, A.E., Bygott, J.D., Cairns, S.J., Hanby, J.P., and Bergerhoff-Mulder, M. 1988. Reproductive success of lions. In Reproductive success. *Edited by* T.H. Clutton-Brock. University of Chicago Press, Chicago. pp. 363–383.
- Patterson, B.D., Dubach, J.M., Gnoske, T.P., Weru, S., Mwangi, E., and Kays, R.W. 1999. Morphologic, genetic, and ecological variation of African lions: the mane story. In Proceedings of the 79th Annual Meeting of the American Society of Mammalogists, University of Washington, Seattle, 17–21 June 1999. p. 317.
- Patterson, J.H. 1914. The man-eaters of Tsavo and other East African adventures. MacMillan and Co., Ltd., London.
- Patterson, J.H. 1925. The man-eating lions of Tsavo. Zoology: Leaflet 7 of the Field Museum of Natural History, Chicago.
- Pease, A.E. 1914. The book of the lion. John Murray, London.
- Pennycuik, C., and Rudnai, J.A. 1970. A method of identifying individual lions, *Panthera leo*, with an analysis of the reliability of the identification. *J. Zool.* **160**: 497–508.
- Pocock, R.I. 1930. The lions of Asia. *J. Bombay Nat. Hist. Soc.* **34**: 638–665.
- Rachlow, J.L., Berkeley, E.V., and Berger, J. 1998. Correlates of male mating strategies in white rhinos (*Ceratotherium simum*). *J. Mammal.* **79**: 1317–1324.
- Randall, V.A. 1993. Androgens and human hair growth. *Clin. Endocrinol.* **40**: 439–457.
- Randall, V., Thornton, M.J., Hamada, K., and Messenger, A.G. 1994. Androgen action in cultured dermal papilla cells from human hair follicles. *Skin Pharmacol.* **7**: 20–26.
- Rodgers, W.A. 1974. The lion (*Panthera leo*, Linn.) population of the eastern Selous Game Reserve. *East Afr. Wildl. J.* **12**: 313–317.
- Schaller, G.B. 1972. The Serengeti lion: a study of predator–prey relations. University of Chicago Press, Chicago.
- Schaller, G.B. 1973. Golden shadows, flying hooves. Dell Publishing, New York.
- Selous, F. 1908. African nature notes and reminiscences. Macmillan and Co., London.
- Smuts, G.L., Whyte, J., and Dearlove, T.W. 1977. A mass capture technique for lions. *East Afr. Wildl. J.* **15**: 81–87.
- Smuts, G.L., Anderson, J.L., and Austin, J.C. 1978. Age determination of the African lion (*Panthera leo*). *J. Zool.* **185**: 115–146.
- Stander, P.E., and Albon, S.D. 1993. Hunting success of lions in a semi-arid environment. *Edited by* N. Dunstone and M.L. Gorman. Zoological Society of London, London. pp. 127–143.
- Swayne, H.C.G. 1895. Seventeen trips through Somaliland. A record of exploration and big game shooting, 1885 to 1893. Rowland Ward and Co., London.
- Thornton, M.J., Laing, I., Hamada, K., Messenger, A., and Randall, V.A. 1993. Differences in testosterone metabolism by beard and scalp hair follicle dermal papilla cells. *Clin. Endocrinol.* **39**: 633–639.
- Thornton, M.J., Kato, S., Hibberts, N.A., Brinklow, B.R., Loudon, A.S.I., and Randall, V.A. 1996. Ability to culture dermal papilla cells from red deer (*Cervus elaphus*) hair follicles with differing hormonal responses in vivo offers a new model for studying the control of hair follicle biology. *J. Exp. Zool.* **275**: 452–458.
- Van Orsdol, K.G., Hanby, J.P., and Bygott, J.D. 1985. Ecological correlates of lion social organization (*Panthera leo*). *J. Zool.* **206**: 97–112.
- Woodroffe, R., MacDonald, D.W., and Cheeseman, C.L. 1997. Endocrine correlates of contrasting male mating strategies in the European badger (*Meles meles*). *J. Zool. (Lond.)*, **241**: 291–300.
- Wrangham, R.W. 1980. An ecological model of female-bonded primate groups. *Behaviour*, **75**: 262–297.
- Yamazaki, K. 1996. Social variation of lions in a male-depopulated area in Zambia. *J. Wildl. Manag.* **60**: 490–497.