The Lion's Mane

Neither a token of royalty nor a shield for fighting, the mane is a signal of quality to mates and rivals, but one that comes with consequences

Peyton M. West

The African lion is one of the world's most admired and best studied species, yet its most striking feature has long been a mystery: Why do lions have manes? Charles Darwin, who knew almost nothing about lions, was one of the first to suggest an answer, writing, "The mane of the lion forms a good defence against the one danger to which he is liable, namely the attacks of rival lions." This unsupported hypothesis prevailed until 1972, when George Schaller published his seminal work, *The Serengeti Lion.* Schaller suggested that males bore sumptuous manes to signal their quality as a prospective mate, similar to the displays of several other polygamous species. Although these two hypotheses were not mutually exclusive, scientists tended to favor one or the other. When I began my research in 1995 neither theory had been systematically tested.

Craig Packer introduced the question to me in a casual conversation about potential thesis projects, months before I started graduate school at the University of Minnesota. "There are really two big mysteries left about the big cats," he said. "Why did saber tooth tigers have saber teeth and why do lions have manes?" I remember thinking that there wasn't much I could do about saber tooth tigers, but the lion's mane—I was hooked. The possibility of answering such a basic question was exactly the reason I got into science in the first place. I soon joined Craig's lab despite his warning: "it's not an easy project…."

Three basic features guide any thinking about the lion's mane. First, the mane is sexually dimorphic (only males have manes); second, the mane begins development at puberty; and third, the mane is highly variable both within and between populations. Manes vary in color from almost white to deep black and in overall size from the slightest "Mohawk" and sidewhiskers to a long, thick coat that covers the shoulders and chest. Furthermore, individual manes are not uniformly sized or colored but are often a patchwork of lengths and hues. These features are consistent with the idea that the mane is a product of sexual selection. Most sex-selective traits are sexually dimorphic, begin development at puberty and are highly variable. According to the theory of sexual selection, such characteristics evolve under the stress of competition for mates.

Sexually selected traits can increase reproductive success in two ways. The first, known as *male-male competition*, increases the ability of males to compete against other males for females. Traits in this category include armor to protect males from opponents, weapons to disable opponents or signals of fighting prowess that males use to assess opponents. Generally, males with more exaggerated features are better competitors. The second role of sexually selected traits, *mate choice*, increases male attractiveness to females. Traits of this sort, such as bright coloration, long feathers or elaborate calls, usually relate to the male's condition. Females that prefer more "ornamented" males may obtain benefits directly, in the form of more offspring, or indirectly, through better genes for their offspring. One of our objectives was to determine whether the mane functioned in male-male competition, mate choice or both.

Figure 1. Manes are unique to lions—no other cat species has them, so they must serve some specialized function. Yet the purpose of the

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Serengeti Story

When Craig said studying the mane would be challenging, he knew what he was talking about. He has studied lions in the Serengeti National Park in

male lion's mane remained unverified until recently. The author's work in East Africa provides comprehensive evidence of the mane's function as a proxy for overall fitness. Depending on the context, lions of both sexes consider mane characteristics when sizing up a male lion. This picture shows a male guarding his chosen female (in repose) on the Serengeti plains. (All photographs courtesy of the author unless otherwise noted.)

Tanzania for almost 30 years and endured all sorts of grueling ordeals in the name of scientific exploration. His hard work made my job easier though, because thanks to his efforts and those of other scientists, there is a vast database on the Serengeti lions. Not only has this work answered most questions about lion behavior, but demographic and physiological data let us study the heritability of traits and other questions that are difficult to answer for wild populations. Studying sexual selection in the field, in a long-lived species like the lion, would have been impossible without this prior research.

To start with, knowledge of lions' social structure allowed us to refine our hypotheses about sexual selection. Female lions live in prides consisting of related females and their dependent offspring. As the cubs grow, young females typically join their mother's pride, and young males form "coalitions" and disperse to look for their own pride. This creates a system in which a small group of males can monopolize many females, leading to severe reproductive competition. Predictably, males compete intensely for mates, and they compete on two levels. At the group level, male coalitions vary in size, and larger coalitions

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Figure 2. Manes can be short or long, nearly black or almost white. The length and color vary considerably within a group, but the greatest variety lies between populations that inhabit different climates. An individual lion's mane may demonstrate a patchwork of hues *(left)* or show a more consistent coloration *(center).* Mane length is also variable: A few hundred miles east of Tanzania's Serengeti National Park, the adult males in Kenya's Tsavo National Park have extremely short manes, frequently bearing only vestigial side-whiskers and a tufty sprout atop their heads *(right).*

sire more offspring than small coalitions. Individuals within a coalition also compete: If a male discovers an estrous female, he will jealously guard her and prevent her from mating with his companions. As Craig and his colleagues discovered, this behavior skews the paternity rates for individuals in larger male coalitions.

In contrast, female lions are egalitarian. Unlike some social carnivores, such as wolves and hyenas, all of the adult females in a pride reproduce, and female lions don't have a dominance hierarchy, which often dictates reproductive success in other species. Furthermore, a key attribute of lion society is that females breed synchronously, which means that there are often more estrous females available at one time than there are resident males. Males cannot usually defend more than one female at a time, but they willingly mate with additional females if possible. Thus, if estrous females outnumber males, the "excess" females—those that aren't actively guarded—are free to choose among coalition males. The bottom line is that this social system provides opportunities for sexual selection based on male-male competition and mate choice. This combination is not entirely surprising. Although historical studies of sexual selection focused on one or the other hypothesis, more recent work demonstrates that the two mechanisms often operate together.

More than 30 years of field observations also helped answer our next question: What kind of trait would be most useful to lions? With lethal claws and teeth, fighting is very costly, even for the victor. For this reason, just as Darwin suggested, males might benefit from a shield to protect them during fights. However, avoiding the fight altogether would be a greater advantage; thus, males would benefit from a signal that conveys their fighting ability to rivals.

From the females' perspective things are slightly more complicated. Unlike many mammals, male lions play an important role in raising offspring, but they are also utterly intent on their own reproductive fitness. When a new coalition of males joins a pride, they immediately kill or evict the offspring of the previous males. This behavior accounts for more than 25 percent of cub deaths and is a major variable in female reproductive success. In the short term, a group of females can fend off infanticidal newcomers, but the pride's resident males bear most of the responsibility for protecting young lions. The displacement or loss of a male coalition generally leads to 100 percent mortality of any unweaned cubs. Females would thus benefit from a signal that advertised a male's ability to fight off would-be usurpers.

Males also help feed the pride. Although male lions are often depicted as parasites, lying around while females do all the work, males are extremely capable hunters of a key prey species: the Cape buffalo. Buffalo are large and slow, and hunting them depends less on the speed and agility evinced by females

Figure 3. Charles Darwin proposed that male lions had manes to shield their vulnerable head and neck from the teeth and claws of other lions. If the mane did evolve to shield its owner, then attacks to these areas would probably be more frequent during fights. However, the author's analysis of records from witnessed fights and an extensive database of injuries showed that wounds to the mane area were no more frequent or lethal than wounds to other parts of the body—even for females and subadults, which lack manes.

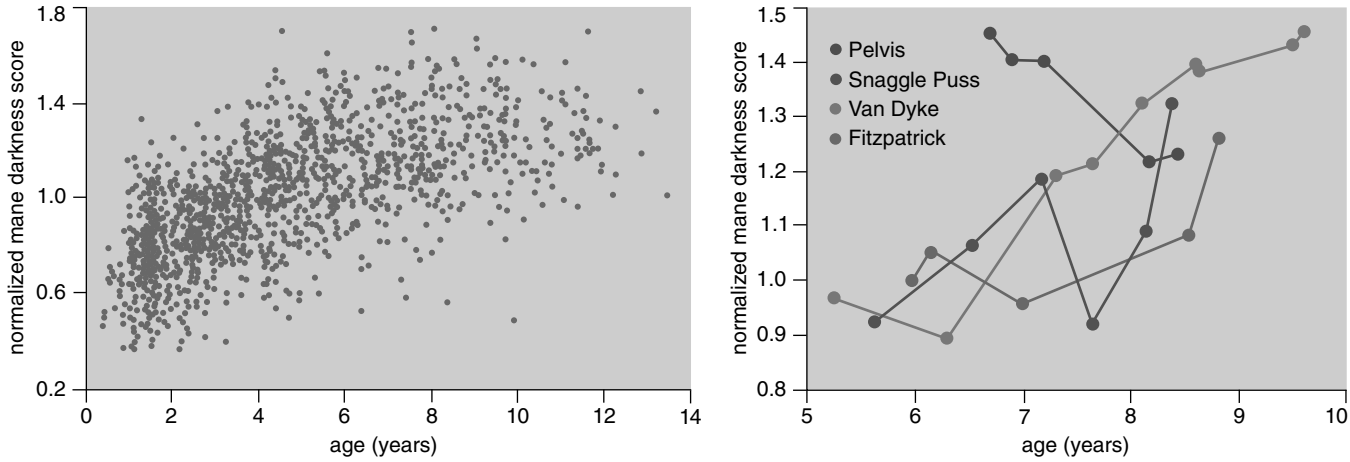

Figure 4. Like other sexually selected traits, the lion mane is sexually dimorphic, begins to develop at puberty and is highly variable. The mane of a male lion usually starts to darken before his first birthday and continues to do so for the next four to five years *(left).* Over the same time period, mane length and serum testosterone show similar increases. However, the manes of individual lions can become darker or lighter during adulthood because of injury or dietary changes, as demonstrated by the records of four individuals over a period of several years *(right).*

and more on the weight and strength characteristic of males. A buffalo will satiate a big pride, and this species is the most important prey throughout much of the lion's range. For females, such contributions are critical because starvation is another common cause of death among cubs. Any trait that advertises male hunting ability or contains general information about a male's nutritional status would be valuable.

This knowledge allowed us to refine our thinking before beginning our fieldwork. We hypothesized that the mane might function in any of three ways: as a shield against injury, as a signal of the male's ability to fight and protect his cubs (essentially the same thing), or as a sign of the male's nutritional status. The physiological attributes of hair support the idea that it could convey such information. Hair growth depends on a variety of factors, including, among other things, hormones, health and nutrition. In sexual selection terms, hair is "condition-dependent," meaning that its appearance is often related to the underlying condition of the animal. More specifically, hair growth and pigmentation are influenced by testosterone, which in turn is related to aggression and might be an indicator of fighting ability. Additionally, malnourished and sick mammals often develop rough, unhealthy-looking hair, and poor nutrition, such as copper and zinc deficiencies, can inhibit hair growth and pigmentation.

The Meaning of the Mane

Our first goal was to address the mane-as-a-shield hypothesis, which makes two simple predictions: that the mane is an effective barrier against the teeth of rival lions, and that males with longer or darker manes are injured less frequently or less severely. Unfortunately, these predictions are almost impossible to verify. Fights between lions are rarely witnessed, and individuals are seldom seen regularly enough to assess the frequency with which they are wounded. Instead, we generated two related hypotheses that were testable. First, we predicted that if the mane's primary function was protection, the "mane area," or the area of the body covered by mane hair, would be a special target during fights and that most lion-inflicted wounds would be found there. Second, we predicted that wounds to the mane area would be more serious and more likely to be fatal.

We addressed our hypotheses by combing the records for descriptions of injuries and eliminating those wounds that were not inflicted by other lions. From these observations we created a database that included the locations and survival rates for wounds to males, females and subadult lions. These data did not support the mane-as-shield hypothesis. Wounds to the mane area were no more frequent or lethal than those to other parts of the body. The observations were true not only for adult males but also for females and subadults, which lack manes. It seems that a lion's teeth provide more than enough incentive to avoid tangling with the front end.

Finding little evidence to support the mane-as-protection hypothesis, we turned to the idea that the mane functions primarily as a signal, asking specifically: What ecological trends predict mane length and darkness? A critical first step was to quantify objectively the length and darkness of a lion's mane. For this task we turned to our photographic archives, which included pictures of virtually every male lion to appear in our study area since the project began in 1966. While in the field, we continued to photograph males every six months to document new animals and record any changes in their manes. We then recruited undergraduate students, who were informed of the general nature of our work but knew nothing about the individual animals, to "grade" the pictures for length and darkness. At least five students graded each picture; we then eliminated the low and high scores and averaged the remainder. These measurements became the backbone of our research.

We first used these data to address several long-standing questions about lion manes. We ascertained, for example, that manes in the Serengeti generally begin developing at just under one year and continue growing until males reach 4.5 years of age. The mane gains pigment rapidly during this time, until the color becomes more stable about a year after growth ends. It continues to darken at a slower rate throughout life. We also demonstrated that the age-related increases in length and color mirrored the increase in testosterone during adolescence.

A welcome surprise was that the manes of individual males were not always constant over time; although the pattern of sharp gains in length and color followed by slow darkening was typical, the manes of some lions