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 side-whiskers 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.

Peyton M. West earned an undergraduate degree in English literature from Yale University, where she avoided science classes altogether. A love of animals led her to take several years of biology coursework, coincident with an internship at the Beardsley Zoo in Bridgeport, Connecticut, and a full-time job studying recombination in the soil bacterium Acinetobacter calcoaceticus. *She received a Ph.D. in ecology, evolution and behavior from the University of Minnesota in 2003 and worked in the Mammal Department at the Bronx Zoo before taking time off to have a baby. Address: 1524 29th Street NW, Washington, DC 20007 Internet: west0302@umn.edu*

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

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.

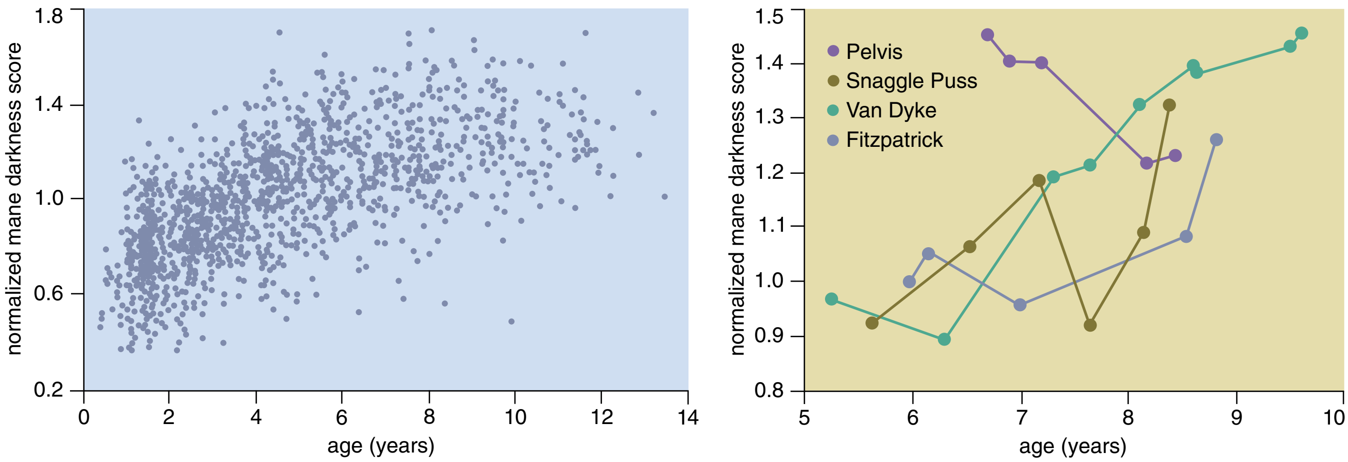

Figure 4. Like other sexually selected traits, the lion mane is sexually dimorphic, begins to develop at puberty and is highly variable. The mane of a male lion usually starts to darken before his first birthday and continues to do so for the next four to five years *(left).* Over the same time period, 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 became lighter or shorter, or changed back and forth. These results were inspiring because they gave further credence to the idea that the mane is condition-dependent—this kind of variation in sexually selected traits often reflects changes in the underlying condition of the animal.

More generally, our analysis revealed that mane length and darkness are correlated with several ecological factors. In males older than five years, mane length was most closely associated with injury. Prior to starting the analysis, we knew anecdotally that the manes of injured males were often reduced and could fall out altogether, and we now discovered that injured males also had more subtle reductions in mane length. This fact is significant because it suggests that mane length might signal a male's current fighting ability—injured males should be less able or less aggressive fighters. Mane color proved more interesting still: In addition to the age effect, we found that males with darker manes had higher levels of testosterone, suggesting greater aggression, and were on average better fed throughout the year, suggesting either general dominance or superior hunting ability. These results implied that both length and color provided interesting information for other lions, and that both males and females would benefit from using it.

Shorthand for Quality

Signaling theory predicts that if information is available animals will take advantage of it, but demonstrating the truth of this principle can prove challenging. Our next step was to look for evidence in our long-term records that males and females were actually using the information contained in the manes. For males, this proof was particularly difficult to get. We knew from previous research that dominance relations in male coalitions do occur—in coalitions consisting of three or more males, generally only two males fathered all of the offspring—but we were unable, because of incomplete photographic data, to link these relations to mane characteristics.

Instead, we turned to an experimental protocol used by previous lion biologists: playbacks. This technique uses recordings of natural animal sounds to mimic situations that we would otherwise seldom witness. We broadcast the roars of single, unfamiliar females to coalition males in order to evoke male competition for access to an estrous female. Because the first male to reach an estrous female generally ends up guarding and mating with her, we reasoned that whichever male led the group would most likely be dominant. If mane color or length were indications of dominance, we predicted that the male with the darker or longer mane would be the first to the loudspeaker. Experiments with 13 resident male coalitions uncovered a revealing and surprising result. Mane length had little relation to "dominance," as measured by our tests, but males with darker manes were significantly more likely to win the race to the female, suggesting that mane darkness does predict male dominance.

We next turned to females, and here our long-term data proved more useful. Because "excess" estrous females choose their own mate, we looked among the records for situations in which a male mated with more than one female in the course of an hour, assuming that at least one of the females was there by choice and was therefore exercising a preference. We found 14 examples of this situation for which we also had good data on the mane characteristics of all the males in the coalition. Again the results contained a surprise. Like coalition males, females appeared to place little value on the length of the mane—in only seven of these examples did the male in question have the longest mane of his coalition. However, color was again a critical factor. In 13 of the 14 observations, the females mated with the male whose mane was darkest.

The consistent results indicated that mane darkness played a role in sexual selection, but they left some nagging questions. Why didn't lions pay attention to mane length when it could betray recent injury? And how did lions respond to strangers, whose arrival had such potentially disastrous consequences? Observational data were inadequate because such meetings are rare, occur mostly at night and are impossible to predict. Thus, we again turned to active experiments, presenting to the real lions "dummies"—two plush, life-sized toy lions that differed only in their mane—to see if mane characteristics influenced the lions' behavior.

Figure 5. The lion's mane often shortens considerably and can even fall out altogether when an animal is wounded. These two photographs show the same lion, "Trojan," within a six-month period before *(left)* and after receiving an injury in a fight with another lion. He was last seen a few months after the second photograph was taken.

Fool Me Once…

We were optimistic about this approach. Ecologists commonly use dummies to study sexual selection in other species, and another graduate student from the Packer lab had successfully used a lion mount (prepared by a taxidermist) in earlier experiments. However, getting the actual dummies was a problem. We couldn't find a source for large, realistic stuffed lions, and custom-made toys were prohibitively expensive. Then, in a stroke of serendipity, Craig was contacted by a documentary filmmaker, Brian Leith, who wanted to make a film about lions. Brian was captivated by the experiments we were planning, and in no time at all he discovered Anna Club Plush, a Dutch company that was willing to donate stuffed toy lions made to our specifications. Within a few months, four beautifully plush, life-sized male lions arrived in the Serengeti. We christened them Romeo (short, dark mane), Lothario (short, blonde mane), Julio (long, dark mane) and Fabio (long, blonde mane).

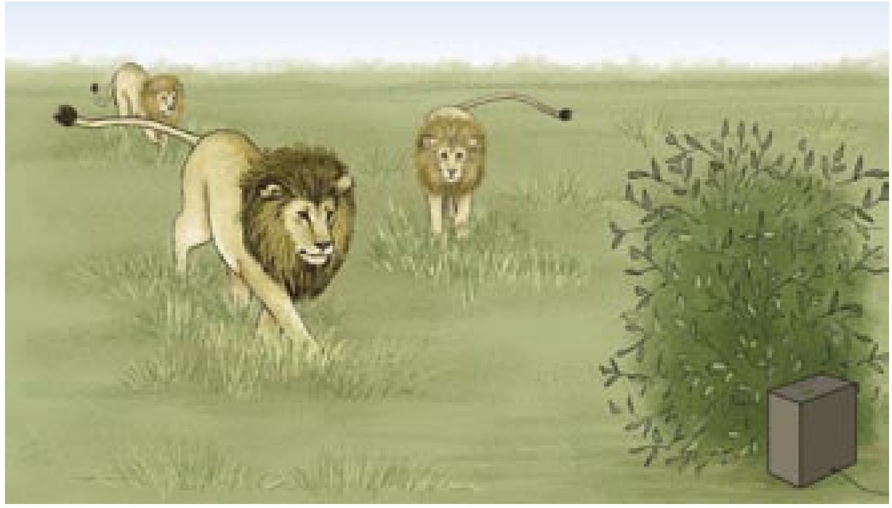

Figure 6. To see if a lion's mane relates to his relative dominance within a coalition of males, the author broadcast the roars of an unfamiliar female lion from a hidden speaker, an act that prompted all the local males to investigate. The scientists reasoned that because the first male to encounter an estrous female usually becomes her mate, the dominant male in a coalition would most often lead the group. Although mane length did not predict the order in which male lions arrived, ones with darker manes were significantly more likely to reach the "female" first.

In each experiment we presented a choice between two dummies to single-sex groups of adult lions. Lothario and Fabio helped us test the importance of mane length, and we used Julio and Fabio to test the effect of mane darkness. The manes were attached with Velcro, a feature that allowed us to switch manes and control for any differences between individual dummies. Once we found a group of lions, we waited until dusk (when lions are more active), set up the decoys downwind (to mitigate any effect of scent) and broadcast recordings of hyenas at a kill. This cue evoked a speedy response from the lions, who gathered to scavenge a meal. As they approached, the lions quickly noticed the two "strangers," and their attention shifted to the dummies. At that point, we turned off the sound and watched.

The early experiments were nail-biting affairs. Would the protocol work? Could the dummies fool real lions? Happily, it was clear from the outset that we were getting good data. After a quick start toward the loudspeaker, the real lions became much more cautious when they caught sight of the plush ones, stopping for a careful look every few feet before proceeding. On reaching a dummy, often their first act was to sniff under its tail. To eliminate the effect of scent on their behavior, we noted on which side the lions approached the dummies, because they usually made that decision at a distance of 100 meters or more. Thus, a female approach on the side of the dark-maned dummy counted as a preference for the darker mane.

Although the initial experiments were promising, it took three years to get enough data to draw meaningful conclusions: To our great surprise, the lions soon became habituated to the dummies. Lions that had seen them before—even years before—were never really fooled again. Their behavior was much less cautious, and they often failed to approach at all. Because lions live in fission-fusion groups, the project became much, much more complicated. Even if three out of four lionesses were dummy "virgins," we couldn't test the group—all four had to be naive. Furthermore, because the tests of males required resident coalitions (nomadic males would flee rather than approach the strange males), we had to expand beyond our study area to get an adequate sample size. But our reward for all this work was a fascinating set of data.

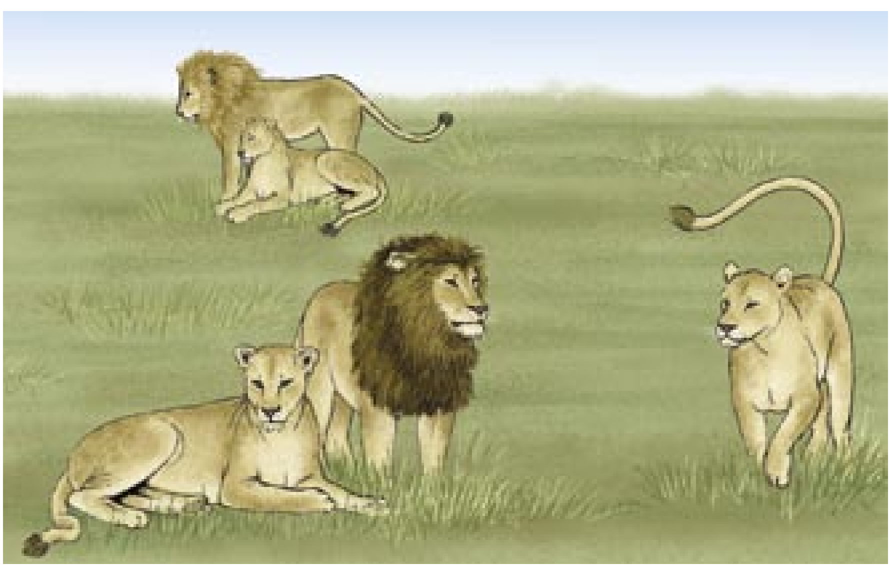

Figure 7. The fundamental unit of lion society is a pride of related females that is dominated and protected by a smaller number of allied males. Females in a pride come into estrus synchronously, but during this time each male is able to guard only a single female from advances by other males. Thus, so-called "excess" females can choose which male to approach as a prospective mate. In 13 of 14 cases, females chose to copulate with the male that had the darkest mane among coalition members. Mane length was not a significant factor in female choice.

Figure 8. The use of dummy lions—life-sized plush toys with mix-and-match manes—allowed the author and her colleagues to test the effects of mane length and darkness on the interactions between unfamiliar lions. The four toy lions sported colorful names as well: *(left to right)* Romeo (short, dark mane), Fabio (long, blonde mane), Julio (long, dark mane) and Lothario (short, blonde mane).

Similar to the long-term mating records, females in this test strongly preferred dark manes, approaching on the side of the black-maned dummy nine out of ten times. They approached the longer-maned dummy in only seven of ten trials (a nonsignificant result). Similarly, males were sensitive to mane darkness, avoiding the darker-maned dummy in five out of five trials. However, unlike the playback study, the tests with Lothario and Fabio showed that males were extremely sensitive to mane length; they avoided the long-haired dummy in favor of the short-haired one in nine out of ten tests. The different results arose from the different contexts for the two experiments: Whereas the earlier study tested dominance within a coalition, the plush lions simulated interactions between unfamiliar males. Because mane length can indicate short-term quality in the form of recent fighting success, this signal may be more relevant when deciding to challenge an unfamiliar opponent than when dealing with a well-known, long-term confederate.

We had established that the mane acts as a signal to other lions, but what were the actual benefits of having or preferring dark or long manes? A further look at our long-term records filled in these gaps. Although mane length had no detectable link with overall fitness, mane darkness was a significant factor. Males with darker manes spent more of their lives residing with a pride and were more

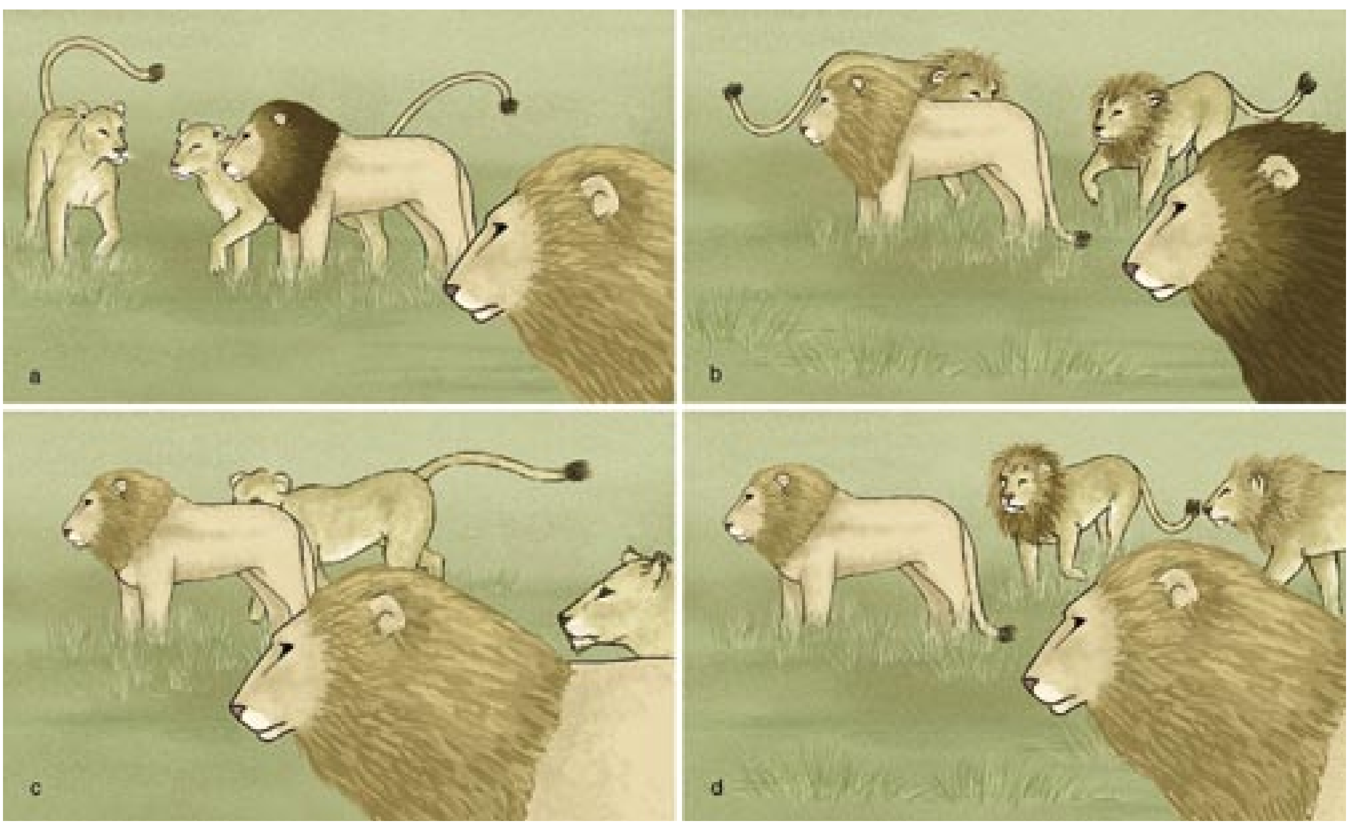

Figure 9. The life-sized dummies provided a tool for testing each sex's response to a pair of unfamiliar lions whose manes varied by length or color. Consistent with the observation that "excess" females in a pride chose mates with dark manes, females who encountered Fabio and Julio approached the latter 90 percent of the time *(a)*. By contrast, male lions avoided the darker "stranger" in four of five trials *(b)*. Females showed less preference for mane length, opting to examine Fabio rather than Lothario in 70 percent of the experiments—a nonsignificant result *(c)*. However, males were wary of the long-haired decoy, cautiously approaching on the side of the short-maned dummy in 90 percent of trials *(d)*. Unlike the earlier study of male lions that found no relation between mane length and dominance within a coalition, this experiment's simulation of an encounter between unfamiliar males indicates that they do attend to mane length when estimating the fighting prowess of an unknown rival.

likely to survive when wounded. Furthermore, their offspring were more likely to reach their second birthday (which also benefits females that chose dark-maned males) and less likely to be wounded, suggesting that darker-maned males provide better protection from other lions (the most common cause of injury).

Degree of Cost

The analysis showed several benefits of having a dark mane. So why don't all males have them? In other words, what prevents "dishonesty" among males who are wooing prospective mates? This is a common question in the study of sexual selection. Scientists generally answer that the production or maintenance of such a phenotype must be so costly that only superior males can afford it. So what is the cost of a black mane? Heat.

Since the early 20th century, naturalists such as Frederick Selous have noted that lions in different regions had different mane characteristics, and they even linked this variety to temperature. Males in colder, higher-altitude habitats tend to have bigger, darker manes than those in hot, humid climates, and all lions are extremely sensitive to heat. Larger animals have more difficulty with high temperatures because of their higher ratio of volume to surface area, and many lion behaviors seek to minimize heat stress. Sleeping in the day and limiting most activity to the night is one example; others include lying on their backs to expose their thin-skinned bellies, resting on high rocky knobs to catch the breeze, and panting after exertion or large meals. Unlike dogs, lions do not have cool, wet noses, and unlike people, they don't sweat. Their only means of thermoregulation are breathing (panting) and radiating heat from the skin. In this context, the mane is a handicap because it prevents the efficient dissipation of heat. Furthermore, dark hairs are thicker than light hairs, creating a better insulator, and dark surfaces absorb more solar energy than light ones.

These facts suggest that heat stress might be the most significant cost associated with the mane, and that lions with long, dark manes would be most affected. Testing these hypotheses was challenging—we couldn't exactly use a thermometer on wild lions. However, the technology of infrared thermog-

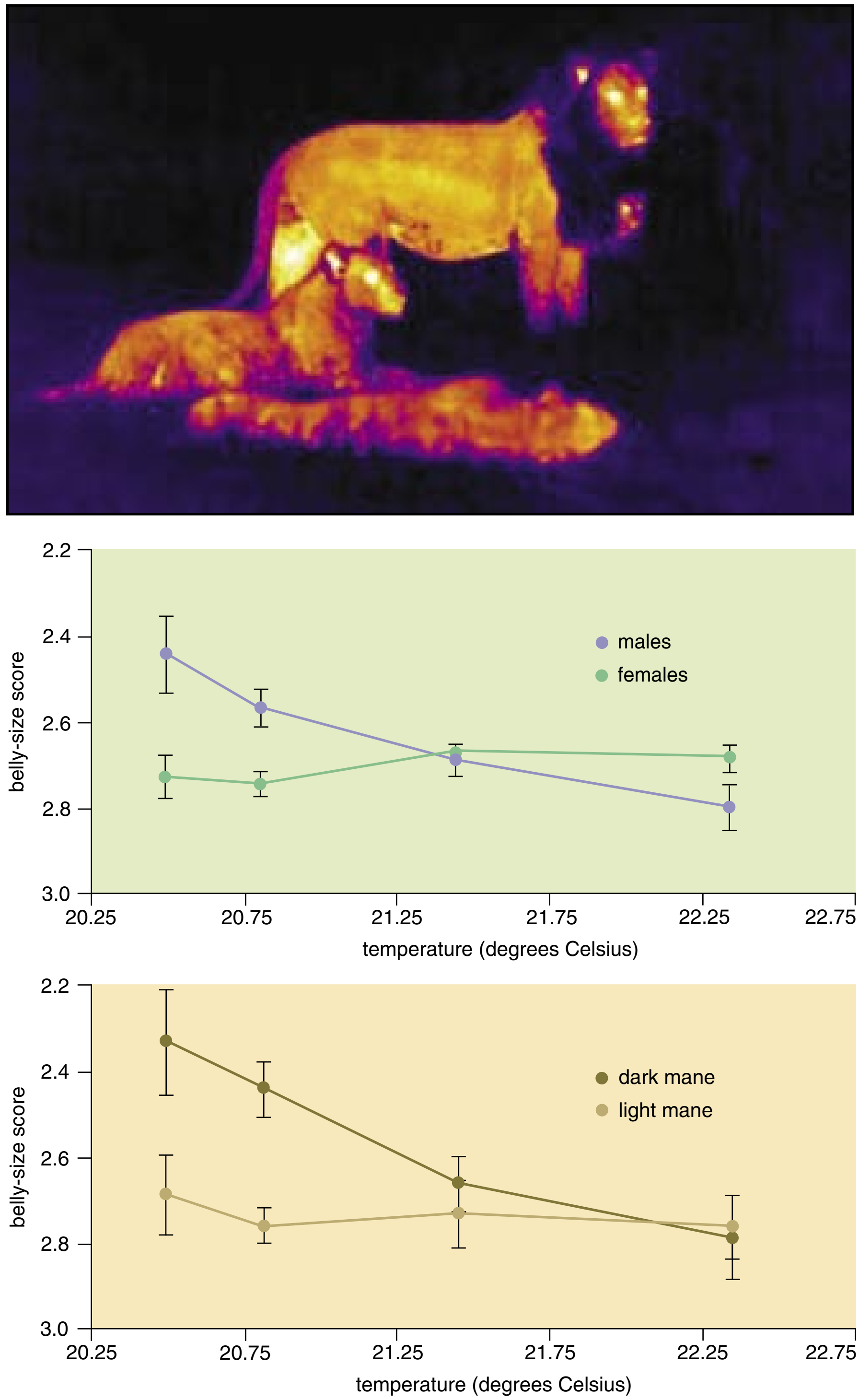

Figure 10. A male lion runs the risk of heat stress in exchange for having a long, dark mane. Unable to sweat, lions must dissipate heat through panting and radiation—mechanisms that are inadequate when the mercury climbs. Remote thermography of a trio of lions *(top)* shows that the surface temperature of the standing male is higher (more yellow) than those of the two reclining females (more orange). This temperature difference between sexes does not exist among lions in Tsavo National Park (a hotter and more humid area where males have slight manes), suggesting that the mane is linked to the buildup of heat. A higher body temperature has negative consequences, including an increased incidence of deformed sperm; not surprisingly, dark-maned males show fewer normal sperm than light-maned males from the same region. Even the metabolic heat generated by the digestion of a big meal can become taxing at the edge of the lion's climatic range. Male lions in the Ngorongoro Crater eat less (judging by measurements of belly size from photographs) when the weather is hot than during cool periods *(upper graph)*. However, this restriction appears to apply preferentially to males with dark manes *(lower graph)*. The scoring system for lion bellies uses a scale of 1 (the fattest) to 5 (the skinniest).

Figure 11. The African lion's sensitivity to temperature leads to behaviors that increase heat dissipation, such as the practice of resting high on rocky outcrops, or *kopjes*, to catch the breeze. Global warming will probably mean that long, dark manes, which trap heat, will become rarer in the future.

raphy, which can measure the precise surface temperature of a distant object, held some promise. The latest generation of such cameras was sufficiently portable to bring to the field, and a manufacturer, Flir Systems Incorporated, agreed to let us rent one of the pricey devices at a discount.

We spent three months snapping infrared pictures of all the adult males in the area, as well as many females and subadults. Our first step was to compare the average surface temperatures of the sexes, reasoning that if the mane had a thermoregulatory cost, males would be hotter than females. This turned out to be true, but there was a problem: Males are 50 percent larger than females and might be hotter just because of a greater ratio of volume to surface area. Unable to solve this conundrum in the Serengeti, we traveled to Tsavo National Park in Kenya, where male lions were reportedly "maneless." Tailed by a crew from *National Geographic*, we took a month-long detour in search of males that lacked manes but retained the size advantage over females. If Tsavo males and females showed different temperatures, then we could infer that lion temperature was a function of size. But if the sexes had similar surface temperatures in Tsavo, then the difference in temperature seen in Serengeti lions must be a result of their manes.

We discovered that many of Tsavo's adult males did have extremely small manes, although not all were maneless. In support of our heat-stress hypothesis, Tsavo was noticeably hotter and more humid than the Serengeti, and the lions there appeared to be more challenged by the climate. For example, we observed the novel behavior of scraping away the topsoil before lying down, presumably to find cooler earth underneath. Yet aside from their manes and their heat-related adaptations, Tsavo's lions were virtually identical to Serengeti lions in appearance and behavior, and the sizes of prides and coalitions were the same. While in Tsavo, we took the opportunity to perform several dummy tests and found that these males behaved in exactly the same way as Serengeti lions, appearing intimidated by longer and darker manes. And despite the challenges of unfamiliar surroundings, thick obscuring brush and the lack of radio collars (which aid tracking), we took many thermal images. What we found was that Tsavo males, despite being bigger than Tsavo females, were no hotter. Thus, we concluded that the temperature difference between males and females in the Serengeti derived from the heat cost of the mane rather than that of a larger body.

Back in the Serengeti, we next compared males' body temperatures to their mane scores to find precisely which mane characteristics were influential. Mane length had little effect, but males with darker manes were significantly hotter than those with lighter manes, even after controlling for ambient temperature, wind, humidity and prior activity. This connection supported our prediction that males with darker manes paid a higher price in terms of heat stress. In addition, we confirmed that males with darker manes had higher proportions of abnormal sperm (the link between testicle temperature and sperm production is well known). We also found that unlike light-maned males, dark-maned males reduced their food intake in hotter weather. Lions with big bellies (from eating big meals) tended to pant more and had higher surface temperatures, suggesting that gorging also causes heat stress. Males with dark manes are already more compromised by the heat, and thus must eat smaller meals when temperatures rise.

Once we had linked individual mane phenotypes to heat stress, we revisited some long-term data to see if similar effects existed at the population level. We wondered whether mane characteristics varied with small-scale changes in habitat or with seasonal differences in ambient temperature. The answer was yes to both questions. Males born into prides in the Serengeti woodlands, the warmest habitat in our study area, had shorter manes throughout life regardless of the climate they lived in as adults. Similarly, males that reached adolescence in warmer-than-average years maintained shorter manes over the course of their lives regardless of their residence as adults. Finally, males from the Ngorongoro Crater, the coolest part of our study area, had significantly darker manes. These results emphasize the importance of heat for determining mane traits and for the species in general: Such sensitivity to the negative consequences of hyperthermia argues that lions may be living at the edge of their tolerance for heat. This possibility raises an interesting conservation issue.

Global warming is real, and as research continues to uncover the negative effects of climate change on wildlife, an exquisite sensitivity to heat takes on an importance that is more than academic. Broadly speaking, we predict that the continued rise in average temperatures in East Africa will lead to fewer lions with long, dark manes. This shift may negatively affect industries such as tourism and legal sport hunting.

More important is the result of such a change on the lions. In the evolutionary past, climate change may have driven to extinction species with sexually selected traits they could no longer afford. Although the mane's phenotypic plasticity makes this scenario unlikely in lions, certain behavioral or physiological adaptations could become necessary. Such changes are impossible to predict, but any effects on a keystone predator like the lion have the potential to influence whole ecosystems. Our research emphasizes the potential consequences of climate change and argues for the importance of behavioral studies to detect its more subtle effects.

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