Of the world’s 40 cat species, lions are the only ones to have manes, and only male lions grow them. This conspicuous difference between male and female lions exaggerates other differences between the sexes: males also have bigger heads, necks, and shoulders, and frequently weigh twice as much as females. The mane amplifies already-impressive differences in these characteristics. Just as lipstick enhances the size and shape of the lips, manes communicate the size and shape of the lion. Although various human cultures have found significance and symbolism in manes, that communicator is targeted first and foremost at other lions, both males and females.

The Meaning of MANES

by Bruce Patterson
Like manes, grosbeak breasts, guppy tails, impala horns, and elk antlers also take on different forms in the two sexes. Such “sexually dimorphic” characters fall into two main classes: “showy” ones for attracting members of the opposite sex (“choice” characters, like bright breast feathers and tails) and ones useful in competing for mating opportunities (“contest” characters, like manes and antlers). “Choice” characters involve communications between the sexes: How alluring are that male’s feathers? How irresistible is his song? Because females contribute more energy to offspring (in yolk, milk, care), but have the same genetic share in the offspring as males, females tend to be choosier about their mates, and most choice characters provide females with the means to identify prospective mates. On the other hand, “contest” characters typically equip males to assert their dominance, and to the victor go the spoils. For example, the final bull elephant seal left on the beach after week-long contests is the one to mate with the females that subsequently arrive there.

Lion manes are clearly a sexually selected character, but are they “choice” or “contest” characters? University of Minnesota researchers Peyton West and Craig Packer have conducted field trials with lion mannequins, showing that females are attracted to lions with manes. They found bigger and darker manes elicited more interest and activity from the females and were seemingly more preferred. But what “say” do female lions have in choosing the males they breed with?

Studies in the Serengeti Ecosystem show that lion societies consist of two principal groupings. “Prides” are groups of related females and their dependent offspring. Prides remain near their birthplace, often occupying the same area for generations, and defend territories that are defined by food and water resources. “Coalitions” are groups of 2-4 related or unrelated males that compete for breeding access to prides. The competitions are fierce and sometimes fatal;

A 5-year old male, Taita Ranch, Tsavo, Kenya

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the stronger, more vigorous coalitions prevail. Head-to-head competition is the pride’s guarantee of genetic quality in their mates; if the incoming males can oust the incumbents, then the females are better off rearing offspring with the newcomers. Besides, a female participating in the frenzy of sometimes-mortal combat with much larger males risks injury or death herself. Better to let males sort things out themselves.

Except for infanticide. In some parts of Africa, competition for prides is so severe that the expected tenure of any male coalition is short, only a year or two, about the time needed for cubs to become fully independent. Under these circumstances, incoming males will kill nursing cubs, the offspring of the ousted males. Lions (like other cats) have a facultative estrus and the cessation of nursing brings them back into “heat” so that all their reproductive efforts—in utero nourishment, suckling of cubs, and months of shared meals—will benefit the newly arrived males. Obviously beneficial to the newly arrived males, infanticide represents a decided cost for females, particularly those with many months already invested in their offspring. Under these circumstances, it would pay for females to tip the balance of power, at least until their cubs are independent and no longer vulnerable. And who better to tip the balance than a group of cooperative hunter-killers which share a genetic stake in successfully rearing those young? Female collusion might influence when coalitions are replaced and alter the mating access of individuals during estrus. Still, “female choice” of mates in lions remains purely theoretical and experimental.

Coalition mates grooming shortly afterwards,
Katavi National Park, Tanzania

However, there is little doubt that manes reflect a lion’s genetic quality. Like other sexually selected characters, manes have very low heritability. Heritability is a biological concept measuring environmental effects on a genetically determined trait—“nature versus nurture.” Heritable traits are influenced little if at all by the environment in which they develop—eye color and blood type are traits in humans with high heritabilities. But antlers and manes all have a different kind of genetic architecture, one that emphasizes the individual’s condition and history. Deer have larger antlers the year following a mild winter, and those larger antlers are correlated with better fat reserves, higher testosterone levels, more frequent calls during the rut, etc. A deer’s antlers reflect whatever combination of environment and individual circumstances his constitution has recently experienced—if they are larger than his competitors, females can be assured that his genes are locally adapted and promise success to her future offspring.

Ditto for manes. We think. We know more about deer antlers, because hundreds of thousands of game licenses in developed nations have funded sound science for managing deer. With 500,000 white-tailed deer harvested each year in Wisconsin alone, there’s plenty of revenue to support biological studies. In nearby universities, theses and dissertations are written on habitat and forage selection, over-winter mortality and twinning rates. Roadside monitoring points can collect a sample tooth from harvested deer for aging purposes or measure coat density or back-fat. For lions, it’s different (enrich the analogy with antlers). Lions range over dozens of countries, are notoriously difficult to manage, and only recently have the lions harvested in a few active concessions been scientifically documented (by dozens, not hundreds or thousands).

Manes develop at the onset of sexual maturity, stimulated by increasing androgen (male hormone) production. Manes are under active hormonal control. C.A.W. Guggisberg wrote of a male lion in Nairobi National Park that accidentally killed two females during inept mating attempts. To safeguard the park’s small lion population, vets castrated the male, but within months, he lost all traces of his mane. Chronically dominated males and those castrated during fights or predation events never develop manes or lose the manes they had. So a lion sporting a large mane proclaims several things to anyone looking at him: he’s in good condition, is sexually competent, and has won more battles than he has lost. He’s a force to be reckoned with.

Communicating those facts to other lions, male and female, is why lions have manes in the first place. Why fight in a potentially mortal contest when all players can tell at a distance who the victor(s) will be, without the bloodshed? In this manner, manes confer social advantages on lions but come with a number of environmental costs. Manes are expensive to grow and maintain, are cumbersome and conspicuous, harbor parasites and pathogens, and can cause their bearers to overheat.

Heat-loading is an especially important determinant of mane size across much of Africa. Historically, the best maned

A 5-year old male with a warthog.
Taita Ranch, Tsavo, Kenya
The full belly and the accompanying female are proof of fitness in this pride male, Selous Game Reserve, Tanzania

Lions were often found at high latitudes and high elevations. Cool conditions softened the manes, and those from Ethiopia, the Mau highlands, and Ngorongoro Crater, without genetic modification, were often carried to outrageous limits in North American and European zoos. With good nutrition and unlimited access to water, manes become enormous, extending over the arms and ribs and onto the belly and flanks. Even an average lion in a North American zoo is more heavily maneled than his most luxurious African peers.

But does this make zoo lions more "macho" than their African relatives? Absolutely not. Manes represent a compromise between social benefits and ecological costs, and the higher costs of manes in hot, arid environments shifts the acceptable range of mane sizes towards shorter and sparser. A good example is provided by the Greater Tsavo Ecosystem of southeastern Kenya, a sprawling wilderness mostly covered by dry grasslands and Acacia-Conilinophora woodlands. Long familiar (or infamous) for its man-eating lions, who literally stopped the British Empire in its tracks at the Tsavo River in 1898 during construction of the Kenya-Uganda Railway, Tsavo is now also famous for its maneless lions. With Samuel Kasiki and Alex Mwazo of the Kenya Wildlife Service and Roland Kays of the New York State Museum, I have studied lions on ranchlands outside of Tsavo with the help of volunteers from the Earthwatch Institute—citizens from all walks of life who travel to Tsavo to help us collect data on the ecology and behavior of lions there. To date, more than 385 volunteers from 30 nations have assisted us.

The picture that is developing underscores the adaptability of lions and the malleability of manes. Manes of lions here vary substantially, depending not
“Bruno”, a 17-year old zoo lion, Houston, Texas

only on age and condition but also on the temperature and rainfall in that part of the 20,000 km² reserve. Near Sobo in Tsavo East, lions are virtually maneless. Sobo has a 9-month dry season when water is scarce-to-nonexistent, and a well-maned lion would squander his daily water allowance simply panting under a bush, with none to spare for patrolling his territory, hunting, or finding mates. For Sobo lions, manes are a luxury they simply can’t afford. Heat stress provides the regulatory trigger that controls hair production. And Sobo males and females never see a Serengeti male, so their choices of who to fight with or mate with are based on local variation.

On nearby Taita and Rukinga Ranches, temperatures are comparable but twice as much rain falls annually; lions have more water for cooling and larger manes as a result. All have something of a Mohawk on the nape, most have a neck ruff, some have chest bibs. One very successful male could even be mistaken for a Serengeti lion. But that is very much the point—although it is possible to characterize mane size and color for any area, the population of lions in that area exhibits a range of variation. It is the relative position of a lion within the local range that tells other lions—and the people cued into them—who’s who.

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All photos by Bruce Patterson

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She

She Whispers to me, whispers to my soul
I listen for Her, I watch for Her, I am spellbound.
Her music lingers on and my heart pulses when
She breathes
Her breath on my neck.

Her fingers tousle my hair,
Her endless beauty lifts me.

She moves with the wind, She brings me light
and happiness

She never leaves, always by my side,
She moves me, inspires me.
Her open arms invite me.

In her bosom she cradles me.
The stars twinkle as they watch over Us.
She is me, I am Her. We are one.
She is mine, in my heart, my soul Forever.
She is My Africa.