individuals from Willow Creek could be tested at common doses (they exhibited a similar but nonsignificant positive relationship); individual whole-animal resistance measures were not available for Bear Lake individuals. The concordance between whole-animal and skeletal muscle TTX resistance indicates that the physiological mechanisms that allow skeletal muscle fibers to function in increased concentrations of TTX are at least one component of individual differences in the effects of TTX on locomotor performance. Unexplained variance suggests that additional underlying mechanisms of whole-animal TTX resistance remain to be identified. Such mechanisms may include the ability of other nerve and muscle tissues to function in TTX.

The coevolutionary arms race between *T. sirtalis* and newts defended by TTX has led to remarkable adaptive divergence in whole-animal TTX resistance among snake populations. This divergence includes independent evolution of resistance in at least two distinct lineages of garter snakes, as well as substantial quantitative variation in level of TTX resistance among populations (*16*). Some of this variation may result in part from observed trade-offs between resistance and other physiological functions (*16, 18*). The results we present here demonstrate one physiological mechanism underlying the adaptive differences among populations, but just as important, they show that variation in the same physiological function exists among individuals within populations. Selection resulting from the interactions of individual predators and prey may therefore act indirectly on this fundamental physiological function. Although we do not know that these individual differences in skeletal muscle resistance are genetically based, two points suggest that the potential exists for this physiological variation to respond to selection. First, whole-animal TTX resistance is known to be highly heritable in garter snakes (*15*), which suggests that heritable variation is also present in the mechanisms that underlie it. Second, the TTX sensitivity of skeletal muscle sodium channels in other vertebrates is affected by genetic changes that alter amino acid sequences (*25, 29, 30*). At this point, it is unclear whether the parallel evolution of TTX resistance in separate lineages of *T. sirtalis* has occurred through identical or unique genetic mechanisms, but the genes that encode sodium channels expressed in the skeletal muscle fibers of resistant snakes appear to be good candidates with which to explore this question.

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Sexual Selection, Temperature, and the Lion's Mane

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The mane of the African lion (*Panthera leo*) is a highly variable trait that reflects male condition and ambient temperature. We examined the consequences of this variation in a long-term study of lions in the Serengeti National Park, Tanzania. Mane darkness indicates nutrition and testosterone and influences both female choice and male-male competition. Mane length signals fighting success and only appears to influence male-male assessment. Dark-maned males enjoy longer reproductive life-spans and higher offspring survival, but they suffer higher surface temperatures, abnormal sperm, and lower food intake during hot months of the year. Maned males are hotter than females, and males have lighter and/or shorter manes in hotter seasons, years, and habitats. This phenotypic plasticity suggests that the mane will respond to forecasted increases in ambient temperature.

Sexually selected indicator traits reflect male health and vigor (*1*), revealing how well individuals withstand environmental stress (*2, 3*). Environmental effects on trait morphology can be substantial (*4, 5*), outweighing both genetic effects (*6*) and reproductive advantages (*7*). Changing environmental conditions can alter trait costs, leading to the evolutionary loss of sexual ornaments (*8*) or possibly even to species extinction (*9*). The global environment is undergoing rapid change due to anthropogenic disturbance (*10*), and these changes have already altered some sexually selected behavior (*11, 12*). Sexually selected morphological traits may also be vulnerable, depending on the relative importance of ecological effects, reproductive benefits, and a trait's phenotypic and/or genetic plasticity, as well as the magnitude of environmental change.

Here we examine the evolutionary and ecological factors influencing the mane of the African lion. Manes are sexually dimorphic, develop at puberty, and are highly variable; thus, the mane has long been considered a sexually selected trait (*13*). Mane size and darkness are reduced in populations and subspecies living in hot climates [see supporting

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online text (*14*)], suggesting that the mane is particularly sensitive to ambient temperature (T_a) (*15*). Subspecies differences in mane characteristics may have a genetic component (*16*), but individual males can grow longer manes when moved to cooler habitats (*15*).

We studied approximately 300 lions residing in the Ngorongoro Crater and the woodlands and plains of Serengeti National Park, Tanzania, from 1996 to 2001; long-term photographic, demographic, and behavioral records date from 1964. Lions are social and defend well-defined territories. "Coalitions"

of 1 to 9 males monopolize "prides" of 1 to 18 females. Females are philopatric, but males disperse and compete for access to prides. Upon defeating resident coalitions, incoming males accelerate the females' return to estrus by killing unweaned cubs and evicting subadults. Males of the resident coalition compete with each other for mating opportunities; a male forms an exclusive consortship with an estrous female and prevents her from mating with his companions (*17*), thereby restricting mate choice. However, breeding is generally synchronized by the

takeover, and estrous females occasionally outnumber coalition males. In these cases, each male guards a single female, leaving "excess" females free to choose among partners (*18*).

The claws and teeth of lions are lethal, so the mane might have evolved to shield the neck and shoulders (*13*, *17*). However, we could find no evidence that lions primarily attack the neck/shoulder region or that wounds to this area are especially harmful (*14*). Further, all felids are similarly armed, yet the lion is the only species with a conspicuous male ornament. Owing to their complex social system, lions are the only felid in which males and females can regularly compare males, and excess females can freely choose among them. Thus, the mane might have evolved to signal male genetic and/or phenotypic condition. Nutritional deficiencies decrease hair pigmentation (*19*) and weaken hair shafts (*20*), and testosterone regulates hair growth (*21*) and melanin production (*22*) and influences male aggression (*23*). Further, prepubertal castration prevents mane growth (*24*).

We analyzed photographs of 568 subadult and adult males from 1964 to 2000 (*18*). Manes lengthen and darken coincidentally with age-related rises in serum testosterone (Fig. 1), and the length and darkness of adult manes can vary monthly (fig. S1). Limiting the analysis to 313 adult males above the age of 4 years, we could find no measurable signs of heritability in either aspect of the mane (*25*). Instead, variations in length and color were associated with age, injury, testosterone, nutrition, and T_a (Table 1). Short manes were associated with serious injury (fig. S2, A and B), and manes darkened with age and with serum testosterone. In Ngorongoro Crater (where the food supply is constant throughout the year), darker males gained higher food intake, suggesting better overall nutrition (Fig. 2). Manes were also darker in

Fig. 1. Mane development patterns. (**A**) Serum testosterone increases from around 1 to 4 years of age. (**B**) Mane hair begins growth around 1 year of age and reaches full size around 4 years. (**C**) Manes become darker with age, but mane color varies from the earliest stages of development. Graphs include multiple observations of each male, and values for length and color have been normalized (*14*).
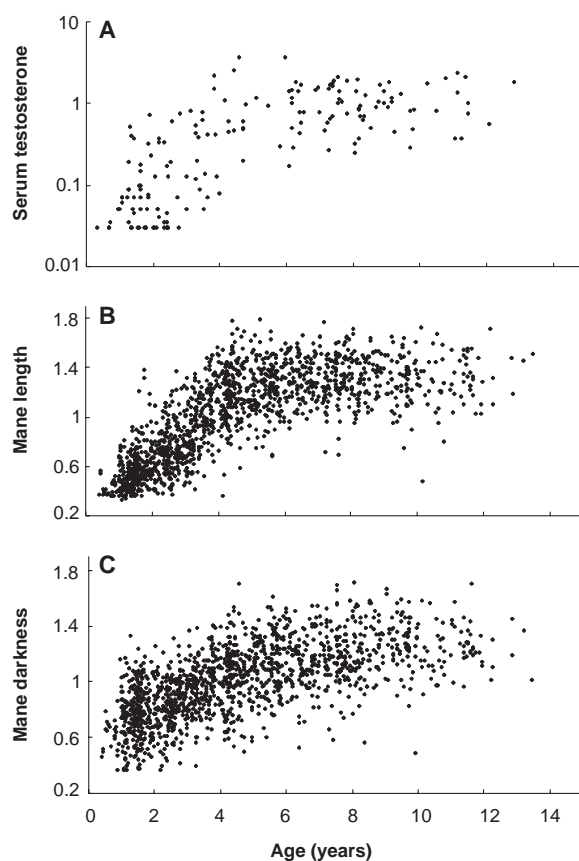

Table 1. Variables influencing mane characteristics of adult males in Ngorongoro and Serengeti. Models are multiple regression; all variables are also significant in univariate analyses. Data were analyzed with the SAS system for Windows software, release 8.02. Both length and darkness are associated with male condition and environmental factors. Full model statistics are presented on the top row of each model.

Independent variable	t	P	Dependent variable	r^2	F	n
Mane length						
Male born in Serengeti woodlands	−3.07	0.0026	Mane length	0.2848	13.44	126
Mane darkness*	2.96	0.0037				
Annual temperature between age 3 to 4 years†	−2.09	0.0387				
Male injured at time of photo	−2.08	0.0398				
Mane darkness						
Male born/resident in Ngorongoro Crater‡	4.47	0.0000	Mane darkness	0.4533	24.42	114
Average temperature during month of photo§	−4.14	0.0001				
Male born in Serengeti woodlands	−3.64	0.0004				
Log of male's age when photographed	2.49	0.0144				
Male resident on Serengeti plains‖	−3.20	0.0021	Mane darkness	0.1599	7.37	68
Log titer serum testosterone‖	2.49	0.0155				

*Mane color was included because dark mane hairs are significantly thicker than light hairs (*14*) and presumably less vulnerable to breakage. †Yearly deviations from average temperature from 1960 to 2000 [data are from the Goddard Institute of Space Studies (www.giss.nasa.gov)]. ‡All resident males in Ngorongoro were also born there. §Average monthly temperature calculated using a 10-year data set collected at Serengeti Wildlife Research Center. ‖These results are reported separately because of the reduction in sample size. Habitat effects on mane darkness are expressed here as a negative correlation between darkness and residency on the plains.

cooler habitats and months and longer if they reached maturity in cooler years.

These data suggest that short manes reflect poor fighting ability or short-term health, whereas dark manes indicate maturity and high levels of testosterone and nutrition. Do lions take advantage of this information? Paternity is often highly skewed between coalition partners (26). The first male to reach an estrous female quickly establishes a consortship (27), but field observations of these "scramble competitions" are rare. We performed playback experiments, broadcasting roars of an unfamiliar female to coalitions of two to three males (14). Dark-maned males were more likely to lead the approach to the broadcast roars (n = 13 coalitions, G = 16, P < 0.05, rank-sum test), but there was no effect of mane length.

Females would gain direct benefits from preferring superior males. Fathers protect their cubs from infanticide, and eviction of the resident coalition generally causes 100% cub mortality (28). In addition, males can provision an entire pride by capturing large prey such as giraffe or Cape buffalo (29); and even in areas where these species are uncommon, well-nourished males would be likely to maintain longer pride tenure. Our long-term records reveal that excess estrous females mostly mated with the darkest-maned male in their coalition (in 13 of 14 cases, P < 0.01, sign test) but showed no preference for long-maned males (7 of 14 cases).

"Model" males are widely used to stimulate sexually selected behavior (1). We set out two life-sized models, differing in either mane length or darkness, and attracted lions with recordings of scavenging hyenas (fig. S2C). The lions typically approached to the side of one model, often moving in to inspect
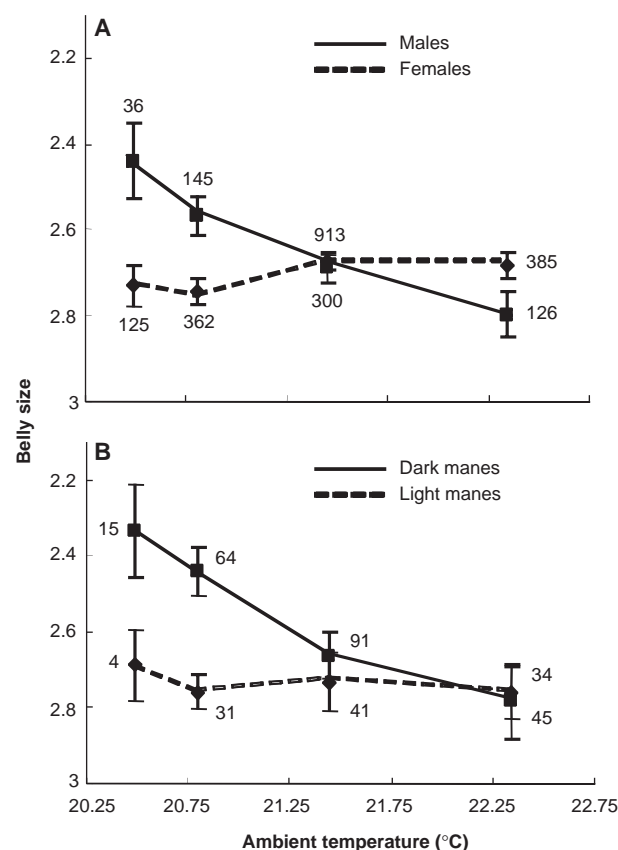

Fig. 2. Belly size versus average monthly temperature in Ngorongoro Crater. Belly size was assessed visually and ranges from 1 (fully expanded) to 5 (emaciated). Numbers beside symbols indicate numbers of individuals assessed. (A) Females do not alter their food intake at different temperatures, whereas males significantly decrease their intake in the hottest months (interaction between sex and temperature: $T = 4.658$, $P = 0.0000$). (B) Dark-maned males feed significantly more than light-maned males in the coldest months but not in the warmest months (interaction between mane color and temperature: $T = 2.018$, $P = 0.0445$).

Table 2. Fitness parameters associated with mane darkness. All variables are significant in univariate analyses unless otherwise noted. Males with darker manes have superior survival and competitive abilities, resulting inoverall increases in offspring fitness. Full model statistics are presented on the top row of each model.

Independent variable	Coefficient/SEM	P	Dependent variable	n	r^2	F
Logistic regression of male's 12-month survival after being wounded						
Male's age when wounded	−3.6	0.0003	Annual survival	110 wounded males		
Number of males in coalition	2.35	0.0187				
Mane darkness	2.17	0.0300				
Linear regression of coalition's lifelong tenure						
Independent variable	t	P	Dependent variable	t	r^2	F
Number of males in coalition	8.63	0.0000	Lifelong tenure	71 coalitions	0.549	43.58
Average mane darkness	2.03	0.0463				
Logistic regression of yearling survival to age 2						
Independent variable	Coefficient/SEM	P	Dependent variable	n		
Yearling's exposure to male takeover	−1.2239	0.0000	Survival from 1 to 2 years	443 yearlings		
Average mane darkness of paternal coalition	2.7837	0.0247				
Maternal survival to yearling's 2nd b'day	1.1983	0.0314				
Logistic regression of yearling risk of wounding						
Number of males in paternal coalition	5.23	0.0000	Risk of wounding	585 yearlings		
Average mane darkness of paternal coalition*	−2.76	0.0059				
Linear regression of litter survival						
Independent variable	t	P	Dependent variable	n	r^2	F
Ngorongoro Crater						
Litter's exposure to male takeover	−4.65	0.0000	Survival to 1 year	155 litters	0.149	14.51
Average mane darkness of paternal coalition	2.99	0.0033				
Serengeti Plains						
Litter's exposure to male takeover	−3.66	0.0004	Survival to 1 year	143 litters	0.147	13.27
Average mane darkness of paternal coalition	−3.33	0.0009				

*Not significant by univariate analysis.

its hindquarters; and although males were extremely hesitant (movie S1), females were generally less cautious. In our only opportunity to test an excess estrous female, she demonstrated explicit sexual behavior, walking sinuously past the models (movie S2). Males and females differed significantly in their response to manes (table S1). Males always approached the light-maned model (in 5 of 5 tests) and were significantly more likely to approach the short-maned model (9 of 10 tests, $P = 0.022$, two-tailed, sign test). Females preferentially approached the dark-maned model (9 of 10 tests, $P = 0.022$) but showed no significant attraction to longer manes (7 of 10 tests).

By assessing mane length and darkness, males avoid healthier, older, more aggressive individuals, thereby lowering the potential costs of fighting. By preferring males with darker manes, females gain mature, better-fed, more aggressive mates, and their preference confers direct fitness benefits. Dark-maned males are more likely to survive 12 months after being wounded, and coalitions with darker manes enjoyed longer residencies over the course of their lives (Table 2). Annual survival rates for yearlings were higher for the offspring of dark-maned coalitions (Table 2). This might reflect superior genes, but yearling offspring of dark-maned coalitions were less likely to be wounded (after controlling for coalition size) (Table 2), suggesting that their improved survival was due to better paternal protection. Paternal mane color had a more complex effect on cub survival. Litters sired by dark-maned coalitions were more likely to survive to their first birthday in Ngorongoro Crater, but mane color had a negative impact on litter survival on the Serengeti plains (Table 2).

This apparently results from contrasting diets: Dark-maned males facilitate cubs' feeding success on the large carcasses typical of the Crater, but they deny cubs access to the small carcasses common on the plains (14).

Mammals generally grow longer, denser fur in the winter, and darker coat color can increase heat load (30, 31). The floor of the Ngorongoro Crater is surrounded by cool highlands; the Serengeti woodlands are adjacent to the hot, humid Lake Victoria basin; and the Serengeti plains are intermediate between these two in T_a. Ngorongoro males have the darkest manes as adults, whereas those born in the Serengeti woodlands have the shortest manes (Table 1) (32). Temporal changes in ambient T_a also influence mane characteristics: Manes are darker during the cooler months of the year, and males that reached adult size during hotter-than-average years maintained significantly shorter manes throughout their lives [see supporting online text (14)] (Table 1).

Male lions may be more sensitive to T_a than females because their larger size reduces their surface-to-volume ratio and their manes limit the area available for heat exchange. We used infrared thermography (33) to investigate the effect of mane length and color on thermoregulation (fig. S2), measuring the surface temperature (T_s) of lions in Serengeti and Ngorongoro as well as in Kenya's Tsavo National Park (where males were largely maneless) (14). In Serengeti and Ngorongoro, T_s was higher in males than in females (after controlling for ambient temperature and the distance from camera to animal), but there was no difference between females and maneless males in Tsavo (Table 3). These results suggest a general thermoregulatory cost of the mane,

because male T_s is only higher in habitats where males grow conspicuous manes.

Dark mane hairs are thicker than blonde hairs (paired t-test statistic = 6.925, $P < 0.0001$, $n = 18$ males) (14), and thicker hair decreases rates of heat transfer (34). In Serengeti and Ngorongoro, T_s was higher in darker males (Table 3). Sperm production is hampered by high testicular temperatures (35), testicular T_s is correlated with overall T_s (Table 3), and dark-maned males have more abnormal sperm (Student's t test = 2.83, $r^2 = 0.8542$, $P = 0.0177$, $n = 15$; the result remains significant after controlling for inbreeding in Ngorongoro lions) (36). Male T_s also increased with belly size (Table 3), suggesting that large meals increase heat load, and dark-maned males in Ngorongoro (where the food supply is constant year-round) ate less during the warmest months of the year (Fig. 2).

Our results demonstrate that the lion's mane reflects a complex interaction between reproductive benefits and environmental costs. Both mane length and darkness are advantageous, but darkness appears to be the dominant signal to other lions. Males were sensitive to both length and darkness when confronted with models (that is, strangers), but only darkness correlated with male dominance within coalitions. Females were only sensitive to mane darkness in their resident males and in the model tests, and only darkness correlated with tenure length and with offspring survival. Darker males have higher testosterone levels, and testosterone is likely to have several relevant consequences. First, dark-maned males may have greater feeding success because of higher dominance at kills; second, testosterone can raise metabolic rates (37), thereby increasing T_s.

Table 3. Infrared measurements of T_s of males and females ≥ age 3.5 years. Maned males are hotter than females, and males with dark manes and full bellies have the highest T_s. Full model statistics are presented on the top row of each model.

Independent variable	t	P	Dependent variable	r^2	F	n
Serengeti/Ngorongoro T_s: *males versus females*						
T_a	7.956	0.0000	T_s	0.6668	29.02	28 males and 15 females
Distance from camera to animal	−3.118	0.0034				
Male versus female	2.196	0.0341				
Tsavo T_s; *males versus females*						
T_a	4.593	0.0007	T_s	0.7562	28.914	5 males and 5 females
Male versus female	−0.4252	n.s.	T_s			
Serengeti/Ngorongoro: male T_s						
T_a	4.334	0.0000	Male T_s	0.7138	23.44	28 males
Distance from camera to animal	−3.178	0.0162				
Mane darkness	3.922	0.0020				
Belly size*	−2.419	0.0340	Male T_s	0.8444	21.36	16 males
T_a	4.334	0.0012				
Distance from camera to animal	−3.178	0.0088				
Mane darkness	3.922	0.0024				
Serengeti/Ngorongoro: testicular T_s						
Male T_s	4.194	0.0018	Testicular T_s	0.6013	17.59	12 males

*Model reported separately because of sample size reduction.

Dark-maned males are presumably better able to withstand heat-related costs, and although we could find no heritability in darkness, mate choice for dark manes might confer indirect genetic benefits as well as direct fitness effects.

Heat appears to be the dominant ecological factor shaping the lion's mane. Mane length showed a significant relationship to annual T_a fluctuations from 1964 to 2000 (Table 1), and manes are darker in cooler habitats and seasons. Long-term climate forecasts predict an increase of 1.3° to 4.6°C in this region by the year 2080 (*38*); thus, manes are likely to become shorter and lighter in these populations. The general importance of ambient temperature to sexual selection is not yet known, and temperature effects may be most obvious in animals where large body size already imposes thermal stress. However, any indicator trait with high energetic costs should be sensitive to ambient temperature, suggesting broad implications for studies of sexual selection.

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Meiotic Arrest in the Mouse Follicle Maintained by a G$_s$ Protein in the Oocyte

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The mammalian ovarian follicle consists of a multilayered complex of somatic cells that surround the oocyte. A signal from the follicle cells keeps the oocyte cell cycle arrested at prophase of meiosis I until luteinizing hormone from the pituitary acts on the follicle cells to release the arrest, causing meiosis to continue. Here we show that meiotic arrest can be released in mice by microinjecting the oocyte within the follicle with an antibody that inhibits the stimulatory heterotrimeric GTP–binding protein G$_s$. This indicates that G$_s$ activity in the oocyte is required to maintain meiotic arrest within the ovarian follicle and suggests that the follicle may keep the cell cycle arrested by activating G$_s$.

Oocytes within mammalian ovarian follicles begin meiosis during embryogenesis but then arrest at prophase of meiosis I until luteinizing hormone acts on the follicle to cause meiosis to resume (*1*). Maintaining this arrest in fully grown oocytes depends on the presence of the surrounding follicle (Fig. 1, A and C); removing the oocyte from the follicle reinitiates meiosis. However, it is unknown how the follicle cells communicate with the oocyte to keep the cell cycle arrested. Signaling depends on maintaining a high level of adenosine 3′,5′-monophosphate (cAMP) in the oocyte, but where the cAMP comes from and how the follicle cells regulate its level is unclear (*1*). One hypothesis is that cAMP enters the oocyte through gap junctions with the follicle cells (*1*, *2*). Alternatively, cAMP could be generated in the oocyte, and the role of the follicle cells could be to maintain the activity of a stimulatory G protein (G$_s$) in the oocyte membrane, thus stimulating oocyte adenylyl cyclase (*1*, *3*). Although some evidence has been obtained for each model, neither possibility has been definitively tested.

Studies of how meiotic arrest is main-

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