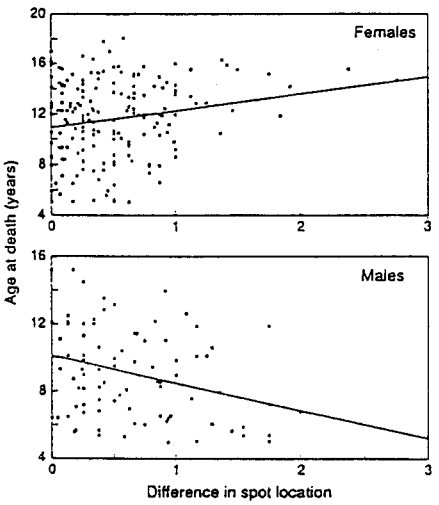
Should a lion change its spots?

SIR — Fluctuating asymmetries can provide important insights into patterns of mate choice[1,2] because asymmetric individuals often show low levels of overall genetic health[3]. But the complex relationship between fluctuating asymmetry and lifespan in African lions suggests that this trend may not be universal.

Lions, like other cats, have conspicuous vibrissae spots on either side of their muzzle. Each spot is a small furless area that surrounds a single 'whisker'. Parallel rows of vibrissae spots are located on each side of each lion's face. Above the topmost row, most lions possess a few additional identification spots, which we recorded systematically when an individual was first observed (usually as a small cub). The precise patterns of these spots are highly variable and vibrissae spots are used for individual recognition in most field studies of lions[4]. We have now examined fluctuating asymmetry in the whisker-spot patterns of 920 lions from our long-term studies[5–7].



Regression of lifespan against horizontal identification spot asymmetry for females (top) and males (bottom). The horizonal location of each spot is scored according to its position above the topmost row of vibrissae spots, or 'reference' row, on that side of the lion's face. Reference-row spots are numbered sequentially from the spot closest to the tip of the lion's nose. If a lion has two spots on the left side of its face directly above the first and second reference-row spots, its position score for that side would be scored as (1+2)/2=1.5. If it has one spot directly above the third reference-row spot on its right side, the horizontal difference in spot location would be 3−1.5=1.5 and the difference in the number of spots would be 2−1=1. Longevity is significantly related to horizontal asymmetry in both sexes: for females, the least-squares linear regression of age at death against horizontal spot differences: r^2=0.0378, n=176, Student's t=2.61, P<0.01. Female lifespan varies across habitats, but the effect of horizontal spot difference remains significant when habitat is included in a multiple-regression model: t=2.78, P<0.01. For males: r^2=0.0844, n=87, Student's t=−2.80, P<0.01. Males in larger coalitions live longer, but horizontal spot asymmetry remains significant in a multivariate model: t=−2.84, P<0.01.

A lion may differ in the number of identification spots on each side of its face or in the location of spots above the topmost 'reference' row, but these patterns do not differ consistently between left and right. Nor is there any correlation between the asymmetry of a mother's and her cubs' spots. Of 793 lions whose spot patterns can be scored for the number and location on both sides of the face, 759 (96%) are unique.

We tested whether any measure of spot-pattern asymmetry is correlated with two factors known to affect fluctuating asymmetry[3]: the extent of close inbreeding and the intensity of nutritional stress during development. The Ngorongoro crater lions are inbred and show significantly reduced levels of genetic variability[5,6], whereas the lions on the Serengeti plains are subject to far greater variation in food supply than lions in either the Serengeti woodlands or the crater[7]. However, the extent of asymmetry in identification spots does not differ across habitats, nor is spot asymmetry correlated with isozyme heterozygosity.

We tested whether asymmetry in the number or horizontal location of identification spots is correlated with specific components of lifetime reproductive success. We restricted our analysis to individuals that died during the course of our study but lived for a minimum of 5 years, by which age both sexes have generally become established breeders[7].

We found no relationship between fitness and asymmetry in the number of spots on each side of the face. However, lifespan in both sexes is significantly correlated with the difference in horizontal location of their identification spots (see figure). Even more surprising, the correlation runs in the opposite direction in each sex. Consistent with other studies of fluctuating asymmetry, asymmetric males die at a younger age than symmetrical males; but asymmetric females live longer than symmetrical females. These results are statistically significant both by simple regression and in multiple-regression models that include the main factors known to influence longevity in the two sexes[7].

Female mammals that are heterozygous for genes on the X chromosome often have mosaic skin patterns in either coat colour (for example, calico cats) or in the distribution of sweat glands (anhidrotic ectodermal dysplasia) due to X-chromosome inactivation (a phenomenon generally, and in this case rather amusingly, known as lyonization). However, our results do not result from lyonization: the degree of spot asymmetry is the same in the two sexes. Thus asymmetric spot patterns in lions are probably generated by a similar mechanism in both sexes.

It is difficult to accept that these correlations reflect direct causality between spot asymmetry and survival. It is more likely that spot asymmetries reflect some underlying genetic or physiological condition expressed during early development that is subject to opposing selective forces in the two sexes. Whatever the underlying mechanism, male and female lions would do better to show divergent preferences in the pattern of their partners' spots.

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