Territoriality, and Population Dynamics in Serengeti Lions

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To test the effects of ecological changes on population dynamics (1–3), we rely on long-term records available from the Serengeti National Park, Tanzania (4). Lions in a 2,000 km² area of the Serengeti have been studied continuously since 1966 (5). “Woodlands” prides reside in regions dominated by Acacia and Commiphora trees, with resident herds of hartebeest, topi, and buffalo. “Plains” prides occur grasslands consisting primarily of Sporobolus, Themeda, Pennisetum, and Cynodon spp., with low densities of resident warthog and Grant’s gazelle. Large numbers of migratory wildebeest, zebra, and Thompson’s gazelle move through both habitats in response to seasonal rainfall patterns each year. Lion prides consist of 1 to 18 adult females, their dependent offspring, and a resident coalition of 1 to 9 males. Females defend joint territories, and larger prides dominate smaller ones (6, 7). As a result, prides of ≤2 females suffer very low reproductive success; prides of >10 females also fare poorly because of high levels of within-group competition (5, 8). Prides persist for generations, and new prides consist of related females that disperse together from preexist-
Fig. 1. Lion population sizes each month: (A) woodlands, (B) plains. Horizontal lines indicate periods where population sizes were statistically homogeneous but different from adjacent periods. Blue lines include all individuals; black lines indicate lions ≥2 years. Diamonds designate change points. Pale green blocks highlight times when the populations were below local equilibrium density; dark green lines demarcate years within these periods with favorable rainfall. Red line shows the CDV die-off in 1994. (C) Serengeti herbivore population sizes. Vertical bars show SE. Green box highlights recovery from rinderpest; brown box highlights drought-related die-off in the wildebeest.

Fig. 2. Wildebeest, fire, and the regeneration of woody vegetation in the Serengeti woodlands. (A) The extent of wildfire is inversely related to the size of the wildebeest population. (B) Wildfire reached a low point in the late 1970s and early 1980s. (C) Population growth rates of acacias in the Serengeti woodlands as measured from fixed-point photography; woodland recovery peaked in the early 1980s. Green band indicates time period when the woodlands lions experienced the greatest increase in prey accessibility.
(16)], 1983 and 1999 were followed by the two driest wet seasons in more than 40 years, and the increase in the plains population occurred during the extreme El Niño rainfalls of 1997–1998, which were the heaviest since 1962. (Migrant herbivores spend less time on the plains in “dry” wet seasons and more time on the plains in “wet” wet seasons.) Thus, the background of long-term change in prey availability is overlain with a stochastic year-to-year pattern of prey distribution, and the first “good year” permitted rapid recruitment in the lion population. Across all significant population increases, the primary demographic response was increased cub survival ($P < 0.01$) rather than larger litter size or shorter interbirth intervals. All the population “leaps” involved successful reproduction in an exceptional number of prides. Five of six woodlands prides successfully raised cohorts of cubs in 1973 and 1983 (four of six was the prior record) and six of seven in 1999. There had never been more than six successful prides in any single year on the plains until 1997, when 11 of 12 prides successfully fledged offspring.

Our data clearly reveal the impact of the wildebeest on the Serengeti lions. Buffalo and gazelle both returned to 1960s levels by 2002 (Fig. 1C) without a concomitant decline in lion numbers, whereas the wildebeest population has remained at about 1.2 million for the past 25 years. The wildebeest were also responsible for two indirect effects on the lions. Increased levels of grazing led to extensive regeneration of woody vegetation, permitting an increase in the woodlands lion population, whereas a temporary decline in the wildebeest population increased the average height of grasses in the intermediate grass community, enabling an expansion of the lion population on the plains. The first significant improvement in local wildebeest abundance during a period of persistent ecological change also permits the simultaneous establishment of viable new prides (with $\geq 4$ females), thus triggering the sudden increase of the population as a whole (13). In contrast, the herbivore community in the nearby Ngorongoro Crater is nonmigratory, and the Crater lion population fell to one-eighth of its local equilibrium density after a disease outbreak in 1962 (19) but subsequently showed a continuous period of exponential growth, doubling every 4 years for 12 years (20).

**Impact of social structure.** To evaluate the importance of group living on population changes in the Serengeti, we developed a detailed simulation model that incorporated long-term data on cub productivity, pride splitting, and adult survival as functions of annual rainfall, pride size, and dispersal status. We modeled the impact of large-scale ecological change as an increase in the number of potential territories in each study area (the magnitude being set by the observed change in equilibrial population size); rainfall followed the observed sequence over the past 40 years, and the simulated population suffered the observed level of disease mortality in 1994. Pride formation was a stochastic process that depended on the number of available territories, the size of the maternal pride, and cub recruitment. Key parameters were varied first to mimic an asocial species. In this initial case, all offspring dispersed and females were solitary (thus the model was deterministic rather than stochastic). In the second scenario, lions lived in stochastically created prides and new prides were only viable if they contained $\geq 4$ females, but there was no within-group den-
sity dependence: Cubs in large prides had similar mortality as those in medium-sized prides. The final model imposed both a threshold minimum viable pride size and the observed levels of cub mortality in excessively large prides.

In a solitary species, gradual changes in the environment in the Serengeti woodlands produce a continuous response in adult population size (Fig. 4A), because females can be added one at a time as the number of potential territories increases. In a social species with a threshold minimum group size but lacking within-group density dependence, adult population growth is less continuous, but the shifts between equilibria are still gradual because daughters can always be added to preexisting prides (Fig. 4B). With both a threshold minimum pride size and within-group density dependence, however, adult population growth is abrupt, and the model often generates the kind of saltatory equilibrium observed in the empirical data (Fig. 4, C and D). With an upper limit on pride size, moderate-sized prides require exceptional circumstances to rear large cohorts of daughters, and this is the only scenario that accurately predicts a delayed (but abrupt) recovery from the 1994 CDV outbreak (see also figs. S1 and S2).

Lion social structure imposes a coarse-grained tempo on population change that is further amplified by synchronous recruitment of large cohorts by multiple prides and stabilized by within-group density dependence. Until now, population models have assumed that population trends could be predicted by extrapolation from the survival and reproduction of individuals. However, a more complete understanding of population dynamics can only be achieved by incorporating the impact of social organization and family structure on the population as a whole.

References and Notes
13. Time-series correlations between the change in the number of adults (age ≥2 years) in a given month and the change in the number of prides during that same month were highest when “prides” were defined as groups containing four adult females: Primes: N = 369 pride months, r = 0.374, P < 0.0001; woodlands: N = 437 pride months, r = 0.249, P < 0.0001. Autocorrelations within each time series were not significant; best fits were found with a zero time lag between the number of adults and the number of prides.
15. An optimal segmentation method (27) determined the number of segments and the date of the change points for each population. This method segments a data series so as to minimize the total sum-of-squares deviations by using the mean and sum of squares for each segment (and assuming a normal distribution and constant variance). The minimum number of equilibria for each habitat was determined by a dynamic programming algorithm that measured the improvement in the sum of squares with each additional segment. A cumulative sum (CUSUM) technique (22) confirmed the number and date of the change points by detecting persistent shifts from a known mean in a time series (table S1).
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SOM Text
Table S1
Figs. S1 and S2
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Grain Boundary Decohesion by Impurity Segregation in a Nickel-Sulfur System

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The sulfur-induced embrittlement of nickel has long been wrapped in mystery as to why and how sulfur weakens the grain boundaries of nickel and why a critical intergranular sulfur concentration is required. From first-principles calculations, we found that a large grain-boundary expansion is caused by a short-range overlap repulsion among densely segregated and neighboring sulfur atoms. This expansion results in a drastic grain-boundary decohesion that reduces the grain-boundary tensile strength by one order of magnitude. This decohesion may directly cause the embrittlement, because the critical sulfur concentration of this decohesion agrees well with experimental data on the embrittlement.

The incorporation of a small quantity of impurities can drastically change the mechanical strength of metals. Auger electron spectroscopy studies, together with various tensile tests, show that the sulfur (S)–induced embrittlement of nickel (Ni) is clearly associated with S segregation to grain boundaries (GBs) and that the transition from ductile to brittle behavior requires a critical intergranular concentration of S (1, 2). However, why and how S weakens the GBs and the significance of the critical intergranular concentration remain unclear. One hypothesis assumes that the embrittlement arises from S-induced changes in the electronic structure that lead to weakening of the Ni-Ni bonds holding the GB (3, 4). A second assumes that the magnitude of the embrittling effect can be estimated by the binding energy difference for S at a GB and at a fractured free surface according to the Rice-Wang model (5, 6). These hypotheses, however, do not directly explain the existence of a critical

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