

Ecological Change, Group Territoriality, and Population Dynamics in Serengeti Lions

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Territorial behavior is expected to buffer populations against short-term environmental perturbations, but we have found that group living in African lions causes a complex response to long-term ecological change. Despite numerous gradual changes in prey availability and vegetative cover, regional populations of Serengeti lions remained stable for 10- to 20-year periods and only shifted to new equilibria in sudden leaps. Although gradually improving environmental conditions provided sufficient resources to permit the subdivision of preexisting territories, regional lion populations did not expand until short-term conditions supplied enough prey to generate large cohorts of surviving young. The results of a simulation model show that the observed pattern of “saltatory equilibria” results from the lions’ grouping behavior.

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 occupy 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-

ing prides (9). Lion territory size varies with overall food availability (10) but not with the number of females in the pride (11), and a pride territory must also contain permanent water and adequate denning sites (5, 12).

Population stasis and transition. To breed successfully, female lions must have sufficient companions to defend adequate food, water, and denning sites. Thus, an expanding food supply can only cause lion populations to grow when preexisting prides can split to form descendant prides that are large enough to establish themselves successfully. Population size should therefore increase as a direct function of the number of breeding groups in the population. The month-by-month change in population size between the 1960s and 2002 was highly correlated with the corresponding change in the number of prides in that habitat, regardless of whether we defined a pride as containing a minimum of two, three, or four adult females (and whether females were defined as “adults” after reaching 2, 3, or 4 years of age). However, the best statistical fit defined prides as groups containing a minimum of four females of at least 2 years of age (13), the age at which young females first participate in territorial defense (14).

Figure 1, A and B, shows the monthly population sizes in each study area. Totals fluctuated slightly from month to month; but at a broad time scale, each population showed long periods of stasis ended by a sudden transition to a new equilibrium (15), and each change point was associated with a specific ecological change in that habitat. Figure 1C shows the population sizes of the major Serengeti herbivore species over the past 40 years. Wildebeest

and buffalo numbers increased dramatically from the early 1960s until the late 1970s because of their release from rinderpest infection in 1963 (4). This was by far the most substantial change in prey abundance over the entire study period, and the lion population showed a clear increase over this same span [also see (16)]. Most striking, however, is that the woodlands lion population suddenly increased to a new equilibrium in 1973. The plains lions were not monitored between 1969 and 1974, so the precise timing and tempo of its increase are not known.

Lions enjoy higher feeding success in areas with greater vegetative cover (17), and each Serengeti habitat has undergone a large-scale increase in cover in the past 20 years. The grazing wildebeest herds remove vast quantities of grass that would fuel wildfires if left to senesce, and the enormous increase in wildebeest numbers led to a striking decrease in grassfires that, in turn, stimulated a regeneration of the Serengeti woodlands during the 1980s (Fig. 2). In November 1983, the woodlands lion population suddenly increased to a new plateau after several years of unprecedented growth of woody vegetation (Fig. 1A). The wildebeest population declined in 1994 (as a result of severe drought); the migration “skipped” the intermediate grass plains in 1995, enabling the tallest species in this community to dominate, and this pattern persisted for the following 5 to 6 years (Fig. 3). The tall grass provided improved cover for the plains lions, and the plains population suddenly increased in February 1997 after remaining at a persistent equilibrium since at least 1975.

The woodland lion population dropped significantly in 1994 because of the canine distemper virus (CDV) epizootic that killed approximately one-third of the Serengeti lions (18). Although the die-off caused the lions to drop well below their equilibrium density, the population remained relatively constant for 5 years until suddenly returning to its previous plateau in May 1999.

Determinants of population change. The irruption of the herbivores, the regeneration of the woodlands, and the expansion of the tall grass plains were all processes that continued over several years, yet the lion populations always reached a new equilibrium in a single year. Similarly, the woodland population recovered suddenly but not until 5 years after the CDV outbreak. What determined the precise timing of these changes? The migratory patterns of the dominant herbivores (wildebeest, zebra, and gazelle) are primarily driven by seasonal rains in the Serengeti, and all of the sudden changes in lion population size coincided with years of unusual rainfall: 1973 was the first in a series of unusually “wet” dry seasons [which attracted the migratory herds to the woodlands study area

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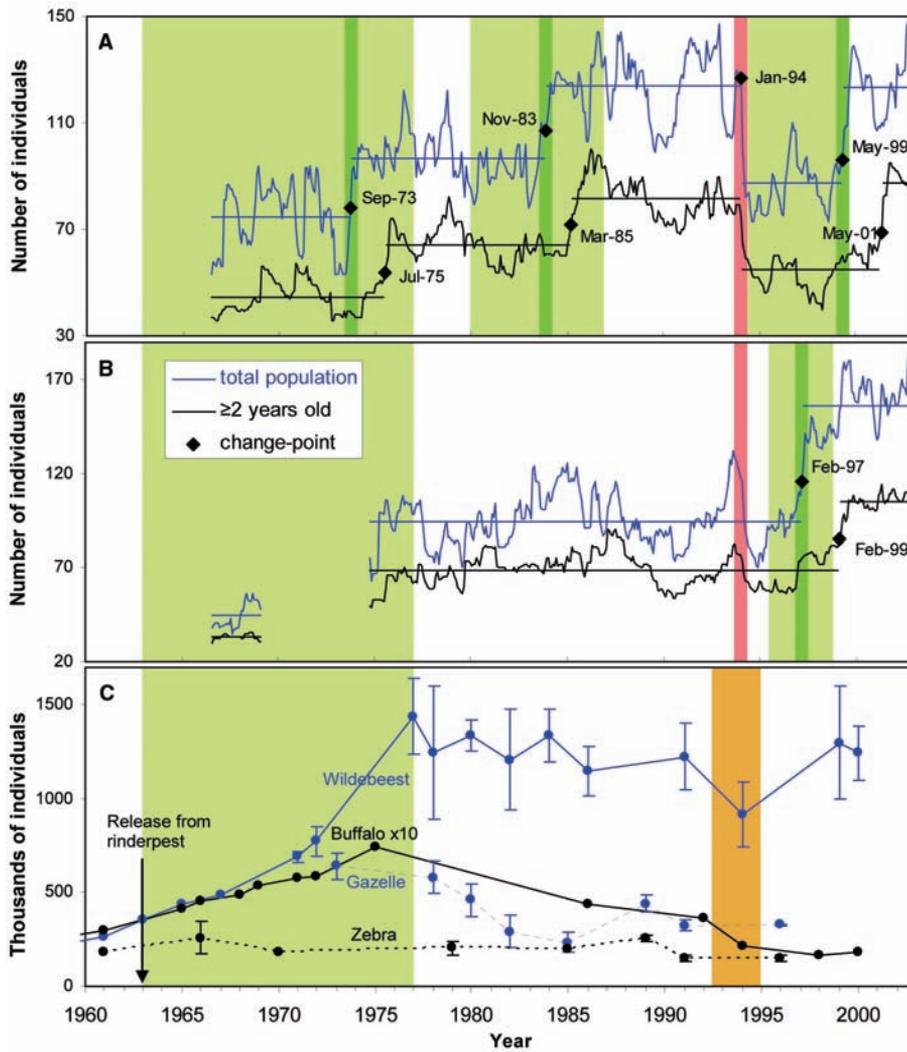


Fig. 1. Lion population sizes each month: (A) woodlands, (B) plains. Horizontal lines indicate periods where population sizes were statistically homogeneous but different from adjacent periods. Blue lines include all individuals; black lines indicate lions ≥ 2 years. Diamonds designate change points. 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.

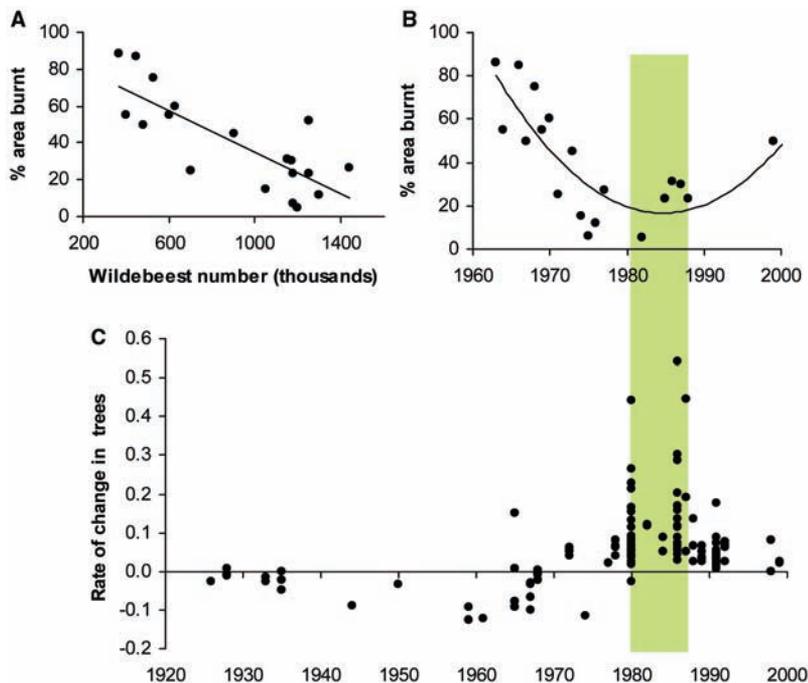


Fig. 2. Wildebeest, fire, and the regeneration of woody vegetation in the Serengeti woodlands. (A) The extent of wildfire is inversely related to the size of the wildebeest population. (B) Wildfire reached a low point in the late 1970s and early 1980s. (C) Population growth rates of acacias in the Serengeti 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 num-

ber 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 ≥ 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 equilibrium 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 ≥ 4 females, but there was no within-group den-

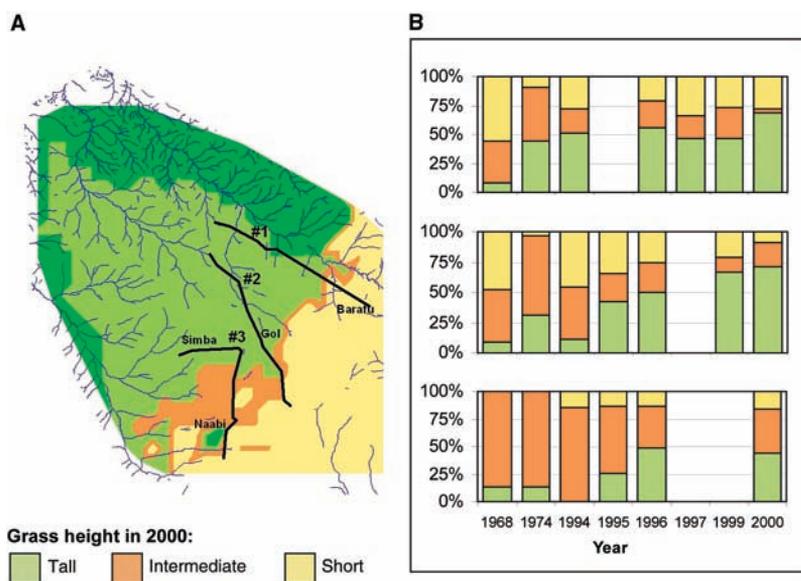


Fig. 3. Long-term changes in grass height. (A) Grasslands map for the Serengeti plains. (B) Bar graphs indicate percentage of each grass type along the three transects in (A). The extent of tall grass has increased since 1994 ($P < 0.01$).

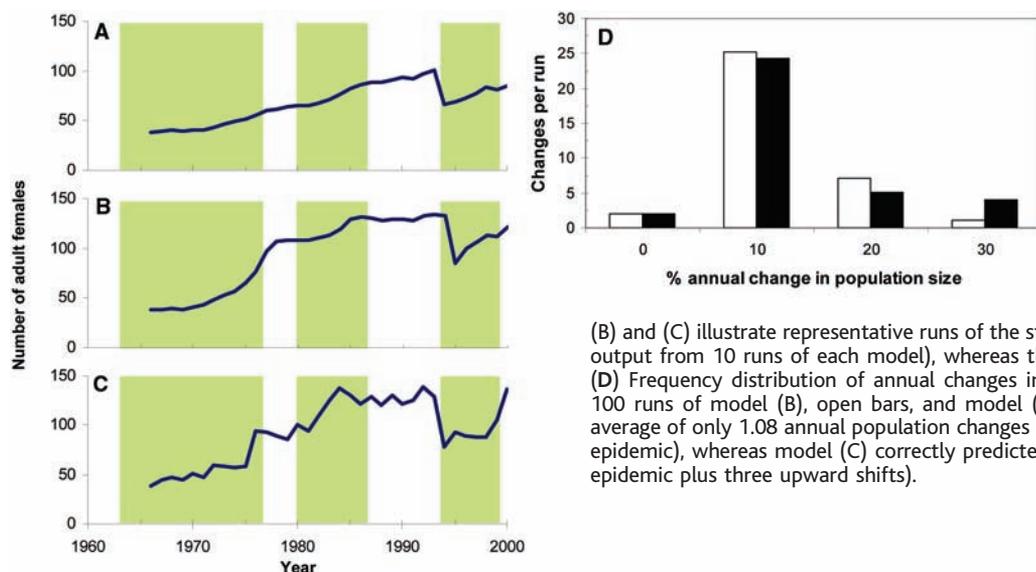


Fig. 4. Number of adult females predicted by simulation models of the Serengeti woodlands population under three different scenarios. (A) Each territory is occupied by only one adult female; all adult daughters disperse. (B) Lions live in prides that must contain ≥ 3 females to be viable, but cubs do not suffer higher mortality in excessively large prides. (C) Prides must be ≥ 3 females to be viable, and cubs born in large prides suffer higher mortality. (D) Frequency distribution of annual changes in female population size averaged over 100 runs of model (B), open bars, and model (C), black bars. Model (B) generated an average of only 1.08 annual population changes larger than 30% (because of the disease epidemic), whereas model (C) correctly predicted an average of 4.08 such changes (the epidemic plus three upward shifts).

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 repro-

duction 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.

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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. Plains: $N = 369$ 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.
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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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Supporting Online Material

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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 asso-

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ciated 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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