containing 1 μM EF protein in 20 mM Tris-HCl (pH 8.5), 500 mM NaCl, 10 mM $MgCl_2$ and 2.5 μM [^{3}H]GDP (specific activity approximately 11.5 Ci mmol^{-1}) (Amersham Pharmacia Biotech) were assayed at different temperatures, first at 10-°C intervals between 0 and 100 °C and then ±5 °C on either side of the temperature optimum. For the ML-meso putative ancestor, binding at 5-°C intervals between 40 and 70 °C was also determined. The amount of [^{3}H]GDP bound to EF was determined as previously described[16].

Received 7 April; accepted 30 July 2003; doi:10.1038/nature01977.

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Supplementary Information accompanies the paper on **www.nature.com/nature**.

Acknowledgements We thank M. Miyamoto, J. Aris, A. Falcon, S. Sassi, C. West and Z. Yang for discussions and assistance with our research. We also thank C. Knudson and A. M. Sanangelantoni for providing EF clones. Funding is provided by the National Research Council and NASA's Astrobiology Institute (E.A.G.), and the NIH and NASA (S.A.B.).

Competing interests statement The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to E.A.G. (gaucher@ufl.edu).
Inferred ancestral sequences have been deposited in GenBank under accession numbers AY305395–AY305397

Patterns of predation in a diverse predator–prey system

A. R. E. Sinclair[1], **Simon Mduma**[1,2] **& Justin S. Brashares**[1]

[1]*Centre for Biodiversity Research, 6270 University Boulevard, University of British Columbia, Vancouver, V6T 1Z4, Canada*
[2]*Tanzania Wildlife Research Institute, Box 661, Arusha, Tanzania*

There are many cases where animal populations are affected by predators and resources in terrestrial ecosystems[1–3], but the factors that determine when one or the other predominates remain poorly understood[4–5]. Here we show, using 40 years of data from the highly diverse mammal community of the Serengeti ecosystem, East Africa, that the primary cause of mortality for adults of a particular species is determined by two factors—the species diversity of both the predators and prey and the body size of that prey species relative to other prey and predators. Small ungulates in Serengeti are exposed to more predators, owing to opportunistic predation, than are larger ungulates; they also suffer greater predation rates, and experience strong predation pressure. A threshold occurs at prey body sizes of ~150 kg, above which ungulate species have few natural predators and exhibit food limitation. Thus, biodiversity allows both predation (top-down) and resource limitation (bottom-up) to act simultaneously to affect herbivore populations. This result may apply generally in systems where there is a diversity of predators and prey.

The influence of predation and resource availability on population dynamics has long been a focus of ecological research[6]. Yet, we know little about how these top-down and bottom-up forces work together to structure diverse ecosystems[4–6,7]. This is particularly true for mammal communities, where effects of predation and resource limitation are usually investigated on single species or in simple systems with low species diversity[8,9]. We examined patterns of predation in the diverse Serengeti ecosystem using data on ungulate populations before, during and after a period of predator removal.

The Serengeti ecosystem (34–36° E, 1–4° S) in Tanzania and Kenya, East Africa, is composed of open grassland and savannah. It supports 28 species of ungulates and 10 species of large carnivores that prey on them[10]. In any one habitat, there can be seven co-

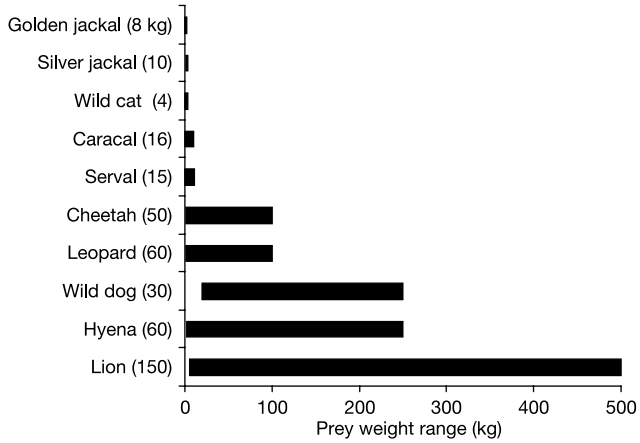

Figure 1 The range of weights of mammal prey consumed by carnivores of different sizes in the Serengeti ecosystem. There is a large overlap in diet at small prey sizes. Data are from our unpublished observations and published sources[17,26].

occurring species of canid and felid carnivores feeding on an array of ungulates. The carnivores show a characteristic pattern in the sizes of their typical prey. Each predator species tends to differ from others in preferring a narrow range of prey sizes within a broader diet range (Supplementary Information). Thus, the lion's (*Panthera leo*) preferred prey is wildebeest (*Connochaetes taurinus*) and zebra (*Equus quagga*) (170–250 kg; 38% of animals consumed), but 44% of the diet is made up of smaller prey (2–45 kg), while buffalo (*Syncerus caffer*) and giraffe (*Giraffa camelopardalis*) comprise 5–15% (refs 11, 12; approximate percentages in terms of biomass consumed are 63, 14 and 15–24, respectively). Each carnivore species includes prey outside their preferred size range but is inefficient at catching such prey. So, while lions are less efficient at catching gazelle (*Gazella sp.*) than catching wildebeest[13], they do so if opportunities present themselves. Hence, gazelle are less vulnerable to lion predation, despite their small size, than are wildebeest[13]. Overall, the diet niche of smaller carnivores is nested within that of larger carnivore species (Fig. 1).

Smaller-bodied ungulates suffer predation from many more predators than do larger ungulates (Fig. 2). Small species of antelope, such as oribi (*Ourebia ourebi*), are prey to five species of cats, two canids, hyena (*Crocuta crocuta*) and many smaller carnivores in Serengeti. We observed this range of predators with oribi where predation was caused by lion (14%), hyena (15%), leopard (*Panthera pardus*; 43%), silver-backed jackal (*Canis mesomelas*; 9%), baboon (*Papio anubis*; 7%), eagle (7%) and python (6%)[14]. Medium-sized antelopes (for example, wildebeest) are prey to three felids, the wild dog (*Lycaon pictus*) and hyena, while larger ungulates such as buffalo and giraffe are depredated by lion only[15]. Very large herbivores (that is, elephant (*Loxodonta africana*), rhinoceros (*Diceros bicornis*) and hippopotamus (*Hippopotamus amphibius*)) almost never suffer predation as adults and only rarely as juveniles.

Approximate densities per km^2 of the major predators in northern Serengeti are lion 0.22, hyena 0.5, leopard 0.12, cheetah (*Acinonyx jubatus*) 0.08, wild dog 0.02, and silver-backed jackal 0.16, providing a total of 1.1 predators per km^2 (ref. 16). These differences in density among species combined with differences in predation rates suggest that some carnivores have a greater effect on prey populations than others. Actual predator densities are likely to be much higher if the golden jackal (*Canis aureus*) and other smaller carnivores (1–10 kg) are included, but these data are not yet complete. Preliminary counts suggest these smaller predators occur at densities at least 2–3 times higher than those of the largest carnivores. Small prey such as oribi or Thomson's gazelle (*Gazella rufifrons*) at approximate densities of 3 per km^2 (see below) are faced with a predator:prey ratio of at least 1:3, which is extremely high. Thus, smaller ungulates should experience greater mortality from opportunistic predation, and we predict their populations should be severely affected by predation.

This prediction was tested with data from long-term studies of ungulate mortality rates and their causes. Using the long-term recruitment and mortality rates of ungulate populations and direct measures of mortality from telemetry[17–20], and information on predator diets[11,12,21], we calculated the proportion of adult mortality of ungulates accounted for by predation (Fig. 3). All records of adult mortality of impala and oribi indicate predation. In contrast, only about 5% of giraffe and 23% of buffalo adult mortality is caused by predators, and the proportion due to predation declines to zero for the largest ungulates. These values reflect adult mortality only, but predation at the juvenile stage will have an additional effect on most herbivore populations, particularly for smaller-bodied species. The relationship between ungulate body size and predation rate is not linear. Above a threshold body size of about 150 kg the proportion of annual adult mortality caused by predators declines rapidly as body size increases, indicating a sharp transition from top-down to bottom-up regulatory processes.

The pattern of predation mortality relative to prey size (Fig. 3) is predicted from differing levels of opportunistic predation through exposure to different numbers of predator species (Fig. 2). Such a pattern may also be predicted if small-bodied prey are uniformly more vulnerable to all predator species. However, data on predation rates, and predator diet and efficiencies[11–13,15,16,21,22], show that prey are differentially vulnerable to different predators, making this alternative mechanism less probable.

A natural experiment allowed a further test of this relationship between herbivore size and mode of population regulation. In a study area of northern Serengeti that has been monitored since 1966, poaching and indiscriminate poisoning removed the majority of carnivores (notably lion, hyena and jackals from evidence on observed carcasses and absence of calls) for an eight-year period (1980–87)[19]. In the contiguous Mara Reserve of Kenya, a part of the same ecosystem, predator populations remained intact[23]. During the predator removal period, five smaller-bodied species (oribi, Thomson's gazelle, warthog (*Phacochoerus africanus*), impala (*Aepyceros melampus*) and topi (*Damaliscus lunatus*)) for which data were available, increased markedly in density in the predator removal area relative to their populations in the non-removal area

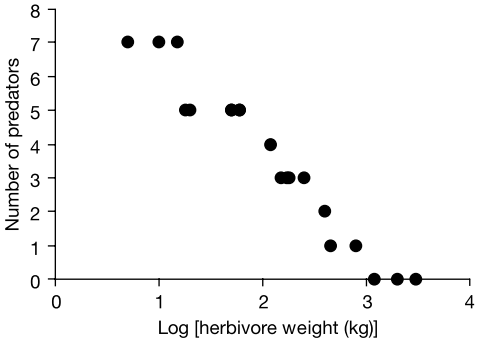

Figure 2 The number of mammal carnivore species that prey upon the savannah ungulates of different body sizes in Serengeti. Adult female body sizes are from published sources[26] and provided in Supplementary Information.

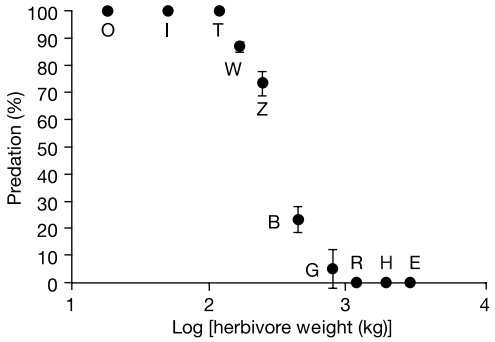

Figure 3 The proportion of annual adult mortality accounted for by predation in ten non-migratory ungulate populations for which data were available in the Serengeti ecosystem. There is a threshold in body size of about 150 kg above which predator limitation switches to food limitation. Error bars are 95% confidence limits. Species are: O, oribi; I, impala; T, topi; W, wildebeest; Z, zebra; B, African buffalo; G, giraffe; R, black rhino; H, hippo; E, African elephant. Data are provided in Supplementary Information.

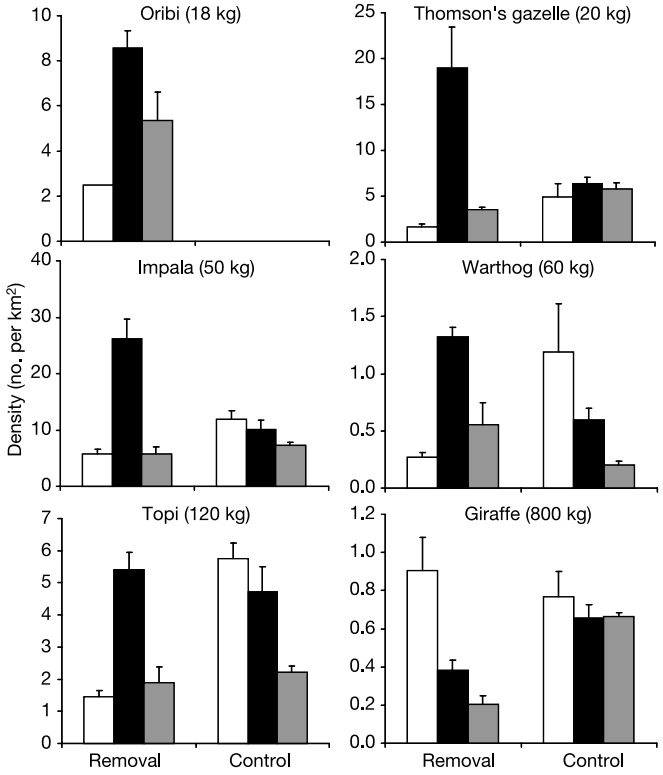

Figure 4 Densities of six ungulates in a predator removal area in northern Serengeti[17,27] compared with an adjacent control in the Mara Reserve[23]. Period before removal (open bar) covered 1967–80, the period of low predator numbers due to poaching (solid bar) covered 1981–87, and the period after predators returned (shaded bar) included years from 1989 onwards[17]. The five smaller species (<150 kg) increased during the predator removal period relative to the control, whereas the larger giraffe did not respond by increasing. These results are predicted from the pattern in Fig. 3. All comparisons of before versus during, and during versus after, periods differed significantly in the removal area ($P = 0.05$–0.001 calculated from standard census formulae[28,29] or *t*-tests assuming unequal variance). All comparisons in the control area were not significant except for warthog and topi ($P < 0.05$) that declined owing to other system-wide processes. There is no control for oribi because they do not occur in the Mara Reserve. Census locations and methods are described elsewhere[17,23,30]. Error bars are 1 standard error. Data are provided in Supplementary Information.

(Fig. 4). These populations declined once predators returned to the area. In contrast, abundance of one of the largest ungulates, the giraffe, did not increase in the predator removal area over the eight-year period (Fig. 4). These results conform to the prediction from Fig. 3 that species below a threshold body size (in this case <150 kg) should be predator limited whereas giraffe should not. If the loss of one predator species were to be compensated by increased predation from another, then we would not have observed the increase in prey populations, especially those of very small prey (Fig. 4).

In summary, evidence from predator diets, predation efficiencies and mortality of prey indicate that the preferences of carnivores impose the pattern of predation pressure on prey populations. This pattern is related to two features of scale—the nested diet niches of carnivores, and the body size of the prey. These two scaling factors result in heavy predation pressure (top-down processes) for small prey and resource limitation (bottom-up processes) for large prey in this diverse prey community. There exists a threshold in body size beyond which the cause of mortality switches to bottom-up control in larger species. These results suggest a mechanism by which the diversity or abundance of predators and the diversity of prey may determine the effect of predation on populations. We hypothesize that the loss of such diversity could disrupt the interaction of these processes and result in outbreaks and extinctions[2,7,24,25]. We suggest that these patterns of predation will emerge in other terrestrial systems that display similar complexity and scaling of predators and prey. □

Received 9 June; accepted 18 July 2003; doi:10.1038/nature01934.

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Supplementary Information accompanies the paper on **www.nature.com/nature**.

Acknowledgements We thank the Tanzania Wildlife Research Institute and Tanzania National Parks for facilitating our research in Serengeti. We thank NSERC Canada and the National Geographic Society for funding.

Competing interests statement The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to A.R.E.S. (sinclair@zoology.ubc.ca).

