THE ROYAL SOCIETY

Mammal population regulation, keystone processes and ecosystem dynamics

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The theory of regulation in animal populations is fundamental to understanding the dynamics of populations, the causes of mortality and how natural selection shapes the life history of species. In mammals, the great range in body size allows us to see how allometric relationships affect the mode of regulation. Resource limitation is the fundamental cause of regulation. Top-down limitation through predators is determined by four factors: (i) body size; (ii) the diversity of predators and prey in the system; (iii) whether prey are resident or migratory; and (iv) the presence of alternative prey for predators. Body size in mammals has two important consequences. First, mammals, particularly large species, can act as keystones that determine the diversity of an ecosystem. I show how keystone processes can, in principle, be measured using the example of the wildebeest in the Serengeti ecosystem. Second, mammals act as ecological landscapers by altering vegetation succession. Mammals alter physical structure, ecological function and species diversity in most terrestrial biomes. In general, there is a close interaction between allometry, population regulation, life history and ecosystem dynamics. These relationships are relevant to applied aspects of conservation and pest management.

Keywords: regulation; population fluctuation; allometry; predation; keystone processes; ecological landscaping

1. INTRODUCTION

The theory of regulation in animal populations has been the cause of one of the major controversies in ecology during the past century (Nicholson 1933; Andrewartha & Birch 1954; Lack 1954, 1966; Chitty 1960; Wynne-Edwards 1962). However, a consensus of understanding is now established with a body of data to support the theory (Sinclair 1989; Royama 1992; Murdoch 1994; Turchin 2003). This theory is fundamental to understanding intraspecific competition, predation dynamics and, ultimately, the causes of natural selection. In mammals, which exhibit the greatest range in body sizes of any animal group, allometric relationships and life-history features influence regulation. These relationships in turn determine how populations respond to environmental disturbances and structure the ecosystems in which they live.

Animal populations can be regulated by either bottom-up processes such as a shortage of food (or some other resource) or top-down processes through predation. Just when each process occurs has been the subject of some controversy (Connell 1983; Roughgarden 1983; Strong *et al.* 1984; Schoener 1989; Polis 1991; Menge 1992; Carpenter & Kitchell 1993) because there is an extensive literature supporting each but no clear rules for predicting them. In mammals some of these rules are becoming more evident and they may apply to other groups.

Mammals have played a significant role in world ecosystems for the past 30 million years since the advent of the gigantic indricotheres, some five times the size of elephants. Normally mammal populations are small compared to those of invertebrates, for example. However, the unique feature of mammals is that some have become very large and consequently they have major impacts on the physical structure of habitats, rates of ecosystem processes and the diversity of communities. In short, they are ecosystem landscapers.

I examine, in this review, our knowledge of mammal populations and ask the following five questions.

(i) What are the important characteristics of population regulation?
(ii) What determines variability of population sizes?
(iii) What are the ecosystem consequences of regulation by predators (i.e. top-down control) and by food (i.e. bottom-up control)?
(iv) What is the link between regulation and keystone processes?
(v) How does regulation affect the conservation of small populations?

These questions pertain mostly to mammal herbivores because they are subject to both bottom-up and top-down processes. I focus on terrestrial species for which we have more information.

2. REGULATION, EQUILIBRIUM AND CYCLES

(a) *Equilibrium domain*

Populations persist in nature through a negative-feedback mechanism termed 'density dependence'. Operationally, *density dependence is observed when the* per capita *rate of increase of a population (r) is negatively related to population density*, as seen for example in the Serengeti
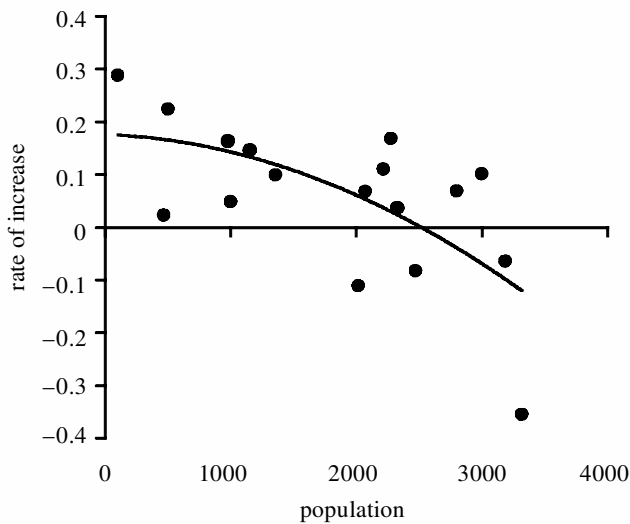
Figure 1. The *per capita* rate of increase of the African elephant in Serengeti shows a curvilinear relationship with population size, illustrating the increasing strength of density dependence at higher numbers (A. R. E. Sinclair and S. Mduma, unpublished data).
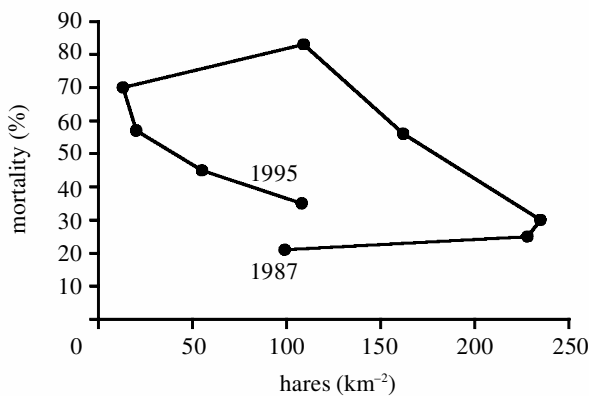

Figure 2. The percentage of the snowshoe hare population in northern Canada killed by carnivores, as measured by telemetry for the years 1987–1995, is related to hare density 3 years earlier (% predation $= 31.076 + 0.1879x$, where x is the density at $t - 3$, $r^2 = 0.84$). From O'Donaghue *et al.* (2001), with permission.

elephant (*Loxodonta africana*) (figure 1). The decrease in r occurs through either an increase in *per capita* mortality or a decrease in *per capita* natality. Populations experiencing such a negative-feedback mechanism are *regulated*.

This negative feedback can be immediate (time-scales are relative to life history) caused by such processes as intraspecific competition. Regulation tends to keep populations near equilibrium. However, negative effects, such as a drop in fertility owing to lack of food, physiological stress, etc., or mortality caused by predators, might take time to affect population numbers (usually one or two life stages or breeding seasons later) and so they could have a 'delayed density-dependent' effect (Hornfeldt 1994). For example, predators such as lynx (*Felis canadensis*) and great horned owls (*Bubo virginianus*) have a delayed effect of 2–3 years on the population numbers of snowshoe hares (*Lepus americanus*) in Canada (figure 2; O'Donaghue *et al.* 2001; Rohner *et al.* 2001). Such a delay produces cycles in numbers where the prey population is always over- or

undershooting equilibrium. Nevertheless, the population is still regulated because there are negative-feedback processes operating on it. We should, therefore, think of an *equilibrium domain* of population densities described by the amplitude of the fluctuations about the virtual equilibrium. Such oscillations should not be described as 'non-equilibrium', a term that should be used only when populations exhibit random drift with no density dependence (Sinclair 1996; Illius & O'Connor 1999, 2000).

(b) *Curvilinear density dependence*

For convenience we can describe the rate of increase of a population (N) by the θ-logistic equation (Gilpin *et al.* 1976)

$$\frac{dN}{dt} = r_m N \left(1 - \frac{N}{K} \right)^\theta \tag{2.1}$$

and

$$r = \left(\frac{dN}{dt} \right) \Big/ N = r_m \left(1 - \frac{N}{K} \right)^\theta, \tag{2.2}$$

where r_m is the maximum or intrinsic rate of increase and K is the carrying capacity of the population and the asymptote of the curve. When $\theta = 1$ the strength of density dependence is uniform over all population sizes and the *per capita* rate of increase (r) declines linearly as population increases. However, in large mammals density dependence is much stronger at high population numbers, producing a more rapid decline in r (as in figure 1). In this case θ is greater than unity. Conversely, in small mammals there is an indication that density dependence is stronger at low numbers than at high numbers (thus $\theta < 1$) (Fowler 1981, 1988), a trend also described for birds (Saether & Engen 2002). Thus, θ is positively related to body size. This allometric relationship has implications for the degree of stability and fluctuation in populations.

In large mammals with high values of θ, regulation is strongest at high density leading to stability and small population fluctuations. The caveat is that there is no overcompensating density dependence that can produce population cycles and chaos (see § 2c). However, at low population numbers there is little density dependence to compensate for disturbances caused by weather, predators or competitors. This means the population is vulnerable to extinction. Conversely, in small mammals the population is buffered against extinction because there is strong compensating density dependence at low numbers, as mentioned already. However, at high numbers there is weak density dependence, the population is vulnerable to perturbations from weather, and it may exhibit collapse or outbreaks in number.

What could produce these different trends in the strength of regulation? Food supply or other resources can produce the pattern where $\theta > 1$ (Sinclair 1977, 1979; Sinclair *et al.* 1985). Predation theory predicts that predators are likely to have strong density-dependent effects on prey at low prey density if this prey species is the primary food source (Pech *et al.* 1995; Sinclair & Pech 1996). Because prey numbers increase interference (e.g. territorial behaviour) and physiology (satiation, shortage of time) constrains predator numbers (Holling 1959, 1965), density-dependent predation not only becomes weaker but
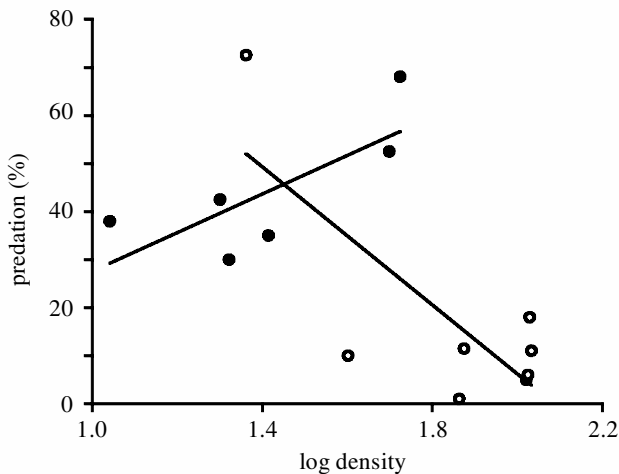
Figure 3. The percentage raptor mortality of the house mouse in the wheatlands of eastern Australia. At the low phase of density (filled circles) predation is density dependent but at the high phase (open circles) predation is inversely density dependent (from Sinclair *et al.* 1990).
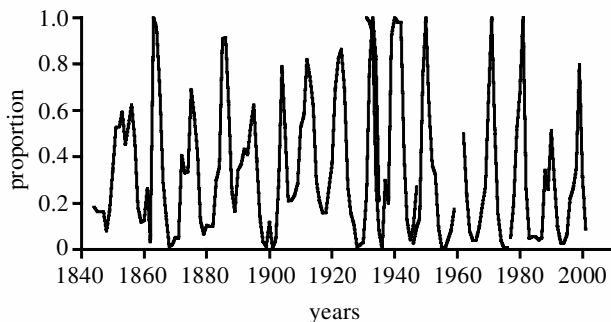

Figure 4. The snowshoe hare cycle from 1844 collated from different datasets and normalized to the peak record in each set (peak = unity). Data for years 1844–1935 from MacLulich (1937); for years 1931–1947 from D. Chitty and H. Chitty in Smith (1983); for years 1946–1959 from Marshall (1954) and Keith (1963); for years 1962–1976 from Cary & Keith (1979); for years 1977–2001 from Krebs *et al.* (2001), C. J. Krebs, personal communication.

changes to inverse density dependence as prey numbers increase. An example of this complex regulatory response is seen in the impact of the black-shouldered kite (*Elanus axillaris*) on erupting house mouse (*Mus domesticus*) populations in Australia (figure 3) (Sinclair *et al.* 1990). Predation, therefore, is one mechanism that can produce the pattern of regulation where $\theta < 1$.

(c) *Population cycles*

Over the animal kingdom, regular periodic fluctuation in population size (cycles) is extremely rare (Keith 1963; Finerty 1980). However, many small mammals exhibit population cycles in higher northern latitudes. These include rodents such as lemmings and voles, shrews and their associated predators such as weasels and raptors, and the period is 3–4 years (Henttonen *et al.* 1987; Erlinge *et al.* 1988; Hanski *et al.* 1991; Hornfeldt 1994; Korpimaki & Krebs 1996). Snowshoe hares in North America exhibit 10 year cycles, evidence for which extends from the early 1800s to the present day (figure 4).

The amplitude of the cycle tends to be more evident in northern ranges of a species, becoming weaker in the south, as seen in shrews and voles in Fennoscandia, (Hansson & Henttonen 1985; Erlinge 1987; Sandell *et al.* 1991). Population cycles are unrecorded in tropical latitudes. Cycle period in mammals is inversely proportional to the intrinsic rate of increase (r_m) and directly proportional to generation time (T) and body weight ($W^{0.26}$) (Calder 1983; Peterson *et al.*. 1984; Sinclair 1996).

Although cycle period is an intrinsic property of a species, the cause of the cycle is largely produced by extrinsic factors. Specialist predators may be the cause of the more pronounced cycles of small mammals in Fennoscandia (Erlinge 1987; Hanski *et al.* 1991; Korpimaki 1994). Experimental studies suggest both bottom-up (food supply) and top-down (predators, parasites) processes produce the snowshoe hare cycle (Murray *et al.* 1998; Krebs *et al.* 1995). In general, time lags in the density-dependent effects produce cycles.

However, overcompensating density dependence can also produce stable limit cycles and chaotic oscillations (May 1975; Bellows 1981; Grenfell *et al.* 1992; Turchin & Taylor 1992; Turchin 2003). In general, small species (less than 950 g) are predicted to exhibit chaotic oscillations, while those in the range 950–8500 g should show cycles, and larger species still should exhibit damped oscillations (Sinclair 1996; Larter *et al.* 2000). These relationships, however, are disturbed when mammals are introduced to novel environments. Species when they are exotic show much greater population variability than when they are indigenous (Sinclair 1997).

3. FLUCTUATIONS IN POPULATION AND LIFE-HISTORY THEORY

Some populations fluctuate more than others. It has been suggested that those with weaker density dependence are more prone to environmental perturbations and so exhibit greater variability in numbers (Fowler 1981; Strong 1986; Sinclair 1989). Weather is known to modify the strength of density dependence (Coulson *et al.* 2001). However, fluctuations also occur through the opposite process, namely strong, overcompensating density dependence as mentioned in § 2, resulting from intrinsic biological properties of the species rather than the environment. When external factors are not limiting, the potential maximum rate of increase, r_m, is determined by species-specific biological features (Fisher 1930). Field data for mammals show that r_m is related to body weight by

$$r_m = 1.375 W^{-0.315}, \tag{3.1}$$

where W is the mean adult live weight of females in kilograms and r_m is the maximum instantaneous rate over a year (Caughley & Krebs 1983; Sinclair 1996). This relationship is similar to others documented in both invertebrates and other vertebrates (Blueweiss *et al.* 1978).

The relationship in equation (3.1) implies that smaller species should respond to environmental change faster than large species. Thus, smaller species should show a greater degree of population variability over time, and published data indicate that this is so. For example, populations of rodents fluctuate to a greater extent than do those of elephants (Sinclair 1996). The rate of change in
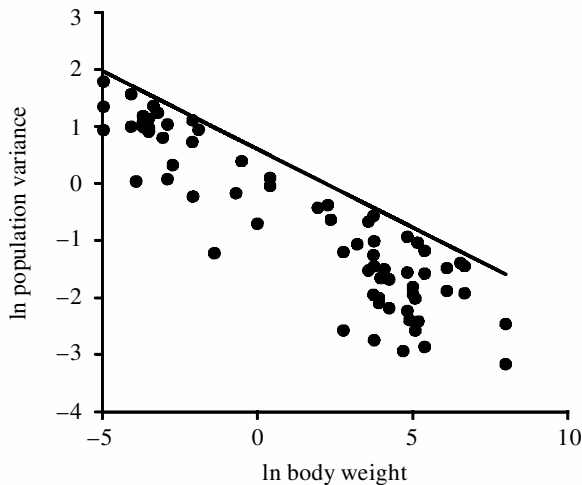
Figure 5. The negative relationship between natural log of population variance per year and natural log body weight (W) in kg of mammals. Data are from populations that were stationary over the time of the collected data. The slope of the envelope line is –0.27 as predicted by the metabolic relationships (from Sinclair 1997).

Figure 6. Natural log of population variability multiplied by generation time is independent of body weight in mammals (from Sinclair 1997).

population can be measured by the multiplication rate per unit time (λ). For analysis we need a symmetrical value for decrease as well as increase, and this is provided by the natural log of λ, the instantaneous rate of change between censuses adjusted to an interval of 1 year (r_t)

$$r_t = \frac{\ln \lambda}{t} = \frac{\ln(N_{n+t}/N_n)}{t}, \qquad (3.2)$$

where N_n and N_{n+t} are consecutive counts, and t is the interval in years between them. Over a period of time populations with little or no long-term trend will tend to fluctuate around a mean rate of increase of zero so that r_t is approximately zero. Variability can then be measured directly by the standard deviation, s.d. (r_t), using absolute values of r_t. Figure 5 shows the relationship between ln [s.d.(r_t)] and ln body weight (W) in kilograms. There is a clear negative relationship between population variability over a year and body weight. Transforming the log relationship of figure 5 we get

$$\text{s.d.}(r_t) = 0.805 W^{-0.316}. \qquad (3.3)$$

Short-term seasonal fluctuations in the environment are tracked through rapid reproduction by small species, resulting in high population variability over absolute time (in this case 1 year), and are buffered through high survivorship by large species, resulting in greater population stability (figure 5). However, species of different size have different generation times (T, the mean age in years of reproductive females), and T is also related to body weight (Miller & Zammuto 1983) by

$$T = 1.74 W^{0.27}. \qquad (3.4)$$

The exponents in equations (3.1), (3.3) and (3.4) have opposite sign because r_m and T are inversely related and so they tend to cancel each other out (Fowler 1988). Thus, both the intrinsic rate of increase and population variability weighted by generation time ($\ln[r_m]T$ and
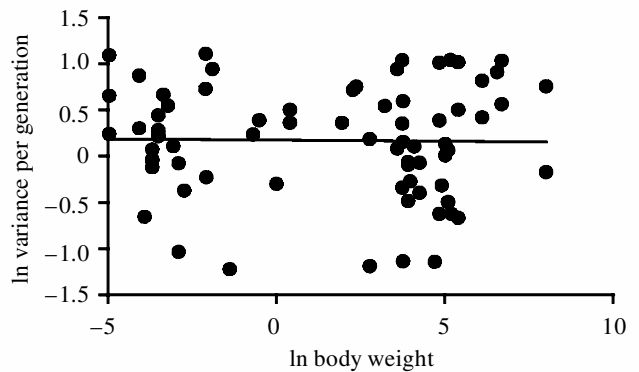
$\ln[\text{s.d.}(r_t)]T$) are independent of body weight (figure 6; Sinclair 1996, 1997).

This result is predicted by life-history theory. Species can adapt to perturbations in their environment either by improving reproduction (r species) or by improving survivorship (K species). However, species cannot do both simultaneously: there is a trade-off such that one parameter is improved only at the cost of the other. In general, small species adapt by increasing reproduction and so survivorship is low. By contrast, large species cannot increase reproduction but can improve survivorship through behavioural and physiological adaptations such as migration, dispersal and fat accumulation. These large species have developed a buffer against environmental changes. Both survivorship and reproduction are important adaptations and, whichever one a species emphasizes in responding to environmental variation, the optimal solution (which is the product of reproduction and survivorship) should be about the same across all species. This prediction is confirmed in figure 6, indicating that the degree of variability in a population is the same for all species, irrespective of size, relative to their generation time. Small species are not intrinsically more variable than larger ones.

In summary, variability in mammal population sizes can be accounted for largely by intrinsic biological properties of the species, in particular the rate of increase (r_m), generation time (T) and body size (W). These biological properties lead both to differential sensitivity and responsiveness to environmental stochasticity.

4. RULES FOR TOP-DOWN AND BOTTOM-UP REGULATION

In the absence of predators (or parasites) bottom-up processes must regulate all populations. Regulation through resources must be the basic rule, and it clearly applies to all top predators. What are the conditions, therefore, when bottom-up processes do not apply? In essence, there are four main conditions that predict when top-down regulation could occur.

(a) *Body size*

As with life-history constraints, body size determines the cause of regulation. Small prey species are vulnerable to predation whereas very large species, especially in mam-

mals, have outgrown all present day predators, and so are regulated by food supply. Thus, a suite of predators account for virtually all mortality of adult snowshoe hares in northern Canada (Boutin *et al.* 1995). By contrast, the wood bison (*B. bison athabascae*) population in the Mackenzie Bison Sanctuary of Canada appears to be regulated by food supply (resulting in emigration of excess animals), despite wolf predation of juveniles (Larter *et al.* 2000).

In Africa, we see a similar effect of body size on causes of regulation. Elephants, rhinos and hippos are too large for predators. Although predators kill a few newborn animals they have no effect on the population (Sinclair 1977). Even animals the size of African buffalo and giraffe are large enough that predators have difficulty killing them, predation accounts for a small proportion of adult mortality, and undernutrition is the predominant cause of mortality (Sinclair 1977, 1979).

(b) *High diversity systems*

In some systems there is a high diversity of large mammal herbivores and carnivores. Nearly all are associated with tropical savannah and grassland. Whether a herbivore species population is limited by predators is determined by its place in the hierarchy of herbivores. In African savannah there are as many as 10 coexisting canid or felid carnivores feeding on ungulates, lagomorphs and rodents. They vary in size from the 200 kg lion (*Panthera leo*) to the 10 kg wild cat (*Felis sylvestris*). The larger the carnivore the greater is its range of prey sizes (Sinclair 2003). Thus, the lions' diet ranges from buffalo (450 kg) to dikdik (*Madoqua kirkii*), a small antelope (10 kg), whereas that of caracal (*Felis caracal*) ranges from duiker (15 kg) to 100 g rodents (Avenant & Nel 1997). The consequence of this is that in the Serengeti system, for example, smaller ungulates have many more predators than larger ungulates. Thus, smaller ungulates must experience more predation and be predator regulated (if they are not migrants, see § 4c). Direct measures of mortality by predators are consistent with this prediction. Beyond a threshold body size of *ca.* 150 kg the proportion of annual adult mortality caused by predators declines as body size increases (Sinclair 1979; A. Sinclair, unpublished data).

(c) *Migration*

There is one adaptation, migration, which overcomes the constraints imposed by body size and biodiversity. Predators cannot follow migrating herbivores because they are confined to territories to raise and protect their young. This general rule is evident in all mammal migration systems such as the wildebeest and gazelles in Serengeti and Botswana, white-eared kob (*Kobus kob*) in Sudan, caribou (*Rangifer tarandus*) in northern Canada, and most probably the original plains bison of the North American prairies (Sinclair 1983; Fryxell & Sinclair 1988). It might also apply to the migration of marine mammals. Migrating species, therefore, escape from predator regulation even when they are relatively small, as in the gazelles. In addition, migration is an adaptation to access ephemeral, high-quality food resources not available to non-migrants. These two features of migration systems allow populations to become an order of magnitude greater in number compared to residents. Thus, migrant wildebeest in Serengeti occur at 64 animals km^{-2} compared to a sympatric resi-

dent population at 15 animals km^{-2} (A. Sinclair, unpublished data).

(d) *Low-diversity ecosystems*

In higher latitudes there are often predator–prey systems with only one major predator and one or a few mammal prey species. We see such systems in temperate woodlands and tundra, and even in mammals of tropical forest (though not in other groups). In these ecosystems we normally see bottom-up regulation of the prey. Nevertheless, there are a few cases of top-down regulation of prey. Wolves might regulate moose in some parts of Canada and Alaska (Gasaway *et al.* 1992; Messier & Joly 2000). However, on Isle Royale in Lake Superior, wolf numbers appeared to track moose numbers and did not regulate that population (Peterson & Vucetich 2001). Thus, we have evidence that regulation of herbivores by both predators and food can occur. It appears that idiosyncratic features of the ecosystem and the species involved determine the direction of regulation. For example, multiple states (see § 5 for a discussion) may occur where regulation can switch in the same system from resource limitation to predation or vice versa. Alternatively, regulation may be determined by the presence or absence of alternative prey for the predator (see § 5).

5. ECOSYSTEM CONSEQUENCES OF REGULATION BY PREDATORS

(a) *Primary and secondary prey*

Regulation of prey populations by predators occurs only under special circumstances of predator behaviour (their functional response) and population dynamics (the numerical response). The underlying theory and biology of these responses have been explained elsewhere (Holling 1959, 1965; Pech *et al.* 1995; Sinclair *et al.* 1998; Turchin 2003). Predators can regulate prey if such prey are the *primary* food source and there are few suitable alternative prey species. When the number of prey is low predation can be density dependent and prey populations can stabilize. In these cases predators cannot cause the extinction of the prey because their own numbers (and hence impact, see figure 3) decline as prey numbers decline. The caveat is that predation is not so overwhelming that it exceeds the r_m of the prey (Sinclair *et al.* 1998). In some cases the functional response of predators is determined by the ratio of predators to prey as well as to prey density. This 'ratio dependence' also affects when predators can regulate prey (Ginsburg & Akcakaya 1992; Abrams & Ginsburg 2000).

In practice, however, there are few good examples demonstrating direct regulation by predators, i.e. showing density-dependent predation and prey stability. Raptors regulate small mammals in Scandinavia (Erlinge *et al.* 1983, 1988). The rates of increase of some marsupial prey in Western Australia indicate density-dependent predation by red fox (*Vulpes vulpes*) when good forest habitat provides refuge for the prey (Sinclair *et al.* 1998). There are some examples of regulation with a time lag as mentioned in § 4c in discussing cycles: carnivores impose a 3 year delayed density-dependent mortality on snowshoe hares in northern Canada (figure 2; O'Donaghue *et al.* 2001). Ratio-dependent predation may also contribute to cycles in mammals (Akcakaya 1992).
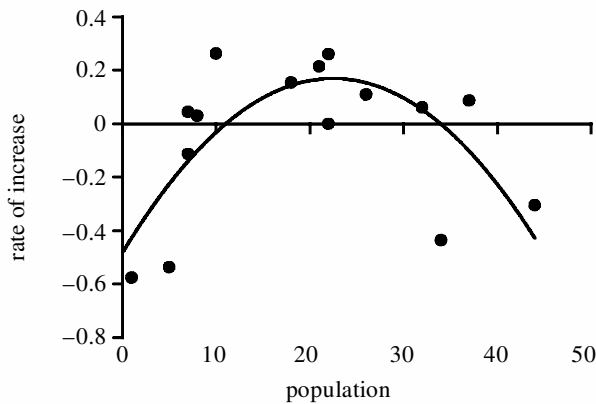
Figure 7. The rate of increase of black-footed wallabies experiencing predation by introduced red foxes in Western Australia. The negative rate of increase at low densities indicates that foxes can cause extinction of these wallabies because foxes depend on European rabbits as primary prey (data from Kinnear *et al.* 1998).

Predators may also have destabilizing effects on the prey through inverse density dependence. This is the more usual effect of predation, resulting from the type II functional response or weak numerical response. In the type II response, the *per capita* feeding rate of a predator increases curvilinearly to an asymptote as the prey density increases. This relationship results in a decreasing proportional mortality of the prey population as it increases. Such an inverse effect has been described for birds feeding on spruce budworm (*Choristoneura fumiferanna*; Crawford & Jennings 1989) and raptors killing snowshoe hares (Rohner *et al.* 2001), and one of the destabilizing consequences is the outbreak of prey numbers. Equally, this type of predation can cause the collapse of prey populations and extinction. Collapse occurs especially when prey are *secondary* species. Normally such species are incidental prey upon which predators do not depend. In this case predators can drive the prey to extinction without themselves declining in numbers (Pech *et al.* 1995; Sinclair *et al.* 1998; Sinclair & Krebs 2002). Foxes that depend upon European rabbits (*Oryctolagus cuniculus*) as their primary prey have driven some highly vulnerable Australian marsupials to extinction (Burbidge & McKenzie 1989; Kinnear *et al.* 1998; Serena 1994; Sinclair *et al.* 1998). For example, small populations of black-footed rock-wallaby (*Petrogale lateralis*) on rock outcrops in Western Australia declined to extinction once they dropped below some lower threshold number as a result of fox predation (figure 7).

(b) *Multiple states*

Operationally, *multiple states can be identified when an external perturbation changes a system from one state to another and the system does not return to the original state once the perturbation has ceased.* This definition excludes situations where different states occur under different environmental conditions (Holling 1973; May 1977). Predation is one process that can produce such multiple states.

Under special circumstances of type III functional responses, predators can theoretically hold prey populations at two levels under the same environmental conditions. In the type III response, the *per capita* feeding rate of a predator shows an S-shaped relationship to prey density with an initial accelerating phase followed by a decelerating phase (as for a type II response). In the accelerating phase, predation is density dependent and prey could be held at low density. Alternatively, in the decelerating phase predation is inversely density dependent, prey exist at high density and predators eat prey but do not regulate them. Prey can, therefore, jump from low to high density or collapse from high to low. Such sudden population changes in the presence of the predator provide circumstantial evidence for multiple states (Scheffer *et al.* 2001).

However, evidence for multiple states in nature is extremely sparse, even in the broader context of ecology. Forest insects may be regulated at low densities by warblers but can erupt to high densities where warblers do not regulate them (Ludwig *et al.* 1978; Crawford & Jennings 1989). The collapse of marine fish stocks from over fishing and their persistent low numbers once fishing has been removed is interpreted as evidence for multiple states. Piscivorous fishes are thought to be the predator (Myers *et al.* 1996). There are a few examples where mammals act as the predator. White-tailed deer (*Odocoileus virginianus*) maintain different plant communities by feeding on young trees. Two tree densities can be found depending on whether young trees can escape this herbivory or not (Augustine *et al.* 1998). Similarly, elephants in the Serengeti can maintain two different densities of *Acacia* trees. If mature trees have been destroyed through fire, elephants maintain a grassland state by feeding on and regulating juvenile trees. When elephants were removed by human hunting (in both the 1880s and 1980s), trees escaped herbivory and formed a mature savannah. After both removal periods the number of elephants increased, they fed on the mature trees but did not return the vegetation to a grassland (Sinclair & Krebs 2002). Examples of multiple states where mammals are prey are also rare. Outbreaks of house mice and European rabbits in Australia may be interpreted as changes from a predator-regulated to a food-regulated state (Sinclair *et al.* 1990; Pech *et al.* 1992). The collapse of the 'forty-mile' caribou herd of Yukon may be evidence of multiple states. Traditionally, this herd numbered in the hundreds of thousands. Hunters reduced the herd in the 1920s and 1930s and subsequently wolves have held numbers below 14 000 for the past 60 years (Urquhart & Farnell 1986). Similarly, high numbers of wildebeest in the Kruger National Park, South Africa were reduced by culling. When culling ceased wildebeest numbers continued to decline through lion predation (Smuts 1978).

6. LANDSCAPING CONSEQUENCES OF FOOD REGULATION

Regulation of herbivorous mammal populations through their food supply has profound consequences on the ecosystems where they occur. Mammals may not be numerous compared with other animal groups but their impact is considerable. Perhaps more than any other group they can determine the physical structure of the habitats, alter the rates of ecosystem processes such as nutrient flow, growth rate or decomposition, and dictate

species diversity (Sinclair 2003). These large-scale effects—at the level of landscapes, watersheds and biomes—can properly be described as *ecological landscaping*. Such impacts are far more extensive than those described as ecological engineering (Jones *et al.* 1997).

(a) *Vegetation structuring*

Plants determine the physical structure of habitats, the particular type being a function of the abiotic conditions—tundra at high latitudes, forest in wet low latitudes, savannah and desert in dry areas. Some periodic environmental effects, such as fire, hurricanes and sand storms can interrupt the normal succession of plant species towards a climax. In savannah, fire typically impedes the succession of trees to produce a 'fire disclimax' of grassland and fire tolerant herbs, shrubs and trees. Herbivorous mammals can have analogous effects to fire in savannah systems (Hobbs 1996) and so produce a 'mammal disclimax'. Plant succession is held in a different state as a result of the restructuring imposed by mammals. Such impacts are evident in most terrestrial biomes where mammals are abundant. However, mammals have their greatest impacts in the tropical savannahs, particularly through feeding by megaherbivores (Owen-Smith 1988); and grasslands throughout temperate and tropical regions owing to grazing and browsing by ungulates (Sinclair 2003).

By contrast, mammal herbivores have little structuring effect in the high latitude tundra biomes, but this is a recent event. During the Pleistocene, tundra supported a substantial biomass of mammoths, woolly rhinos and bison. Herbivorous mammals also do not substantially alter tropical forest, though mammals do influence the dispersal of tree seedlings (Janzen 1970). In both arctic tundra and tropical forest the low impact of herbivores may be the result of the top-down effects of mammal carnivores limiting herbivore densities in these systems (Terborgh 1988; Oksanen 1990).

(b) *Ecosystem rates*

Mammals influence the rates of nutrient cycling in addition to altering physical structure. High densities of mammals can influence the soil processes through their deposition of faeces and urine. The Serengeti plains have very high nutrient turnover rates owing to the large herds of ungulates in the wet season and the plethora of dungbeetle species that act to bury the dung. This leads to high protein and mineral content of the grasses eaten by the grazing herds. In essence, ungulates fertilize their own food and so create a positive feedback, increasing their own density (Botkin *et al.* 1981; McNaughton *et al.* 1997).

In boreal forests moose decrease nitrogen mineralization of the soil by decreasing the return of high-quality litter: their browsing on deciduous trees reduces their leaf fall while promoting low-quality white spruce inputs (Pastor *et al.* 1993). By contrast, soil nitrogen cycling in Yellowstone and other prairie areas of USA is increased by large mammal grazers (Hobbs 1996; Frank & Evans 1997).

(c) *Plant species composition*

Herbivory by mammals not only alters structure but also the type of plants that can withstand such impacts.

On the North American prairies, rodents such as black-tailed prairie dogs (*Cynomys ludovicianus*) live in large colonies. These species graze grasses to a low level (a few centimetres) around their colonies. Grazing changes the grass species composition to low growing forms, and many dicotyledonous species survive owing to reduced competition from grass. American plains bison preferentially graze these short grasses and pronghorn antelope (*Antilocapra americana*) feed on the dicotyledons (Huntly & Inouye 1988; Miller *et al.* 1994).

Rabbits (*Oryctolagus cuniculus*) maintain short grasslands with many dicotyledons on the South Downs of Sussex, UK. When the epizootic myxomatosis removed rabbits in 1953, plant species composition changed to one of tall tussock grasses with few dicotyledons, and there were subsequent changes in ants and lizards dependent on these plant forms (Ross 1982).

7. MAMMALS AS KEYSTONE SPECIES

Although mammals can have major landscape structuring effects and sometimes regulate prey populations, these impacts are unevenly distributed between species. Some carnivores and herbivores, particularly among large mammals, have major top-down effects, whereas others have little impact. This uneven distribution of top-down influences is at the heart of the concept of 'keystone species'. By definition *a keystone species has a disproportionately greater impact on other species than that predicted by their abundance* (Paine 1969; Bond 1993; Power *et al.* 1996). Top predators are often presented as keystone species: for example, the presence or absence of sea otters (*Enhyra lutris*) as top predators of inshore marine communities determines the abundance and species composition of other members (Estes & Duggins 1995).

However, there are two major problems with the keystone concept (Mills *et al.* 1993; Power *et al.* 1996). First, there are operational problems with identifying keystone species. What parameters should be measured—abundance, biomass, species composition or something else? What degree of change in the community defines a keystone species? Second, communities are open ended and it is unclear how far into the foodweb we should trace the impacts. Should the impacts of top predators be traced only as far as the herbivores and plants, or through other indirect links to more distant herbivores, detritivores, protozoans, even microbes? There is no natural limit.

These problems have led some to abandon the concept (Hurlbert 1997). Nevertheless, it is generally agreed that some species define the community composition, and removal of these can produce changes in state, whereas the loss of other species has little effect on the rest of the community. Thus, for both conceptual and applied (conservation) reasons, we need to find a way of operationally identifying keystones. Some approaches to detect keystones have used Markov chain models (Wootton 2001) or the fraction of secondary extinctions following species removals (Sole & Montoya 2001).

I suggest that a *keystone effect* (e_i) can be defined as the amount of change for one particular parameter in a community (D_2) resulting from the loss of species i measured relative to an intact community (D_1), so that

$$e_i = \frac{|\,[\ln(D_2/D_1)/t]\,|}{N_i}, \tag{7.1}$$

where e_i is measured as the absolute value, t is the time interval (years) to standardize for different periods of impact and N_i is the density of the lost species i. Equation (7.1) highlights the point that a keystone species can only be detected by removal experiments and their impacts measured relative to those of other species that are removed in the same community.

The extent of a keystone's impact through the foodweb can be arbitrarily defined *a priori*. To compare the effect of a potential keystone with that of some other species we need to measure the impact over the same range of guilds, but this range is determined by practical considerations. The total effect (E_i) over several guilds is the sum of the e_i values for each guild. For example, in the Serengeti ecosystem we can estimate the impact of changes in two large mammal herbivores on various guilds within the community. The two species are wildebeest and African buffalo. The number of wildebeest was reduced through the exotic disease rinderpest during the period 1890–1963 (Sinclair 1977; Dobson 1995). When the disease itself disappeared in 1963 wildebeest numbers increased fivefold. This species grazes the eastern treeless plains of the Serengeti during the wet season and they maintain today a short grass–herb plant community (McNaughton & Sabuni 1988; Augustine & McNaughton 1998). However, when wildebeest numbers were low (before 1963) the eastern plains comprised a very different long grass plant community that still exists in parts of the western plains today. At the same time two major predators, lion and spotted hyena, have increased as the number of wildebeest has gone up, and I use data for lion here (Scheel & Packer 1995). Thus, we can compare the long grass and short grass communities as an index for the direct effect impact of wildebeest on lion and dicotyledonous herb guilds. In addition, I have used bird diversity and density as two indirect effects. For illustration I include other indirect effects on butterfly and grasshopper species (table 1).

There are many more dicotyledonous herbs on the grazed plains relative to the ungrazed plains, and these herbs support a much higher density of butterflies. By contrast, grasshoppers are direct competitors with wildebeest, and both grasshopper species and abundance decline in the presence of wildebeest. This decline was observed during the period when wildebeest were increasing: before 1963 the number of grasshopper species was probably similar to that now found in the long grass areas today (49 species). In 1972 I collected 13 species near Gol Kopjes in the eastern plains, and by 1986 only one species was found there (A. Harvey, unpublished data). The community of small insectivorous and granivorous birds also changed with grazing intensity, largely owing to changes in the physical structure of the grass sward (A. Sinclair, unpublished data).

Buffalo were also severely depleted in number by rinderpest prior to 1964. Subsequently they increased fivefold and by 1976 they were the dominant resident large mammal herbivore in northern Serengeti. Between 1977 and 1984 large scale poaching effectively eradicated the buffalo in this area and the species has remained at very low numbers since (Sinclair 1977; Dublin *et al.* 1990; S.

Mduma, unpublished data). Despite these marked changes in biomass there were no detectable changes in lion population, grass plant community or in bird species composition (other guilds were not recorded). However, buffalo may have had some effect on the dynamics of the riverine forest trees. In the dry season buffalo depend upon, and graze down, the forest interior rank grass, *Setaria sphecelata*. In the absence of buffalo this grass has overgrown and killed small seedlings of forest trees. Thus, buffalo were probably directly reducing the grass biomass in forests and indirectly raising the recruitment rate of forest canopy trees.

Table 1 shows that the direct population effect from wildebeest removal is some 15 times that of the direct effect from buffalo removal. The *per capita* direct effect of wildebeest is twice that of buffalo. Indirect effects from buffalo removal were not detected but I have included them to illustrate how they can be analysed. In summary, for guilds measured during the perturbation of both species the combined population effect of wildebeest is some 20-fold that of buffalo while the *per capita* effect of wildebeest is about three times that of buffalo. Wildebeest have an extensive indirect effect on the ecosystem, but because the same measures were not available on grasshoppers, butterflies, etc. from buffalo removal, comparisons could not be made. I would predict that when similar measures are obtained from the removal of other ungulates we would see that the effects of wildebeest are uniquely greater than those of other ungulates—and this result would be the essential criterion to identify a keystone species. This example serves to illustrate in principle how keystone effects can be measured.

8. REGULATION AND THE CONSERVATION OF LARGE MAMMALS

(a) *The extinction of the mammoths*

The special characteristics of large mammals, particularly their slow rate of increase, their curvilinear density dependence that is weak at low numbers, and their structuring effects on landscapes, make them especially prone to factors causing decline and extinction. Declining populations, particularly small ones, are cause for the greatest concern in conservation (Caughley 1994). In many cases we are unable to establish the reasons for the decline; mortality is often not observed, predation is secretive and degraded habitat has insidious, subtle effects. We can, however, advance our understanding of the process of decline by first analysing the demographic rates of the population using a simplified stage-structured population projection matrix (Caswell 1989). In essence, all conservation problems are concerned with four components of a population: the instantaneous rate of increase; the *per capita* reproductive rate; the *per capita* juvenile survival; and the *per capita* adult survival.

By illustration we can apply this approach to the extinction of megaherbivores in the late Pleistocene. Owen-Smith (1988) believed that human hunting was the cause of their demise because in all continents other than Africa these mammals had no appropriate defensive behaviour against group hunting by humans. By contrast, others believe humans could not have killed every last one of them, and have postulated either unrelated habitat change

Table 1. Keystone effects.

(Changes in the parameters of different guilds in the Serengeti community resulting from the removal of two ungulate species (A. Sinclair, unpublished data). *Per capita* effects for each parameter are given by e_i. Total *per capita* effects (E_i) for several parameters combine both diect (a) and indirect (b) impacts and can be compared between the two removed species. Changes owing to wildebeest are much greater than those caused by buffalo indicating the former might be a keystone species.)

guild parameter	species absent (D_2)	species present (D_1)	K_i (km^2)	t	population effect $|\ln(D_1/D_2)/t|$	*per capita* effect (e_i)
wildebeest						
(a) direct effects						
grass biomass (kg ha^{-1})	1750	3600	63.93	20	0.036 07	0.000 564
dicotyledonous herb (species number m^{-2})	6	15.3	63.93	20	0.046 80	0.000 732
lion density (km^{-2})	0.048	0.1375	63.93	20	0.052 62	0.000 823
(b) indirect effects						
bird species number	37	25	63.93	20	0.019 60	0.000 307
bird density (km^{-2})	90	160	63.93	20	0.028 77	0.000 450
(c) other indirect effects						
butterfly density (n ha^{-1})	500	6100	63.93	20	0.125 07	0.001 956
grasshopper number	47	13	63.93	20	0.064 26	0.001 005
grasshopper density (n m^{-2})	1.2	0.572 055	63.93	20	0.037 04	0.000 579
total direct effects (a)					0.135 49	0.002 119
total indirect effects (b)					0.048 37	0.000 757
total both effects (E_i)					**0.183 86**	**0.002 876**
African buffalo						
(a) direct effects						
grass biomass (kg ha^{-1})	3600	3000	10	20	0.009 12	0.000 912
dicotyledonous herb (species number m^{-2})	9	9	10	20	0.000 00	0.000 000
lion density (km^{-2})	0.02	0.02	10	20	0.000 00	0.000 000
(b) indirect effects						
bird species number	148	148	10	20	0.000 00	0.000 000
bird density (km^{-2})	67.85	67.85	10	20	0.000 00	0.000 000
total direct effects (a)					0.009 12	0.000 912
total indirect effects (b)					0.000 00	0.000 000
total both effects (E_i)					**0.009 12**	**0.000 912**

owing to climate warming, or that an epizootic disease finished them off once they had dropped to low enough numbers (MacPhee & Marx 1997).

Matrix analysis indicates that hunters did not have to kill all of these megaherbivores, or even any of the adults. From demographic data on elephants, maximum birth rates per female are one baby every 4 years, or 0.125 per adult per year. Protected stationary populations have an adult survival of 99% per year (A. Sinclair, unpublished data). Matrix analysis shows that hunters need only kill 90% of juveniles in their first 3 years of life to create a 1% rate of decline per year. As we know hunters did kill some adults (Owen-Smith 1988), and birth rates are likely to be lower than elephants owing to much lower productivity in ice-age tundra and forest, the proportion of juveniles hunted could be much lower: juvenile mortality need only be 30% with a 2% adult mortality from hunting for extinction to occur.

In summary, no extraordinary additional mortalities are required to explain the disappearance of the megaherbivores through human hunting. A modest hunting mortality of juveniles is all that is needed because there is effectively no density-dependent compensation at low numbers in these large beasts. Understanding of regulation provides insight into the mode of extinction processes.

9. CONCLUSION

In this paper I identify some important features of population regulation as they apply to mammals and examine how body size modifies this regulation. In turn, the type of regulation determines the dynamics of the ecosystem. First, the particular curvilinear characteristics of regulation relative to population size have consequences for the stability of populations and vulnerability to extinction:

large species may be more stable at high densities but are more vulnerable to extinction at low densities. Second, population fluctuations can be caused by both extrinsic features of the environment as well as characteristics to do with body size. However, all species show approximately the same degree of population variability per generation, as predicted by life-history theory.

Third, populations can be regulated by either resource limitation (bottom-up) or by predators (top-down). Resource regulation occurs under four conditions as follows:

(i) when body size is large enough to avoid predators;
(ii) when in high-diversity communities with a range of predator and prey sizes (savannah, grassland), only the largest species can avoid predation and they simultaneously subsidize predators that regulate smaller prey species;
(iii) when populations adopt large scale migration behaviour because predators are unable to follow them; and
(iv) when in low-diversity systems with a single predator and one or a few prey (tundra, desert, boreal and temperate forests) the presence or absence of secondary (alternative) prey determines whether or not predators regulate prey.

Fourth, the large size of mammals results in major landscaping effects in ecosystems. Their role is to modify vegetation structure, alter pathways of nutrients and thereby change species' composition. These effects make large mammals, in particular, functionally important as 'keystone species'. Mammals act as keystones when they have a top-down regulating effect and so are themselves regulated by food. The keystone role maintains species diversity not just through direct effects on vegetation and predators, but also through indirect effects along the food chain. As a consequence, mammals are prime candidates as 'umbrella species' for conservation—protection of these species and their habitats also supports a large part of the remaining community. It also means that such mammals become the 'indicator species' for the health of the ecosystem. Knowledge of how mammals are regulated and their impacts on ecosystems is required to manage such systems and conserve endangered species.

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