

Are big mammals simply little mammals writ large?

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Summary. Populations are regulated intrinsically (self-regulated) when the animals lower their rate of increase behaviorally or physiologically as a reaction to rising density. They are regulated extrinsically if the equilibrium is a mechanical consequence of interaction between the population and the organisms providing its food. We suggest that, at least for mammalian herbivores, self-regulation is unlikely to evolve unless the population's intrinsic rate of increase exceeds about 0.45 on a yearly basis. That value corresponds to a body weight of about 30 kg, the intrinsic rate being related inversely to body weight by $r_m = 1.5 W^{-0.36}$ with W in kg.

The two dynamic strategies, self-regulation and extrinsic regulation, should enforce a bimodality of the frequency distribution of observed intrinsic rates of increase. This in turn might be reflected in a bimodality of body sizes, the smaller herbivores constituting the lower mode generally showing intrinsic regulation and the larger herbivores of the upper mode generally being regulated by extrinsic mechanisms. There is some empirical support for these predictions but it is by no means clearcut.

Mechanisms of self-regulation can evolve either by individual or group selection. Individual selection may act in two ways. By inhibiting their neighbours with some form of interference, individuals may increase their relative fitness without increasing their reproductive rate. Alternatively, individual selection may raise the absolute fitness of individuals and thereby raise the population's intrinsic rate of increase. The population is destabilized if that process continues beyond a certain threshold and the population is then at significant risk of extinction at the troughs of the consequent oscillations. Selection between such populations will favour those carrying the beginnings of a self-regulating mechanism, and with that mechanism strengthened and fixed by continuing group selection, individual selection is again freed of the dynamic restraints on raising further the intrinsic rate of increase.

Introduction

Populations do not increase without limit. Mechanisms proposed to explain this truism can be arranged under two broad heads: *extrinsic* regulation on one hand and *intrinsic*

regulation (or self-regulation) on the other. The equilibrium of the first is a consequence of interaction between a population and its resources, predators or diseases. The second kind of equilibrium is the consequence of a mechanism built into the population and transmitted by its genes.

Most advocates of one or other of these modes have, in their stretch for generality, assumed that the kind of population regulation that seems appropriate to the animals they study is likely also to characterise those species with which they are unfamiliar. We will argue, in contrast, that there are two kinds of populations, one for which self-regulation is a necessity, the other for which self-regulation would provide no selective advantage and therefore would not evolve.

Extrinsic regulation. If a population has no intrinsic regulating mechanism it may be expected to increase until a resource is utilised fully or weather, predators and diseases intervene to reduce density. That resource may be inert (e.g. the nesting sites of penguins) or growing (e.g. grass eaten by buffalo). Either way there comes a point at which the resource is saturated as in the first case, or utilised at its rate of renewal as in the second. Both lead towards an equilibrium, the dynamic adjustment being simple in the first case because only the animal population adjusts, or complex in the second because both the population and the resource hunt for a mutual accommodation. Since the level of resources is influenced by factors other than utilisation by the animals, and since the density of the animals is itself influenced by year-to-year variation in weather, the equilibrium has little reality beyond that of a mathematical concept. The biological reality lies not in a unique equilibrium point but in the dynamics of the system comprising the animals and their resources being centripetal.

Nicholson (1933), Lack (1954) and Andrewartha and Birch (1954) were the main proponents of extrinsic regulation, the last pair favouring an additional control enforced by the shortage of time over which the environment allows rate of increase to remain positive.

Intrinsic regulation (=self-regulation). This category embraces a plethora of postulated mechanisms with a common denominator: regulation is achieved more by things the animals do than by direct interaction of the animals with one or more resources or predators. Rate of increase is held to a mean of zero before extrinsic regulating mechanisms can come fully into play because the animals' physiology

is upset by crowding, with (Chitty 1967) or without (Christian 1971) concomitant genetic changes, or the animals limit their rate of increase by dispersal (Krebs et al. 1973, Lidicker 1975, Gaines and McClenaghan 1980) or by a complex of behavioral conventions (Wynne-Edwards 1962).

Intrinsic regulation is not an alternative to extrinsic regulation but an addition to it that comes into play at population levels below which extrinsic mechanisms would otherwise wind rate of increase down to zero. The system thus has two modes of regulation which may interact. Environmental conditions may determine the density at which intrinsic regulation operates or hold the population below the level at which intrinsic mechanisms manifest.

Regulation in mammals

Ecologists that work on mammals may be classified informally into those that work on little mammals and those that work on big mammals. Alternatively they can be categorised according to whether they consider the populations on which they work are regulated intrinsically or extrinsically. Combining those classifications gives four categories: little-extrinsic, little-intrinsic, big-extrinsic and big-intrinsic. These categories are occupied unevenly: the middle two, little-intrinsic and big-extrinsic, delimit the positions of the overwhelming majority of ecologists who work on mammals. The other two positions are occupied so sparsely that we had to think hard to identify even a few occupants. The phenomenon is clear-cut notwithstanding the rare exceptions. Ecologists that work on mammals form two groups. At one pole are those working on mammals weighing less than about 30 kg and who are excited about self-regulation. At the other are those working on heavier mammals and who see little necessity to look beyond extrinsic regulation as a model explaining the dynamics of the populations they choose to study.

The two authors of this paper exemplify that dichotomy. One of us, working principally on small herbivorous mammals, has published a good deal of evidence that the dynamics of these are inexplicable without self-regulation (Krebs 1964, 1978, 1979). This judgment is reinforced by that of other small mammal workers such as Christian (1971, 1978), Chitty (1960, 1967), Bujalska (1973), Armitage (1975), Madison (1980), Tamarin (1980), and Terman (1980).

The other author also works mainly on herbivorous mammals but seldom has much to do with animals weighing less than 40 kg. He has never found it necessary to invoke the hypothesis of self-regulation to explain the dynamics of the animals he has worked on, but instead has been impressed by the evidence favouring extrinsic regulation (Caughley 1970, 1976a, 1976b, 1979). The most recent detailed studies on large mammals (Sinclair 1977, on African buffalo; McCullough 1979, on white-tailed deer) tread the same path. Fowler et al. (1980) reviewed most of the ecological studies of large mammals and concluded that "resources, either directly or indirectly, seem to be at the base of most or all density dependent relationships observed..." Peck (1980) suggested that "general agreement prevails that ungulate populations are externally controlled by changing environmental conditions rather than through intrinsic regulating mechanisms".

Three possible explanations suggest themselves for the dichotomy in perceived modes of regulation. It may reflect

simply a difference of ethos between the two groups of ecologists. Small-mammal ecologists and large-mammal ecologists do not talk to each other very often, and a glance at the literature cited in a dozen papers from each of the two fields demonstrates clearly that they seldom read each other's papers or that they consider them irrelevant to their own work. Perhaps one group has found the truth, the other is in error, and the truth has not yet permeated through the barrier of mutual indifference.

Secondly, the dichotomy might reflect a difference in methodology. Small mammals are more amenable to experimental manipulation and the experiments on them are often designed with care. Most work on large mammals is descriptive, and even when experimental manipulation is attempted the controls are frequently inappropriate (Romesburg 1981). Most workers on large mammals still believe that 'before' is a control on 'after'. Hence one might argue that large mammal research exhibits approximately the same level of rigor today as did small mammal work in the 1930s when all small mammal workers thought that extrinsic factors controlled numbers.

The third possibility is that large mammals and small mammals really do have different ecologies and that both groups of ecologists are right about their animals. We are attracted to this explanation. We think there may be a break-point in the interval 25–35 kg body weight below which regulation tends to be intrinsic and above which it tends to be extrinsic. More important, we think we know why.

Theory

The theory of interaction between populations in two adjacent trophic levels has made numerous advances over the last few years, thanks particularly to the efforts of Rosenzweig and MacArthur (1963), May (1975, 1977), Tanner (1975), Gilpin (1972, 1975) and Noy-Meir (1975, 1978). Some authors envisage the interaction as between prey and predator, others as between host and parasite, and still others as between plant and herbivore. We will consider the last specifically but recognise that our arguments may generalise loosely to the higher levels.

The growth of a population of ungrazed plants may be modelled by the logistic equation

$$dV/dt = rV(1 - V/K) \quad (1)$$

implying that the population grows initially at an exponential rate r (the intrinsic rate of increase) but that the rate is slowed progressively by root competition and by a continuing reduction in photosynthetic rate as some leaves shade other leaves. When the population reaches a density of K units of biomass its rate of increase reaches zero. This model of plant growth has moderate empirical backing (Noy-Meir 1975; Harper 1977).

With the introduction of a herbivore Eq. (1) must be extended to account for the plant material removed by grazing. One possibility is the functional response term introduced by Holling (1965):

$$y = c_1 [V/(V + D_1)] \quad (2)$$

where y is the rate of intake of a single herbivore at a density V of vegetation. Here c_1 is the maximum rate of intake when the herbivore has more food available to it than it can eat. D_1 is inversely proportional to a herbivore's

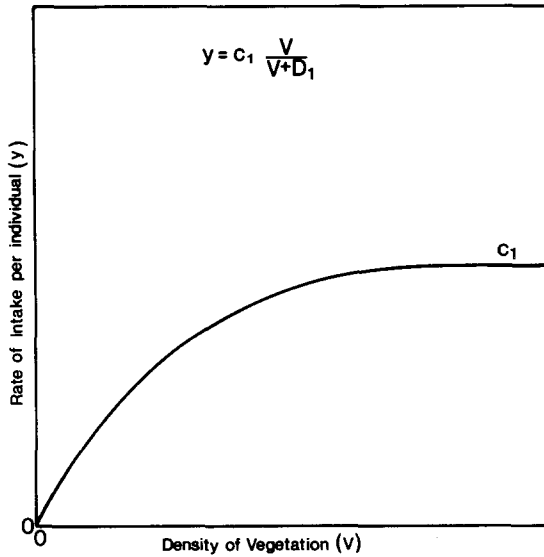


Fig. 1. The functional response used in this paper: rate of intake per head (y) against biomass of edible plants

grazing efficiency, being the biomass of edible vegetation at which the herbivore's rate of intake is half its satiating diet. The lower is D_1 the higher is the herbivore's rate of intake when plants are sparse. In a prey-predator model D_1 is proportional to the time a predator takes to find a prey at a given level of prey density. In a plant-herbivore system, where eating time and digesting time are important constraints, and where the food items vary greatly in nutritional value, the interpretation of D_1 is necessarily less precise. Figure 1 indicates the kind of functional response generated by Eq. (2).

Rate of increase of grazed plants can be modelled by combining Eq. (1) and (2):

$$dV/dt = rV(1 - V/K) - c_1 H [V/(V + D_1)] \quad (3)$$

where H is the number of herbivores eating the plants. Setting $dV/dt = 0$ and solving for H yields

$$H = (r/c_1) (1 - V/K) (V + D_1) \quad (4)$$

which gives the equilibrium level of plant biomass, if an equilibrium is possible, for any level at which H is held constant. It is called the zero-isocline of plants or alternatively the vegetation's critical line. Figure 2 shows such a curve. By Eq. (4) it is necessarily a parabola truncated at $V=0$ and peaking at $V = (K - D_1)/2$.

Tanner's models. Tanner (1975) constructed two basic models of a prey-predator system by combining Eq. (3), representing the growth of the prey population, with two alternative equations for growth of the predator population. His Model A bestows self-regulation on the predators in that the population's growth rate per head is a function of both prey density and predator density. Growth rate per head of predator in his Model B was a function only of prey density, any tendency towards regulation being thereby extrinsic. By replacing prey with plants and predators with herbivores, and translating his notation to ours, we obtain the growth rate of herbivores by Model A as

$$dH/dt = sH(1 - HJ/V) \quad (5)$$

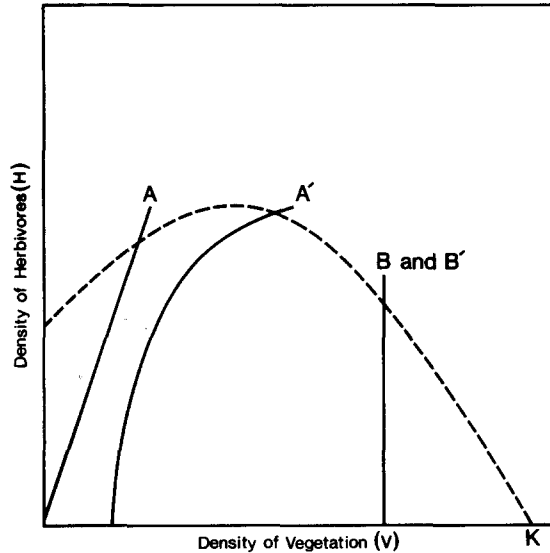


Fig. 2. The critical line of plants common to all models and the form of the critical line of animals in Models A, A', B and B'

where s is the herbivore's intrinsic rate of increase and J is the biomass density of plants sufficient to support one herbivore when the system is at equilibrium. The herbivore's critical line, defining the equilibrium to which herbivore numbers would converge if plant biomass were held constant, is solved as $H = V/J$, a line sloping out from the origin as in Fig. 2.

The stability properties of the model here presented as Eq. (3) and (5) have been explored by May (1975) and Tanner (1975). If the herbivore's critical line cuts that of the plants to the right of the hump in their critical line, the equilibrium between plants and herbivores is stable. If the critical lines intersect to the left of the hump (as in Model A, Fig. 2) the equilibrium is stable only when r (the intrinsic rate of increase of the plants) is less than s (the intrinsic rate of increase of the herbivores). Otherwise a limit cycle is generated around the intersection of the two critical lines.

Tanner's (1975) Model B links Eq. (3) for plant growth with one for the growth of a herbivore lacking a self-regulating mechanism. The details of its construction do not concern us because its outcome is consistent with that of a whole family of models in which the lack of self-regulation of the herbivore is proclaimed by the verticality of its critical line (Model B, Fig. 2). We note however that the architecture of Tanner's Model B differs in style from that of Model A.

The stability properties of Models A and B have features in common and also important differences. For both, an equilibrium is stable if the critical lines intercept to the right of the hump, and that outcome is independent of the r/s ratio. No point equilibrium is possible when the critical lines of the Model B cross to the left of the hump, that outcome again being independent of the r/s ratio.

Tanner (1975) argued from these findings that a system comprising eaters and eaten will be stable only when the eaten are strongly self-regulated (i.e. K is small and therefore the hump in the zero-isocline of the eaten is positioned well to the left), or when the intrinsic rate of increase of the eaters is greater than that of the eaten (i.e. $r/s < 1$). He provided an analysis of the demography of several prey

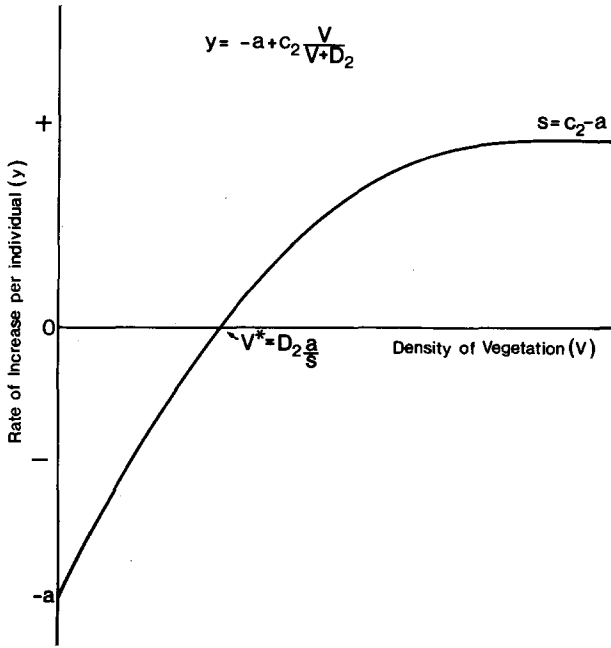


Fig. 3. Numerical response of Model A': rate of increase of the animals against biomass of edible plants

predator pairs to show that these predictions were generally confirmed by nature.

An alternative model. We were uneasy about comparing the effects of intrinsic and extrinsic regulation simply by contrasting the behaviors of Tanner's two models. They differ too much in other respects to provide a clean comparison. Consequently we devised an alternative pair that differed only in that one contained a term for self-regulation, the other being capable only of extrinsic regulation. We adopted Tanner's equation for the growth of the eaten, given here as Eq. (3), and substituted for the growth of the eaters the equation

$$dH/dt = H[-a + c_2 V / (V + D_2) - bH] \quad (6)$$

in which b is an explicit constant for the strength of the eaters' self-regulation. Setting $b = 0$ dismisses self-regulation and converts the model into one where any tendency towards an equilibrium must necessarily be blamed on extrinsic mechanisms. Of the other constants, a is the rate at which the eaters decline when they run out of food, c_2 is the maximum rate at which this decline is alleviated when food is abundant (hence $c_2 - a = s =$ intrinsic rate of increase of the eaters), and the term $V / (V + D_2)$ erodes this maximum rate as V (the food) declines. Figure 3 diagrams that numerical response.

Our models are cross-referenced with Tanner's by labeling as Model A' our version in which the eaters are self-regulated (Eq. 3 and 6, the second with $b > 0$) and the version in which they are not as Model B' (Eq. 3 and 6, the second with $b = 0$). The critical line of the eaten common to all models (A and A', B and B') is that given in Eq. (4). The critical line of the eaters in Model A' is

$$V = D_2(a + bH) / (s - bH) \quad (7)$$

and in Model B' simply

$$V = D_2 a / s \quad (8)$$

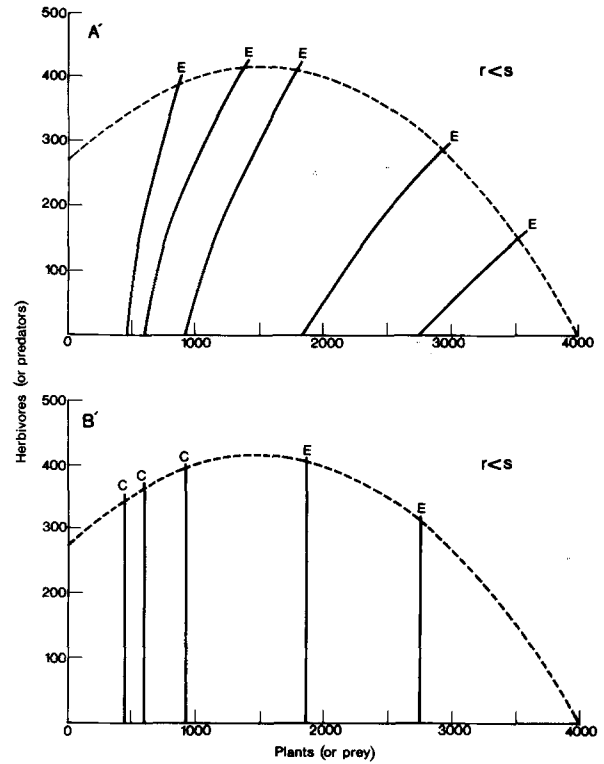


Fig. 4. Critical line of plants and of herbivores in Model A' (top) in which the herbivore is self-regulated, and for Model B' (bottom) in which it is not. Each intersection is labelled according to whether the outcome is an equilibrium (E) or cycles (C). In all examples the intrinsic rate of increase of the herbivore is greater than that of the plants

Both critical lines leave the x -axis at $V = D_2 a / s$, that of Eq. (7) curving up to the right (Fig. 4A) and that for Eq. (8) being upright (Fig. 4B).

Lacking the mathematical expertise to deduce the stability properties of these two models by analysis, we investigated them by electronic brute force guided by a Runge-Kutta algorithm. After enough runs to convince us that our conclusions were independent of the values of our fake data we deduced that the stability properties of our model lacking self-regulation (Model B') were the same as Tanner's analogous Model B. An intersection of critical lines to the right of the hump led to a stable point equilibrium. An intersection to the left produced limit cycles (Figs. 4B and 5B). The r/s ratio had no bearing on that result.

In contrast, the two models ascribing self-regulation to the eaters (Tanner's Model A, our Model A') produced incongruent outcomes. Remember that when the critical lines intersected left of the hump, Model A was stable only when $r < s$. An intersection to the right provided stability irrespective of the r/s ratio. Our analogous Model A' conformed with Model A for intersections right of the hump, but not for those to the left. By Model A', an intersection left may presage stability if self-regulation is strong enough (b is high) or limit cycles if self-regulation is weak (b is low); but those outcomes were not dependent on the r/s ratio (see Figs. 4A and 5A).

Conclusions from the models. By our Model B' a population of herbivores without intrinsic regulation will reach a stable

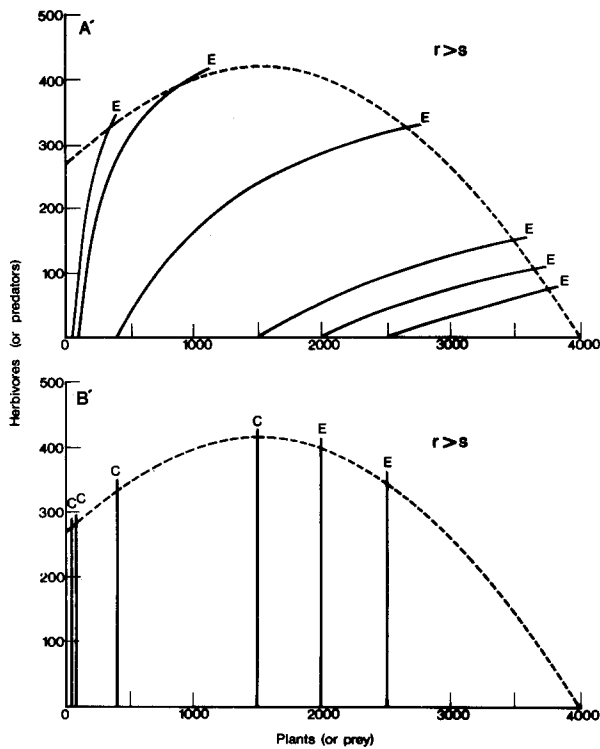


Fig. 5. Caption as for Fig. 4 but intrinsic rate of increase of the herbivore is less than that of the plants

point equilibrium only when

$$D_2 a/s > (K - D_1)/2. \quad (9)$$

Hence the stability of the plant-herbivore system of Model B' is maximised when the plants compete vigorously amongst themselves for resources (K is low), and when the herbivore is an inefficient grazer (D_1 is high) and an accident-prone (a is high), indifferent parent (D_2 is high, s is low). The most stable plant-herbivore system is thus one in which the plants give each other a bad time but are troubled little by a bumbling herbivore that has somehow escaped the discipline of natural selection. Such a prototype system is described by Milne (1928). Of those numerous parameters we select s (the intrinsic rate of increase of the herbivore) as perhaps the most representative, and suggest that selection to increase s will lead to instability unless the herbivores regulate themselves.

Tanner (1975) used the outcome of his Model A to argue that a population with an intrinsic regulating mechanism must, to be stable, have an intrinsic rate of increase higher than that of the organisms it eats if the two critical lines intercept to the left of the hump. The contrary outcome of our Model A' indicates that his conclusion reflects not generality but the details of his model. Nonetheless, there is a generalisation that embraces Models A, A', B and B': if s is high the system is unlikely to be stable unless the eaters have evolved a self-regulatory mechanism. That prediction is made also by every other model that we know of in this general area. For example, the most contracted of them, the logistic, is adamant that the higher is the intrinsic rate of increase the greater must be the force of competition or self-regulation (i.e. the lower must be K) to enforce stability (May 1974). We suspect that the generalisation is robust.

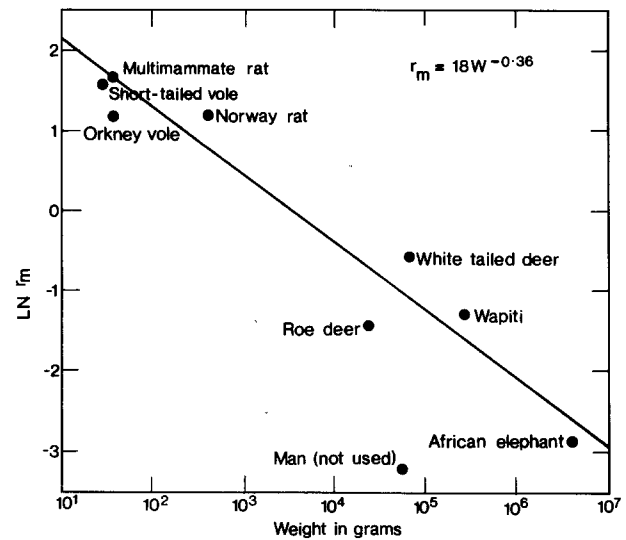


Fig. 6. Regression of intrinsic rate of increase against body weight

Although we have questioned Tanner's conclusion that the r/s ratio is an important determinant of point stability, on the grounds that it is special to his model, we cannot reject it solely on these grounds because his model may turn out ultimately to be right. Tanner himself thought it was probably a reasonable approximation because its prediction that stability results from $r/s < 1$, or from K being small, was confirmed by the observed dynamics of eight prey-predator pairs. We have reinvestigated these and conclude that his data are not adequate to determine the r/s ratios with sufficient precision and that independent data suggest that some of his r/s ratios reported as less than 1 are either greater than 1 or very close to 1 (see Appendix I). Thus there is little empirical support for his r/s hypothesis.

Big versus little

Initially we categorised alternative regulatory strategies in terms of the size of the animal, but theory suggests that the intrinsic rate of increase is the determining variable, or more specifically the a/s ratio with modifying inputs from D_1 , D_2 , b and K . Size as such is obviously only an index of those parameters and we choose s to examine the nature of that correlation. The literature provides a trend for generation length against body length (Bonner 1965), for intrinsic rate of increase against generation length (Smith 1954, Heron 1972) and for intrinsic rate of increase against body weight (Fenchel 1974). We have constructed a relationship between intrinsic rate of increase and body weight for herbivorous mammals only (Fig. 6), using the rates from Table 9.2 of Caughley (1977), references to the sources of the data being in that table. Weights were calculated as the average of mean adult weight of males and mean adult weight of females as given by Southern (1964) or Banfield (1974). Two additional rates are included. The intrinsic rate of increase of African elephants (*Loxodonta africana*) was taken as 0.06 on a yearly basis (Hall-Martin 1980), and their average weight calculated from Laws et al. (1975). Intrinsic rate and body weight of the multimammate rat (*Rattus natalensis*) is from Oliff (1953). Figure 6 gives data from nine mammalian species ranging in weight from

30 g (short-tailed vole) to 3,700 kg (elephant). Man was judged an outlier and excluded from the analysis which yielded

$$s = 1.5 W^{-0.36} \text{ (weight in kg), or} \\ s = 18 W^{-0.36} \text{ (weight in g)} \quad (10)$$

Intrinsic rate of increase s ($=r_m$) has been measured on a yearly basis. The regression accounts for 92% of variation in s . Thus the smaller the mammal the greater its intrinsic rate of increase and, we postulate, the less stable its population dynamics unless it is self-regulated.

Equation (9) suggests that maximum rate of decrease a of the eaters may also have an important bearing on stability if the eaters are not self-regulated. Since a is a rate of decline when food runs out it is largely a function of the rate of mobilisation of stored reserves, mainly fat and protein. Hence a is likely to be indexed closely by metabolic rate per unit of body weight. Kleiber (1961) gives the standard metabolic rate of eutherians as

$$\text{SMR (cal/hr)} = 16.4 W^{0.75} \text{ (g);}$$

Dawson and Hulbert (1970) give

$$\text{SMR} = 12.3 W^{0.737}$$

for marsupials. The exponents are similar so we will argue only from the 0.75 of eutherians. Dividing Kleiber's equation by W gives

$$\text{cal/hr/g} = 16.4 W^{-0.25}. \quad (11)$$

Hence the larger the animal the lower is its metabolic rate per unit of mass, and we would argue that the same relationship holds between maximum rate of decrease and body weight. Taken at face value, large a promotes stability, and since little animals appear to have a larger a than big animals their populations should be more stable, other things being equal.

However, by Eq. (9) it is the a/s ratio that promotes stability, not so much a or s in isolation. That ratio's trend on weight can be examined roughly by combining Eq. (10) and (11) to give

$$\frac{a}{s} = \frac{A W^{-0.25}}{B W^{-0.36}}$$

where A and B are proportionality constants of no interest in this context. By cancelling,

$$a/s = (A/B) W^{0.11} \quad (12)$$

the positive exponent of 0.11 suggesting that the a/s ratio rises with increasing body weight. If maximum rate of decrease is proportional to metabolic rate per unit of body weight as we assume, and if our estimate of the exponent of intrinsic rate of increase regressed on weight is a reasonable approximation, the implied trend of a/s suggests that the larger the animal the greater its potential for stability without self-regulation.

We are not entirely comfortable with those calculated exponents and therefore do not wish to push this argument too far. Our exponent of -0.36 relating intrinsic rate to body weight of mammals is at variance with Fenchel's (1974) exponent of -0.275 calculated from numerous unicellular organisms and heterotherms. He showed that intrinsic rates and body weights of five mammals had a similar trend, and if he is right the a/s ratio for mammals will

have little or no trend on body weight. However, Fenchel's trend for mammals is determined largely by one point. His other four points, representing the intrinsic rates and weights of small mammals, cluster at one end of the regression, the remaining point representing the cow being at the other. The four small mammals are the same species as those in Fig. 6, but the estimate of r_m we use for the Norway rat (Leslie et al. 1952) is more dependable than Fenchel's value which is Leslie's (1945) first approximation from scant data provided by King (1939). Fenchel's $r_m = 0.365$ annually for the cow, critical to the slope of his regression, is taken from a diagram presented by Smith (1954). It was not measured but rather was 'based on general information' (Smith 1954: 282). Consequently we put marginally more faith in our exponent than in Fenchel's.

Discussion

The speculative generalisation that we introduced previously – that little animals have intrinsic regulating mechanisms usually not possessed by big animals – is here elevated temporarily to the level of an axiom, thereby allowing us to explore its ramifications as if its truth were not in doubt. We ask how such a dichotomy might have arisen and how it might be enforced, assuming for purposes of argument that extrinsic regulation is the evolutionarily primitive condition and that selective pressure is required for self-regulation to evolve.

To start with, we consider the simple case of plants eaten by a herbivore lacking predators, and focus on the intrinsic rate of increase of the herbivore. Ungrazed plants are almost invariably limited in potential density, we think by extrinsic mechanisms, and there are obvious mechanical constraints limiting how fast a herbivore can eat even when food is super-abundant. Given those two conditions, a limit on the potential density of plants and a saturating functional response for the herbivore, the plants' critical line must necessarily have a hump. Its position is a function of the biomass of the vegetation when ungrazed and the ability of the herbivore to obtain food when food is scarce. Models A, A', B and B' are representatives of a suite of models with the attribute that an intersection of plant and herbivore critical lines to the right of the hump promotes stability and an intersection to its left promotes cyclicity unless the herbivore is strongly self-regulated. Physiological and demographic rates are scaled to body size in mammals (Western 1979, Damuth 1981, Lindstedt and Calder 1981) in a way likely to separate progressively with increasing body size the hump in the critical line of vegetation from the critical line of the herbivores. There are few circumstances in which the critical line of a large herbivore might be expected to lie left of the hump. Providing that the environment did not fluctuate too wildly the animals and their food supply would tend towards an equilibrium determined only by extrinsic forces. There would be no pressure of selection favouring the evolution of self-regulation.

A smaller mammal with a higher intrinsic rate of increase would, other things being equal, have a critical line intersecting that of the vegetation closer to the hump. Individual selection would favour a rise in intrinsic rate s , a rise in grazing efficiency (i.e. a lowering of D_1) and a rise in demographic efficiency (i.e. a lowering of D_2) because each of these modifications improves an individual's fitness. Equation (9) indicates that each of these trends expected

as a necessary consequence of individual selection will force the herbivore's critical line farther to the left towards the region where limit cycles are precipitated. The further left the intersection the larger will be the limit cycles and the greater will be the probability of extinction.

A critical assumption of this model is that cyclic populations under extrinsic controls are at high risk of extinction, and that the only cyclic populations which have persisted in evolutionary time are those which are self-regulated. There is some evidence for this assumption in small mammals (c.f. Krebs 1978) but some exceptions exist as well. The snowshoe hare cycle, for example, is believed to be driven by food shortage and predation (Keith and Windberg 1978). The larch budmoth cycle may be driven by epidemic disease (Anderson and May 1980).

Selection on species which stray into this region can act in two different ways. First, individual selection may operate to select for mechanisms that produce self-regulation. Individuals will be favoured if they can reduce the fitness of their neighbours relative to themselves (Rothstein 1979). A variety of behavioural and physiological mechanisms are available for accomplishing this interference, and the collective impact could be that the population is restricted somewhat in size so that extrinsic limitation through the food supply no longer obtains (Healey 1967, Krebs 1978).

Alternatively, group selection may operate to produce self-regulation. Group selection will favour those populations whose average individual fitness (as measured by ability to increase and ability to utilise resources) lags behind that of the majority, and it will favour those populations that carry latent the beginnings of a self-regulatory mechanism. Individual selection raising the intrinsic rate of increase of the animals, and group selection acting against the development of instability, are pushing in opposite directions, the condition identified by Gilpin (1975) as that in which group selection is most likely to overwhelm the effects of selection acting on individuals. In these circumstances group selection would be helped by the force of individual selection because the further individual fitness is raised the higher the proportion of populations culled by group selection. However, when group selection has fixed a self-regulating mechanism into a population, the restraints against a further increase of individual fitness are relaxed and the base of the herbivore's critical line may then move farther to the left as intrinsic rate of increase is again raised by individual selection.

Although we have postulated two mechanisms whereby self-regulation might evolve from simple extrinsic regulation we do not argue that the trend of evolution was necessarily always in that direction. The opposite process requires no additional element beyond reversal of selection pressures. If for any reason selection acted to increase body size, intrinsic rate of increase would have been reduced in parallel as would have been the necessity for self-regulation. The energetic cost of that mechanism would at first overhaul and then exceed its selective benefit. Self-regulation would then be selected against. That is what might have happened with mammalian lines that started small, as did most, and evolved into larger forms during the Tertiary. The early mammals might well have inherited self-regulatory mechanisms from reptilian ancestors.

Our verbal model predicts that a population should either have its critical line a safe distance to the right of

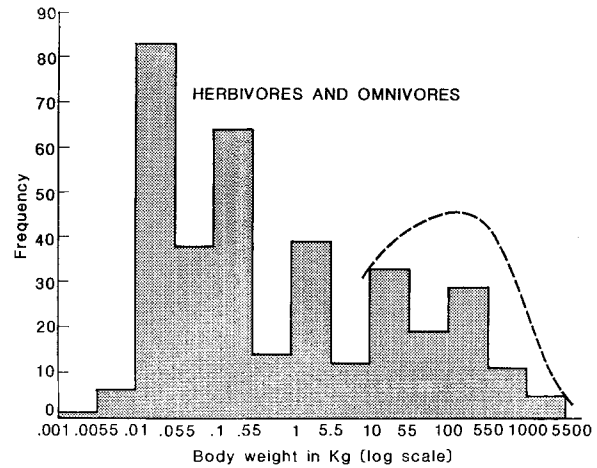


Fig. 7. Distribution of body weights for herbivorous and omnivorous mammals, excluding primates. Data are pooled from Europe, Canada, East Africa and Thailand, the sources given in the text. The dashed line represents diagrammatically the frequencies of large mammals before the late Quaternary die-offs occurred

the hump, the verticality of that line indicating a lack of self-regulation, or it should be anchored well to the left of the hump but curved to the right by self-regulation.

That postulated polarity might be reflected in a weak bimodality in the intrinsic rates of increase of mammalian herbivores, weak because the position of the hump in the vegetation's zero-isocline differs between grazing systems. Since the two are negatively correlated, a bimodality in the intrinsic rates should show up also as a somewhat weaker bimodality in body size.

Bourliere (1975) suggested that the body weights of extant mammals are bimodal. He commented that most cluster between a few grams and a few kg and between a few tens and a few hundreds of kg. Frequency distributions of mammalian body weights presented and discussed in Appendix II indicate that the postulated bimodality is not particularly convincing. The distribution of weights of herbivores and omnivores (primates excluded) exhibit at least three troughs. The one that interests us shows up in Fig. 7 (Appendix II) as between 5.5 and 10 kg but its position is largely an artefact of logging the weights. Dissection of the 5–50 kg body weight into 5 kg intervals indicates that the trough lies at about 25–35 kg. Owen-Smith (1977) provided a list of ungulates 'reportedly exhibiting territoriality' and a second of 'ungulate species reportedly nonterritorial'. Only the first includes species below 30 kg. While we find that interesting we are reluctant to push it further because the data on ungulate territoriality are simply not yet comprehensive enough to determine in which species territoriality regulates density and in which it serves only to facilitate mating.

Nonetheless, we select the body weight of 30 kg (corresponding to an intrinsic rate of increase of about 0.45) to provide a testable hypothesis: that the vast majority of herbivorous mammals lighter than 30 kg are self-regulated whereas the vast majority of heavier herbivores are regulated only by extrinsic mechanisms. One quick way of falsifying it is by way of fencing experiments. A fence thrown around a population regulated intrinsically by spacing behaviour will disrupt that population's dynamics by hold-

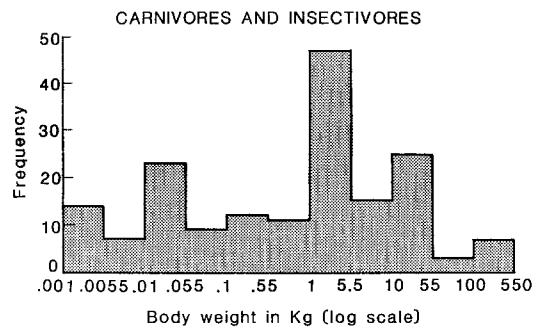


Fig. 8. Distribution of body weights of carnivorous and insectivorous mammals, excluding bats. Regions and sources are as for Fig. 7

ing within it those individuals that would otherwise disperse. The ‘fence effect’ can be spectacular for small herbivores (Krebs 1971). If our hypothesis is true a fence should not perturb the dynamics of populations of large herbivores unless it cuts a migration route. We know of only one study in which a fenced population of large herbivores was compared with appropriate unfenced controls. Rate of increase of two species of kangaroo within a fenced area of 440 km² did not differ significantly from that of kangaroos outside the fence (Bayliss 1980, and summarised by Caughley in press). Similar experiments on other species of large herbivores are needed to test the generality of that negative result.

Figure 8 of Appendix II is a frequency distribution of weights of terrestrial insectivores and carnivores. It differs markedly from that of herbivores and omnivores (Fig. 7). That may or may not be pointing to something important but it provides a caution against assuming that plant-herbivore systems and prey-predator systems are dynamically interchangeable. The first is a two-layered system in the absence of predation. The second is always a three-layered system, and its behavior need not conform to that of the plant-herbivore system with its two isoclines (May 1976).

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Appendix I

On r/s ratios

Tanner’s (1975) prediction that stability results from $r/s < 1$ or from K being small was confirmed by the observed demography of eight prey-predator pairs which he reported in detail. May’s (1976) Table 4.2 summarises the data and we have used this as the basis of our expanded Table 1.

Tanner’s reasoning goes like this: if the prey is strongly self-regulated (i.e. K is small) the hump in the prey’s critical line will lie well to the left. Therefore, other things being equal, the chances are good that the predator’s critical line will fall to the right of it. By Models A and B, and irrespective of the r/s ratio, an intersection to the right of the hump imposes equilibrium whether or not the predator is self-regulated. Hence the predicted outcome of the first two prey-predator pairs of Table 1. The prey of the remaining six pairs are not considered strongly self-regulated and so the chances are that the predator’s critical line cuts to the left of the hump which itself will be well to the right. Model A predicts that in these circumstances stability is possibly only when $r/s < 1$, and so it is for the five pairs that observation confirms are stable. The snowshoe hare-lynx pair has an r/s ratio of about unity. That system should therefore be cyclic, and it is.

Because the first two prey-predator systems are predicted as stable irrespective of the r/s ratio the critical test of the r/s hypothesis rests only with the last six cases. We are not convinced that Tanner’s empirical estimates of r/s for these six pairs are accurate enough to differentiate an $r/s < 1$ from an $r/s > 1$, but before we give our reasons we must contrast Tanner’s method of estimating r and s with ours. Tanner extracted from the literature the highest observed rates of fertility and survival he could find for each species, and married them by the basic demographic equation ($\sum l_x m_x e^{-rx} = 1$) to estimate r . This gave an observed fertility – observed survival rate of increase. He then combined observed survival with maximum fertility to give a second estimate, “‘maximum’ meaning that which I judge to be the highest likely in an optimal environment” (Tanner 1975: 861). Then observed fertility was combined with maximum survival to give a third estimate for rate of increase, and maximum survival combined with maximum fertility gave a fourth. Note that, as Tanner was at pains to point out, the maximum values are guesses, their only empirical

Table 1. Summary of Tanner’s (1975) analysis of eight prey-predator systems

Prey-predator	Intrinsic rates ^a		r/s	Is prey strongly self-regulated? (K is small?)	Outcomes	
	Prey r	Predator s			predicted	observed
sparrow-sparrow hawk	1.3	0.8	1.6	yes	equilibrium	equilibrium
muskrat-mink	1.4	0.5	2.8	yes	equilibrium	equilibrium
snowshoe hare-lynx	1.0	1.0	1.0	no	cycles	cycles
mule deer-mountain lion	0.2	0.5	0.4	no	equilibrium	equilibrium
white-tailed deer-wolf	0.3	0.5	0.6	no	equilibrium	equilibrium
moose-wolf	0.2	0.5	0.4	no	equilibrium	equilibrium
caribou-wolf	0.2	0.5	0.4	no	equilibrium	equilibrium
dall sheep-wolf	0.1	0.5	0.2	no	equilibrium	equilibrium

^a Taken from Tanner’s “maximum survival and maximum fertility” column

component being supplied by the observed value setting a lower limit. Hence the r/s values in May's (1976) Table 4.2 and in our Table 1 are each two guesses divided by two guesses. Tanner himself was more restrained when comparing r with s . He used all four estimates for the intrinsic rate of increase of a species. "The estimated rates for the wolf exceed those of all its prey species studied here with the single exception that the lowest value for the wolf is less than the highest value for the white-tailed deer" (Tanner 1975: 861). On that basis he reached the reasonable conclusion that $r < s$ for those prey-predator pairs.

Our approach was to search for rates of increase in the literature rather than attempting to estimate them indirectly from reported age-specific fertility and survival rates. The highest rate of increase we could find for wolves was $s = 0.28$, calculated from the increase on Isle Royale from 31 in 1974 to 41 in 1975 (Peterson and Stephens 1980). It is higher than Tanner's observed survival – observed fertility rate, about the same as his observed survival – maximum fertility rate, and considerably lower than those from the other two combinations. We think his maximum-maximum rate may be a severe overestimate and, by analogy, so also might be that for mountain lion.

In contrast, his maximum-maximum rates of r for the five prey species paired with these predators look rather too low. That for white-tailed deer certainly is. Six deer were introduced to the George Reserve in 1928, and a drive count six breeding seasons later logged 160 (O'Roke and Hammerstrom 1948): $r = 0.55$. McCullough (1979) derived a correction factor for drive counts which suggests that the 160 is too low by at least 20: $r = 0.57$. Tanner's maximum-maximum estimate for this species was $r = 0.30$. McCullough's (1982) estimates of rate of increase of this herd are in error. They must be multiplied by 2.303, the factor converting base-ten logarithms to natural logarithms.

We can find no useful rates of increase for mule deer but agree with Tanner that r for this species is probably lower than that of white-tailed deer. We would guess at around $r = 0.40$, against Tanner's maximum-maximum estimate of 0.24.

We have been unable to locate a rate of increase of caribou from low density but note that the closely-related reindeer increased at about $r = 0.3$ on St. Matthew Island between 1944 and 1957 (Klein 1968; Caughley 1976a). The Barff reindeer herd on South Georgia increased from low density at about $r = 0.38$ between 1912 and 1916, and at about 0.32 between 1916 and 1922 (Leader-Williams 1978). Tanner's maximum-maximum estimate for caribou was $r = 0.20$.

Nor do we know of any useful direct estimate for dall sheep but we are certain, by analogy with rates of increase of species of that size, that Tanner's maximum-maximum rate of $r = 0.11$ is impossibly low. Domestic sheep increase at about double that rate from an economic carrying-capacity level (Caughley 1967). Their intrinsic rate of increase should therefore be something like 0.35–0.40. That for dall sheep is probably lower, but we would be surprised if it were much below 0.3

Data on the rate at which moose erupt are of dubious accuracy. Mech (1966) quotes P.F. Hickie's unpublished report of a population of around 300 on Isle Royale in 1920. Hickie (1936) reckoned the population in 1928 as between 1,000 and 5,000. The lower estimate returns $r = 0.17$ over the seven years, the higher $r = 0.40$. We do not

challenge Tanner's maximum-maximum estimate of $r = 0.20$ on the basis of these data.

In summary, Tanner's conclusion that r/s ratios of five prey-predator pairs were less than 1 is not confirmed by this reappraisal. We suspect $r/s > 1$ for white-tailed deer and wolf, and probably also for mule deer and mountain lion. The ratio is probably close to 1 for caribou and wolf and for dall sheep and wolf; and Tanner is probably correct that $r < s$ for moose and wolf. If, as Tanner suspected, the predator's critical was left of the hump in these systems, his model predicts from our r/s estimates more cyclicity within this suite of species than has been observed. Alternatively the intersection of critical lines may yet be to the right of the hump, in which case the r/s ratios are without relevance. But either way we do not accept Tanner's estimates as evidence of the importance of the r/s ratio to the stability of prey-predator pairs.

It is unfortunate that much of our commentary on Tanner's (1975) paper has been restricted to those areas where his conclusions clashed with ours. We wish to remedy this by affirming that his paper is one of the most stimulating we have read in the last ten years.

Appendix II

The distribution of mammalian body weights

Figure 7 is a distribution of body weights of herbivorous and omnivorous mammals other than primates. It combines species from Britain and Europe (data from Van den Brink 1967 and Burton 1976), Canada (Banfield 1974), East Africa (Kingdon 1971, 1974, 1978, 1979, 1982; Dorst and Dandelot 1970) and Thailand (Lekagul and McNeely 1977 with some weights from Harrison 1966 and Medway 1969). The body weight of a species is taken as the average of male and female adult weight.

The dashed line on the right side of the histogram is a conservative reconstruction of what the frequencies of the heavier species would have been before selective extinctions in the late Quaternary. Martin (1966) suggests that 70% of genera heavier than 50 kg died out in North America over that period, as did 40% in Africa. The European fauna was similarly affected.

Distinct troughs in body-weight frequencies occur at 0.055–0.1, 0.55–1 and 5.5–10 kg. Table 2 gives a breakdown of the frequencies by Order and region. The first trough is entirely within the Rodentia. It shows up well in the Holarctic and Thailand rodents but does not appear in the African data. We have no explanation for it.

The second trough, at 0.55–1 kg, is marked in the Canadian rodents but unconvincing for the other regions. It is generated in the pooled data of Fig. 7 mainly by a suite of lagomorphs peaking in frequency in the following weight class.

The third trough, 5.5–10 kg, although visually no more striking than the others, may be of more significance in the context of regulatory strategies. Its position in Fig. 7 is largely an artefact of the log scale of body weights. When the range 5–50 kg is dissected into constant 5 kg intervals the trough lies at 25–35 kg. Essentially it divides rodents and small ungulates from large ungulates.

Figure 8 gives for comparison a frequency distribution of the weights of carnivorous and insectivorous mammals, bats excluded, from the same four regions. The histogram

Table 2. Frequencies of body weights for herbivorous and omnivorous mammals (primates excluded) in (A) Britain and Europe, (B) Canada, (C) East Africa and (D) Thailand. See text for sources

Weight (kg)	Lagomorpha				Rodentia				Perissodactyla				Artiodactyla				Hyracoidea				Proboscidea				Total ^a				
	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D					
0.001–0.0055					0	0	1	0																					1
0.0055–0.01					2	1	3	0																					6
0.01–0.055					22	24	27	14																					87
0.055–0.1					3	5	23	9																					40
0.1–0.55	0	1	0	0	15	12	12	25																					65
0.55–1	0	1	0	0	0	3	6	5																					15
1–5.5	2	5	5	0	0	7	5	5					0	0	4	2	0	0	3	0									38
5.5–10					2	2	1	2					0	0	4	0													11
10–55					1	1	2	0					4	1	21	3													33
55–100													2	4	11	1													18
100–550									0	0	2	1	5	5	16	4													33
550–1,000									0	0	0	1	2	0	4	4													11
1,000–5,500									0	0	2	1	0	0	1	0					0	0	1	1					6

^a A few species common to two or more regions contribute more than once to these totals

is very different from that of herbivores and omnivores depicted in Fig. 7.

References

- Anderson RM, May RM (1980) Infectious diseases and population cycles of forest insects. *Science* 210:658–661
- Andrewartha HG, Birch LC (1954) The distribution and abundance of animals. University of Chicago Press, Chicago
- Armitage KB (1975) Social behavior and population dynamics of marmots. *Oikos* 26:341–354
- Banfield AWF (1974) The mammals of Canada. Toronto University Press, Toronto
- Bayliss P (1980) Kangaroos, plants and weather in the semiarid. MSc Thesis University of Sydney
- Bonner JT (1965) Size and cycle: an essay on the structure of biology. Princeton University Press, Princeton
- Bourliere F (1975) Mammals, small and large: the ecological implications of size. In: Golley FB, Petruszewicz K, Ryszkowski L (eds). Small mammals: their productivity and population dynamics. International Biological Programme 5, Cambridge University Press, Cambridge, pp 1–8
- Bujalska G (1973) The role of spacing behaviour among females in the regulation of reproduction in the bank vole. *J Reprod Fertil Suppl* 19:465–475
- Burton M (1976) Guide to the mammals of Britain and Europe. Elsevier Publishing projects SA, Lausanne
- Caughley G (1967) Parameters for seasonally breeding populations. *Ecology* 48:834–839
- Caughley G (1970) Eruption of ungulate populations with emphasis on Himalayan thar in New Zealand. *Ecology* 51:53–72
- Caughley G (1976a) Wildlife management and the dynamics of ungulate populations. In: Coaker TH (ed) Applied Biology Vol I. Academic Press London, pp 183–246
- Caughley G (1976b) Plant-herbivore systems. In: May RM (ed) Theoretical ecology: principles and applications. WB Saunders, Philadelphia, pp 94–113
- Caughley G (1977) Analysis of vertebrate populations. John Wiley and Sons, Chichester
- Caughley G (1979) What is this thing called carrying capacity? In: Boyce MS, Hayden-Wing LD (eds) North American elk: ecology, behavior and management. The University of Wyoming, Laramie, pp 2–8
- Caughley G (In press) Dynamics of large mammals and their relevance to culling. In: Owen-Smith N (ed) Proc symposium on management of large mammals in African conservation areas. Pretoria 1982
- Chitty D (1960) Population processes in the vole and their relevance to general theory. *Can J Zool* 38:99–113
- Chitty D (1967) The natural selection of self-regulatory behaviour in animal populations. *Proc Ecol Soc Aust* 2:51–78
- Christian JJ (1971) Population density and reproductive efficiency. *Biol Reprod* 4:248–294
- Christian JJ (1978) Neurobehavioral-endocrine regulation of small mammal populations. In: Snyder DP (ed) Populations of Small Mammals under Natural Conditions. Pymatuning Lab Ecol Spec Publ No 5
- Damuth J (1981) Population density and body size in mammals. *Nature* 290:699–700
- Dawson TJ, Hulbert AJ (1979) Standard metabolism, body temperature, and surface areas of Australian marsupials. *Amer J Physiol* 218:1233–1238
- Dorst J, Dandelot P (1970) A field guide to the larger mammals of Africa. Collins, London
- Fenchel T (1974) Intrinsic rate of natural increase: the relationship with body size. *Oecologia* 14:317–326
- Fowler CW, Bunderson WT, Ryel RJ, Steele BB (1980) Comparative population dynamics of large mammals: a search for management criteria. Report to Marine Mammal Commission NTIS No PB80-178627
- Gaines MS, McClenaghan Jr LR (1980) Dispersal in small mammals. *Ann Rev Ecol Syst* 11:163–196
- Gilpin ME (1972) Enriched prey-predator systems: theoretical stability. *Science* 177:902–904
- Gilpin ME (1975) Group selection in predator-prey communities. Princeton University Press, Princeton
- Hall-Martin A (1980) Elephant survivors. *Oryx* 15:355–362
- Harper JL (1977) Population biology of plants. Academic Press New York
- Harrison J (1966) An introduction to mammals of Singapore and Malaya. Malayan Nature Society, Singapore
- Healey MC (1967) Aggression and self-regulation of population size in deer mice. *Ecology* 48:377–392
- Heron AC (1972) Population ecology of colonising species: the pelagic tunicate *Thalia democratica*. *Oecologia (Berlin)* 10:269–312
- Hickie PF (1936) Isle Royale moose studies. *Proc North American Wildlife Conf* 1:396–398
- Holling CS (1965) The functional response of predators to prey density and its role in mimicry and population regulation. *Mem Ent Soc Canada* 45:3–60

- Keith LB, Windberg LA (1978) A demographic analysis of the snowshoe hare cycle. *Wildl Monogr* No 58:1–70
- King HD (1939) Life processes in grey Norway rats during fourteen years in captivity. *Amer Anat Mem* No 17:1–72
- Kingdon J (1971–1982) East African mammals. An atlas of evolution in Africa Vols I–IIID. Academic Press London
- Kleiber M (1961) *The fire of life: an introduction to animal energetics*. Wiley and Sons, New York
- Klein DR (1968) The introduction, increase, and crash of reindeer on St Matthew Island. *J Wildl Manage* 32:350–367
- Krebs CJ (1964) The lemming cycle at Baker Lake, Northwest Territories during 1959–1962. *Arctic Inst N Amer Tech paper* No 15:1–104
- Krebs CJ (1971) Genetic and behavioral studies on fluctuating vole populations. In: Boer PJ den, Gradwell GR (eds) *Proc Advanced Study Institute on dynamics of numbers in populations*. Oosterbeek 1970, pp 243–256
- Krebs CJ (1978) A review of the Chitty Hypothesis of population regulation. *Can J Zool* 56:2463–2480
- Krebs CJ (1979) Dispersal, spacing behaviour, and genetics in relation to population fluctuations in the vole *Microtus townsendii*. *Fortschr Zool* 25(2/3):61–77
- Krebs CJ, Gaines MS, Keller BL, Myers JH, Tamarin RH (1973) Population cycles in small rodents. *Science* 179:35–41
- Lack D (1954) *The natural regulation of animal numbers*. Oxford University Press London
- Laws RM, Parker ISC, Johnstone RCB (1975) *Elephants and their habitats: the ecology of elephants in North Bunyoro, Uganda*. Clarendon Press Oxford
- Leader-Williams N (1978) The history of the introduced reindeer of South Georgia. *Deer* 4:256–261
- Lekagul B, McNeely J (1977) *Mammals of Thailand*. Kurusapha Ladprao Press Bangkok
- Leslie PH (1945) On the use of matrices in certain population mathematics. *Biometrika* 33:183–212
- Leslie PH, Venables UM, Venables LSV (1952) The fertility and population structure of the brown rat (*Rattus norvegicus*) in corn-ricks and some other habitats. *Proc Zool Soc Lond* 122:187–238
- Lidicker WZ Jr (1975) The role of dispersal in the demography of small mammals. In: Golley FB, Petruszewicz K, Ryszkowski L (eds) *Small mammals: their productivity and population dynamics*. International Biological Programme 5, Cambridge University Press Cambridge, pp 103–128
- Lindstedt SL, Calder III WA (1981) Body size, physiological time, and longevity of homeothermic animals. *Quart Rev Biol* 56:1–16
- Madison DM (1980) Space use and social structure in meadow voles, *Microtus pennsylvanicus*. *Behav Ecol Sociobiol* 7:65–71
- Martin PS (1966) Africa and Pleistocene overkill. *Nature* 212:339–342
- May RM (1974) Biological populations with non-overlapping generations: stable points, stable cycles, and chaos. *Science* 186:645–647
- May RM (1975) *Stability and complexity in model ecosystems*. Princeton University Press Princeton, Second Edition
- May RM (1976) Models for two interacting populations. In: May RM (ed) *Theoretical ecology: principles and applications*. WB Saunders, Philadelphia pp 49–70
- May RM (1977) Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature* 269:471–477
- Mech LD (1966) The wolves of Isle Royale. *Fauna of the National Parks of the United States Fauna Series* 7:1–201
- Mech LD (1970) The wolf. *Am Mus Nat Hist Press* New York
- Medway Lord (1969) *The wild mammals of Malaya and offshore islands including Singapore*. Oxford University Press London
- McCullough DR (1979) *The George Reserve deer herd*. The University of Michigan Press, Ann Arbor
- McCullough DR (1982) Population growth rate of the George Reserve deer herd. *J Wildl Manage* 46:1079–1083
- Milne AA (1928) *The house at Pooh Corner*. Chaucer Press Bungay
- Nicholson AJ (1933) The balance of animal populations. *J Anim Ecol* 2:132–178
- Noy-Meir I (1975) Stability of grazing systems: an application of predator-prey graphs. *J Ecol* 63:459–481
- Noy-Meir I (1978) Stability in simple grazing systems: effect of explicit functions. *J Theoret Biol* 71:347–380
- Oliff WD (1953) The mortality, fecundity and intrinsic rate of natural increase of the multimammate mouse, *Rattus (Mastomys) natalensis* (Smith) in the laboratory. *J Anim Ecol* 22:217–226
- O'Roke EC, Hammerstrom Jr FN (1948) Productivity and yield of the George Reserve deer herd. *J Wildl Manage* 12:78–86
- Owen-Smith N (1977) On territoriality in ungulates and an evolutionary model. *Q Rev Biol* 52:1–38
- Peek JM (1980) Natural regulation of ungulates (what constitutes a real wilderness?). *Wildl Soc Bull* 8:217–227
- Peterson RO, Stephens PW (1980) *Ecological studies of wolves on Isle Royale. Annual Report 1979–1980*, p 19
- Romesburg HC (1981) *Wildlife Science: gaining reliable knowledge*. *J Wildl Manage* 45:293–313
- Rosenzweig ML, MacArthur RH (1963) Graphical representation and stability conditions of prey-predator interactions. *Amer Nat* 97:209–223
- Rothstein SI (1979) Gene frequencies and selection for inhibitory traits, with special emphasis on the adaptiveness of territoriality. *Amer Nat* 113:317–331
- Sinclair ARE (1977) *The African buffalo. A study of resource limitation of populations*. University of Chicago Press Chicago
- Smith FE (1954) Quantitative aspects of population growth. In: Boell EJ (ed) *Dynamics of growth processes*. Princeton University Press Princeton, pp 277–294
- Southern HN (ed) (1964) *The handbook of British mammals*. Blackwell Scientific Publications Oxford
- Tamarin RH (1980) Dispersal and population regulation in rodents. In: Cohen MN, Malpass RS, Klein HG (eds) *Biosocial mechanisms of population regulation*. Yale University Press New Haven, pp 117–133
- Tanner JT (1975) The stability and intrinsic growth rates of prey and predator populations. *Ecology* 56:855–867
- Terman CR (1980) Behavior and regulation of growth in laboratory populations of prairie deer mice. In: Cohen MN, Malpass RS, Klein HG (eds) *Biosocial mechanisms of population regulation*. Yale University Press, New Haven, pp 23–36
- Van den Brink FH (1967) *A field guide to the mammals of Britain and Europe*. Collins, London
- Western D (1979) Size, life history and ecology in mammals. *Afr J Ecol* 17:185–204
- Wynne-Edwards VC (1962) *Animal dispersion in relation to social behaviour*. Oliver and Boyd, Edinburgh

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