

# Population dynamics of large and small mammals: Graeme Caughley's grand vision

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**Abstract.** Ecologists that study the population dynamics of large and small herbivorous mammals operate in two worlds that overlap only partly, and in this paper I address whether the conjecture that these worlds represent two distinct and valid paradigms is currently justified. I argue that large mammals fall into three groups depending on whether they have effective predators or not, and whether they are harvested by humans. Because of human persecution of large predators, more and more large herbivorous mammals are effectively predator-free and are controlled bottom-up by food. But in less disturbed systems, large herbivorous mammals should be controlled top-down by effective predators, and this can lead to a trophic cascade. Small herbivorous mammals have been suggested to be controlled top-down by predators but some experimental evidence has challenged this idea and replaced it with the notion that predation is one of several factors that may affect rates of population increase. Intrinsic control (territoriality, infanticide, social inhibition of breeding) appears to be common in small herbivorous mammals with altricial young but is absent in species with precocial young, in ecosystems with strong stochastic weather variation (deserts) and in areas of human-induced habitat fragmentation in agricultural monocultures. The extrinsic control of large herbivores with precocial young validates part of Graeme Caughley's Grand Vision, but the relative role of intrinsic and extrinsic mechanisms for small herbivores with altricial young is still controversial. An improved knowledge of population control mechanisms for large and small herbivores is essential for natural resource management.

## Introduction

The conventional view of science is that it solves problems and moves on but a variety of ecologists have argued that we do not operate this way in ecology (Peters 1991; O'Connor 2000). The problems of population dynamics have been addressed with vigour for more than 50 years and some ecologists have argued that they are now solved and we can move on. Unfortunately, the solutions expressed by various ecologists differ and yet it is important for the management of our natural resources that useful generalisations are carefully analysed and presented.

In 1983 Caughley and Krebs presented a set of arguments about why we should expect large and small herbivorous mammals to have different population dynamics based on first principles. Large herbivorous mammals (intrinsic rate of increase  $<0.45$  per year, body mass  $>30$  kg) ought to have extrinsic controls while small herbivorous mammals would be expected to show intrinsic controls. Given that extrinsic control is typically identified with predators, diseases, and food shortage, these ought to be the critical factors that managers dealing with large mammals need to consider. For small mammals intrinsic control is typically identified with territoriality, infanticide, physiological stress, and other social interactions, and small mammal ecologists should thus deal with a completely different set of mechanistic forces in trying to understand population changes. Managers dealing with small mammal pest problems rarely consider intrinsic control and often adopt the extrinsic approach instead. I will refer to this set of large-and-small-mammal generalisations

as Graeme Caughley's Grand Vision because it satisfied his lifelong quest for mechanistic generality in population dynamics. But have these generalisations turned out to be correct in the light of further research?

Soon after that paper was published in 1983, several challenges appeared to these generalisations. Within those who work on large herbivorous mammals, individuals have fallen into two camps identified as 'top-down control via predation' versus 'bottom-up control via food supplies'. Sinclair and Krebs (2002) proposed that primary control in all herbivorous vertebrate populations was bottom-up from food supplies, and this control could be secondarily modified by top-down natural enemy effects, social interactions, or stochastic weather events. Korpimäki *et al.* (2002, 2003, 2004) argued that top-down control was the norm for small mammal populations and implicitly argued against the dichotomy proposed by Caughley and Krebs (1983). In this paper I explore further the recent evidence bearing on these potential generalisations.

I do not discuss here the problems of populations of large mammals, such as orangutans, whose dynamics are being driven by habitat loss associated with agriculture or forestry land use. There is no interesting scientific question here to be debated because the principle that *if there is no habitat, there can be no population* is as close to a scientific law as is possible in ecology. My background assumption is that we are dealing with populations that occupy habitats suitable in landscape scale to their size and feeding requirements. This assumption excludes many species of conservation concern because of habitat loss.

Many factors interact to affect the changes in numbers of any population, and the job of the population ecologist could be described in two ways: (1) to catalogue all the factors affecting changes in population size, or (2) to determine the major factors driving changes in numbers. I adopt the second approach here with the background assumption that this will provide the most useful information for natural resource management. I have described this elsewhere as the mechanistic paradigm (Krebs 2002), and I use the term 'control' in this paper to refer to any mechanistic factor that affects population growth rates. My concern here is with the mechanistic paradigm and not with the density-dependent paradigm, which I have argued is less useful for understanding population dynamics (Krebs 2002).

### Large mammal population dynamics

Caughley (1981) argued that for large herbivores we should first thoroughly study the large mammal–food supply nexus before we try to understand how predators and competitors affect this balance. Few large-mammal ecologists appear to have heeded his advice, but rather seem to operate on the assumption that if effective predators exist for a large mammal population, one should study the predation nexus before considering the vegetation interactions. For the most part, this is understandable, given a shortage of time, personnel and funds for any particular project. One of the contradictions of Graeme Caughley was that he did not always take his own advice. His classic paper on the dingo fence (Caughley *et al.* 1980) inferred that dingo (*Canis lupus dingo*) predation controlled the abundance of red kangaroos and emus in South Australia, outside the dingo fence. To reach this conclusion he did not investigate plant–herbivore dynamics for these populations but reached the direct conclusion of a top-down system where predators were removed by humans in western New South Wales. This conclusion was supported by subsequent more-detailed research (Pople *et al.* 2000).

To evaluate Caughley's conjectures in the light of recent studies, I begin with the dynamics of large herbivorous mammals. I wish to deal with current populations, many of which have been strongly affected by human activities, and thus I divide all large mammal populations into two classes: (1) large herbivorous mammals with no predators (e.g. elephants (*Loxodonta africana*), white-tailed deer (*Odocoileus virginianus*) in eastern North America), and (2) large mammals with effective natural predators (e.g. red kangaroos (*Macropus rufus*) in central Australia, woodland caribou (*Rangifer tarandus caribou*) in Canada, zebra (*Equus burchellii*) in Africa). Inevitably, there are populations that fall between these two groups, like eastern grey kangaroos (*Macropus giganteus*) in eastern New South Wales, where most, but not all, of the predators have been suppressed by poisoning (Banks *et al.* 2000; Fletcher 2006) but, in general, most of these populations have predators that are not highly effective so they operate like the first group.

Clearly, the first group of large herbivorous mammals with no predators is the simplest to analyse. The study of kangaroos at Kinchega in New South Wales by Caughley *et al.* (1987) is a paradigm on this approach, since these kangaroo populations existed in the virtual absence of dingo predation. If predators are not present or effective, population changes must be caused by changes in food resources (in the absence of disease limitation).

The general message for these kinds of large mammal populations is to analyse carefully plant–herbivore dynamics as the key to understanding population changes, a point made effectively by Caughley (1976) and shown well by the Soay sheep (*Ovis aries*) study on St Kilda (Crawley *et al.* 2004).

A special case exists for those large mammals in which human hunting or poaching is the main cause of population changes. Conservation for these species becomes a case of setting proper harvesting quotas along with effective law enforcement, often easier said than done. The black rhinoceros (*Diceros bicornis*) in east Africa is a good example, showing the complications introduced by poaching driving the dynamics (Metzger *et al.* 2007). The hunting of elephants for ivory is another example (Caughley *et al.* 1990; Milner-Gulland and Beddington 1993).

When natural predator communities are more or less intact, it is tempting to reverse the onus of proof and to begin with the assumption of top-down control by predators. A good example is the woodland caribou in Ontario. Woodland caribou have been declining in southern Canada for more than 30 years, presumably as a result of predation by wolves, bears, and lynx. Bergerud *et al.* (2007) obtained the data shown in Fig. 1 on two populations of woodland caribou, one isolated from predators on offshore islands in Lake Superior and one mainland population with predators. No studies were carried out on the food supplies of these populations, but the presumption is that the island population is food-limited. But from a management perspective, predation is the key process threatening mainland populations and the question is what can be done to reduce predator kills of caribou.

Eastern North American white-tailed deer populations are an example of top-down control of ungulate numbers, and a trophic cascade that has resulted from the killing of wolves and bears in the highly settled areas of eastern United States. Trophic cascades are a form of strong top-down control in which impacts flow down the food chain as a series of positive and negative impacts on successive trophic levels in the community. White-tailed deer are

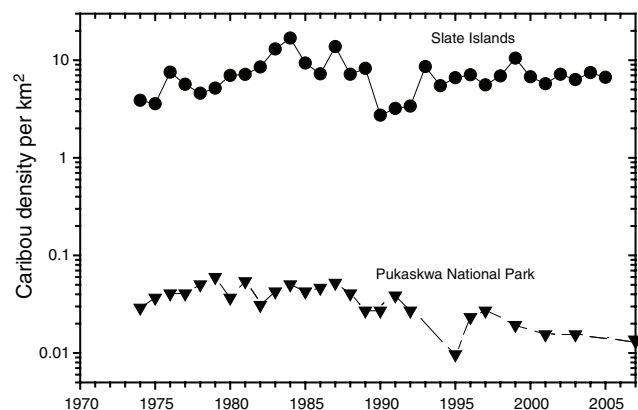


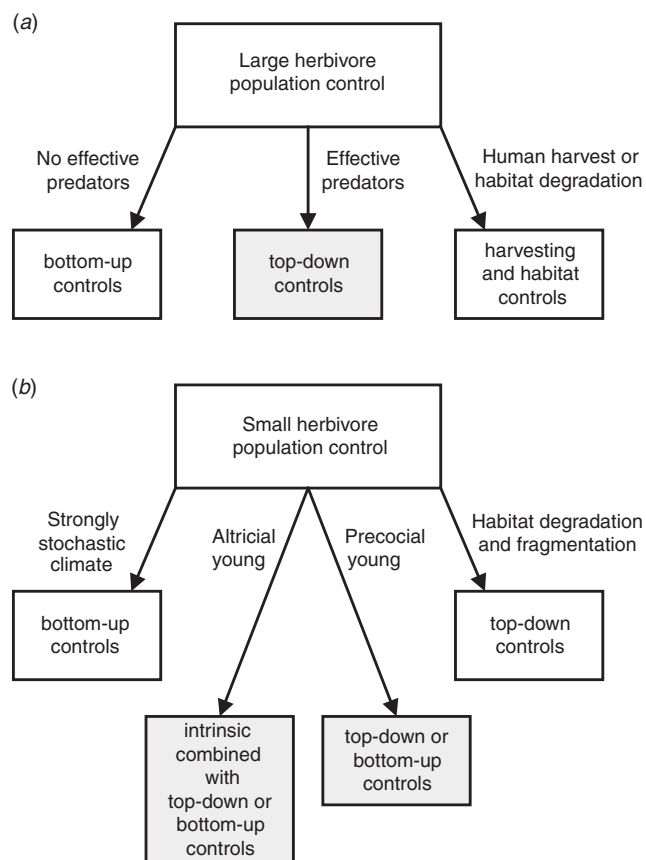
Fig. 1. Woodland caribou densities on the Slate Islands of Lake Superior and on the adjacent mainland in Pukaskwa National Park, Ontario, from 1974 to 2007. Island populations free of predators exist at 100-times the density of mainland populations that occur with predators. Predators are driving the mainland populations of woodland caribou towards extinction. From 1987 to 2007 the mainland herd showed a significant decline of 6% per year ( $P < 0.01$ ). (Data from Bergerud *et al.* 2007.)

now overabundant and the resulting highway collisions and damage to regenerating forests (Mladenoff and Stearns 1993; Stromayer and Warren 1997) are an on-going conservation dilemma. A trophic cascade is not a necessary consequence of top-down control, and will occur only when the herbivores involved are dominant species in a community. Rare species may well be controlled top-down but not be abundant enough to affect plant resources.

Fryxell *et al.* (1988) pointed out that large-mammal migrations were one strategy that reduced predator effectiveness and permitted some migratory species to escape predator limitation and thus be controlled bottom-up by food supplies. The wildebeest of the Serengeti are the classic example of this strategy, which is a version of a spatial refuge for the prey. Group formation among large mammals is a second strategy that also helps to reduce the effectiveness of predators (Fryxell *et al.* 2007). Migration typically evolves to track seasonal food supplies, and one secondary consequence of this strategy is that predators may become less effective. Migration and group formation, however, will not be effective as predator-escape strategies if the predators themselves are migratory, as is the case with wolves and barren ground caribou in North America.

Figure 2 gives a schematic diagram of population control processes in large and small herbivorous mammals and attempts to update the conjectures of Caughley and Krebs (1983). For large herbivores Caughley's Grand Vision has been little changed by recent research. I do not distinguish as a separate category in Fig. 2 populations of large herbivores limited by weather. Large-mammal herbivores, in general, are not greatly affected directly by weather, with a few exceptions. Peary caribou (*Rangifer tarandus pearyi*) in the Canadian arctic islands are periodically reduced by autumn episodes of freezing rain that render their food plants unavailable and cause starvation (Caughley and Gunn 1993). Reindeer (*Rangifer tarandus*) on Svalbard are another example of this situation in which weather may be a driving variable of population changes (Solberg *et al.* 2001). Winter mortality of Soay sheep is strongly affected by wet, windy weather interacting with *per capita* food supplies (Hone and Clutton-Brock 2007). More typically, weather affects vegetation growth and the direct effect on the herbivores is via food shortage, a classic response demonstrated by Caughley *et al.* (1987) for kangaroos. Direct weather effects on large mammals operate as an interaction with bottom-up controls via food supplies.

Some of the tension in the literature about large herbivore population dynamics could be avoided if the objectives of each study were carefully outlined. The dichotomy in all mechanistic population studies is between, on the one hand, finding out what variables are the main causes of population changes (so that management activities can be assigned accordingly) and, on the other hand, understanding how the nexus of food supplies, predation, disease, weather, social interactions, and habitat structure operate to control changes in numbers. These different objectives demand different experimental designs. The key is to specify exactly the objectives of each population study so that an end point for understanding can be specified. There is no doubt that there are factor interactions that need to be analysed; for example, whether poor food supplies permit increased parasite



**Fig. 2.** Global model of population control in large and small herbivorous mammals. Typical pathways are shown in grey shading. For large mammals the key questions are whether numbers are driven by human harvest and whether effective predation is impossible. For small mammals the three key variables are whether the species has altricial or precocial young, the strength of climatic variability, and the severity of habitat disturbances associated with agriculture and land management. Harvesting controls and habitat degradation can be viewed as top-down controls with humans as the apex predator.

loads that contribute to higher predation rates. Management agencies typically have only a few major variables they can manipulate within their budgets to change population trends, and knowing the details of how factors interact may not be necessary for effective management action.

For large mammals I propose to extend the conjecture of Sinclair and Krebs (2002) that for mammalian herbivores the primary control is bottom-up with a tripartite separation for those populations with and without natural predator assemblages, and those completely subject to human control via harvesting and habitat changes (Fig. 2). I suggest that primary control for large mammalian herbivores in intact ecosystems is top-down with secondary modifications produced by food supplies, disease, and weather. The Serengeti wildebeest (*Connochaetes taurinus*) is the exception to this generalisation because its migration strategy sheds potential predator controls on abundance (Fryxell *et al.* 2007). Almost no large herbivore studies consider the potential role of intrinsic processes in population dynamics and the

assumption is that these social processes are not important for populations of large herbivores.

### Small mammal population dynamics

The conjecture of Caughley and Krebs (1983) that small herbivorous mammals show intrinsic control was challenged by an array of Scandinavian researchers who, in general, postulated top-down control of small mammal numbers. If this were correct, we could simplify population dynamics by adopting the same paradigm for large and small mammals, and it is important to examine the evidence provided for top-down control.

Small mammal population changes illustrate all too well the potential confusion of correlation and causation in population dynamics. Many factors change as numbers rise and fall. For example, a population regulated top-down by predators that show a time lag in their numerical response will, of necessity, show a correlation of population changes with food supply *per capita*. Observing such a correlation is not proof of bottom-up control. Factor interactions make these kinds of observations even more difficult, for example, when parasite infections change individual susceptibility of prey to predation or extreme weather events. The solution, which has been known for some time, is to adopt an experimental approach.

But this is not easy because every field experiment has its limitations (Raffaelli and Moller 2000). A series of large-scale field experiments by Korpimäki and his colleagues in Finland has attempted to establish the viewpoint that small mammal population fluctuations are caused by predation (Klemola *et al.* 1997; Korpimäki and Norrdahl 1998; Korpimäki *et al.* 2004). I cannot provide a detailed analysis here of all the important research done by this group of ecologists. But all their experiments suffered from serious limitations; in the end the field data were equally consistent with the view that predation has a modifying effect on rodent population changes but may not be the primary driver. Limitations of these experiments involved predator-removal treatments that could be applied only in the summer months and were effectively pulse treatments rather than press treatments due to technical problems of locating predators in the winter snowy season, and the difficulty in assessing population densities of both prey and mammalian predators on a landscape scale.

The conclusion of top-down control for small mammals has been widely accepted because it can be modelled successfully (Hanski *et al.* 2001; Korpimäki *et al.* 2002). We have argued elsewhere that models cannot test hypotheses (Lambin *et al.* 2002), and this is a source of prime disagreement among ecologists. Models of small rodent population dynamics typically contain several parameters that are not known with any degree of confidence. Since it is possible to produce models that mimic cyclic population changes in small mammals from a completely bottom-up approach (Turchin and Batzli 2001) and from a completely top-down approach (Hanski *et al.* 2001; Gilg *et al.* 2003), one or both types of model must be an inadequate representation of the field dynamics. To complicate it further, recent models involving only intrinsic control of breeding season length also produce population fluctuations that resemble changes seen in field populations (Smith *et al.* 2006).

We can evaluate a plethora of models that purport to explain population changes in small mammals only if they make some specific predictions that do not follow from any other model (Platt 1964). As a secondary check on model validity, we can determine whether the parameters used in the models are based on detailed data from field populations and include the range of values that have been observed in the real world.

Graham and Lambin (2002) attempted to test the predation model for small mammal population fluctuations on Scottish populations of *Microtus agrestis*. They specified the predictions of the predation model, and looked for evidence for or against these predictions. They rejected the predation model because the primary predator, the weasel (*Mustela rixosa*), did not show a delayed density-dependent response to vole densities and had no impact on juvenile vole mortality.

The Scottish experiment was highlighted by Oli (2003a) as a critical test of a popular hypothesis. Oli's commentary was in turn vigorously attacked by Korpimäki *et al.* (2003), who argued that the vole population fluctuations in Scotland were different in kind from those of Scandinavia, and that the scale of the Scottish experiments was too small. This attack was responded to by Lambin and Graham (2003) and Oli (2003b). The bottom line in this controversy seems to be that every experiment can be improved, but it is counterproductive to claim that the local conditions of every study area in every year should require a different explanation for population changes, the opposite view from the Grand Vision suggesting some generality (Lambin *et al.* 2006).

If social factors such as territoriality and infanticide are critically important in small mammal population dynamics, this generalisation will not automatically translate into methods for the management of pest-control problems in agriculture but may be useful in planning control programs. Social interactions in house mice in grain fields of south-eastern Australia have important effects on population growth (Sutherland and Singleton 2006), and this knowledge can assist a program of fertility control to reduce damage. Similarly, rats in Asian rice fields illustrate too well the failure of predation to restrict densities, but management can be achieved by a variety of cultural controls and crop management (Singleton *et al.* 2005). Knowing the limiting factors can help to minimise setting up programs for management that cannot succeed. The classic examples for pest rodents in tropical countries are programs encouraging predators such as cats and barn owls for rodent control in situations where predator offtake is minimal in relation to rates of increase of the rodents (Singleton *et al.* 2003).

For small herbivorous mammals I separate species with altricial young from those with precocial young, following Wolff (1997). I propose that the primary control of population change in species with altricial young is via an interaction of intrinsic controls with extrinsic controls. Small mammals with precocial young will not be controlled with intrinsic, social mechanisms and will be subject to top-down or bottom-up controls depending on the ecosystem. There are two important exceptions for small mammals. In severe environments, such as deserts (Dickman *et al.* 1999), bottom-up control is enforced by pulsed climatic events driving food production so that social interactions, although present, are not the main cause of population changes. In disturbed habitats, such as agricultural



fields, a similar scenario will occur (Fig. 2). By contrast, if habitats are sufficiently broken up by agriculture or forestry operations, generalised predators supported by human activities can become major drivers of population dynamics as habitat patches become a minor part of the landscape. Many of the results of Scandinavian studies of small rodents must be viewed in the light of these landscape effects. I suggest that primary control for small mammal populations is a combination of top-down, bottom-up, and intrinsic mechanisms, as diagrammed in Fig. 2.

There is abundant evidence of intrinsic processes limiting population growth rates in small rodents (Krebs *et al.* 2007), and it is important for small mammal ecologists studying species with altricial young to recognise that population changes through intrinsic processes exist. The fact that it is very difficult to study intrinsic processes such as infanticide in field populations must be recognised as one important reason that more data are not available on the role of intrinsic processes in governing population changes.

The woylie or brush-tailed bettong (*Bettongia penicillata*) is a classic small mammal conservation case in Australia because it has been driven to near extinction by red fox (*Vulpes vulpes*) predation (Risbey *et al.* 2000). As such, it would appear to contradict the generalisations in Fig. 2. But I would classify introduced predators in the category of habitat degradation, and would not expect a species like the woylie to show any intrinsic population control in the face of such changes arising from invasive pests like the red fox.

## Discussion

I have discussed population changes only in herbivorous mammals, and have not covered predator population dynamics. Predator populations are typically thought to be food limited, but this generalisation needs further analysis because different predator species show an array of controls from food shortage, territoriality and infanticide in wolves (*Canis lupus*) and lions (*Panthera leo*) to intraguild predation of predators on other predators. A review of population control in predatory mammals is needed to address the kinds of issues raised in this paper for herbivores.

To test the conjectures of Caughley and Krebs (1983), Erb *et al.* (2001) analysed time series of long-term data on 30 populations of large and small mammals to look for evidence of direct or delayed density dependence. They identified delayed density dependence with extrinsic control, and direct density-dependence with intrinsic control. On the basis of 30 time series, they found that almost all time series showed delayed density dependence, and consequently rejected the Caughley–Krebs conjectures. But this analysis is deeply flawed by the initial assumption that direct and delayed density dependence can be mapped on to intrinsic and extrinsic control, and I can see no justification for this assumption. Many time series will show both direct and delayed density dependence without informing the user about the mechanisms behind these relationships. Their finding of reduced variability within time series of population changes in large mammals relative to small mammals is correct, although, as Sinclair (1996) showed, when variability is expressed on a time base of per generation, small and large mammals have equal variability.

Graeme Caughley discussed the dynamics of large mammals largely within the mechanistic paradigm (Sibly *et al.* 2003). He approached the plant–herbivore dynamics of kangaroos and caribou (Caughley and Gunn 1993) with a mechanistic understanding of how these species responded to weather-induced variations in food availability. The surprising conclusion that Caughley and Gunn (1993) reached was that little understanding in these systems could arise from the standard population dynamics approach through density dependence. As time has passed, the literature is less and less occupied with arguments about density dependence and more and more occupied with trying to find the mechanisms behind the population changes we observe. These mechanisms must be known to apply proper management to populations and to conserve populations in decline.

Management and conservation have both profited from the conjectures of Caughley in his many papers on population dynamics. His main points have been that management must address mechanisms if they are to achieve changes in both pest and endangered species, that these mechanisms can be explored with simple models, and that alternative hypotheses should always be present. While these ideas have been taken up strongly in conservation biology, they have also become an important component in kangaroo management (Cairns and Grigg 1993; Jonzen *et al.* 2005) and in pest management (Hone 2007).

One of the failures of the Caughley and Krebs (1983) paper was to attempt to explain the evolution of intrinsic population control via group selection. This type of natural selection might occur but is unlikely, and a much more testable model of the evolution of intrinsic control was provided by Wolff (1997). Wolff (1997) argued that the division was not between large and small mammals, as Caughley and Krebs (1983) suggested, but instead was based on the potential for infanticide that follows from having altricial young. Mammals that have altricial young are likely to evolve social mechanisms to prevent infanticide, and these social mechanisms have as a secondary consequence the possible control of population density. The Wolff hypothesis thus provides an explanation for the example of snowshoe hares (*Lepus americanus*), which are both small mammals and yet are controlled top-down by predation rather than by social mechanisms (Krebs *et al.* 2001). Similar top-down controls are suggested for mountain hares (*Lepus timidus*) by Newey *et al.* (2007), who postulate that predators and parasites exert control for these hare populations in Europe and Asia. Life-history characteristics are one potential key to population control in herbivores, in contrast to a simple body size dichotomy used by Caughley and Krebs (1983).

There is no doubt that both extrinsic and intrinsic controls operate in small herbivore populations for species with altricial young, as shown in Fig. 2, and the key is to determine the relative strength of intrinsic controls, top-down and bottom-up mechanisms in changing the rate of population increase. As more and more of the Earth's habitats are degraded by human activities, the generalisations that once held for natural ecosystems may not apply to many of the populations that are the focus of natural resource management.

The approach Graeme Caughley took to understanding population changes in large mammals has now a long history

of successes in the use of functional responses to changes in food resources. And he did appreciate that some large mammals with intact predator communities could be controlled with no food resource limitation, and thus that it is not necessary to study plant–herbivore dynamics for all species in order to carry out proper management. As in most ecological generalisations, there are exceptions, and overall the simple conjectures of Caughley and Krebs (1983) have been superseded by further research on the mechanisms of population control in large and small mammals. Although the devil is in the details of population control, and there is much biological interest in the quirks shown by many species, the Grand Vision of Caughley still provides an outline of how to approach population dynamics of both large and small vertebrate species.

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