Acta Oecologica 53 (2013) 73–87

Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Original article

Experimental and observational evidence reveals that predators in natural environments do not regulate their prey: They are passengers, not drivers

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ARTICLE INFO

Article history:
Received 17 June 2013
Accepted 24 September 2013
Available online 10 October 2013

Keywords:
Bottom–up/top–down
Carrying capacity
Doomed surplus
Food limitation
Outbreaks
Limitation/regulation
Survival of the young

ABSTRACT

Among both ecologists and the wider community there is a tacit assumption that predators regulate populations of their prey. But there is evidence from a wide taxonomic and geographic range of studies that predators that are adapted to co-evolved prey generally do not regulate their prey. This is because predators either cannot reproduce as fast as their prey and/or are inefficient hunters unable to catch enough prey to sustain maximum reproduction. The greater capacity of herbivores to breed successfully is, however, normally restricted by a lack of enough food of sufficient quality to support reproduction. But whenever this shortage is alleviated by a large pulse of food, herbivores increase their numbers to outbreak levels. Their predators are unable to contain this increase, but their numbers, too, surge in response to this increase in food. Eventually both their populations will crash once the food supply runs out, first for the herbivores and then for the predators. Then an "over-run" of predators will further depress the already declining prey population, *appearing* to be controlling its abundance. This latter phenomenon has led many ecologists to conclude that predators are regulating the numbers of their prey. However, it is the same process that is revealed during outbreaks that limits populations of both predator and prey in "normal" times, although this is usually not readily apparent. Nevertheless, as all the diverse cases discussed here attest, the abundance of predators and their co-evolved prey are both limited by their food: the predators are passengers, not drivers.

1. Introduction

The debate as to whether the abundance of animals is determined by active top–down regulation by mortality factors or passive bottom–up environmental limitation continues unabated. However, my purpose here is not to review this controversy with an analysis of the pros and cons in the debate. There are already a large number of arguments in the literature supporting the top–down view. Instead I present an over-view of published studies that reveal that predators – the most commonly invoked regulating mortality factor – are, like their prey, subject to bottom–up limitation of their populations. These studies provide experimental and observational evidence across a wide taxonomic and geographical range that there is a common pattern running throughout the animal kingdom – predators follow the prey dynamics rather than regulate them. They also reveal that the processes that lead to both irregular outbreaks and cyclic peaks of great abundance are the same as those that limit the size of endemic populations during "normal" times.

Today, however, the belief that predators regulate their prey is firmly established as the dominant view among ecologists. To prevent prey populations from increasing until they destroy their environment, or dwindling to extinction, it is said to be necessary that the numbers in a prey's population must be regulated by the negative feed-back actions of their predators that tend to return the prey's numbers to an "equilibrium" or "mean" density. I have previously discussed this concept, the definition of regulation, and the fallacy that there is such a thing as a mean population in nature (White, 2001, 2004, 2007). To a great extent this thinking has been based on uncritical acceptance of the Lotka–Volterra theoretical description of these trophic interactions. Only recently has the correctness of this long-standing paradigm been seriously questioned (Murray, 2011; Arditi and Ginzburg, 2012). Furthermore, experimental research that supports the concept has come largely from work with closed laboratory populations: protozoans in solutions of nutrients (Gause, 1931); beetles confined in jars of measured amounts of flour (Park, 1933); maggots eating controlled amounts of meat (Nicholson, 1933); mice living in a confined space

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http://dx.doi.org/10.1016/j.actao.2013.09.007

and supplied with unlimited food (Southwick, 1955). In the field the concept has been reinforced by studies of animals confined in fenced enclosures or on small islands (Coulson et al., 2004). And computer models – closed populations framed around carefully selected (or excluded e.g. Gilg et al., 2003) parameters – have continued its widespread acceptance.

Beyond ecology, however, the concept has percolated into and become deeply ingrained in society generally. In radio, television and press articles, and in everyday conversation, the belief that predators regulate their prey is widespread and unquestioned. The immediate response to any reference that an animal has become a pest, or is proliferating in a new environment, is that this is because its "natural enemies" are absent or it has, in some unspecified manner, "escaped" from being "regulated" by one or more of its predators. Furthermore, the whole concept and practise of biological control has been built on this assumption.

This widespread and ready acceptance among the general public and ecologists alike, that animals must be regulated by the action of their predators, probably stems from a combination of deeply ingrained prejudices and fears. Not least of these is the innate need of humans to control the world around them and therefore assume that the natural world is similarly regulated. Then there is the ingrained ancestral fear of both our own predators and those of our domestic and managed animals, coupled with the knowledge of the impact that human harvesting has had on populations of wild animals. At the same time the "tooth and claw" activity of predators in nature is still readily observed (and frequently highlighted in television documentaries), while there is usually no obvious sign of resources (or space) being limiting in the environment.

There are, however, some situations where predators would appear to be regulating their prey. But these have all been brought about where the original evolved predator–prey interactions have been significantly altered or eliminated by human intervention. As such they should not be used to draw conclusions about the functioning of undisturbed natural predator–prey interactions.

First, the congregating of predators to attack easily caught livestock kept enclosed in large dense herds does not equate to their hunting of scarce and scattered prey in a natural environment.

Second, once humans invented weapons and traps for hunting and catching other animals, they ceased to be predators. They became harvesters able to access a far greater pool of available food than they would ever have done as unaided predators. With modern techniques they have reduced many species to near or actual extinction. Similarly, populations of wild animals can be artificially managed at numbers well below the capacity of the habitat to support them.

Third, the introduction of foreign predators to new environments has caused changes to the evolved predator–prey interactions that originally prevailed in both the original and new environment. In particular, native species have no evolved capacity to avoid the attacks of invaders, resulting in the extermination of many.

These exceptions aside, however, there are a great many studies of many and diverse species in all parts of the world that demonstrate that native predators are not able to control the numbers in, nor the ultimate size of the populations of their co-evolved prey. Rather than there being top–down regulation of prey by their predators, there is bottom–up limitation of both prey and predator. The only times in a natural evolved situation when predators appear to be regulating their prey is when a decrease in the rate of reproduction of the prey allows the inevitably lagged increase in the numbers of the predators to "over-run" the remaining prey. Some of these necessarily short-lived events are discussed in the following examples.

2. Examples of predators not regulating their prey

Many studies that reveal how predators are limited, just like their prey, by the availability of food have already been reported (White, 1993, 2008). Here I discuss studies that more specifically reveal the converse of this; that predators are not normally able to regulate the abundance of their food.

2.1. Predators of small mammals

The belief that predators regulate the numbers of their prey is probably strongest and most widespread in studies of cyclic populations of a variety of sub-Arctic animals. In the case of voles most emphasis is on the role of their mammalian predators, especially the mustelids (stoats and weasels) that are said to be specialist predators controlling cyclic changes in their abundance (Oli, 2003a, and references therein). However, it is a misnomer to label them as specialists. A truly specialist predator (such as a parasitoid of the eggs of but a single species of insect) must be wholly dependent for its survival on access to its prey. These mustelids, on the other hand, simply preferentially attack the most abundant and easily captured prey available at the time. When food is scarce they will eat anything they can catch.

Apart from that, however, this hypothesis is based primarily on mathematical modelling. But these models "… simply formalise hypotheses" (Lambin and Graham, 2003), and produce results depending mainly upon what environmental factors are included in them (Krebs, 1995) – or more importantly, *excluded* from them (Gilg et al., 2003; Okamoto et al., 2012). And there is, anyhow, much experimental and observational evidence that these predators do not control the abundance of their prey. Specifically, Graham and Lambin's (2002) study of the field vole (*Microtus agrestis*) and its predator, the weasel (*Mustela nivalis*) in a plantation in northern England (called by Oli, 2003b " … one of the most rigorous experimental tests of the specialist predator hypothesis") disproves the hypothesis. Their results conclusively demonstrated that "… changes in weasel predation rate were not responsible for driving the population cycles of field voles …" that predation by weasels "… was neither sufficient nor necessary to initiate and drive cyclic decline of field vole populations", explaining "… only 5% or less of the variation in field vole survival." Graham and Lambin's (2002) findings were strongly questioned by a number of prominent proponents of the predation hypothesis (Korpimaki et al., 2003), but without demolishing them.

Furthermore, this is not an isolated case. In Norway Ekerholm et al. (2004) excluded mammalian predators (principally stoats, *Mustela erminea*, and weasels) from the common habitat of the field, grey-sided (*Clethrionomys rufocanus*), red (*Clethrionomys rutilus*), and root (*Microtus oeconomus*) voles. During the increase phase of the vole cycle the authors found that predators had no effect on their rapidly multiplying prey. There was no difference between the numbers of voles in the exclusion and control plots. But during the declining stages of the cycle the density of voles was significantly lower in the presence of predators, the difference becoming four-fold in the final crash year. And the strongest response was displayed by the reproducing females and young of the field voles that are considered to be the major prey of weasels. So the lagged "over running" of a declining prey by its predators was clearly demonstrated, and the authors concluded that their results confirm those of Graham and Lambin (2002) as supported by Oli (2003a,b): predation by these small mustelids is neither necessary nor sufficient to drive the cycles of abundance of the voles.

Similarly, Norrdahl et al. (2004) have reported that reducing the numbers of weasels and stoats had no significant effect on changes