

Reappraisal of the role of big, fierce predators!

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Abstract The suggestion in the early 20th century that top predators were a necessary component of ecosystems because they hold herbivore populations in check and promote biodiversity was at first accepted and then largely rejected. With the advent of Evolutionary Ecology and a more full appreciation of direct and indirect effects of top predators, this role of top predators is again gaining acceptance. The previous views were predicated upon lethal effects of predators but largely overlooked their non-lethal effects. We suggest that conceptual advances coupled with an increased use of experiments have convincingly demonstrated that prey experience costs that transcend the obvious cost of death. Prey species use adaptive behaviours to avoid predators, and these behaviours are not cost-free. With predation risk, prey species greatly restrict their use of available habitats and consumption of available food resources. Effects of top predators consequently cascade down to the trophic levels below them. Top predators, the biggies, are thus both the targets of and the means for conservation at the landscape scale.

Keywords Biodiversity · Conservation · Costs of predation · Indirect effects · Non-lethal effects · Predators · Top-down control

Amid concern over the increasing impact of humans on earth's biota, ecologists have increasingly sought clues to the maintenance of biodiversity. A growing number of studies point to the powerful role played by top predators. The loss of predators, particularly top predators, leads to biodiversity loss (Terborgh et al. 2001; Estes et al. 2001), thus jeopardizing ecosystem integration. Top predators, the biggies, are thus heralded as both

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the target of and the means to conserve biodiversity at the landscape scale (Ray et al. 2005). Such efforts are epitomized by slogans like, ‘Save the tiger’, ‘Save the white shark’, ‘Save the grizzly’, or other large carnivore-orientated campaigns (Seidensticker 1997) and are reflected in ecologists’ present endeavors to scientifically justify the connection between predators and biodiversity (Soulé and Terborgh 1999; Estes et al. 2001). Various claims are made that charismatic species such as large carnivores can act as important flagships, umbrellas or indicators (Simberloff 1998) for the conservation of the rest of the biodiversity, and even that some are vital keystone species for ecosystem function (Noss et al. 1996). The mounting evidence of a tight association between apex predators and high biodiversity justifies targeting top-predator species for their conservation utility on ecological grounds (Ray et al. 2005; Sergio et al. 2005, 2006).

Here we examine the recent arguments concerning the role of apex predators on ecosystem structure and function from an historical perspective. We will show that Ecologists are reinventing the wheel (cf. Oksanen 1991)! We consider the reasons why, and we end with a reminder that old science can be good science, and knowledge of the historical development of a field can be a potent component of a scientist’s intellectual arsenal.

Over half a century ago, Leopold (1943) suggested that predation was a necessary component of all ecosystems and that its loss could lead to grave ecological consequences. He argued that the loss of predators set the stage for an irruption of the Kaibab (mule) deer population followed by a degradation of habitat and an eventual reduction in carrying capacity. This study, once considered a classic, was widely reported in the ecology textbooks of the 1960s as an example of an ungulate population eruption in the absence of their predators. In a powerfully constructed article, Caughley (1970) criticized Leopold’s interpretations and forwarded alternative hypotheses for the deer irruptions, such as interrelationship of livestock grazing and fire control. New analyses of aspen tree rings from the Kaibab are, however, consistent with Leopold’s hypothesis of extreme deer herbivory following predator removal, as well as the importance of predation in controlling deer populations on the Kaibab (Ripple and Beschta 2005). Using modern analyses, today ecologists are finding Leopold’s interpretations to be right on the mark, several decades after their publication. In fact, Leopold may have been more correct than he could know. Given modern paradigms, one can envision situations in which, in the absence of predators, an herbivore species depletes its food reserves simply by experiencing no fear. In the absence of fear, herbivores can increase both their use of available habitats and food resources.

The classic view of predators, likely held by Leopold, was that predators were important because they helped maintain a balance of nature—between population growth and mortality; between food supply and herbivore, and between herbivore and predator. Today we would say that the classic view is based on the premise of equilibrium. We now recognize that while equilibrium is a most useful theoretical construct, it probably rarely manifests in nature. Top-down effects of big, fierce carnivores occur regardless of an assumption of equilibrium.

Naturally, one wonders why was there such a delay reinventing the wheel. Perhaps Caughley’s (1970) devastating re-analysis of the Kaibab deer story made ecologists “gun shy” over the potential of top-down community effects. Alternatively, perhaps due to small sample sizes, large ranges, and the logistical challenges of performing manipulative experiments with top predators, our understanding of the role of large carnivores in ecosystem function has remained unclear and contentious (Soulé and Terborgh 1999). Or, as suggested recently by Knight et al. (2006), ripple effects of predators on lower trophic levels, particularly the producer, depend on relative consumption of mutualists versus

antagonists of producers. Trophic cascades are not likely observed when predators consume producer mutualists, which may obscure their ecosystem-wide effects.

Science emerged from the Second World War with a new paradigm, systems analysis (Bode 1945). Under this view, complex systems are conceptualized as interconnected components with feedback loops that stabilize the system at equilibrium. This paradigm established the notion that living and non-living parts interact via fluxes of matter and energy. Further, apex predators, as end points of those fluxes, are of minor consequence to ecosystem function (Estes et al. 2001). Ecosystems are regulated by forces acting from lower to higher trophic levels. With these views dominant, it is perhaps unsurprising that top-down control by predators was not considered an essential process in shaping communities.

As argued earlier by others (Cody and Diamond 1975; see also *American Naturalist* 122(5) 1983), competition was long held to be the principal factor structuring natural communities. Emphasis on competition may be traced to Darwin (1859), who asserted that the struggle for existence should be most keen among the most similar species. Gause's (1934) laboratory experiments in the early 1930s, the first controlled tests of species interactions, bolstered that competition could decide the outcome of the struggle. By the mid-20th century, competition was widely viewed as the principle organizing force in communities, and the niche was the fundamental unit of that organization (MacArthur 1972). Given that the Lotka–Volterra predator-prey model was neutrally stable and that Gause's predator-prey system usually went to extinction, the ecological realm fortified by the process of competition seemed impenetrable. The period from the 1960s through the early 1970s was indeed the heyday of competition.

The questioning of the ubiquity of competition as the dominant factor structuring natural communities, coupled with increasing use of field experiments in the 1970 and 1980s, led to a growing consensus regarding the importance of predation relative to competition (Sih et al. 1985). This was a much delayed response following the first incontrovertible evidence of the keystone role of predators in regulating the diversity of the prey community (Paine 1966). This is surprising when considering that the keystone concept fit nicely with the notion of cascading effects of predators in a food chain (Hairston et al. 1960). Paine's manipulations of seastar densities provided a central body of evidence in the formative period of the predation paradigm (*sensu* Kuhn 1962) that was characterized by innovative field experiments and hypothesis testing in the context of historical arguments of competition theory (Robles and Desharnais 2002). Evidence from field studies was also encouraging: a principal result of the first scientific effort to understand tiger ecology (Schaller 1967) posited the tiger as the main factor limiting the growth of the populations of its prey.

We suggest that the full significance of predation on communities was not possible until all the costs of predation were more fully appreciated. Predation, even on large prey, can often be of large magnitude. The percent mortality among large herbivores—such as buffalo, springbok, and wildebeest—by predators in natural ecosystems in Africa ranges from 59% to 96% (Prins and Iason 1989). No surprise that predation affects prey population directly via mortality (Crawley 1992): predators consume prey, thus affecting their density. But prey try to avoid being eaten, often at considerable costs (though obviously not as great a cost as death). The former is the domain of population ecology and the latter is that of evolutionary ecology. Classic population ecological studies and models of community dynamics incorporate only how changes in predator densities affect community dynamics by directly killing their prey (e.g. Hairston et al. 1960; Rosenzweig 1973; Oksanen et al. 1981). Evolutionary ecology teaches us that prey adopt adaptive behavioural strategies that reduce or eliminate their probability of death by predation (Mangel and Clark 1988; Lima

and Dill 1990; Lima 1998; Brown et al. 1999)—and that these strategies come with significant costs to the prey species using them.

Traits that allow prey to avoid predation and thus strongly affect fitness will be under strong selection (Abrams 2000). Today, many evolutionary biologists believe that predation has played a major role in determining patterns in the history of life on this planet. The mere presence of predators in a community can force prey to make behavioural choices between vital activities such as feeding and avoiding contact with predators. The effects that ripple through the food web via evasive behaviour of herbivores are known as higher order (Werner 1992) or behavioural or trait-mediated indirect interactions (Abrams 1995; Werner and Peacor 2003; Schmitz et al. 2004). This recent avenue of research has brought new insights into how predation risk, in addition to actual predation, affects populations, communities and entire ecosystems (Sinclair and Arcese 1995; Berger et al. 2001; Brown and Kotler 2004; Ripple and Beschta 2005). Recently, Creel et al. (2007) show that in large ungulates (elk) these antipredator responses are associated with costs that can be measured by changes in reproductive physiology and demography. Today ecologists recognize the significance of trait-mediated interactions. The 91st Annual Meeting of the Ecological Society of America (2006) held in Memphis, TN (USA) devoted an entire oral session (out of 18) on implications of trait-mediated effects (<http://www.esa.org/memphis/session-Schedule2.php>). Interestingly, trait effects have been shown as large as (Preisser et al. 2005) or even larger (Schmitz et al. 1997) than density effects. When faced with predation risk, prey select relatively safe habitats which are often poor in resources (Bergerud et al. 1983; Creel et al. 2005) and they increase vigilance in risky habitats (Elgar 1989). By constraining habitat selection and adaptive shifts in foraging behaviour, predators may have greater effects on prey dynamics than would be predicted on the basis of direct predation alone. Apparently, a predators' mere presence may bring changes in prey's behaviour, i.e. foraging mode, habitat use patterns, mating system and life history traits that determine prey's niche. Subsequently, by the early 1990s assumption that competition primarily determines niches was no longer held, but instead biologists suggested that both competition (resource related) and anti-predator needs affect niche characters (Sih et al. 1985).

With the onset of the current millennium, ecologists have amassed a plethora of evidence demonstrating that predators can have tremendous influences on the structure of and the dynamics of ecological populations and communities. Apparently, predators do so (1) by limiting or even regulating their prey, (2) by their keystone effect (wherever keystone predators are present) and the subsequent cascading impacts down the food chain and (3) via higher order interactions. Such insight was made possible by looking at predation with broader perspectives in light of the conceptual framework and present techniques of population, community and evolutionary ecology. From our current perspectives, Leopold (1943) was correct in his predictions about the consequences of predation on communities and ecosystems.

Although we directed our comments toward top predators, the biggies, we suspect that the same points hold for many other predators, independent of body size (Terborgh 1988). Insectivorous birds control herbivorous insects and can significantly affect plant fitness (Marquis and Whelan 1994; Mols and Visser 2002), effects that could affect forest composition and structure (Whelan and Marquis 1996). The composition of tallgrass prairies of North America can be profoundly affected by vole herbivores (Howe and Brown 1999), but this effect is likely strongly modulated by lethal and non-lethal effects of their predators. With predators, voles restrict their habitat use and reduce damage to favored food plants (Desy and Batzli 1989). The mere presence of spiders affects habitat use and foraging activity of grasshoppers (Schmitz et al. 1997). Effects of these smaller predators, too, clearly

transcend consumption of prey. Now, where should we go? First, this mini-review bolsters the suggestion that not only density effects, but also trait effects, must be integrated into empirical and theoretical studies (Luttbeg and Kerby 2005; Creel et al. 2007). Second, conservationists and managers should continue to incorporate the role of predators into the doctrine and practice of conservation (see special issue of the *Israel Journal of Zoology* 50, numbers 2–3). Third, conservation biologists should develop monitoring programs capable of detecting trends in predator populations and their effects on biodiversity.

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