

COMMENTARY

Subsidized predators, landscapes of fear and disarticulated carnivore communities

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The subsidization of predators occurs when humans directly or indirectly alter resource availability in such a way as to increase the density of a predator population above levels that would occur without the additional resources. Subsidized predators can drastically impact prey populations because subsidies insulate the predator populations from the effects of declines in prey populations (Sinclair *et al.*, 1998). Such scenarios become problematic for conservation practitioners when the enhanced predator population influences species of conservation concern. Examples of this are widespread: subsidized ravens influence tortoise ecology (Boarman, 2003); subsidized predatory beetles influence insect herbivore populations (Rand & Louda, 2006); subsidized mountain lions influence bighorn sheep demographics (Rominger *et al.*, 2004); and in the example presented by Shapira, Sultan & Shanas (2008), subsidized red foxes *Vulpes vulpes* influence gerbil ecology.

Shapira *et al.*'s fox-gerbil example is particularly interesting because the influence of foxes is best seen not in altered densities of gerbils *per se*, but in the behavior of these taxa. In areas near farms, the availability of crops and favorable habitat apparently subsidize foxes. As a result, in areas where foxes are putatively more abundant, gerbils are not only less abundant but are also less active, and show decreased foraging efficiency. This suggests that foxes in this agricultural region have altered gerbil biology not by direct predation alone, but also by creating a landscape of fear (Brown, Laundré & Gurung, 1999; Laundré, Hernandez & Altendorf, 2001), from which the gerbils have somehow rendered a microhabitat-level map of the perceived risk of predation. It is harder, however, to address the effect of actual predation on gerbils as Shapira *et al.* do not present information on the diet of foxes.

Indeed, the differential activity rates and behaviors of gerbils at sites near and far from foxes are potentially confounded by several concerns. Foxes are not uniformly distributed but are found near farms. While this is, of course, a primary point of Shapira *et al.*'s paper, it none-

theless means that many of the factors making the farmed areas so different from the more natural surrounding areas are also presumably correlated with fox distributions and may also influence gerbil biology. In addition, which of the two gerbil species, or the ratio of the two species, that is being examined at each study site is not clear. This is important, because if the two gerbil species differ in their foraging and behavior, then observed differences in gerbil ecology and behavior that are attributed to foxes may in fact be a function of which gerbil species is visiting the seed tray. Finally, the foraging behavior of the predator itself may differ across study sites. Shapira *et al.* did not study the ecology of the foxes, but we know that predator behavior is not static. Just as prey alter their behavior to address perceived risks of predation, predator behavior also changes as a function of prey density and behavior (Lima, 2002; Quinn & Cresswell, 2004).

Nonetheless, differential intensity of fox use of the landscape does appear to be the most parsimonious explanation for the observed patterns of gerbil ecology, as these patterns match our understanding of how subsidized predators and their prey should interact. In a world in which anthropogenic landscape change is a seemingly ubiquitous concern for conservationists, can we predict *a priori* where and which predators are likely to become problematic in such situations, and can we make recommendations as we attempt to identify solutions? Although a full examination of these two questions is beyond the scope of this commentary, we know enough about the ecology of predators, of prey and of their intra- and interguild interactions to make some generalizations that may carry predictive power and applied relevance.

For instance, we know that larger carnivores may suppress populations of other guild members in the same way in which predators influence prey: through predation and by creating landscapes of fear (Linnell & Strand, 2000; Creel, Spong & Creel, 2001). At the Israeli–Jordanian study sites, the generalist and mid-sized red fox apparently outcompetes

the sand fox *Vulpes ruepelli*, which is smaller and a more habitat specialist (Ilani, 1988). Given the differential abilities of predator species to make use of human-modified habitats, generalists like red foxes are probably much more likely to become subsidized predators than are specialists like sand foxes. Elsewhere across the globe, however, red foxes are limited by still larger carnivores (e.g. in the Middle East, see Scheinin *et al.*, 2006), and this often occurs despite a relatively low degree of dietary overlap between the larger and smaller predators. Therefore, a decline in the smaller, subsidized carnivore population due to the presence of larger carnivores could alleviate some of the predatory pressures on the prey that are caused by increased numbers of the smaller carnivore. At Shapira *et al.*'s study sites, this has apparently not occurred, as the larger carnivores that might serve to limit red fox numbers are either controlled (free ranging domestic dogs) or are still in early stages of range expansion (golden jackals). Thus, red foxes have become a pernicious problem for two reasons: the species is subsidized by the agricultural landscape, and it also benefits by inhabiting a region where the natural carnivore community is fractured, thus releasing red foxes from competition with larger carnivores.

It would seem that the most simplistic management scenario to solve the problem of subsidized predators would be to target the predator species. While this might work, there are several potential difficulties with such an approach. First, intervention would be required in perpetuity and at large spatial scales, and even then the efficacy of culling programs is sometimes unclear (Harding, Doak & Albertson, 2001; Baker & Harris, 2005). A better approach might involve enhancing the quality of prey habitat, because the foraging decisions of generalist predators are a function of prey vulnerability (Quinn & Cresswell, 2004). However, while such a solution might ameliorate the effects of the subsidized predator on the prey species of concern, from a community perspective, it does not fully solve the problem as the predation pressures may merely shift to other potential prey species. Ultimately, long-term solutions for these problems might involve restoring the broader carnivore community, whose intraguild feedback loops could mitigate many of the issues identified in this paper.

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