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COMMENTARY

Does agriculture drive predator-mediated behavioral effects on prey?

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Agriculture may create or destroy habitat for native species, and some species may do better when land is converted to agricultural uses. For instance, populations of human commensals, such as rats, and some predators, such as foxes, may increase following agricultural land conversion. Shapira, Sultan & Shanas (2008) capitalized on the apparent agriculturally induced increase in red fox populations to study the behavioral decisions made by two species of gerbils.

Their 'natural experiment' was conducted along the border between Israel and Jordan in the arid Arava desert ecosystem. On the Jordanian side, pastoralists and traditional farmers live and work in the arid landscape. On the Israeli side, modern, irrigated, agricultural farms fill the land. As the authors first assumed, and then tried to verify with track counts, red fox density was higher on the Israeli agricultural lands than on the Jordanian side of the border.

The authors designed a 'giving-up-density' experiment – a method widely used by behavioral ecologists to study risk assessment (Brown, 1999). Gerbils visiting trays containing a fixed quantity of seeds mixed with sand would forage until they assessed the marginal benefits of remaining at the trays to begin to decline. We assume the decision to leave a tray is a function of both the amount of food in the tray (presumably assessed by the harvest rate), and predation risk. Assuming that gerbils would not want to spend more time foraging for less food, the amount of food they leave (the giving-up density) reflects the gerbil's assessment of risk.

Shapira, Sultan and Shanas put these trays with a fixed amount of food in close to and far from cover near and 6 km away from Israeli farms in the more rustic Jordanian landscape. They also conducted these experiments on full-moon nights and nights without moonlight because many small prey (including gerbils) are sensitive the greater risk associated with foraging when the moon is out. Gerbils left more food on full-moon nights than on moonless nights, but there was no effect of distance to cover on giving-up density.

They then conducted a more complex experiment where they created trays with diminishing returns by putting lower densities of food at a lower level of the tray and higher density of food at the top level of the trays. By putting these trays in different locations, they aimed to infer something about 'apprehension' – which is vigilance diverted toward predator detection and away from foraging (Dall, Kotler & Bouskila, 2001). Again, moon phase significantly influenced gerbil selectivity to these trays where gerbils preferred to forage on the high-density trays, rather than the low-density trays on moonless nights in Jordan, but not in Israel.

Taken together, the authors inferred that differences in fox density influenced gerbil foraging decisions. In areas where foxes were denser (Israel), the gerbils were more sensitive to variation in illumination-related risks than they were in the lower density area (Jordan).

I believe that the method of giving-up densities has an important role to play in documenting such indirect effects of predators on prey as a function of anthropogenic habitat modifications. However, I have several concerns about this particular study and its specific inferences.

First, while the authors have shown that gerbils behaved differently as a function of moon phase in Jordan than they did in Israel, they have not convincingly demonstrated this difference in risk assessment was caused by foxes. Fox-density estimates were based solely on tracking, rather than mark–recapture, so all that is really known is that there were more tracks on their transects in Israel than in Jordan (one individual that moved around a lot – which could have conceivably been moving away from humans – would leave more tracks than one individual that did not move that much). Species have multiple predators (Lima, 1992), and current behavior may be influenced by past predators (Blumstein, 2006). While Shapira, Sultand & Shanas claim that owls and snakes are unimportant and rare in this habitat, the current or historical abundance of owls and snakes may also affect prey behavior. While the authors assert that animals were protected, it is possible to imagine scenarios whereby owls or snakes were harassed differentially on either side of the border. Thus, without a better understanding of the relative abundance of all predators, it seems premature to assert that this effect was solely due to foxes.

Second, assuming that there were in fact more foxes in Israel than in Jordan, the authors assert that the increase in foxes was a direct result of agriculture, but they fail to demonstrate this convincingly. Other uncontrolled factors might be responsible for the increased density of foxes in Israel.

Third, and this is an issue with many, but not all, giving-up-density studies, the authors failed to look at the behavior of individuals. It was impossible for them to determine which species foraged at the trays and they were unable to determine how many different individuals foraged at the trays. While studying multiple species is a bit of worry, I do not feel that the issue of multiple foragers is as substantial a problem if they wish to draw inferences about the gerbils at a location. However, if one wants to assert that individual risk assessment varies, it becomes more of an issue.

Despite these shortcomings, let us step back and put this potentially important result in context.

This study suggests that agriculture may have unanticipated indirect effects on prey if agricultural practices increase predator abundance. Predators affect prey populations directly through predation, and indirectly through fear (Brown & Kotler, 2007). This study has shown that the presence of foxes may have an indirect effect on gerbils. Acting through fear, foxes may reduce gerbil carrying capacity, not only directly through predation, but also indirectly if gerbil reproductive success is tied to foraging success. Thus, we should generally look for such indirect as consequences of anthropogenic actions that increase the populations of human commensal predators.

Direct and indirect effects of commensal predators may happen on a relatively small spatial scale. Presumably, the effect is associated with the size of the carnivore's home range. Larger carnivores range over larger distances (e.g. Carbone *et al*., 2005), so larger commensal carnivores will have a larger spatial effect on prey. Future studies could formally test this hypothesis, in this and other systems, by having multiple giving-up-density plots different distances from the Israeli farms (a design that might not work in this area because of border security issues).

The increase in commensal carnivores also could affect other carnivores, which may have consequences for their prey. Typically, larger carnivores compete with and displace smaller ones (Caro & Stoner, 2003), and by favoring one species, smaller competitors may be displaced and populations of smaller prey may increase. The ecological consequences of this imbalance need to be studied fully.

Ultimately, we wish to develop the link between individual foraging decisions (and how they are impacted by humans directly or indirectly) and fitness (Tarlow & Blumstein, 2007). I believe that combining giving-up density and other feeding tray studies along with other more direct observations of foraging behavior can be very revealing. Such individually focused studies are essential to develop mechanistic models that will allow us to better predict the effects of anthropogenic impacts on wildlife (Blumstein & Fernández-Juricic, 2004) which are likely to be both complex and wide ranging.

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