most modern insects and who can collapse their wings posteriorly). In fact, the basal splits of Pterygota remain a contentious issue, even in current analyses of large genomic data. Interestingly, early scholars like Anton Handlirsch believed all winged insects evolved from Palaeodictyopterida, and that this group originated directly from trilobites. However, current hypotheses support either placement of palaeodictyopterids with mayflies and dragonflies or alternatively as the extinct sister group to the Neoptera (Figure 2).

Where can I find out more?

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Primer

Ecology of fear

Liana Y. Zanette* and Michael Clinchy

The 'ecology of fear' refers to the total impact of predators on prey populations and communities. The traditional view in ecology is that predators directly kill prey, thereby reducing prey survival and prey numbers — and that this is the limit of their ecological role. The ecology of fear posits that the behavioural, physiological and neurobiological costs of avoiding predation ('fear' for short) may additionally reduce prey fecundity and survival, and the total reduction in prey numbers resulting from exposure to predators may thus far exceed that due to direct killing alone. If this is the case, then failing to consider fear as a factor risks profoundly underestimating the ecological role predators play.

The ecology of fear is not only of academic interest but is directly relevant to conservation, in particular the conservation of large carnivores. Lions, tigers and wolves are among the most charismatic animals on the planet, and as with most large carnivores, their numbers have dwindled dramatically in recent decades, such that tigers are officially endangered and lions are considered vulnerable to extinction. Wolves were effectively extinct in the contiguous United States, and much of Europe, by the mid-20th century. The merits of their reintroduction or recolonization have been the subject of much debate, centered on whether the fear wolves instill in their prey significantly augments their impacts on prey and the maintenance of natural ecosystems.

Fear can be readily seen in prey fleeing from its predator. Darwin was struck by the absence of fear in birds on the Galapagos Islands, noting that they did not flee at the approach of a dangerous predator (himself), causing him to write in *The Voyage of the Beagle* about the "fear of man [as] an acquired instinct". Referring to anti-predator behaviour as 'fear' is thus something students of nature have been doing for centuries, and lay readers have had no difficulty understanding. The fundamental challenge associated with studying the ecology of fear is that while one can see fear-related behaviours, and one can see a predator killing a prey, one cannot directly see fear reducing the reproduction or survival of prey, but must instead infer its effects. This means that manipulative experiments are essential to making strong inferences about the effects of fear. The debate about whether fear augments the ecological role of large carnivores continues precisely because of a lack of manipulations in those systems. Instead, virtually all research has been based on correlations, which critics may correctly claim could be spurious. Evidence that fear affects prey populations has so far come from manipulations in other systems, but are likely to apply across the animal world.

Prey can 'die of fright'

Fear can kill, and it can also reduce fecundity, and as a consequence fear can be as important as direct killing by predators in affecting prey numbers. These remarkable facts are supported by hundreds of elegant manipulative experiments on invertebrate and aquatic species, typically conducted in terrariums or aquariums. Measuring effects on populations is made considerably easier if the animals are small, and the population is 'closed', so there is no immigration or emigration. And, if the population is actually enclosed, this makes it relatively easy to find the prey, to count how many young they have had, or how many have survived. This capacity to account for all the additions (births) and losses (deaths) in the prey population was critical to first establishing that fear itself can affect prey numbers. The second critical requirement was to demonstrate that predators can affect prey numbers in the absence of direct killing. This can be done in invertebrate systems by gluing the predator's mouthparts shut, thus rendering them 'toothless'. In a classic experiment, researchers contrasted the number of deaths of grasshopper nymphs under control conditions (no predator), with that in the presence of a 'toothless' predator (a spider with its mouthparts glued), and a predator that could directly kill its prey (an intact spider). That prey can literally 'die of fright' was demonstrated by deaths being increased by 20% in the presence of the 'toothless' predator compared to the control. Fear can be as important as direct killing, as deaths increased by just a further 9% in the presence of the intact

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Figure 1. Fearsome predators and their frightened prey.
Spiders (Photo: Opoterser/Wikimedia Commons) can literally frighten grasshoppers (Photo: Mister Light/ Wikimedia Commons) to death. Fear of wolves (Photo: Mas3cf/Wikimedia Commons) may reduce the pregnancy rate in elk (Photo: California Department of Fish and Wildlife), and it is an open question whether the fear of lions (Photo: Yathin S. Krishnappa/Wikimedia Commons) can affect the reproduction of megaherbivores, such as elephants (Photo: Liana Zanette) — though new research suggests fear of the human 'super predator' likely can.

predator that could both frighten and directly kill its prey.

Spiders and grasshoppers in a terrarium may seem a far cry from wolves and elk in North America's Rocky Mountains, or lions and elephants on the African savanna (Figure 1), but is this apparent difference a biological one? There are compelling reasons to expect that the ecology of fear may manifest itself differently across different taxa, but that the net effect of fear on populations may be largely the same.

One fundamental difference is parental care. Parental care defines what it is to be a mammal and is present in virtually all birds, but it is largely absent in other taxonomic groups. For most birds and mammals, the survival of young will depend on the actions of their parents, but it is not pertinent in the majority of other species. Manipulative experiments testing the 'ecology of fear' in birds and mammals need to evaluate effects on the survival of dependent young, given that fear is well-known to affect parental care. Related to this are effects of fear on adult survival, which may be more or less relevant, depending on the species, particularly as prey body size increases. Elephant bulls, for example, have no predators to fear (except for humans of course).

Regardless of whether it is fecundity, offspring survival, or adult survival, that is most affected, the most compelling reason to expect that fear is likely to almost universally affect prey populations is because scared prey eat less. Grasshoppers, elk and most elephants alike all have to divert attention from eating to pay attention to predators, and if eating is significantly impaired for protracted periods this will definitively reduce fecundity and survival.

Of the manipulative experiments testing the 'ecology of fear' in free-living wildlife that have now been conducted, the evidence to date demonstrates that fear can kill, and it can affect fecundity, and the consequences can be considerable. In the wild, predators not only kill adult prey but also prey offspring. Apparent reductions in fecundity or offspring survival in the presence of predators could thus be due to fear, or undetected direct killing by predators. Researchers have disentangled these two effects and isolated the impact of fear in an experiment on free-living wild songbirds. Gluing shut the mouthparts of predators is obviously not possible for wildlife. Instead, the researchers rendered predators 'toothless' by preventing direct killing by predators at every bird's nest. Then, the researchers manipulated fear by broadcasting predator calls and sounds on some territories, while others heard non-predator calls and sounds. Parent birds that heard predators, laid fewer eggs, incubated them less well such that fewer hatched, and fed their offspring less often such that fewer survived, with the net result that they produced 40 % fewer offspring than parents that heard non-predators (Figure 2). Comparable effects of fear itself have been demonstrated in subsequent similar experiments on other songbirds and small mammals.

The magnitude of fear effects on fecundity and survival as a result of scared prey eating less can be further revealed by manipulating food availability. Once again this has been repeatedly demonstrated in experiments on invertebrate and aquatic species. That the same is true in wildlife is strongly indicated by the results of a large-scale (multiple km^2) multi-annual experiment on snowshoe hares and arctic ground squirrels, and a comparable experiment on songbirds. Both experiments employed a bi-factorial design involving adding supplemental food or not, at sites with more or fewer predators, and the results in all three species demonstrated that the effects of increased food availability were completely contingent on predator abundance. Adding food where there were more predators led to only modest benefits to populations as did reducing predator numbers without the addition of food. By contrast, adding food where predators were fewer led to greater than expected benefits to populations. These results are all consistent with the notion that scared prey eat less, and furthermore, do so even when the food supply is unlimited, with ensuing demographic consequences. Indeed, the behavioural evidence further indicated that fear was the cause of prey venturing out less (and hiding more) to use the supplemental food when there were more predators around (and thus more to fear).

Fear cascading through communities

That prey can avoid their predators by hiding from them reflects the fact that the danger from predators is not uniformly distributed in space and time in natural environments, and there are both more dangerous places and times to be active and safer places and times. This spatial and temporal variation in the danger posed by predators has been termed the 'landscape of fear'. Whether and how the 'landscape of fear' has a bearing on prey fecundity or survival (i.e. how it might affect the ecology of fear) could depend on the distribution of the prey's food. If food and danger co-occur, for example, then prey fecundity and survival would be expected to be low, but if food and safety co-occur, fecundity and survival might be high. This interaction between the prey's food and its predators is why the 'ecology of fear' concerns impacts on both populations and communities, because most prey are predators themselves in the sense that they consume other organisms, and the magnitude of fear effects are thus a function of — and in turn affects — the food chain. The rippling effects of fear down the food chain can thus cause a trophic cascade. For example, the fear predators inspire in their prey, by causing the prey to eat less and reducing the prey's fecundity and survival, can alleviate fear in the prey's prey (i.e. food), permitting the prey's prey to eat more and so increase their fecundity and survival. The classic experiment described above on grasshopper nymphs and toothless spiders has demonstrated that fear can cause a trophic cascade, as have numerous other experiments on invertebrate and aquatic species.

Fear of large carnivores has been demonstrated to cause a trophic cascade in a pair of recent experiments. For impala in east Africa areas of thick vegetation are dangerous because that is where their predators lurk (leopards and African wild dogs), and experimentally thinning the vegetation to create more open areas demonstrated that impala prefer these, because they can more easily see and flee their predators and there is accordingly less to fear. Having less to fear in these areas the impala eat more, and as a result only the thorniest and thus most well-defended species of *Acacia* persist in these locations. Consequently, the 'landscape of fear' created by the distribution of large carnivores, by affecting the feeding behaviour of impala, determined the distribution of thorny plants. Large carnivores not only hunt and kill herbivores, such as impala, but also smaller carnivores, like raccoons, as well. In an experiment on islands in the North Pacific, where the resident raccoons obtain much of their food by feeding on crabs in the intertidal, researchers manipulated the raccoons' fear of large carnivores by broadcasting playbacks of large carnivore vocalizations along some stretches of shoreline, and non-predator (control) vocalizations along others. Hearing large carnivores caused raccoons to spend 66 % less time feeding in the intertidal, leading to a significant increase in the raccoon's prey, with a concomitant decrease in the prey of the raccoon's prey. Specifically, less foraging by scared raccoons made

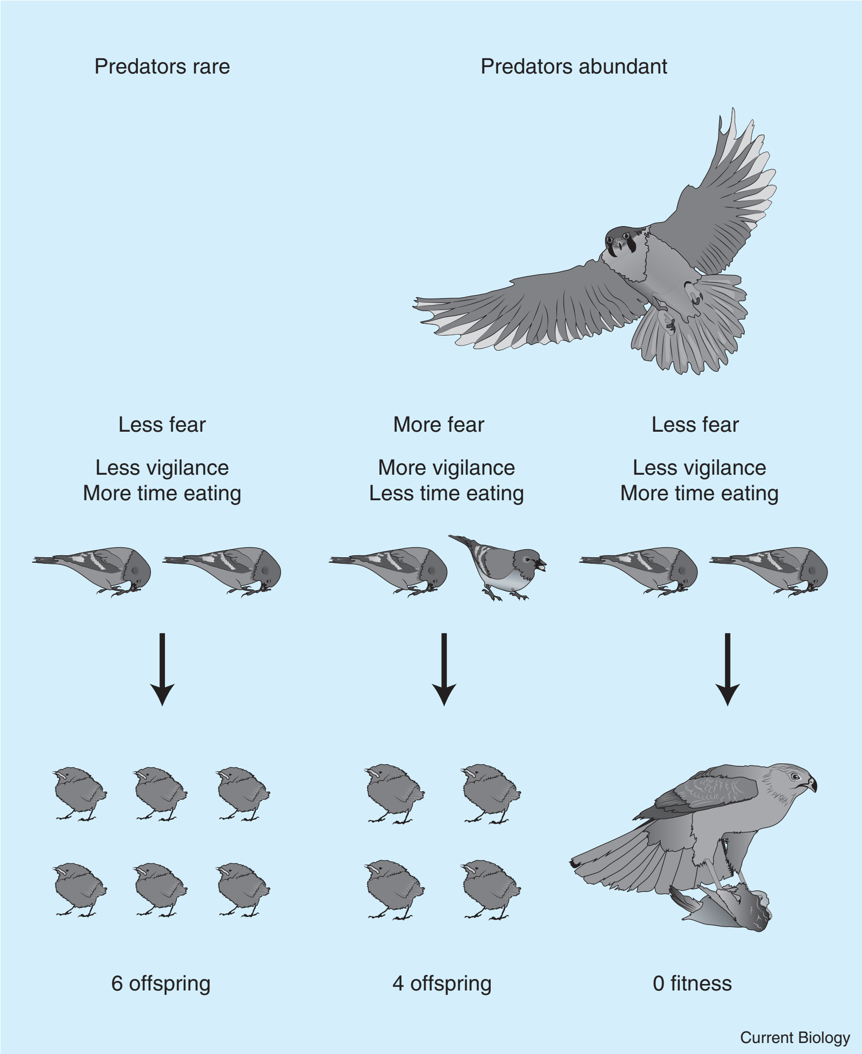

Figure 2. The ecology of fear concerns trade-offs prey make to stay alive.
Where predators are rare (left panel) there is less to fear and prey can spend more time eating, permitting them to produce more offspring. Where predators are abundant the cost of avoiding predation (fear) commonly entails spending more time vigilant and consequently less time eating, which manipulative experiments have demonstrated can reduce the number of offspring produced (middle panel). The cost of not being fearful and consequently failing to avoid predation (right panel) entails the individual's future Darwinian fitness immediately being reduced to zero — the worst of possible outcomes.

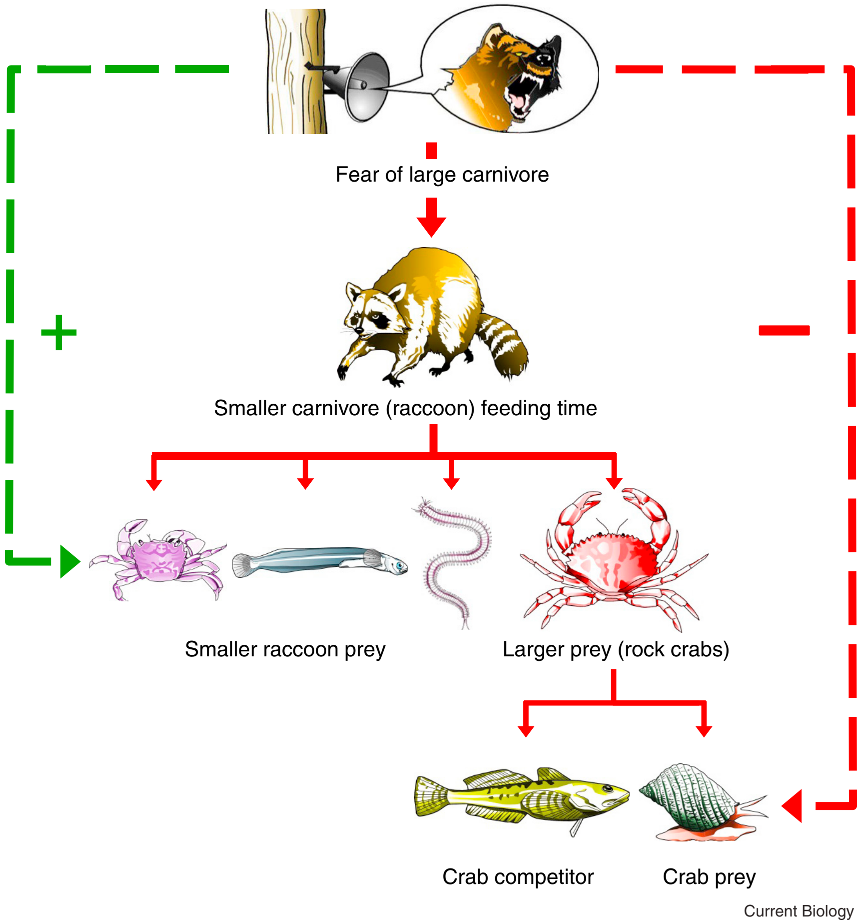

Figure 3. Fear of large carnivores can cause a trophic cascade.
Experimentally manipulating the fear of large carnivores in a smaller carnivore (raccoons), by broadcasting playbacks of large carnivore vocalizations from speakers hung on trees along lengths of shoreline on small islands in the Pacific, had cascading effects on predation and competition — in the ocean. Green and red arrows represent positive and negative effects, respectively, on feeding time, abundance or survival. Solid arrows connect predator and prey; dashed arrows connect species affected, but not directly eaten, by another. Fear of large carnivores caused raccoons to spend less time feeding in the intertidal, reducing raccoon predation, which thus benefited (green arrow) smaller raccoon prey and made it safer for larger red rock crabs to move up from the subtidal and feed closer to shore, enabling the red rock crabs to supplant a competitor (staghorn sculpins) and eat more snails.

it safer for crabs to emerge from the depths and feed closer to shore, with the result that the crabs ate more snails and supplanted a similarly-sized competitor (Figure 3). These demonstrations that the fear large carnivores inspire so impacts their prey's feeding that it has effects down the food chain strongly suggest that the fecundity and survival of their prey might also be affected, but no manipulative experiment has yet tested this.

Fear of the human super-predator

New research on the ecology of fear is focusing on the impacts of animals' fear of the human 'super-predator'. A recent analysis of worldwide data has documented that humans, as predators, have a unique ecology that includes killing prey, and particularly medium and large carnivores, at many times the rate they are killed by non-human predators, meriting humans being called a 'super-predator'. Two subsequent meta-analyses correspondingly indicated that the danger from humans has created a global 'landscape of fear', affecting the movement and degree of nocturnal behaviour in virtually every species of land mammal. Experiments testing how fearful wildlife are of the human super-predator have demonstrated that impala, deer, European badgers and mountain lions fear hearing playbacks of humans (simply conversing calmly) far more than hearing the vocalizations of their non-human predators; and even elephants flee at hearing people speak. The landscape of fear of the human super-predator affecting mammals at multiple trophic levels, indicated by the aforementioned meta-analyses, has recently been experimentally demonstrated in a large-scale manipulation in which the researchers broadcast playbacks of humans, or non-predator (control) vocalizations, across 1 km^2 blocks of forest, for five weeks, in California's central coast mountains. Fear of humans suppressed the movement and activity of carnivores, causing avoidance and more cautious movement in mountain lions, more nocturnal behaviour in bobcats and reduced activity and feeding in skunks and opossums; which in turn evidently alleviated the fear experienced by small mammals, resulting in deer mice moving more and woodrats spending more time feeding. A previous manipulative experiment in the same system demonstrated that mountain lions reduce the time they spend feeding on prey they have killed when they hear humans. Correlational evidence indicates that being scared from their kills means that mountain lions have to kill more prey (deer), thereby causing a trophic cascade. Manipulative experiments testing whether fear of humans reduces fecundity and survival in wildlife have yet to be conducted, but given how profound and widespread fear of the human 'super predator' appears to be, it seems highly likely such effects will be found to be commonplace — adding to the list of human impacts on the environment.

Conclusion

The ecology of fear recognizes that predators play a dual role in affecting prey populations with knock-on effects down the food chain. Predators kill prey, which in itself will affect populations; one kill means one fewer animal. However, predators also scare prey who mount a variety of anti-predator defenses to avoid being killed. While helping prey survive another day, anti-predator defenses carry costs. One of the most well-established trade-offs is that scared prey eat less, because you cannot have your head up looking for predators and your head down looking for food at the same time. Humans have recently been referred to as a 'super-predator' and many animals are most terrified of humans with potential repercussions on prey demography and trophic cascades. Because animals across all taxa engage in some sort of anti-predator defense, the ecology of fear may be widely applicable. Experimental manipulations provide the clearest evidence of fear operating, and many experiments in mesocosms on invertebrates and aquatic species demonstrate that fear is powerful enough to affect prey populations and communities. Manipulations in terrestrial vertebrate systems are relatively scarce but experiments thus far are revealing the importance of fear. More manipulations, especially in terrestrial vertebrate systems, are necessary to assess whether and how fear operates across animal taxa, and within taxa, across species.

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The mirror-based eyes of scallops demonstrate a light-evoked pupillary response

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Light levels in terrestrial and shallow-water environments can vary by ten orders of magnitude between clear days and overcast nights. Light-evoked pupillary responses help the eyes of animals perform optimally under these variable light conditions by balancing trade-offs between sensitivity and resolution [1]. Here, we document that the mirror-based eyes of the bay scallop *Argopecten irradians* and the sea scallop *Placopecten magellanicus* have pupils that constrict to ~60% of their fully dilated areas within several minutes of light exposure. The eyes of scallops contain two separate retinas and our ray-tracing model indicates that, compared to eyes with fully constricted pupils, eyes from *A. irradians* with fully dilated pupils provide approximately three times the sensitivity and half the spatial resolution at the distal retina and five times the sensitivity and one third the spatial resolution at the proximal retina. We also identify radial and circular actin fibers associated with the corneas of *A. irradians* that may represent muscles whose contractions dilate and constrict the pupil, respectively.

Positioned along the edges of their valves, scallops (Mollusca; Bivalvia) have dozens of eyes, each measuring ~400–800 μm in diameter. Like camera-type eyes, these eyes are single-chambered and have both a lens and a cornea. Unlike camera-type eyes, the eyes of scallops primarily use a concave mirror to focus light; they also contain two separate retinas, the proximal retina that lies close to the mirror at the back of the eye and the distal retina that lies between the proximal retina and the lens [2]. These eyes provide scallops with spatial vision that is surprisingly acute for a bivalve: behavioral trials [3], electrophysiological experiments [4], and ray-tracing models [5] all indicate that the eyes of scallops have angular resolutions of ~2°. In 1886, it was reported that scallops can constrict the pupils of their eyes to half of their maximum diameters through the coordinated activities of radial and circular muscle fibers [6]; however, this report was challenged in 1910 [7] and pupillary responses in scallops were not explored again until now.

Using time-lapse imaging, we documented that the onset of light causes pupils from the eyes of intact, un-anesthetized specimens of *A. irradians* and *P. magellanicus* to constrict to 50–60% of their fully dilated areas within several minutes (Figure 1A). After ten minutes of exposure to light, the pupils of *A. irradians* and *P. magellanicus* dilated fully after 45 and 15 minutes in the dark, respectively. Light intensity influenced the magnitudes of the pupillary responses of scallops (Figure 1A). The pupils of *A. irradians* constricted the most under the brightest conditions we tested, which were similar to an overcast day (~1,000 lux) and constricted the least under the dimmest conditions we tested, which were similar to late civil twilight (~1 lux). Compared to other pupillary responses, such as those of vertebrates and cephalopods [8], those of scallops are small in magnitude and slow in action. The pupillary responses of scallops most closely resemble those of the camera-type eyes of box jellyfish, in which a minute of light exposure causes pupils to constrict to half of their fully dilated areas [9].

To test how pupillary responses may impact visual performance in scallops, we used a ray-tracing model to predict the sensitivity and resolution at both retinas in the eyes of *A. irradians*. Across the full range of pupil apertures we observed in our trials (200–400 μm), we found that the sensitivity of the proximal retina (3–15 μm^2 sr) was consistently higher than that of the distal retina (1–3 μm^2 sr) and that the resolution at the proximal retina (30°–100°) was always coarser than the resolution at the distal retina (~2°); further, we found that aperture has a more pronounced effect on the function of the proximal retina than the distal retina (Figures 1B,C, and S1 in Supplemental Information, published with this article online).