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Struggle for safety

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Mortality-driven versus fear-driven predator-prey dynamics

Predator-prey interactions involve two opposing selection pressures as the predator's ability to catch and kill prey is counteracted by the prey's ability to avoid predation. Yet, this interaction is asymmetric, as an individual prey has more to lose by failure to avoid a predator, than predators by failing to catch a prey. To be able to work with the prey's and predator's asymmetric and opposing selection pressures, Brown *et al.* (1999) introduced the concepts of 'fear-driven population interactions' as opposed to 'mortality-driven interactions'. This distinction was inspired by the "r/a" measure of apparent competition by Holt (1977). The N-driven component reflects the prey's intrinsic growth rate r in the face of predation. The fear-driven component measures the predator's ability to catch prey, in other words the predator's rate of encountering the prey, a .

Brown *et al.* (1999) define 'fear' as an organism's perceived cost of injury or mortality. In contrast to mortality-driven systems, in a fear-driven system the predators do not appear to control their prey's population through mortality. Contrary to fear-driven systems, in mortality-driven systems predators would "*have little effect on the behaviour of their prey*" (italics PJH) and would influence the dynamics and abundance of prey only through direct mortality (Brown & Kotler, 2007). Classic predator-prey models like the lynx-hare cycle and the weasel-vole-cycle are suggested to be typical mortality-driven systems.

Although it is perfectly understandable that anti-predation behaviour limits predation rate in fear-driven systems, how *the lack of* anti-predation measures would be the *ultimate* cause of mortality-driven dynamics remains largely implicit. This is unfortunate, especially because the statement is not readily intuitive. Firstly, because natural selection would be expected to penalize relaxed anti-predation traits; secondly, because the argument that fear-driven systems are dominated by the intimidating influence of fierce predators (Brown & Kotler, 2007) implicitly suggests that the predators (like Canada Lynx *Lynx canadensis*) in mortality-driven systems (like the lynx-hare cycle) would not be fierce enough to scare their prey. In fact, fear-driven (non-lethal) effects were ubiquitous in Snowshoe Hares *Lepus*

americanus (Hik, 1995, Sheriff *et al.*, 2009), in Arctic Ground Squirrels *Spermophilus parryii* (Karels *et al.*, 2000) and House Mice *Mus musculus* (Arthur *et al.*, 2004). Thirdly, because it does not explain why, for instance, Snowshoe Hares (actors in a supposedly N-driven system) would be less “sophisticated” in escaping from lynx than squirrels from foxes (actors in a supposedly fear-driven system).

Essentially, high levels of direct consumption by predators occur as a result of density effects among rapidly increasing prey populations, which prey overcome with large reproduction potential. Such density-dependent effects may include the lack of refuges inevitably exposing more prey to predators, which then can feast on this booming population until decreasing numbers of prey forces them to shift to alternative prey (Newton, 1998). Rather than being an attribute of the predator, it is the prey, through density-dependent effects causing its anti-predation measures to be less effective, that causes high mortality. So, even if this behaviour would be regarded as ‘fearless’ behaviour, it seems at best the proximate cause of mortality, but not the ultimate one; density-dependence is.

