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The experimental evolution of parasite resistance in wild guppies: artificial selection, resource availability and predation pressure

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In a recent paper, 'Experimental elimination of parasites in nature leads to the evolution of increased resistance in hosts', Dargent *et al.* [1] reported on a transplant experiment using wild guppies, *Poecilia reticulata*. Fish were collected from a source population in a downstream, high productivity site where they experienced parasitism and predation. They were held in the laboratory and chemically treated four times to remove parasites before being introduced into four guppy-free, upstream, low productivity sites without predators. Fish were collected after one year from two of the introduced populations, and after both one and two years from the other two introduced populations. Along with synchronized collections from the source population, these fish were again chemically treated for parasites and bred under standard laboratory conditions for two generations. The authors then used standard protocols to test whether fish descended from the introduced and source populations differed in their resistance to *Gyrodactylus turnbulli*, a dominant guppy parasite. If parasite resistance is costly to hosts, theory predicts that relaxed selection pressure will result in the evolution of decreased resistance [2,3], and evidence from laboratory studies supports this prediction [4]. Surprisingly, Dargent *et al.* [1] found that the introduced populations had repeatedly evolved greater resistance compared to the source population. After considering various alternative methodological and biological explanations, Dargent *et al.* [1] suggest that, 'relaxed selection for defence against parasites (owing to parasite removal) can be overpowered by the evolution of a slower life history (owing to predator removal) that, through pleiotrophic or functional associations, leads to increased resistance'.

While I agree that this is a reasonable explanation, I believe other factors may have contributed to the intriguing result presented by Dargent *et al.* [1]. Here, I consider additional methodological then biological factors not discussed by the authors. I conclude by suggesting an experimental design that would help elucidate the effect experimental elimination of parasites may have on the evolution of parasite resistance in guppies.

As part of their methodology, Dargent *et al.* [1] may have imposed artificial selection for parasite resistance. Capture, laboratory conditions and chemical treatment may have caused mortality among both stress-prone individuals, which are likely to be less resistant to *Gyrodactylus* infection [5], and those fish already weakened by the heaviest *Gyrodactylus* infections. Whilst the authors state that 'all fish were monitored to ensure that they were in good health', they do not provide mortality data. In a mesocosm experiment, van Oosterhout *et al.* [6] report 14% mortality among their captured wild fish, 24% of which was after re-introduction. If, as one could predict, there was higher mortality among stress-prone, less resistant fish either before or soon after the introductions by Dargent *et al.* [1], or, as is implied, the authors only released fish in 'good health', these introduced populations would have been a non-random sample of the more resistant fish from the source population. Even in the absence of artificial viability selection, this process may have reduced the contribution of stress-prone, less resistant individuals to the next generation. Although fish from the source population were exposed to similar conditions before being transferred to the laboratory during the final collection, the effects of this artificial selection are

likely to be stronger in natural than in laboratory conditions. Additionally, the source population only underwent this process once (during the final collection), compared to twice for the introduced populations (before introduction and during the final collection). For the two introduced populations sampled both one and two years after introduction, a significant increase in resistance between these time points could undermine this parsimonious explanation of the result. Dargent *et al.* [1] do not explicitly test for such a difference statistically, however, and from their fig. 2 it is clear that none exists.

Differences in *per capita* resource availability between the source and introduced populations may also have contributed to the observed differences in parasite resistance. Dargent *et al.* [1] highlight that the introduction sites had more extensive canopy cover and thus lower primary productivity than the source site. They state that the evolution they observe ‘was not owing ... to differences in productivity among the sites’, arguing that lower productivity would lead to a reduction in resistance in guppies due to selection for more efficient use of limited resources. I suggest, however, that the difference in resource availability rather than stream primary productivity is the index more relevant to their argument. The *per capita* resource availability would have been far higher for introduced guppies than for those from the source population, and is unlikely to have been greatly affected by the 4% experimental canopy thinning referred to by Dargent *et al.* [1]. The authors do not report fish densities for any of the populations, but at the introduction sites it would have been approximately 0.26 fish m⁻² (estimated from a description of the sites in [7]) following introduction. This density is an order of magnitude lower than those reported for natural, resource-poor, upstream populations (mean density = 6.5 fish m⁻², in [8]). Increased resource availability can lead to the evolution of increased parasite resistance in other species—moths [9], and may have contributed to the findings of Dargent *et al.* [1]. Even in the unlikely event that resources were limited for the introduced guppies, the reduction in parasite resistance suggested by the authors is not the only possible outcome [9]. The few studies to investigate the effect of food availability on response to

Gyrodactylus infection in guppies have described a complex relationship [10,11], and how this relates to an evolutionary response is untested. It is therefore difficult to predict how resource availability may have influenced the results of Dargent *et al.* [1].

The experimental design employed by Dargent *et al.* [1] does not enable assessment of the effect of experimental elimination of parasites on the evolution of parasite resistance. Although they are to be commended for conducting their experiment under natural conditions, the authors do not control for the change in predation regime, resource availability, or the effects of artificial selection on the source and introduced populations. Disentangling these effects from that of parasite removal on the evolution of resistance is therefore beyond the scope of their data. To elucidate the mechanisms behind the results of Dargent *et al.* [1], it would be interesting to compare their results to differences in parasite resistance between the source and introduced guppies from experiments by Haskins, Endler or Reznick (described in [12]). These classic experiments did not remove parasites, but moved guppies from high predation sites to low predation sites. Additionally, adapting the methodology of Dargent *et al.* [1] to avoid the possibility of imposing artificial selection, and choosing an upstream, low predation source population would also help disentangle the relative roles of the elimination of parasites, predators and resource availability in the evolution of guppy traits.

The findings of Dargent *et al.* [1] indicate that the interaction between the selective pressures of parasites, predators and resource availability in guppy evolution is in need of more comprehensive investigation. Natural evolution experiments are a vital part of the research required to understand these forces. In order to maximize their contribution, however, they should be designed to answer specific questions unambiguously.

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