

Invited reply



Cite this article: Samaš P, Kysučan M, Honza M, Grim T. 2019 Multiple costs are relevant for evolution of host anti-parasite defences. Reply to Yang C *et al.* (2018). *Proc. R. Soc. B* **286**: 20191690.
<http://dx.doi.org/10.1098/rspb.2019.1690>

Received: 18 July 2019

Accepted: 4 October 2019

Subject Category:

Evolution

Subject Areas:

behaviour

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The accompanying comment can be viewed at
<http://dx.doi.org/10.1098/rspb.2018.2430>.

Multiple costs are relevant for evolution of host anti-parasite defences. Reply to Yang C *et al.* (2018).

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Studies of brood parasite-host coevolution have generally assumed that hosts invest more parental care to rear parasite progeny than their own offspring; this view was taken for granted in cases when a parasite chick (e.g. the common cuckoo *Cuculus canorus*; hereafter 'cuckoo') was dramatically larger than a host chick (small passerines in the case of cuckoos [1]). This seemed obvious because a cuckoo fledgling weighs as much as the whole family of a host, i.e. all chicks and both male and female fosterers combined (own unpublished data). Recently, we reported results that question this view: rearing the cuckoo was not associated with overall higher immediate rearing costs to common redstarts *Phoenicurus phoenicurus* (hereafter 'redstart') above the natural baseline levels that are imposed by efforts to rear their own progeny anyway [2]. Additionally, we suggested that such low costs may *partly* help explain low levels of host counterdefences in this host. In their comment, Yang *et al.* [3] do not contradict our main conclusions (rearing the cuckoo is not extra costly) but disagree with our suggestion that surprisingly low immediate rearing costs can be relevant for the evolution of host defences. Here, we address this criticism.

Yang *et al.* [3] claim that individual hosts that are successfully parasitized by cuckoos do not contribute their genes to the next generation, which provides a strong selective pressure on hosts, whereas an excessive parental care for parasite progeny can hardly drive the evolution of anti-parasitic adaptation in hosts. Further, [3] argue that even if the immediate costs of rearing a cuckoo chick do not exist, parasitism itself should be sufficient to promote anti-parasitic defences in hosts.

We agree that the loss of the host's own progeny after successful parasitism is the most important cost that provides a strong selective pressure on hosts to evolve defences. We also agree that the loss of progeny *per se* is sufficient to promote anti-parasitic defences in hosts even in the *potential* absence of immediate rearing costs. However, all this does not mean that other costs are irrelevant. Indeed, the lost progeny cost is the same or very similar in all regular cuckoo hosts because the cuckoo chick kills all its nest-mates in all host species [1] (with a single exception of redstarts); therefore such invariable lost progeny cost cannot explain the large variability in host defences. Therefore, we suggest that multiple costs—i.e. not only the lost progeny cost—play a non-negligible role in the evolution of anti-parasitic defences and can thus better explain variability in levels of anti-parasitic defences across various host species.

Such costs include high demands to raise the cuckoo because host parents exhausted by care for the cuckoo more likely fail to transmit their genes in potential *next* breeding attempts when caring for their own progeny (i.e. the trade-off between the current and future reproduction). Specifically, in the redstart, [2] reviewed factors considered by previous studies as important for the evolution of anti-parasitic defences (length of coevolution, parasitism rate) but these could not explain why the anti-parasitic defence is so weak in this host. For example, an alternative explanation proposed by [3] that 'the redstart may be a recent host species' is rejected by the genetic data: redstart-cuckoo coevolution lasts for at least approximately 2.5 Myr [4].

However, [2] did not test directly the effect of excessive parental care on the evolution of anti-parasitic defences, and thus they only suggested the unexpectedly low immediate rearing costs as a possible *additional* (i.e. not exclusive, see phrasing ‘may, in part, explain’ in the Abstract of [2]) and *post hoc* explanation of low host anti-parasitic defences in the redstart. We also note that the redstart is the only regular cavity breeding cuckoo host and this different breeding strategy can contribute to a lower cuckoo virulence in this species [2].

Liang *et al.* [3] assume that parasitized redstarts ‘fail to pass their genes onto the next generation’. This is not true because many cuckoos fail to evict redstart chicks and such host chicks from ‘mixed broods’ often fledge even from parasitized nests [2,5].

Liang *et al.* [3] claim that ‘nest predators impose no immediate cost on bird parents’. This is incorrect because parents defend their nests and nest defence is considered highly costly for parents [6]. Also, the claim that ‘the cost of parasitism is larger than that of nest predation, and thus anti-parasitic defences should still evolve to a level that is equal to or stronger than antipredator defences’ [3] is not valid. This is because predation of progeny at any stage (egg, nestling, fledgling) entails, *just like in the case of brood parasitism*, lost rearing costs invested by parents from which they gain zero fitness. Predation always zeroes parental breeding success. By contrast, parasitism in redstarts often leads to mixed broods where ‘at least some of the chicks typically survive and fledge, while cuckoo chicks often die’ [5]. Given relatively low parasite rearing costs [2], the overall cost of parasitism might be *lower* than that of offspring predation in redstarts (i.e. the opposite of what [3] suggested).

Finally, [3] claim that comparing costs of rearing own versus foreign progeny are not comparable because the costs of rearing own progeny contribute to host fitness whereas costs of rearing foreign progeny do not. The claim that these costs are ‘totally different’ [3] is not true if we consider the *types* of costs—a female host incubating an egg is expending identical currencies of time, energy, and opportunity no matter what the taxonomical identity of the egg is. This is the reason why *all* studies of rearing costs published to date have always used the same measures of costs for both host and parasite offspring (reviewed in [2]). The only reason why these costs are known to affect parasite-host coevolution (see [7]) is exactly because the ‘genetic background’ [3] differs between hosts and parasites: any investment into a parasite cannot be invested into a host progeny and that is *one of the reasons* why host defences evolve.

Yang *et al.* [3] refer to ‘high and low costs’ without specifying what they mean. In our view, the amount of care for the host’s own offspring is a natural ‘yardstick’ against which any amount of care for foreign offspring should be compared because this directly affects trade-offs in host investment. Thus, ‘high’ costs of care for parasites are best defined as ‘higher than typical baseline levels of care for the host’s own offspring’: hosts exhaust themselves *more* than under natural non-parasitized conditions and are left with *less* resources to invest into their future reproduction (unless being parasitized again). By contrast, ‘low’ costs of care for parasites are best defined as ‘lower than typical baseline levels of care for the host’s own offspring’: hosts exhaust themselves *less* than under natural non-parasitized conditions and are left with *more* resources to invest into their future reproduction (unless being parasitized again). The cost measures we used in our study supported the latter, counterintuitive, scenario [2].

That our argument is realistic is best illustrated by an empirical example [8]: a higher cost can manifest, e.g. in a

longer care for a parasite (measured by us: [2]). Unsurprisingly, the extended care for a cuckoo nestling and fledgling has been traditionally given as a major reason why host individuals that care for the cuckoo until its independence are not left with enough time to breed again before migrating to wintering grounds [1]. This represents an extreme cost of parasitism—one lost breeding attempt represents a huge cost for a typical short-lived cuckoo host. By contrast, host individuals that desert a nest with the cuckoo egg save much time (approx. five weeks) of care for the alien chick in and outside the nest and do have a chance to breed again [1]. Deserting the nest early leads to an almost negligible cost of parasitism, compared to not deserting the nest, *even though the host has lost all its progeny*: in this example, the latter host has a zero fitness in this breeding season whereas the former host reared one (the second) brood. The difference between the two host’s fitness is huge and the reason is not the lost progeny cost (which was paid identically by both hosts): the *only* reason is the rearing cost [2].

Between these two extremes, there is a continuum of host decisions and costs of parasitism: a host that deserts the cuckoo chick before fledging [8] saves approximately three weeks of time and has a chance to breed again, more likely without being parasitized. This is because (i) parasitism is generally rare and thus chances of repeated parasitism of the same individual is even rarer and (ii) the risks of parasitism decline throughout the season and are non-existent after parasites departed to wintering grounds: e.g. cuckoos in our Czech study sites [9] depart several weeks before the end of the breeding period of their warbler (*Acrocephalus*) hosts. Thus, low rearing costs, i.e. shortening of the length of care for the parasite (which we found in our study [2]), have direct fitness benefits for hosts. In other words, high versus low time-related rearing costs make a fundamental difference between low and high host fitness. An identical principle applies to any other measure of cost, e.g. physiological stress, energy expenditures, etc.

To conclude, *variable* host defences across species and populations cannot be explained by ‘failure of transmission of genes in hosts’ [3] because hosts *invariably* lose all their progeny (except for redstarts [2,5]). Further, that one kind of cost is extreme whereas another kind of cost is low does not mean that only the former cost is relevant: also the latter is important but with a lower impact on the evolution of a trait and there is plenty of empirical evidence for this principle [10]. There is also no question whether the high costs of parasitism, no matter whether in the form of lost progeny or rearing, provide stronger selection pressure on hosts than the lower costs of parasitism, no matter whether in the form of lost progeny or rearing or any combination of the two: this is a fundamental assumption behind any study of parasitism.

However, we agree with [3] that lines of further research to explain the low levels of anti-parasitic defences in any hosts should include both intraspecific and interspecific comparisons of costs of rearing a parasite across different populations of the same host species and different species, respectively, to determine if and how costs are correlated with host defences. We recently performed such metareplication in a different host [9]. We also agree with [3] in that the use of mathematical models will be useful only if based on empirically determined and quantified costs and benefits of host and parasite behaviour [2,9].

Data accessibility. This article has no additional data.

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