

CORRESPONDENCE

Remarks on the article on life-history traits in *Drosophila* populations selected for rapid development by Yadav and Sharma

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We are writing about a paper recently published in *The Journal of Experimental Biology* (Yadav and Sharma, 2014). We wish to point out that (i) our work, and that of others, has been cited inappropriately in support of statements that the cited work either refutes or, at the least, does not support; (ii) one principal conclusion drawn about greater reproductive fitness in populations selected for faster development is wrong; (iii) a principal result about populations selected for faster development evolving greater fecundity per unit dry weight is not novel, as depicted, but has been shown before twice; and (iv) the authors provide no discussion of an unexpected and counter-intuitive result of fecundity increasing from young to middle age in some of their populations.

(i) The first two sentences of the Introduction are erroneous citations of Prasad and Joshi (Prasad and Joshi, 2003). We did not state that fruitfly populations in nature are subject to directional selection for faster development. On the contrary, we stated that recent studies on the evolution of development time challenged the earlier held view that fruitflies were subject to selection for faster development in the wild, and then went on to review those studies [see p. 55 of Prasad and Joshi (Prasad and Joshi, 2003)]. Indeed, over the past 18 years, one of us (A.J.) has been consistently writing and speaking about why the earlier held view is wrong. Similarly, we (Prasad and Joshi, 2003) have nowhere claimed that studies on *Drosophila* led to the development of life history theory, or that this theory ‘posits that natural selection enhances organismal fitness’. Both these statements have not been made by us and, moreover, are incorrect. The fourth sentence of the Introduction is also incorrect: Chippindale et al. (Chippindale et al., 1994) do not report on any populations subjected to selection for slower development. Populations selected for postponed aging showed slower development as a correlated response (Chippindale et al. 1994). The second sentence of paragraph 3 of the Introduction is likewise incorrect. Resistance to starvation and desiccation are not fitness components under laboratory conditions and are not used to assess fitness in fruit flies. The references cited in support of this statement are also erroneously cited: those authors have not claimed that these traits are used to assess fitness. In the section headed ‘Adult lifespan’, Sheeba et al. (Sheeba et al., 2000) are cited in support of the statement that there are deleterious effects of light on lifespan and these are supported by experiments showing greater lifespan in constant darkness than in constant light or a light:dark cycle. However, this is also a poor citation: the main thesis of Sheeba et al. (Sheeba et al., 2000), as the title indicates, was that we need to be careful in determining deleterious effects on fitness through lifespan alone, because fruit flies kept under constant light had lower lifespan but higher reproductive output compared with flies kept in constant darkness or in a light:dark cycle.

(ii) The authors observed that faster developing populations produced fewer eggs overall, but more eggs per unit dry weight, as

compared with ancestral controls (Abstract, fig. 1D,E and final sentence of paragraph headed ‘Higher fecundity per unit body weight in faster developing flies’). Reproductive fitness depends on total egg production, not fecundity per unit dry weight. Yet, the authors repeatedly and erroneously claim that their faster-developing flies have higher reproductive fitness than controls (Abstract, and elsewhere in the paper). What the results on fecundity suggest is that the faster-developing flies, which have higher Darwinian fitness than slower-developing flies under the authors’ selection regime, are achieving this partly at the cost of reproductive fitness that is reduced as a consequence of the smaller size that accompanies rapid development, as has also been shown earlier in the context of selection for rapid development by Prasad and Joshi (Prasad and Joshi, 2003) and Chippindale et al. (Chippindale et al., 2004) (see below).

(iii) The authors’ observation that faster-developing populations produced more eggs per unit dry weight compared with ancestral controls is presented as though it were a novel finding. Exactly this result has been seen twice before in fruit fly populations selected for faster development under constant light (Prasad and Joshi, 2003; Chippindale et al., 2004). Both these papers are cited by the authors, but it is nowhere mentioned that the authors’ finding is, thus, a confirmatory result and not a novel one. Indeed, the fact that the authors, selecting under constant darkness, got essentially the same pattern of correlated responses to selection for faster development as Prasad and Joshi (Prasad and Joshi, 2003) and Chippindale et al. (Chippindale et al., 2004) did when selecting under constant light (when the fruitfly circadian clock is arrhythmic), clearly suggests that these correlated responses of life-history traits to selection for faster development are related to development time per se, and are unlikely to be clock-mediated, contrary to what the authors infer in the final paragraph of their Results section. Similarly, in the Abstract, the authors write ‘In order to rigorously examine correlations between pre-adult development and other life history traits...’ as if this is the first such study, when such rigorous examinations of correlated responses to selection for faster development have been done at least in four independent studies on *D. melanogaster* by Len Nunney, Bas Zwaan, Adam Chippindale and N. G. Prasad. In the paragraph headed ‘Reproductive output’, the authors contrast their finding of both lifespan and fecundity being depressed in their selected populations with some previous studies, but do not mention that exactly the same result was also seen by Chippindale et al. (Chippindale et al., 2004).

(iv) In their control populations, the authors observed higher fecundity on days 21 and 11 of adult life than at day 4 (fig. 1D). This is somewhat unprecedented in *D. melanogaster*, which has a typical triangular fecundity function, with maximum fecundity very early (days 2–5) in adult life. Strangely, there is no discussion

whatsoever about this rather surprising and counter-intuitive result. We hope that the authors will take appropriate measures to set the record straight on these points.

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doi:10.1242/jeb.117366

Response to ‘Remarks on the article on life-history traits in *Drosophila* populations selected for rapid development by Yadav and Sharma’

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While we agree that citations of the review article of Prasad and Joshi (Prasad and Joshi, 2003) could have been done more perceptively in our recent paper (Yadav and Sharma, 2014), most other comments made by Prasad and Joshi (Prasad and Joshi, 2015) are certainly out of place.

We would like to clarify that citation of the review (Prasad and Joshi, 2003) in lieu of the original papers was done to reduce the number of citations. However, Prasad and Joshi’s article does state that there is a long-standing view that ‘...*Drosophila* populations in the wild were subjected to directional selection for rapid development as a consequence of the larvae inhabiting ephemeral habitats like rotting fruits...’ (p. 55). Similarly, it also mentions that trait combinations under selection are constrained by trade-offs (‘...evolution of body size in *Drosophila* is constrained by a trade-off between adult reproductive fitness and the fitness costs of increasing larval growth rates...’ on p. 49). However, we concur that Prasad and Joshi (Prasad and Joshi, 2003) do not endorse these views, and therefore it would have been more appropriate for us to either cite the primary references or use ‘reviewed by’ or ‘cited in’ to reflect this.

We agree that Prasad and Joshi do not claim that ‘studies on...organismal fitness’, our intention was to refer to the review only for the latter part of the sentence regarding constraints. However, contrary to their claim, such views are not uncommon in the evolutionary biology literature [e.g. ‘The principle of optimality assumes that there is some measure of fitness that is maximized by natural selection’ (Roff, 1992), and ‘Life history theory posits that natural selection leads to the evolution of mechanisms that tend to allocate resources to the competing demands of growth, reproduction, and survival such that fitness is locally maximized’ (Vitzthum, 2008)].

In the fourth sentence the Introduction (Yadav and Sharma, 2014), we used the term ‘development’ to include adult stages as well (otherwise, we use the phrase pre-adult development). Hence, this is a technicality that is arguable.

Resistance to starvation and desiccation have been considered as traits that impinge upon fitness and hence are considered as fitness-related traits [‘Stress resistance characters are of pervasive

importance in evolutionary physiology impinging upon a wide variety of characters, from fitness itself, to...’ (Chippindale et al., 1996)]. The cited papers assay the above two traits and infer to them as being indirectly related to fitness.

Prasad and Joshi take the citation of Sheeba et al. (Sheeba et al., 2000) completely out of the context to which it refers. It is cited in support of the results showing greater lifespan under constant darkness than in constant light or light:dark cycles, and therefore it is perfectly valid.

Indeed, total fecundity is taken as a measure of reproductive fitness. In the three instances (Abstract, Introduction, Discussion) where we suggest enhanced reproductive fitness, it is preceded by a statement that it is a relative measure (egg-output normalized by body weight).

The main question and the framework of our study are quite different both from Chippindale et al. (Chippindale et al., 2004) and that reviewed in Prasad and Joshi (Prasad and Joshi, 2003) where flies were selected for faster pre-adult development and also early reproduction under constant light. Our selection approach was designed precisely to avoid the pitfalls associated with such a regime on the evolution of circadian clocks (Yadav and Sharma, 2014, p. 581). In this context, our study is indeed novel (although nowhere did we claim novelty) and therefore any similarity in correlated adult traits between ours and previous studies is merely coincidental.

The argument that similar correlated responses to selection were seen in two very different regimes and hence would infer a lack of the role of the clock is flawed because, firstly, the clock could easily alter the ‘extent of changes’ in life history traits. Secondly it should be noted that many aspects of circadian organization are not affected by constant light (reviewed by Howlader and Sharma, 2006). Moreover, we and others have quite convincingly demonstrated circadian-clock-mediated regulation of life history traits (citations in Yadav and Sharma, 2014) including pre-adult development time, and therefore any skepticism on this matter is misplaced.

Because of constraints of space, we did not discuss the results on fecundity of control flies as it is only tangential to our study. Our control populations (maintained under constant darkness for over

200 generations) exhibit higher fecundity at later life stages, unlike others, where fecundity decreases after about 6 days. We speculate that this could be because, under constant darkness, flies shift their egg-laying peak towards the age when eggs are collected for regular maintenance.

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doi:10.1242/jeb.117507