



Invited reply

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The role of genes and environment in the phenotypic expression of alternative mating tactics: a reply to Buzatto *et al.*

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Buzatto *et al.* [1] state that our recommendation to bring together previous, dichotomous game-theoretical approaches of modelling alternative strategies and a conditional strategy is unnecessary as fusion synthesis of this kind has already been carried out via the environmental threshold model. By presenting a verbal model in the conclusion and future direction section of our review paper, these authors state that we have developed a 'new theory' that is unnecessary.

As detailed in our review paper [2], we generally agree with the authors that there has been excellent past work on the quantitative genetics of polyphenisms, including in the area of alternative mating tactics. Indeed, we did cite numerous papers in this area, including several written by Hazel and Tomkins. For example, we cite such papers in the general context of identifying problems with the game-theoretical approach for modelling alternative mating tactics [3] as well as for work detailing genetic variation underlying conditional polymorphisms [4–6]. While our citation list is by no means exhaustive, we do feel we have reviewed key developments in the field, including quantitative genetic models of polyphenisms.

We do, however, disagree with Buzatto *et al.*'s [1] comments on the verbal model we propose and its necessity. First, our verbal model is as much a summary of our perspective on the roles that genes and environment play in governing alternative mating tactics as it is a model, and certainly it is not a formalized mathematical model. For example, in reference to the game-theoretical and status-dependent selection frameworks, Neff & Svensson [2, p. 8] state:

Here, we propose that these two frameworks instead represent the extremes on a continuum and that most AMTs fall somewhere in between the two, with both genes and environment contributing to phenotypic expression of the tactics (figure 2). $G \times E$ interactions play predominately into our framework, which will lead to variation among individuals in the status-dependent switch points.

We see no utility in contrasting such statements to formal mathematical or quantitative genetic models for discrete polyphenisms as is advocated by Buzatto *et al.* [1]. Those authors also seem to have a very restrictive use of the term *model*; one gets the impression that only formal mathematical models are counted as models. We disagree with such a restrictive use of the term. Second, Buzatto *et al.* [1, p. 1] falsely claim that a monomorphic 'decision' gene is the driver of our verbal model:

Neff and Svensson do cite this [...] correction of the record, but in our view failed to convey an understanding of its content, since the assumption of monomorphism reappears as the driver of Neff and Svensson's [...] 'new model'.

Whereas Neff & Svensson [2, p. 8] actually state:

We envision that, regardless of whether there is a single decision gene in the population that shows no variation in DNA sequence ('monomorphism'), other loci are likely always to be important in modifying the expression or effect of the decision gene through epistasis ... The modifier loci are unlikely to be genetically monomorphic in a population, and their effects are also likely to be influenced by the environment, resulting in the $G \times E$ effects on tactic phenotypic expression.

We bring up the concept of a genetic monomorphism in our review of the literature: Gross [7] uses the term genetic monomorphism in the development of his status-dependent selection model for a conditional strategy, a paper that is cited

over 800 times and thus has been quite influential and we felt worthy of review. Moreover, in the conclusion and future directions section, we emphasize and advocate that more genomic work is needed in this area to understand the *actual* molecular genetic architecture and mechanistic basis of tactic expression and reaction norms. We believe that a better understanding of the systems biology along with integration between classical quantitative genetic models and genomic information is necessary to understand the evolution of alternative mating tactics. Such a line of research that integrates molecular and classical quantitative genetics, as opposed to a more restricted quantitative genetic statistical approach advocated by Buzatto *et al.* [1], is likely to lead to novel insights. A more integrative approach could, for instance, uncover the core 'decision' gene that underlies Gross's [7] status-dependent selection model for a conditional strategy.

Finally, we get the impression that Buzatto *et al.* [1] equate *genetics* with *quantitative genetics*, which is a restricted view of the field of genetics. Genetics encompasses several subfields, including Mendelian, population and quantitative genetics, molecular genetics, genomics and transcriptomics. Although the environmental threshold model advocated by Buzatto *et al.* [1] is one mechanism by which discrete and discontinuous tactics or strategies can emerge from quantitative traits, we certainly would not put all our eggs in one basket and claim that the threshold model is the *only* way such discrete phenotypic clusters could develop. Rather, we anticipate that future research incorporating multiple approaches, as we have argued above, is likely to lead to new insights and perhaps surprises regarding the genetic basis of alternative mating tactics. Ultimately, we feel this is an empirical question and not a rhetorical issue.

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