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Title: Manipulating genetic architecture to reveal fitness relationships

Year: 2014

Version: Published version

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Please cite the original version:

Ketola, T., Boratynski, Z., & Kotiaho, J. S. (2014). Manipulating genetic architecture to reveal fitness relationships. *Proceedings of Peerage of Science*, 2014(January), Article e1.
<https://doi.org/10.14726/procpos.2014.e1>

Manipulating genetic architecture to reveal fitness relationships

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Citation: Ketola T et al. (2014) Manipulating genetic architecture to reveal fitness relationships. ProcPoS 1:e1

DOI: 10.14726/procpos.2014.e1



Traits are often claimed (rather than shown) to be closely related to fitness. Sometimes this leads to contrasting predictions for the direction of the association between the trait value and fitness, a prime example of which is the debate over how (Darwinian) fitness links with the rate of energy turnover at rest (see: [Burton et al. 2011](#), for definitions). To resolve this debate [Burton et al. \(2011\)](#) suggested manipulation of traits and measuring changes in fitness. In this perspective, we propose that we should do the opposite – manipulate genetic architecture underlying fitness and measure the traits response.

Evolutionary theories frequently focus on the role of resource allocation and resource trade-offs in determining fitness traits ([Nilsson 2002](#); [Tomkins et al. 2004](#); [Boratyński and Koteja 2010](#); [Ketola & Kotiaho 2009](#)). One common empirical measure of resource use is resting metabolic rate, and there are

two avenues of thinking in how resting metabolic rate is related to fitness. High resting metabolic rate is either assumed to allow higher rates of energy turnover when needed, or high resting metabolic rate is expected to be negatively related to fitness as high metabolic rate per se can restrict the use of limited energy on fitness traits ([Nilsson 2002](#); [Boratyński and Koteja 2010](#); [Ketola & Kotiaho 2009](#)). Interestingly, there are only a handful of studies that have thoroughly addressed the validity of these hypotheses and most of the evidence is correlative ([Burton et al. 2011](#) see also: [White & Kearney 2012](#)).

To overcome the limitation of correlative studies [Burton et al. \(2011\)](#) rightly advocated a manipulative approach. However, they suggested using artificial selection experiments or hormonal manipulations to modify resting metabolic rate and then measuring changes in fitness to determine the outcome of these manipulations. Due to difficulties in measuring fitness, laborious procedures involved in production of selection lines and potential confounding factors included in hormonal manipulations, these methods may be less than optimal. We fully agree that manipulations are called for, but propose manipulating genetic architecture underlying fitness and measuring the traits values, rather than manipulating resting metabolic rate and then measuring fitness.

One very potent, but underused, fitness manipulation is based on directional dominance and revealing hidden harmful recessive alleles by inbreeding. This method relies on a few well established principles (Falconer & Mackay 1996; Lynch & Walsh 1998). By definition, fitness is under directional selection, which is important as conditions for the build-up of directional dominance would otherwise not exist. With a neutral trait, the expectation is that roughly equal number of alleles has positive and negative effects (Lynch & Walsh 1998, p.257, 270). When a trait with such genetic background is subjected to directional selection for increased trait value, recessive alleles increasing the trait value (due to direction of selection: beneficial alleles) will be fixed rapidly. Recessive alleles that decrease trait value (harmful recessives) will be much harder to remove because they are revealed for selection only in a small subset of offspring in the population. Therefore, the likelihood of harmful recessive alleles remains high in traits under directional selection (Falconer & Mackay 1996; Lynch & Walsh 1998). When there is directional selection, directional dominance develops, and, when revealed, recessive alleles will always change trait values in the direction opposing the long term past selection, i.e. away from fitness (Falconer & Mackay 1996; Lynch & Walsh 1998). Therefore, experimentally manipulated inbreeding can be used to infer whether the focal trait is related to fitness and if smaller or larger trait values have increased the fitness.

Although, we advocate the use of inbreeding method for revealing fitness associations, one needs to be cautious when applying it. For example the recessive alleles in very important fitness traits may have been purged by strong directional selection, which can substantially lower inbreeding depression and it is clear that the method should not be applied on already inbred populations, where inbreeding manipulation does not cause increased inbreeding depression. Moreover, while inbreeding can be useful in revealing the course of past directional selection, it is also clear that fitness may be a result of optimization of trait expression in several traits (Falconer & Mackay 1996). Exploring inbreeding on trait to trait interactions can be used to determine whether inbreeding is associated with concurrent changes in other traits, as was for example done in Mallet & Chippindale (2011) and in Ketola & Kotiaho (2012), testing also existence of non-linear selection behind the fitness. In the simplest case, calculating an interaction between two (mean

standardized) traits provides a new index that can be tested for a linear association with fitness. For example, if selection has been against high metabolic rate in large individuals, and against low metabolic rates in small individuals the magnitude of this index is increased when individuals are inbred. Thus, the existence of non-linear selection is not preventing the use of this method. On the contrary, it provides extra information on how traits interactively affect fitness, extending applicability of the method for multiple traits that work in concert for better fitness (Ketola & Kotiaho 2012).

The inbreeding method has been used few times before in the context of identifying sexually selected traits (see: Cotton et al. 2004), in comparing the strength of selection on male and female traits (Mallet & Chippindale 2011), and in determining whether high maintenance metabolism increases or decreases fitness (Ketola & Kotiaho 2009, 2012; Boratyński et al. 2012). Current, albeit limited, evidence suggests that inbreeding increases the maintenance metabolism and greatly elevates expression of maintenance genes (Ketola & Kotiaho 2009, 2012; Boratyński et al. 2012; Mattila et al. 2012; Kristensen et al. 2005). Thus, it seems that high levels of maintenance metabolism may be connected to decreased fitness.

Although fitness is the most important concept in evolutionary biology, it is a bugger of a concept not easily amenable to empirical measurement. To overcome the problem of measurement, the inbreeding method described above is useful and will provide important insights into the nature of the fitness related traits. Despite the rare usage of inbreeding for resolving the trait's relationship with fitness, there is a large body of literature suggesting that life-history traits (that are closely related to fitness) are indeed affected more by inbreeding than for example morphological traits (reviewed in: DeRose & Roff 1999) showing that inbreeding manipulation is a potent, but clearly underused, tool in evolutionary biology.

ACKNOWLEDGEMENTS

We thank Academy of Finland for funding and R. Hegna for revising the language.

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Funding: No specific funding is attributed for this work

Competing interests: Authors declare no competing interests exist

Public Patron #2:



Altmetric

Public Patron #3:

Anonymous Patron