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Correlated-response-to-selection experiments designed to test for a genetic correlation between female preferences and male traits yield biased results

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The genetic correlation between mating preferences and sexually selected (epigamic) traits is a central issue in both Fisherian and good genes models of mate choice (Fisher 1930; O'Donald 1980; Lande 1981; Pomiankowski 1988). One method of demonstrating the existence of a genetic correlation is to select on one trait, and observe if a second trait shows a correlated response to selection (Lande & Arnold 1983; Falconer 1989). This has become the most commonly adopted method of testing for a genetic correlation between mating preferences and epigamic traits: eight of 12 studies reviewed by Bakker & Pomiankowski (1995) used this method. In this commentary, we extend and clarify methodological issues first raised by Butlin (1993), and argue that correlated-response (CR) methods will overestimate the genetic correlation, and may even incorrectly identify a genetic correlation when none in fact exists.

The logic behind applying the CR method is fairly straightforward: if a genetic correlation between traits X and Y exists, then individuals selected for X should harbour genes for Y different from the population mean of Y. Thus selection on X produces a response not only in trait X (given that X is heritable), but also a response in trait Y (also given heritability of Y). One can then determine the extent to which an XY phenotypic correlation reflects an XY genetic correlation. In the special case of mate choice, individuals do not express both X (preference) and Y (epigamic trait), thus no phenotypic correlation exists. If a genetic correlation exists, then selection on the male trait should produce a CR in the female preference (and vice versa). The genetic correlation is specifically due to the selected males (or females) harbouring unexpressed preference (trait) genes. For example, high trait-selected males possess high-preference genes, and low trait-selected males possess low-preference genes. These unexpressed genes (in whichever sex) are the proximate cause of the genetic correlation.

A common experimental procedure is as follows. A source population contributes selected males and randomly chosen females. Their offspring are measured for the male trait, and the procedure is repeated: unselected females from that line are mated with selected males from that line. After several generations, the females are tested to determine whether their preference differs from that of the initial population, a line selected in the other direction and/or unselected control lines. Issues such as genetic drift, replicated lines, control lines and advantages of bidirectional selection have been discussed elsewhere (Bakker & Pomiankowski 1995).

How can CR methods give erroneous results? For selection experiments across several generations, mating is obviously required. The problem arises because by artificially selecting on one sex, researchers alter selection acting on the other sex (altered sexual selection on males in the case of experimenter-selected females; altered natural selection on female preference in the case of experimenter-selected males). For example, if researchers have selected a low male-trait line, then high-preference females are likely to mate reluctantly (if at all) and invest less in current reproduction than are low-preference females. Thus by imposing artificial selection on the male trait, researchers facilitate the imposition of selection on female preferences. An observed response to selection could be due to (1) low-selected males carrying unexpressed low-preference alleles (the genetic correlation of interest), (2) fecundity selection favouring low-preference females (an artefact not of interest in this context), or both. The situation is similar, perhaps even more obvious, if researchers select on the female preference. For example, if a female high-preference line is placed with a random (unselected) group of males, it is reasonable to expect that the males that mate will not be a random subset of the unselected group. The experimenter-selected, high-preference females will, in all likelihood, mate more with high-trait males. Thus the male offspring of the high-preference females are likely to express high-male trait values both because their high-preference mothers had unexpressed high-trait genes (genetic correlation), and because their fathers were not a

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Table 1. Predicted effects of unintended selection acting on the sex not selected by the experimenter; all methods bias the genetic correlation upwards

Selected line	Unintended selection	Strength
Females		
High	SS against low-trait males	Moderate to strong, dependent on mating system
Low	SS against high-trait males	Weak to moderate, dependent on mating system
Males		
High	FS against low-preference females	Weak to moderate
Low	FS against high-preference females	Moderate to strong, dependent on female mating decision rule

SS: Sexual selection; FS: fecundity selection.

random subset of the population (sexual selection); although the fathers were not selected by the experimenter, they were selected by the high-preference females.

Consideration of the possible effects of unintended selection are presented in Table 1. We consider the four combinations of the experimenter-selected sex (female and male) and the direction of selection (high and low). All cases lead to an increase in the apparent genetic correlation. The magnitude of the effect, we suspect, will be strongest, and thus the results least reliable, in the case of experimenter-selected, high-preference females. This should impose fairly strong sexual selection on the male trait, but the strength of selection naturally depends on the mating system. All combinations give biased results, however.

What can be done to remedy the above problem? The most obvious solution would be not to use the CR method to test for genetic correlations between preference and trait (see Arnold & Halliday 1992, for a similar conclusion regarding estimating the genetic correlation between male and female multiple mating). Butlin (1993) proposed that random mating and equal progeny representation would solve this problem. In the case of the genetic correlation between female preferences and male traits, the genetic correlation may be maintained only by nonrandom mating. If the genetic correlation is due to linkage disequilibrium arising from nonrandom mating, then experimenter-imposed, random mating is expected to decrease the strength of the genetic correlation by 50% per generation (Bakker & Pomiankowski 1995). Thus, this previously proposed solution may underestimate the genetic correlation in the case of female preferences and male traits.

We conclude that CR methods are unlikely to provide accurate estimates of the genetic correlation between female preferences and male traits. Alternative methods, such as half-sibling, full sibling, and parent–offspring comparisons, can provide estimates of the genetic correlation (Falconer 1989; for examples with sexually selected traits and female preferences, see Bakker 1993; Gray & Cade 1999). Not using CR methods may seem to be too restrictive a suggestion, but consider the alternatives: the real issue is eliminating differential reproduction of the unselected (by the experimenter) sex, while maintaining natural levels of assortative mating.

There are, of course, other considerations when adopting an experimental design for quantitative genetic estimation. In particular, the sample sizes required to achieve a particular standard error depend on the values of the parameters estimated as well as the method chosen (see, e.g. Reeve 1955; Robertson 1959; Klein et al. 1973; Klein 1974). A second issue is the nature of the answer sought: some researchers may be more interested in a qualitative interpretation of the estimate, that is, 'is there a significant genetic correlation or not', independent of the magnitude of the estimate obtained? We argue that the magnitude of the estimate is important information. This is increasingly true as sexual selection theory becomes more refined, and models indicate that the strength of the genetic correlation required to sustain runaway evolution varies dependent upon natural selection acting on the male trait and the female preference (Kirkpatrick & Barton 1995). We conclude that CR methods should be avoided.

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