The causes of variation in the presence of genetic covariance between sexual traits and preferences

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ABSTRACT

Mating traits and mate preferences often show patterns of tight correspondence across populations and species. These patterns of apparent coevolution may result from a genetic association between traits and preferences (i.e. trait–preference genetic covariance). We review the literature on trait–preference covariance to determine its prevalence and potential biological relevance. Of the 43 studies we identified, a surprising 63% detected covariance. We test multiple hypotheses for factors that may influence the likelihood of detecting this covariance. The main predictor was the presence of genetic variation in mate preferences, which is one of the three main conditions required for the establishment of covariance. In fact, 89% of the nine studies where heritability of preference was high detected covariance. Variables pertaining to the experimental methods and type of traits involved in different studies did not greatly influence the detection of trait–preference covariance. Trait–preference genetic covariance appears to be widespread and therefore represents an important and currently underappreciated factor in the coevolution of traits and preferences.

Key words: Fisherian selection, Fisherian covariance, trait–preference coevolution, sexual selection, speciation, genetic covariance, genetic correlation, runaway.

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I. INTRODUCTION

Sexual traits and preferences often show patterns of tight correspondence across populations and closely related species (West-Eberhard, 1983; Andersson, 1994; Gerhardt & Huber, 2002; Greenfield, 2002; Kokko *et al.*, 2002; Coyne & Orr, 2004; Prum, 2010). This apparent coevolution of traits and preferences occurs in a wide range of traits used during reproductive interactions, including acoustic, vibrational, tactile, visual, and chemical signals, and genitalic structures (Eberhard, 1985, 1996; Greenfield, 2002; Coyne & Orr, 2004; Schärer *et al.*, 2011). For simplicity, we refer to all of these male sexual traits as 'traits' herein. Coevolution between traits and preferences can produce divergence among species in these traits, ultimately leading to pre-zygotic reproductive isolation between species (Panhuis *et al.*, 2001; Ritchie, 2007; Kraaijeveld, Kraaijeveld-Smit & Maan, 2011). Consequently, one of the most important questions in speciation research is which evolutionary mechanisms generate trait–preference coevolution.

A very simple, and potentially pervasive, mechanism that can generate trait–preference correspondence, and divergence in those traits across populations and species, is a genetic coupling (i.e. genetic covariance) between a sexual trait and preference (Fisher, 1958; Mead & Arnold, 2004; Kokko, Jennions & Brooks, 2006; Prum, 2010; Servedio & Bürger, 2014). Genetic covariance between traits and preferences is predicted to arise from starting conditions that are likely to be widespread in nature: whenever genetic variation in male traits and female preferences is found in conjunction with assortative mating, trait–preference genetic covariance will arise. This is because females preferring males with certain trait types will preferentially mate with those males; their sons will exhibit the same trait types and their daughters will bear similar mate preferences (Fisher, 1958). The mate preference and assortative mating may originate in many ways, including various mechanisms of sexual selection as well as natural selection on mate choice (Fisher, 1958; West-Eberhard, 1983; Mead & Arnold, 2004; Kokko *et al.*, 2006; Prum, 2010; West-Eberhard, 2014). Regardless of the initial reason(s) that assortative mating arises, once established, it generates genetic covariance between trait and preference that leads to self-reinforcing loops of coevolution because the preference will exhibit a correlated response to selection favouring the trait (Fisher, 1958; Lande, 1981; Mead & Arnold, 2004). These self-reinforcing loops of coevolution are termed Fisherian selection, and can lead to the rapid elaboration of traits and preferences, and also rapid divergence when initial small differences in the trait or preference arise among groups (Fisher, 1958; Lande, 1981; Kirkpatrick, 1987; Kirkpatrick & Ryan, 1991; Pomiankowski & Iwasa, 1998; Higashi, Takimoto & Yamamura, 1999; Kokko *et al.*, 2002, 2006; Mead & Arnold, 2004). Fisherian runaway selection will interact with other aspects of sexual selection and with natural selection in ways that may halt the runaway

process, or make other aspects of mate choice important in trait–preference evolution (Fisher, 1958; Kirkpatrick & Ryan, 1991; Rowe & Houle, 1996; Chandler, Ofria & Dworkin, 2012; Servedio & Bürger, 2014). However, regardless of which additional selective processes operate in concert with Fisherian selection, Fisherian selection itself will be in operation whenever the requisite conditions occur and therefore constitutes the default mechanism of sexual selection (Prum, 2010).

Despite the potential generality of Fisherian selection as a mechanism for trait–preference coevolution, trait–preference genetic covariance is often found to be absent or weak in empirical tests (for review: Zhou, Kelly & Greenfield, 2011; Greenfield *et al.*, 2014). In fact, the results of empirical tests of trait–preference genetic covariance have a long history of being 'mixed', with some studies detecting covariance and others not (Bakker & Pomiankowski, 1995; Zhou *et al.*, 2011; see Section III). Here, we review the empirical literature to determine the prevalence and biological relevance of trait–preference genetic covariance. It has been nearly 20 years since the first comprehensive review of studies on the topic (Bakker & Pomiankowski, 1995), and in the intervening time, there has been a substantial increase in the number of empirical tests for trait–preference genetic covariance. A recent review examining the incidence of trait–preference covariance among studies testing for covariance in the same species found overall weak levels of covariance but a large range of variation in its strength (Greenfield *et al.*, 2014). Here we aim to explain this type of variation in results by examining potential underlying factors determining whether covariance is detected or not.

We test a series of hypotheses that may explain variation among studies in the detection of trait–preference genetic covariance. Our aim is to understand the factors that may influence whether or not trait–preference covariance is detected. We tested four hypotheses that focus on the conditions required for trait–preference covariance to be established and on the methodology used in tests of its presence, as follows. Hypothesis 1: the amount of genetic variation in traits and preferences influences the detection of trait–preference covariance. Hypothesis 2: implemented patterns of mating in quantitative genetics experiments influence the detection of trait–preference covariance. Hypothesis 3: using artificial selection can bias tests for trait–preference covariance. Hypothesis 4: the method used to describe mate preferences influences the likelihood of detecting trait–preference covariance. We provide background and predictions for each hypothesis below (Sections IV–VII). We also tested for the following additional variables that may influence the likelihood of detecting trait–preference covariance: the type of sexual trait, the quantitative genetic experimental design, and whether mating crosses to produce offspring for estimating genetic parameters involved hybridization with a second species.

II. DATA COLLECTION

We searched the primary literature for empirical tests of trait–preference covariance using the ISI *Web of Knowledge* database (1987 to present; search conducted May 2014). We started with broad search criteria, using the following combination of key words: one key word from group 1 ('covariance', 'genetic correlation', 'Fisherian', 'Fisher', 'genetic association' or 'linkage') and one key word from group 2 ('female preference', 'mate preference', 'male display', 'mate/mating display', 'female display', 'female choice', 'mate choice', 'male choice', 'mating', 'cue', 'signal', 'ornament', 'male trait' or 'female trait'). We supplemented this search by including sources that either cited key papers or were cited by key papers relevant to signal–preference genetic covariance, as well as papers in our own literature collection.

In our analyses we used only studies that quantified variation in sexual traits and preferred trait values. This criterion resulted in the inclusion of 43 studies (Table 1). It excluded studies that assayed female preference or male traits indirectly, for example by measuring female preference strength or selectivity and male attractiveness rather than trait values and preferred values (Table 2).

We found two major categories of study based on the goal of each study's author(s): (*i*) those that test for linkage disequilibrium; and (*ii*) those that test for physical linkage and/or pleiotropy. However, any covariance detected can come from a combination of mechanisms (i.e. a mix of LD, physical linkage, and pleiotropy). To tease the contribution of each apart, one would need to extend studies to a few generations and observe how quickly the genetic association breaks down. Because genetic covariance between traits resulting from LD is established and maintained by assortative mating, LD can break down quickly, whereas genetic covariance due to physical linkage or pleiotropy would persist for several generations (Roff, 1997). Thus, the exact mechanism is typically not determined. However, the fundamental approach for testing for physical linkage/pleiotropy differs from that of testing for LD (Table 1), and thus our tests of the hypotheses take into account the type of study to determine any systematic biases associated with each.

As it is generally assumed that very few empirical studies test for trait–preference covariance, the sample size of $N = 43$ studies was quite surprising to us. However, it was too low to conduct a formal meta-analysis that tested multiple hypotheses simultaneously. We therefore focused on descriptive statistics, simple linear models, and contingency tables to test potential explanations for variation in the detection of trait–preference genetic covariance. We conducted all analyses with JMP 7.0.1 (SAS Institute).

III. HOW COMMON IS TRAIT–PREFERENCE GENETIC COVARIANCE?

The majority of studies detected trait–preference genetic covariance: this was the case for 63% of LD studies

($N = 27$), and for 62.5% of physical linkage/pleiotropy studies ($N = 16$). Although the likelihood of detection did not vary across the LD *versus* physical linkage/pleiotropy studies ($\chi^2 = 0.2$, $P = 0.70$; Fig. 1), there was considerable variation within each of these groups of studies in whether trait–preference covariance was present. We used this variation to test the four hypotheses about biological and experimental factors that might influence the presence and detectability of trait–preference covariance.

Many studies have been published with a result of no covariance ($N = 16$). Thus, we do not anticipate that our overall analysis of the literature is highly confounded by publication bias. We outline in the discussion (Section IX) some cases in which publication bias may influence the more detailed analyses of studies.

IV. HYPOTHESIS 1: THE AMOUNT OF GENETIC VARIATION IN TRAITS AND PREFERENCES INFLUENCES THE DETECTION OF TRAIT–PREFERENCE GENETIC COVARIANCE

Two of the three basic conditions for trait–preference genetic covariance to arise are genetic variation in preferences and genetic variation in traits (Fisher, 1958). These criteria apply generally to covariance between any two traits (Roff, 1997), and the magnitude of genetic covariance is, in part, a product of the heritabilities of the two traits (Kirkpatrick & Barton, 1997). In essence, the heritability of each trait provides an upper limit to covariance, and thus genetic covariance is more likely with greater genetic variation in each of the traits of interest (Lande, 1981). Following from this, the first of two predictions of this hypothesis is that the likelihood of detecting trait–preference covariance should be positively related to the amount of genetic variation expressed in both the trait and the preference (Bakker & Pomiankowski, 1995; Allison *et al.*, 2008; Roff & Fairbairn, 2014). Additionally, mathematical simulations show that the amount of genetic variation in preference will need to exceed that of the preferred trait for high covariance to arise (Roff & Fairbairn, 2014). Thus, we also test the prediction that heritability in preference should have a higher correspondence with the likelihood of detecting covariance than heritability in the trait.

We tested these predictions with studies that reported estimates of genetic variation in the trait and preference (not all studies tested for genetic variation, including the vast majority of studies looking at physical linkage). All such studies reported heritability as an estimate of expressed genetic variation, with the majority using broad-sense heritability. Thus, when both narrow-sense and broad-sense heritability were measured, we used the broad-sense estimate to provide consistency across studies. Based on the magnitude of heritability estimates, we assigned each study to one of four categories: (*i*) heritability not statistically different from zero; (*ii*) low heritability: estimates less than 0.3; (*iii*) medium heritability: estimates between 0.3 and 0.5; (*iv*) high heritability: estimates greater than 0.5.

Table 1. Studies included in our review of tests of trait–preference genetic covariance. We have divided them into (A) linkage disequilibrium between the two traits, and (B) physical linkage or pleiotropy.

Study organism	Trait type	Trait-preference covariance	Heritability of trait	Heritability of preference	Experimental design	Risk of eroding LD	Assay of preference	Notes	Citation
(A) Studies focusing on linkage disequilibrium									
Insects									
Achroia grisella (moth)	Acoustic	No	Low	Low	Breeding design (full-sib/half-sib)	High risk	Preference – artificial		Zhou *et al.* (2011)
Argyrotaenia velutinana (leafroller)	Chemical	Yes	Medium		Breeding design (parent–offspring regression)		Preference – artificial		Roelofs *et al.* (1986)[a]
Cadra cautella (almond moth)	Chemical[b]	No		None	Correlated response	Risk	Preference – artificial		Allison, Roff & Cardé (2008)
Chorthippus brunneus (field grasshopper)	Acoustic	No	(Present)	(Present)	Correlated response	High risk	Mate choice	No replicate lines	Charalambous, Butlin & Hewitt (1994)
Cyrtodiopsis dalmanni (stalk-eyed fly)	Visual	Yes	Medium		Correlated response	Risk	Preference – live	Yes in low lines, no in high lines	Wilkinson & Reillo (1994)
Drosophila mercatorum (fruit fly)	Acoustic	Yes	Medium		Correlated response	High risk	Preference – artificial	Yes in control and low lines and no in high lines	Ikeda & Maruo (1982)
Drosophila sp. (fruit fly)	Genitalic	Yes	Medium	Medium	Correlated response	Risk	Mate choice		Miller & Pitnick (2002)
Ephippiger ephippiger (bushcricket)	Acoustic	Yes			Hybrid cross	No risk	Preference – artificial		Ritchie (2000)
Gryllus integer (field cricket)	Acoustic	Yes	Medium	Medium	Breeding design (full-sib)	No risk	Preference – artificial	No covariance in next generation	Gray & Cade (1999b)
Gryllus texensis and *G. rubens* (field cricket)	Acoustic	Yes	Low	Medium	Breeding design (full-sib)	No risk	Preference – artificial		Gray & Cade (2000)
Nauphoeta cinerea (cockroach)	Chemical	Yes	High		Breeding design (parent–offspring regression)	High risk	Preference – artificial		Moore (1989)
Onthophagus taurus (dung beetle)	Genitalic	Yes	High	High	Breeding design (full-sib/half-sib)	Risk	Morphological match		Simmons & Kotiaho (2007)
Pectinophora gossypiella (pink bollworm)	Chemical[b]	Yes	Medium	(Present)	Correlated response	High risk	Preference – artificial		Collins & Cardé (1989)
Pectinophora gossypiella (pink bollworm)	Chemical[b]	No	High		Correlated response	Risk	Preference – artificial		Collins, Rosenblum & Cardé (1990)
Pectinophora gossypiella (pink bollworm)	Chemical[b]	No	Low	Low	Correlated response	Risk	Preference – artificial		Collins & Cardé (1990)
Ribautodelphax imitans (planthopper)	Acoustic[b]	Yes	High	High	Correlated response	High risk	Mate choice		De Winter (1992)
Scathophaga stercoraria (dung fly)	Genitalic	Yes	Medium	Medium	Animal model	High risk	Morphological match		Thüler *et al.* (2011)
Sepsis cynipsea (dung fly)	Size	No	Medium	High	Breeding design (full-sib/half-sib)	Risk	Preference – live		Mühlhäuser & Blanckenhorn (2004)
Fish									
Gasterosteus aculeatus (stickleback)	Visual	Yes	Low	Medium	Breeding design (parent–offspring regression)	Risk	Preference – live		Bakker (1993)
Gasterosteus aculeatus (stickleback)	Visual	Yes			Breeding design (parent–offspring regression)	Risk	Neurological response		Rick, Mehlis & Bakker (2011)
Haplochromis spp. (Lake Victoria cichlid)	Visual	No	(Present)		Hybrid cross	Risk	Preference – live	Limited number of sires	van der Sluijs *et al.* (2013)
Poecilia reticulata (guppy)	Visual	Yes			Correlated response	Risk	Preference – live	Covariance eroded after few generations	Houde (1994)
Poecilia reticulata (guppy)	Visual	No	Low		Correlated response	High risk	Preference – live		Breden & Hornaday (1994)

Table 1. Continued

Study organism	Trait type	Trait-preference covariance	Heritability of trait	Heritability of preference	Experimental design	Risk of eroding LD	Assay of preference	Notes	Citation
Poecilia reticulata (guppy)	Visual	Yes			Correlated response	No risk	Preference – live		Brooks & Couldridge (1999)
Poecilia reticulata (guppy)	Genitalic	Yes	High	High	Breeding design (full-sib/half-sib)	High risk	Morphological match		Evans, van Lieshout & Gasparini (2013)
Pandamalia pandamilia and *P. nyererei* (cichlid)	Visual	No	(Present)	(Present)	Hybrid cross	Risk	Preference – live	Limited number of sires	van der Sluijs *et al.* (2010)
Birds									
Ficedula albicollis (collared flycatcher)	Visual	No	Medium	Low	Animal model	No risk	Mate choice		Qvarnström, Brommer & Gustafsson (2006)
(B) Studies focusing on physical linkage or pleiotropy									
Insects									
Achroia grisella (moth)	Acoustic	No			Hybrid cross	High risk	Preference – artificial		Limousin *et al.* (2012)
Achroia grisella (moth)	Acoustic	No			Hybrid cross	High risk	Preference – artificial		Alem *et al.* (2013)
Coelopa frigida (seaweed fly)	Size	Yes	High		Breeding design (inversion karyotypes)	No risk	Mate choice		Gilburn, Foster & Day (1993)
Coelopa frigida (seaweed fly)	Size	No	High		Breeding design (inversion karyotypes)	No risk	Mate choice		Gilburn & Day (1994)
Heliconius sp. (butterfly)	Visual[b]	Yes			Hybrid cross	High risk	Preference – artificial		Kronforst *et al.* (2006)
Heliconius cydno chioneus and *H. melpomene rosina* (butterfly)	Visual	Yes			Hybrid cross	Risk	Preference – artificial and live; mate choice[c]		Merrill *et al.* (2011)
Laupala spp. (Hawaiian cricket)	Acoustic	Yes			Hybrid cross	High risk	Preference – artificial		Shaw & Lesnick (2009)
Laupala spp. (Hawaiian cricket)	Acoustic	Yes			Hybrid cross	High risk	Preference – artificial		Wiley & Shaw (2010)
Laupala spp. (Hawaiian cricket)	Acoustic	Yes			Hybrid cross	High risk	Preference – artificial		Wiley, Ellison & Shaw (2012)
Ostrinia nubilalis (European corn borer)	Chemical	No				High risk	Neurological response		Roelofs *et al.* (1987)
Ostrinia nubilalis (European corn borer)	Chemical	No				High risk	Neurological response		Löfstedt *et al.* (1989)
Ostrinia orientalis (moth)	Chemical	No			Hybrid cross	Risk	Preference – artificial		Fu *et al.* (2005)
Utetheisa ornatrix (arctiid moth)	Size	Yes		High	Breeding design (father–daughter regression)	Unknown	Preference – live		Iyengar, Reeve & Eisner (2002)
Fish									
Danio rerio (zebrafish)	Visual	Yes			Mutants	High risk	Preference – live		Gumm, Snekser & Iovine (2009)
Oryzias latipes (medaka fish)	Unknown	Yes			Mutants	Risk	Preference – live		Fukamachi *et al.* (2009)
Birds									
Erythrura gouldiae (Gouldian finch)	Visual	Yes			Breeding design (parent–offspring regression)	Risk	Preference – live		Pryke (2010)

The studies are listed in alphabetical order within study organism, and we extracted the following information from each: trait type, whether there is support for trait–preference genetic covariance, heritability of the trait, heritability of the preference, experimental design, risk of eroding linkage disequilibrium (LD) due to patterns of mating, and assay of the mate preference (preference for artificial stimuli, preference for live animals, or choice for live animals).
Unknown values are indicated by blank entries.
[a]Female trait and male preference.
[b]Cited in Bakker & Pomiankowski (1995).
[c]Used 'Preference – artificial' category for analyses; the results did not depend on the choice of assay used for the test.

Table 2. Studies that did not meet the full criteria for inclusion in our review of tests of trait–preference genetic covariance, divided into (A) linkage disequilibrium between the two traits, or (B) physical linkage or pleiotropy

Study organism	Trait type	Trait-preference covariance	Heritability of trait	Heritability of preference	Experimental design	Risk of eroding LD	Assay of preference	Notes	Citation
(A) Studies focusing on linkage disequilibrium									
Insects									
Drosophila melanogaster (fruit fly)	Unknown	Yes	Present	Present	Breeding design (10 inbred lines)	High risk	Mate choice	Attractiveness	Ratterman *et al.* (2014)
Drosophila serrata (fruit fly)	Species identity	Yes	Present	Present	Breeding design (hybrid cross)	High risk	Mate choice		Blows (1999)
Drosophila sp. (fruit fly)	Acoustic	No	High	Present	Breeding design (full-sib)	No risk	Mate preference	Female responsiveness	Ritchie, Saarikettu & Hoikkala (2005)
Fish									
Poecilia reticulata (guppy)	Unknown	No	None	None	Correlated response	No risk	Preference – live	Attractiveness; selection on trait and preference	Hall, Lindholm & Brooks (2004)
Birds									
Gallus domesticus (chicken)	Unknown	No	None–high		Correlated response	Risk	Mate choice	Attractiveness	von Schantz *et al.* (1995)
(B) Studies focusing on physical linkage or pleiotropy									
Insects									
Drosophila melanogaster (fruit fly)	Chemical	Yes					Mate choice	Discrimination of sex; mutation approach	Marcillac, Grosjean & Ferveur (2005)
Drosophila mauritiana and *D. simulans* (fruit fly)	Unknown	Yes			Hybrid cross		Mate choice	Attractiveness; introgressed backcrosses	McNiven & Moehring (2013)
Drosophila serrata (fruit fly)	Species identity	Yes			Hybrid cross		Mate choice	Mating likelihood	Blows (1998)
Haliotis spp. (abalone)	Fertilization success	Yes					Fertilization proteins	Used single nucleotide polymorphisms	Clark *et al.* (2009)
Birds									
Ficedula hypoleuca and *F. albicollis* (flycatchers)	Species identity	Yes			Hybrid crosses		Mate choice (in wild)	Testing for Z-linkage	Sæther *et al.* (2007)

As in Table 1, studies are listed in alphabetical order within study organism, and we extracted the following information from each: trait type, whether there is support for trait–preference covariance, heritability of the trait, heritability of the preference, experimental design, risk of eroding linkage disequilibrium (LD) due to patterns of mating, and assay of the mate preference (preference for artificial stimuli, preference for live animals, or choice for live animals). Blank entries in (B) indicate either missing values or columns in which the above information was not relevant. Unknown values are indicated by blank entries.
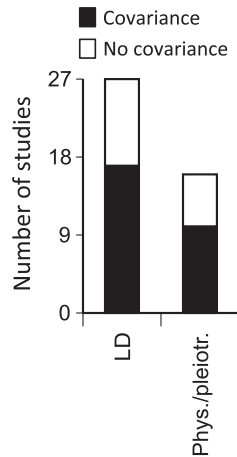
Fig. 1. Detection of trait–preference genetic covariance across the literature surveyed. Rates of detection were similar for studies testing for linkage disequilibrium (LD) between trait and preference, and physical linkage/pleiotropy (Phys./pleiotr.).

Table 3. Tests of the association between the heritability of preference and trait indicating whether covariance between traits was detected

	Factor	N	d.f.	χ^2	P
Heritability of preference	All studies	13	3	12.8	0.005
	LD only	12	3	12.5	0.006
Heritability of trait	All studies	21	2	0.6	0.74
	LD only	19	2	0.9	0.63

d.f., degrees of freedom.

We found that the likelihood of detecting trait–preference genetic covariance varied significantly with the heritability of preference (Table 3). Of the studies with low heritability in the preference, none detected covariance; however, of the studies with medium to high heritability in the preference ($N = 9$), 88.9% detected covariance (Table 3; Fig. 2A). On the other hand, we found that the likelihood of detecting trait–preference genetic covariance did not vary with the heritability of male traits (Table 3; Fig. 2B). We repeated these analyses using only studies testing for LD, because physical position of the traits on the chromosome should not change based on genetic variation. However, we found a similar pattern (Table 3). A linear model was not included for this factor, as there were limited numbers of studies of physical linkage/LD that tested for the heritability of the preference and traits.

When we consider that expressed genetic variation is environment specific, and therefore likely to vary among populations and laboratory conditions (Roff, 1997; Lynch & Walsh, 1998; Sgrò & Hoffmann, 2004), a corollary of this hypothesis emerges. Because covariance should vary with heritability, not every study on the same species should produce the same result: covariance in different populations of a single species should be in accordance with the amount of genetic variation expressed in traits and preferences (Bakker
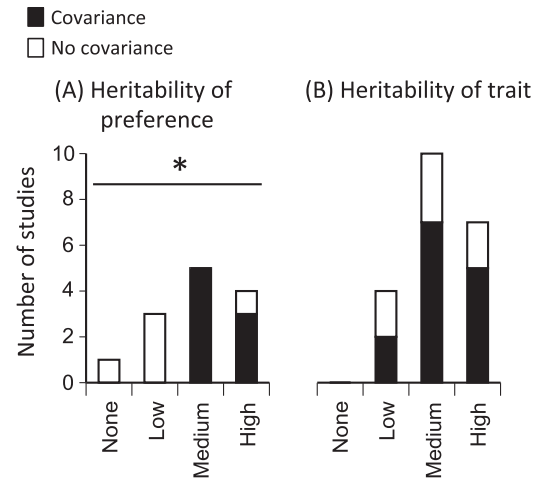
Fig. 2. Detection of trait–preference genetic covariance in studies that detected no, low, medium, or high heritability in the (A) mate preference and (B) trait. The star indicates significant differences among categories.

& Pomiankowski, 1995). The limited number of studies that focus on the same species are not sufficient to test this prediction quantitatively. However, we can test whether experiments conducted in the same species provide similar or different results from one another.

We found six species that were used in multiple studies of trait–preference covariance ($N = 16$ studies). Of these, one species yielded support for covariance across both studies (*Gasterosteus aculeatus*: Bakker, 1993; Rick *et al.*, 2011); two species yielded support against covariance across studies (*Achroia grisella*: Limousin *et al.*, 2012; Alem *et al.*, 2013; *Ostrinia nubilalis*: Roelofs *et al.*, 1987; Löfstedt *et al.*, 1989); and the other three species yielded mixed results (*Pectinophora gossypiella*: Collins & Cardé, 1989, 1990; Collins *et al.*, 1990; *Poecilia reticulata*: Breden & Hornaday, 1994; Houde, 1994; Brooks & Couldridge, 1999; Evans *et al.*, 2013; *Coelopa frigida*: Gilburn *et al.*, 1993; Gilburn & Day, 1994). Thus, variation in the conditions of the source populations, or in the experiments, seems to influence the detection of trait–preference covariance.

V. HYPOTHESIS 2: EXPERIMENTAL PATTERNS OF MATING INFLUENCE THE DETECTION OF TRAIT–PREFERENCE GENETIC COVARIANCE

This hypothesis represents the third basic condition for trait–preference genetic covariance to arise: assortative mating (Fisher, 1958). Except for cases of physical linkage or pleiotropy, covariance is linkage disequilibrium established and maintained by assortative mating. Thus, any experimental design that disrupts assortative mating will reduce the likelihood of detecting covariance (Bakker & Pomiankowski, 1995). This effect could be generated merely by restricting the pool of potential mates to 5–10 individuals (Roff & Fairbairn, 2014). Under experimental conditions of random mating, linkage disequilibrium should be eroded at a rate of ~50%

every generation (Pomiankowski & Sheridan, 1994; Bakker & Pomiankowski, 1995; Allison *et al.*, 2008). Thus, genetic covariance can be completely lost in just a few generations of random mating in the laboratory (Houde, 1994; Roff, 1997). The problem is that quantitative genetics experiments often begin with a period of random mating in the parental generations to eliminate environmental or maternal effects from the estimates of genetic parameters, or with laboratory colonies maintained with breeding regimes that seek to prevent inbreeding (Roff, 1997; Lynch & Walsh, 1998). Consequently, there is a risk that failures to detect trait–preference covariance may be due to the use of experimenter-induced random mating (Pomiankowski & Sheridan, 1994).

The first prediction of this hypothesis is that studies with experimental designs involving greater risk of disrupting assortative mating should have a lower likelihood of detecting trait–preference genetic covariance. In particular, the likelihood of detecting covariance should be highest in studies with no experimentally imposed random mating. This primarily includes studies with experimental designs that incorporate measures of genetic parameters from individuals mated in the field or within laboratory conditions allowing for mate choice among a large sample of males rather than a restricted number of males.

To test this prediction, we assessed the risk that that LD was eroded due to experimentally imposed random mating. Studies were classified as 'no risk' when genetic parameters were estimated using animals mated in the wild. Studies were classified as 'risk' when there was one generation of a reduced ability of females to express their mate preferences: those in which females were given either limited or no choice of mates. Studies were categorized as 'high risk' when limitations on female preference occurred over multiple generations in the laboratory: studies using laboratory lines in which random mating is imposed in order to avoid inbreeding, or studies in which genetic parameters were estimated from the offspring of forced mating crosses.

The likelihood of detecting trait–preference genetic covariance was highest in LD studies with no risk of eroding LD (Fig. 3A). However, we found no overall statistically significant relationship between the detection of covariance and the risk of eroding LD due to random mating (Table 4). A lack of a significant interaction term indicates the same relationship between detection of trait–preference genetic covariance and the risk of eroding LD in both types of studies (Table 4; Fig. 3). We may be limited in our ability to detect such patterns due to a low sample size.

VI. HYPOTHESIS 3: USING ARTIFICIAL SELECTION CAN BIAS TESTS FOR TRAIT–PREFERENCE GENETIC COVARIANCE

One popular approach for testing for covariance is to select for an increase or decrease in either the trait or preference and determine the correlated response to selection of the other. There are two major criticisms of this approach. On the one
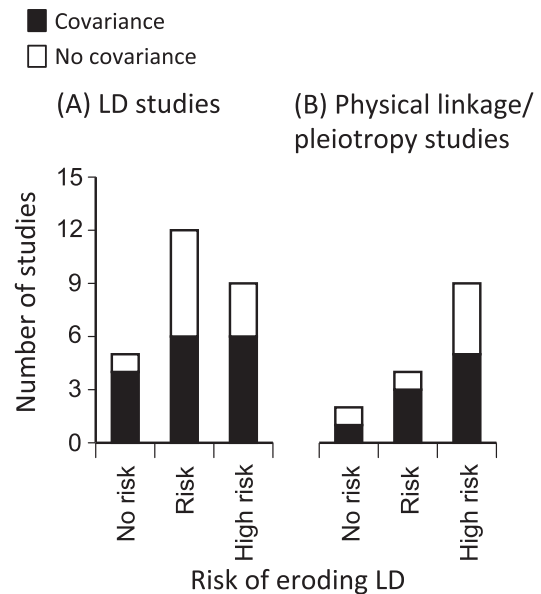
Fig. 3. Detection of trait–preference genetic covariance across studies that vary in the risk of eroding linkage disequilibrium (LD) between the trait and preference due to patterns of mating. (A) Studies testing for linkage disequilibrium (LD), (B) studies testing for physical linkage/pleiotropy.

Table 4. Tests of whether the likelihood of detecting trait–preference genetic covariance varied with the following factors: the risk of eroding linkage disequilibrium (LD) due to patterns of random mating in the laboratory, study type (tests of LD *versus* tests of physical linkage/pleiotropy), and their interaction

Factor	N	d.f.	χ^2	P
Risk of erosion	41	2	0.1	0.97
Study type		1	0.1	0.75
Risk × study type		2	1.6	0.45

d.f., degrees of freedom.

hand, studies that look for correlated responses to selection often impose random mating across multiple generations, which will break down LD and lead to an underestimation of genetic covariance (Bakker & Pomiankowski, 1995; Gray & Cade, 1999*a*). On the other hand, correlated responses to selection experiments may overestimate genetic covariance because selection on, for example, the trait, will also impose natural selection favouring less choosy females because only those willing to mate with males of the selected trait value will contribute to the next generation (Gray & Cade, 1999*a*; Fuller, Baer & Travis, 2005). The outcome of using a correlated response to selection approach will depend upon a complex set of factors as outlined above. We therefore do not make specific predictions, but rather tested for systematic biases. Because we might expect that LD studies would be influenced to a greater degree by this aspect of experimental design, in addition to the overall analysis, we also analysed LD studies separately.
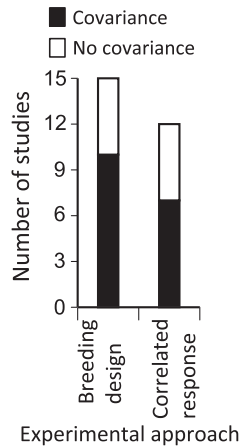
Fig. 4. Detection of trait–preference genetic covariance across studies using a breeding design *versus* a correlated response to selection approach.

We found that the likelihood of detecting trait–preference genetic covariance did not vary between studies testing for a correlated response to selection *versus* other approaches ($N = 43$; d.f. = 5; $\chi^2 = 4.8$, $P = 0.44$). We found a similar lack of effect of the design when analysing only those studies looking for LD ($N = 27$; d.f. = 2; $\chi^2 = 1.0$, $P = 0.59$; Fig. 4). None of the physical linkage/pleiotropy studies used a correlated response to selection approach.

VII. HYPOTHESIS 4: THE METHOD USED TO DESCRIBE MATE PREFERENCES INFLUENCES THE LIKELIHOOD OF DETECTING TRAIT–PREFERENCE GENETIC COVARIANCE

Mate choice is the expression of a mate preference within environments that may vary in the set of available potential mates (among other factors), and how these individuals interact with the choosing individual (reviewed in Rodríguez, Rebar & Fowler-Finn, 2013; Miller & Svensson, 2014). Observed mate choice decisions may vary among social contexts (Jennions & Petrie, 1997; Hunt, Brooks & Jennions, 2005; Cotton, Small & Pomiankowski, 2006), even if the underlying mate preference remains the same. Consequently, assays of mate preference that rely on interactions among individuals may, in part, reflect non-genetic variation in the expression of mate preferences. Because context dependence of preference could lower the genetic covariance between trait and preference (Roff & Fairbairn, 2014), studies with live interactions may underestimate genetic variation and genetic covariance.

This hypothesis makes the prediction that that studies conducted with assays that directly describe preferences, e.g. by using artificial stimuli rather than live males, should be more likely to detect covariance than studies using assays that involve interactions between live individuals. To test this prediction, we assigned each study to one of five categories reflecting the method for describing mate preferences. (*i*)

Table 5. Tests of whether the assay of mate preference, study type [tests of linkage disequilibrium (LD) *versus* tests of physical linkage/pleiotropy (Phys./pleiotr.)], and their interaction, corresponded with the likelihood of detecting trait–preference covariance

| Factor	N	d.f.	χ^2	P
Assay of preference	43	4	4.9	0.29
Study type		1	0	0.96
Assay × study type		3	7.8	0.05
LD only	27	4	4.5	0.34
Phys./pleiotr. only	16	3	7.8	0.05

d.f., degrees of freedom.

Mate preference assayed with artificial stimuli: in these studies, the assay of mate preference was a measure of a female's response to experimentally controlled artificial stimuli. Such experiments rule out the possibility that the behaviour of other individuals influences female responses. (*ii*) Mate preference for live males: in these studies, females interacted with live males, and the assay of mate preference was a measure of association/response with certain males. Both the trait values and other behaviour of the 'stimulus' males may influence female responses, thereby potentially introducing confounding variation. (*iii*) Mate choice: in these studies, the assay of preference was the male type with which the female mated (e.g. by measuring mating decisions, fertilization success, paternity, etc.). Such experiments have a high potential to introduce sources of variation from social and non-social environmental contexts. (*iv*) Morphological match: in these studies, the assay involved the degree of match between morphological measures of trait and preference. (*v*) Neurological measures: in these studies, the preference was measured by either a neurological response to a trait, or the receptor cells that responded to a trait.

We expected this prediction to hold for both studies of LD and physical linkage/pleiotropy (as it deals with the measurement of a proxy for preference that is influenced by sources of variation additional to genetic variation). However, we found that the relationship between the likelihood of detecting covariance and the method of describing mate preferences differed between LD and physical linkage/pleiotropy studies, as indicated by a significant interaction term (Table 5; Fig. 5). Within the LD studies, those testing for a neurological response and morphological match always detected covariance (Fig. 5). This contrasts with the physical linkage/pleiotropy studies, within which none of the neurological response studies detected trait–preference genetic covariance, but all of the studies using live preference did (Fig. 5).

VIII. OTHER VARIABLES THAT MAY INFLUENCE THE LIKELIHOOD OF DETECTING TRAIT–PREFERENCE GENETIC COVARIANCE

We also explored the following additional factors that may influence the likelihood of detecting trait–preference
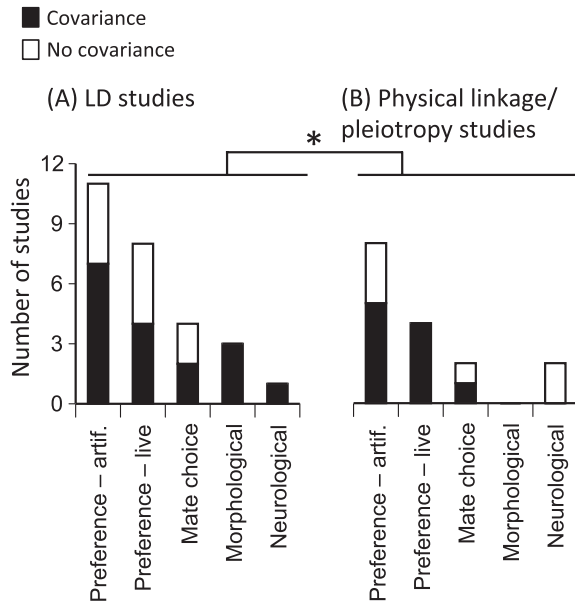
Fig. 5. Detection of trait–preference genetic covariance across studies that differed in the assay of female preference. The star indicates significantly different patterns between (A) linkage disequilibrium (LD) studies and (B) physical linkage/pleiotropy studies. The star indicates significant differences among categories.

covariance: (1) the type of trait, (2) the quantitative genetic experimental design, and (3) whether mating crosses to produce offspring for estimating genetic parameters involved hybridization with a second species. While some of these analyses address specific critiques of methodology commonly found in the literature (e.g. factor 2), they are primarily meant to be exploratory.

(1) Type of trait

We found five categories of trait used in tests of trait–preference genetic covariance; acoustic, visual, genitalic, chemical, and size. The detection of trait–preference covariance varied across trait types, and this relationship differed between studies testing for LD *versus* physical linkage/pleiotropy (Table 6). The incidence of detection of trait–preference covariance did not vary statistically across trait types in studies testing for LD, but did in studies testing for physical linkage/pleiotropy, as covariance was always found for visual traits, but never for chemical traits (Fig. 6).

(2) Quantitative genetic experimental design

We classified LD studies that did not take the correlated response to selection approach into four types of quantitative genetics experimental designs: parent–offspring regression, full-sibling design, full-sibling half-sibling design, hybrid crosses (among laboratory lines, populations, or species), and animal model. We found no difference in the detection of covariance across these study types ($N = 15$; d.f. $= 3$; $\chi^2 = 2.0$, $P = 0.58$).

Table 6. Tests of whether the trait type, study type [tests of linkage disequilibrium (LD) *versus* tests of physical linkage/pleiotropy (Phys./pleiotr.)], and their interaction, corresponded with the likelihood of detecting trait–preference covariance

Factor	N	d.f.	χ^2	P
Trait	43	4	12.2	0.016
Study type		1	1.7	0.19
Trait × study type		3	9.2	0.026
LD only	27	4	6.5	0.16
Phys./pleiotr. only	16	3	10.6	0.014

d.f., degrees of freedom.
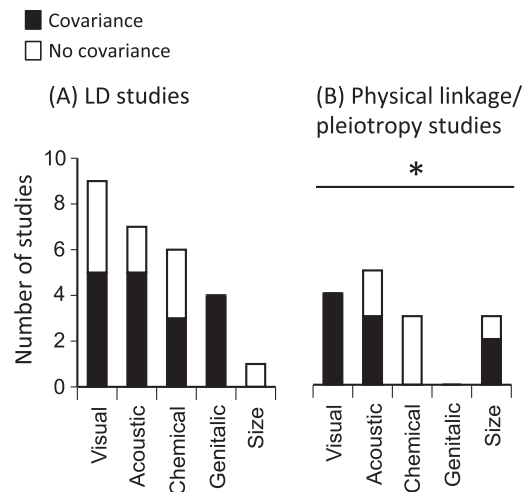
Fig. 6. Detection of trait–preference genetic covariance across studies differing in the type of trait investigated for (A) linkage disequilibrium (LD) studies and (B) physical linkage/pleiotropy studies. LD, linkage disequilibrium. The star indicates significant differences among categories.

(3) Mating crosses involving a second species

We found that some studies tested for covariance using within-species crosses while others used between-species crosses. The relationship between the type of cross and whether covariance was detected or not depended on whether the study involved tests of LD or physical linkage/pleiotropy (Table 7). For LD studies, 63% of those using crosses within species detected genetic covariance, whereas the two studies using crosses among species did not (Table 7). However, these two studies had a limited number of sires (one or two per study), which may have influenced the results. For the physical linkage/pleiotropy studies, the likelihood of detecting covariance did not vary between the between-species and within-species crosses (Table 7).

IX. DISCUSSION

Our review revealed high rates of detection of trait–preference genetic covariance. Of the studies we surveyed,

Table 7. Tests of whether the type of mating crosses (within-species *versus* between-species crosses), study type [tests of linkage disequilibrium (LD) *versus* tests of physical linkage/pleiotropy (Phys./pleiotr.)], and their interaction, corresponded with the likelihood of detecting trait–preference covariance

Factor	N	d.f.	χ^2	P
Cross type	43	1	1	0.31
Study type		1	3	0.08
Cross type × study type		1	6.2	0.01
LD only	27	1	4.3	0.04
Phys./pleiotr. only	16	1	1.9	0.17

d.f., degrees of freedom.

63% detected covariance. This percentage increases to 89% for the studies that best met the conditions required for trait–preference covariance to be established (see Section IV). We investigated several potential factors that could explain why covariance is detected in some studies and not in others. The likelihood of detecting covariance varied with the heritability of female preference: the greater the heritability, the higher the rate of detection. This same relationship did not hold for heritability of the male trait. Detection of trait–preference covariance was not influenced by patterns of mating imposed by the experimenter, whether a correlated response to selection approach was implemented, or by the assay of preference.

The higher correspondence between trait–preference genetic covariance and the heritability of female preference *versus* the trait has been predicted by mathematical simulations (Roff & Fairbairn, 2014). We recommend that empirical tests of this relationship should include accurate estimates for the heritabilities of both traits. Currently, comparable estimates of both in a single study are rare (Roff & Fairbairn, 2014; this study). Publication bias could also lead to the observed asymmetry between heritability of preference *versus* trait in the detection of genetic covariance. Genetic variation in male traits has historically been measured more often (see Table 1), and so studies that find no genetic variation in male traits and no covariance may be likely to remain unpublished. However, because genetic variation in female preferences has been measured less frequently (Hosken & House, 2011), studies that find no genetic variance (and no covariance) may be more likely to reach publication. The magnitude of potential confounding issues is hard to judge accurately, however, because several studies that tested for trait–preference covariance reported no information about the magnitude of genetic variation in traits or preferences (Table 1).

The heritability of preference and trait can vary across populations or generations, and so it is not surprising that we found that studies of the same species do not always produce the same result. In fact, it has previously been suggested that mixed results from a single species may reflect variation in the level of genetic variation expressed across populations (Bakker & Pomiankowski, 1995). Thus, when discussing

the prevalence and biological relevance of trait–preference genetic covariance, the context specificity of the expression of genetic variance and covariance must be taken into account (e.g. Zhou *et al.*, 2011).

We divided studies into two types based on the goals of the studies: those testing for LD between preference and trait, and those testing for physical linkage or pleiotropy. Our thinking was that studies testing for LD would be susceptible to missing covariance for two reasons. First, high sampling error inherent in empirical studies on LD (Roff & Fairbairn, 2014) may make low yet still significant levels of genetic covariance difficult to detect. Second, traditional quantitative genetics breeding approaches often incorporate a period of controlled breeding, during which LD can break down. However, we found no difference in the rates of detection of covariance across the two study types, nor any association between the level of risk of eroding LD and detection of covariance. Extending studies to a few generations would allow assessment of how quickly a genetic association breaks down; genetic covariance due to pleiotropy would persist for several generations (Roff, 1997). In those studies that have estimated covariance across generations (see Tables 1 and 2) the erosion of covariance has varied from one or a few generations (e.g. Houde, 1994; Gray & Cade, 1999*b*), to several generations (e.g. Blows, 1999). This variation in the rate of erosion suggests that perhaps different mechanisms may be responsible for generating or maintaining covariance across different populations or studies. This same reasoning can help explain why the expected problem of using a correlated response to selection approach seems not to be present to any greater extent than the underlying problem of random mating eroding covariance.

The data did not support the prediction that the assay of preference influences the likelihood of detecting trait–preference covariance. While there was an effect for the physical linkage/pleiotropy studies, it was not in the predicted direction and may be a result of small sample sizes. We suggest that this lack of correspondence between the assay and the likelihood of detection may arise if pleiotropy influences multiple traits that determine the outcome of mating interactions. Also, one difficulty of any study on mate preference/choice is that of determining the trait that females are actually assessing. Thus, it is difficult to know whether a lack of genetic covariance reflects a true lack of genetic association between display and preference, or whether the biologically relevant trait and preference were not properly identified by the experimenter.

X. CONCLUSIONS

(1) Trait–preference genetic covariance arises from simple and widespread initial conditions: genetic variation in the trait and preference in conjunction with assortative mating driven by any type of selection favouring some males (direct benefits, good genes, etc. Fisher, 1958; West-Eberhard, 1983; Prum, 2010). Even certain conditions in the social and biotic

environment may promote runaway processes without direct trait–preference genetic covariance (Bailey & Moore, 2012), or may recruit genetic variation in traits and preferences into such runaway processes (Rebar, D. and R. L. Rodríguez. In press.).

(2) We find that the detection of trait–preference genetic covariance is more likely with higher heritability in the preference, but not the trait, with 89% of studies finding medium to high heritability of preference also detecting trait–preference covariance.

(3) Trait–preference genetic covariance may not persist indefinitely (Fisher, 1958; Prum, 2010) and may not necessarily act alone (Servedio & Bürger, 2014). However, it appears to be widespread and therefore represents a potentially important mechanism of trait–preference coevolution and divergence that is currently underappreciated.

XI. ACKNOWLEDGEMENTS

XII. REFERENCES

ALEM, S., STREIFF, R., COURTOIS, B., ZENBOUDJI, S., LIMOUSIN, D. & GREENFIELD, M. D. (2013). Genetic architecture of sensory exploitation: QTL mapping of female and male receiver traits in an acoustic moth. *Journal of Evolutionary Biology* **26**, 2581–2596.

ALLISON, J. D., ROFF, D. A. & CARDÉ, R. T. (2008). Genetic independence of female signal form and male receiver design in the almond moth, Cadra cautella. *Journal of Evolutionary Biology* **21**, 1666–1672.

ANDERSSON, M. (1994). *Sexual Selection*. Princeton University Press, Princeton.

BAILEY, N. W. & MOORE, A. J. (2012). Runaway sexual selection without genetic correlations: social environments and flexible mate choice initiate and enhance the Fisher process. *Evolution* **66**, 2674–2684.

BAKKER, T. C. M. (1993). Positive genetic correlation between female preference and preferred male ornament in sticklebacks. *Nature* **363**, 255–257.

BAKKER, T. C. M. & POMIANKOWSKI, A. (1995). The genetic-basis of female mate preferences. *Journal of Evolutionary Biology* **8**, 129–171.

BLOWS, M. W. (1998). Evolution of a mate recognition system after hybridization between two *Drosophila* species. *American Naturalist* **151**, 538–544.

BLOWS, M. W. (1999). Evolution of the genetic covariance between male and female components of mate recognition: an experimental test. *Proceedings of the Royal Society of London B* **266**, 2169–2174.

BREDEN, F. & HORNADAY, K. (1994). Test of indirect models of selection in the trinidad guppy. *Heredity* **73**, 291–297.

BROOKS, R. & COULDRIDGE, V. (1999). Multiple sexual ornaments coevolve with multiple mating preferences. *American Naturalist* **154**, 37–45.

CHANDLER, C. H., OFRIA, C. & DWORKIN, I. (2012). Runaway sexual selection leads to good genes. *Evolution* **67**, 110–119.

CHARALAMBOUS, M., BUTLIN, R. K. & HEWITT, G. M. (1994). Genetic variation in male song and female song preference in the grasshopper *Chorthippus brunneus* (Orthoptera: Acrididae). *Animal Behaviour* **47**, 399–411.

CLARK, N. L., GASPER, J., SEKINO, M., SPRINGER, S. A., AQUADRO, C. F. & SWANSON, W. J. (2009). Coevolution of interacting fertilization proteins. *PLoS Genetics* **5**, e1000570.

COLLINS, R. D. & CARDÉ, R. T. (1989). Selection for altered pheromone-component ratios in the pink bollworm moth, *Pectinophora gossypiella* (Lepidoptera: Gelechiidae). *Journal of Insect Behavior* **2**, 609–621.

COLLINS, R. D. & CARDÉ, R. T. (1990). Selection for increased pheromone response in the male pink bollworm, *Pectinophora gossypiella* (Lepidoptera: Gelechiidae). *Behavior Genetics* **20**, 325–331.

COLLINS, R. D., ROSENBLUM, S. L. & CARDÉ, R. T. (1990). Selection for increased pheromone titre in the pink bollworm moth, *Pectinophora gossypiella* (Lepidoptera: Gelechiidae). *Physiological Entomology* **15**, 141–147.

COTTON, S., SMALL, J. & POMIANKOWSKI, A. (2006). Sexual selection and condition-dependent mate preferences. *Current Biology* **16**, R755–R765.

COYNE, J. A. & ORR, H. A. (2004). *Speciation*. Sinauer Associates, Sunderland.

DE WINTER, A. J. (1992). The genetic basis and evolution of acoustic mate recognition signals in a *Ribautodelphax* planthopper (Homoptera, Delphacidae) 1. The female call. *Journal of Evolutionary Biology* **5**, 249–265.

EBERHARD, W. G. (1985). *Sexual Selection and Animal Genitalia*. Harvard University Press, Cambridge.

EBERHARD, W. G. (1996). *Female Control: Sexual Selection by cryptic Female Choice*. Princeton Univerity Press, Princeton and Chichester.

EVANS, J. P., VAN LIESHOUT, E. & GASPARINI, C. (2013). Quantitative genetic insights into the coevolutionary dynamics of male and female genitalia. *Proceedings of the Royal Society B* **280**, 20130749.

FISHER, R. A. (1958). *The Genetical Theory of Natural Selection*, A complete variorum edition. Oxford University Press, Oxford and New York.

FU, X., TATSUKI, S., HOSIZAKI, S. & ISHIKAWA, Y. (2005). Study of the genetics of female sex pheromone production and male behavioral response in a moth, *Ostrinia orientalis*. *Entomological Science* **8**, 363–369.

FUKAMACHI, S., KINOSHITA, M., AIZAWA, K., ODA, S., MEYER, A. & MITANI, H. (2009). Dual control by a single gene of secondary sexual characters and mating preferences in medaka. *BMC Biology* **7**, 1–10 (doi: 10.1186/1741-7007-7-64).

FULLER, R. C., BAER, C. F. & TRAVIS, J. (2005). How and when selection experiments might actually be useful. *Integrative and Comparative Biology* **43**, 391–404.

GERHARDT, H. C. & HUBER, F. (2002). *Acoustic Communication in Insects and Anurans*. University of Chicago Press, Chicago.

GILBURN, A. S. & DAY, T. H. (1994). Evolution of female choice in seaweed flies: fisherian and good genes mechanisms operate in different populations. *Proceedings of the Royal Society B: Biological Sciences* **255**, 159–165.

GILBURN, A. S., FOSTER, S. P. & DAY, T. (1993). Genetic correlation between a female mating preference and the preferred male character in seaweed flies (*Coelopa frigida*). *Evolution* **47**, 1788–1795.

GRAY, D. A. & CADE, W. H. (1999a). Correlated-response-to-selection experiments designed to test for a genetic correlation between female preferences and male traits yield biased results. *Animal Behaviour* **58**, 1325–1327.

GRAY, D. A. & CADE, W. H. (1999b). Quantitative genetics of sexual selection in the field cricket, *Gryllus integer*. *Evolution* **53**, 848–854.

GRAY, D. A. & CADE, W. H. (2000). Sexual selection and speciation in field crickets. *Proceedings of the National Academy of Sciences of the United States of America* **97**, 14449–14454.

GREENFIELD, M. D. (2002). *Signalers and Receivers: Mechanisms and Evolution of Arthropod Communication*. Oxford University Press, Oxford.

GREENFIELD, M. D., ALEM, S., LIMOUSIN, D. & BAILEY, N. W. (2014). The dilemma of Fisherian sexual selection: mate choice for indirect benfits despite rarity and overall weakness of trait-preference genetic correlation. *Evolution* **68**, 3524–3536.

GUMM, J. M., SNEKSER, J. L. & IOVINE, M. K. (2009). Fin-mutant female zebrafish (*Danio rerio*) exhibit differences in association preferenes for male fin length. *Behavioral Processes* **80**, 35–38.

HALL, M., LINDHOLM, A. K. & BROOKS, R. (2004). Direct selection on male attractiveness and female preference fails to produce a response. *BMC Evolutionary Biology* **4**: 1.

HIGASHI, M., TAKIMOTO, G. & YAMAMURA, N. (1999). Sympatric speciation by sexual selection. *Nature* **402**, 523–526.

HOSKEN, D. J. & HOUSE, C. M. (2011). Sexual selection. *Current Biology* **21**, R62–R65.

HOUDE, A. (1994). Effect of artificial selection on male colour patterns on mating preference of female guppies. *Proceedings of the Royal Society of London B: Biological Sciences* **256**, 125–130.

HUNT, J., BROOKS, R. & JENNIONS, M. D. (2005). Female mate choice as a condition-dependent life-history trait. *American Naturalist* **166**, 79–92.

IKEDA, H. & MARUO, O. (1982). Directional selection for pulse repitition rate of the courtship sound and correlated responses occurring in several characters in *Drosophila mercatorum*. *Japanese Journal of Genetics* **57**, 241–258.

IYENGAR, V. K., REEVE, H. K. & EISNER, T. (2002). Paternal inheritance of a female moth's mating preference. *Nature* **419**, 830–832.

JENNIONS, M. D. & PETRIE, M. (1997). Variation in mate choice and mating preferences: a review of causes and consequences. *Biological Reviews of the Cambridge Philosophical Society* **72**, 283–327.

KIRKPATRICK, M. (1987). Sexual selection by female choice in polygynous animals. *Annual Review of Ecology and Systematics* **18**, 43–70.

KIRKPATRICK, M. & BARTON, N. H. (1997). The strength of indirect selection on female mating preferences. *Proceedings of the National Academy of Sciences of the United States of America* **94**, 1282–1286.

KIRKPATRICK, M. & RYAN, M. J. (1991). The evolution of mating preferences and the paradox of the lek. *Nature* **350**, 33–38.

Kokko, H., Brooks, R., McNamara, J. M. & Houston, A. I. (2002). The sexual selection continuum. *Proceedings of the Royal Society of London Series B: Biological Sciences* **269**, 1331–1340.

Kokko, H., Jennions, M. D. & Brooks, R. (2006). Unifying and testing models of sexual selection. *Annual Review of Ecology, Evolution, and Systematics* **37**, 43–66.

Kraaijeveld, K., Kraaijeveld-Smit, F. J. & Maan, M. E. (2011). Sexual selection and speciation: the comparative evidence revisited. *Biological Reviews of the Cambridge Philosophical Society* **86**, 367–377.

Kronforst, M. R., Young, L. G., Kapan, D. D., McNeely, C., O'Neill, R. J. & Gilbert, L. E. (2006). Linkage of butterfly mate preference and wing color preference cue at the genomic location of *wingless*. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 6575–6580.

Lande, R. (1981). Models of speciation by sexual selection on polygenic traits. *Proceedings of the National Academy of Sciences of the United States of America* **78**, 3721–3725.

Limousin, D., Rejane, S., Courtois, B., Dupuy, V., Alem, S. & Greenfield, M. D. (2012). Genetic architecture of sexual selection: QTL mapping of male song and female receiever traits in an acoustic moth. *PLoS ONE* **7**, e44554.

Löfstedt, C., Hansson, B. S., Roelofs, W. & Bengtsson, B. O. (1989). No linkage between genes controlling female pheromone production and male pheromone response in the European cornborer, *Ostrinia nubilalis* Hubner (Lepidoptera: Pyralidae). *Genetics* **123**, 553–556.

Lynch, M. & Walsh, B. (1998). *Genetics and Analysis of Auantitative Traits*. Sinauer, Sunderland.

Marcillac, F., Grosjean, Y. & Ferveur, J. F. (2005). A single mutation alters production and discrimination of *Drosophila* sex pheromones. *Proceedings of the Royal Society of London Series B: Biological Sciences* **272**, 303–309.

McNiven, V. T. K. & Moehring, A. J. (2013). Identification of genetically linked female preference and male trait. *Evolution* **67**, 2155–2165.

Mead, L. S. & Arnold, S. J. (2004). Quantitative genetic models of sexual selection. *Trends in Ecology & Evolution* **19**, 264–271.

Merrill, R. M., Van Schooten, B., Scott, J. A. & Jiggins, C. D. (2011). Pervasive genetic associations between traits causing reproductive isolation in *Heliconius* butterflies. *Proceedings of the Royal Society of London Series B: Biological Sciences* **278**, 511–518 (doi: 10.1098/rspb.2010.1493).

Miller, C. W. & Svensson, E. I. (2014). Sexual selection in complex environments. *Annual Review of Entomology* **59**, 427–445.

Miller, G. T. & Pitnick, S. (2002). Sperm-female coevolution in *Drosophila*. *Science* **298**, 1230–1233.

Moore, A. J. (1989). Sexual selection in *Nauphoeta cinerea*: inherited mating preference? *Behavior Genetics* **19**, 717–724.

Mühlhäuser, C. & Blanckenhorn, W. U. (2004). The quantitative genetics of sexual selection in the dung fly *Sepsis cynipsea*. *Behaviour* **141**, 327–341.

Panhuis, T. M., Butlin, R., Zuk, M. & Tregenza, T. (2001). Sexual selection and speciation. *Trends in Ecology & Evolution* **16**, 364–371.

Pomiankowski, A. & Iwasa, Y. (1998). Runaway ornament diversity caused by Fisherian sexual selection. *Proceedings of the National Academy of Sciences of the United States of America* **95**, 5106–5111.

Pomiankowski, A. & Sheridan, L. (1994). Linked sexiness and choosiness. *Trends in Ecology and Evolution* **9**, 242–244.

Prum, R. O. (2010). The Lande-Kirkpatrick mechanism is the null model of evolution by intersexual selection: implications for meaning, honesty, and design in intersexual signals. *Evolution* **64**, 3085–3100.

Pryke, S. R. (2010). Sex chromosome linkage of mate preferece and color signal maintains assortative mating between interbreeding finch morphs. *Evolution* **64**, 1301–1310.

Qvarnström, A., Brommer, J. E. & Gustafsson, L. (2006). Testing the genetics underlying the co-evolution of mate choice and ornament in the wild. *Nature* **441**, 84–87.

Ratterman, N. L., Rosenthal, G. G., Carney, G. E. & Jones, A. G. (2014). Genetic variation and covariation in male attractiveness and female mating preferences in *Drosophila melanogaster*. *Genes Genomes Genetics* **4**, 79–88.

Rebar, D. W. and Rodríguez, R. L. In Press. Insect mating signal and mate preference phenotypes covary among host plant genotypes. Evolution.

Rick, I. P., Mehlis, M. & Bakker, T. C. M. (2011). Male red ornamentation is associated with female red sensitivity in sticklebacks. *PLoS ONE* **6**, e25554, 1–6.

Ritchie, M. G. (2000). The inheritance of female preference functions in a mate recognition system. *Proceedings of the Royal Society of London Series B: Biological Sciences* **267**, 327–332.

Ritchie, M. G. (2007). Sexual selection and speciation. *Annual Review of Ecology, Evolution, and Systematics* **38**, 79–102.

Ritchie, M. G., Saarikettu, M. & Hoikkala, A. (2005). Variation, but no covariance, in female preference functions and male song in a natural population of *Drosophilia montana*. *Animal Behaviour* **70**, 849–854.

Rodríguez, R. L., Rebar, D. W. & Fowler-Finn, K. D. (2013). The evolution and evolutionary consequences of social plasticity in mate preferences. *Animal Behaviour* **85**, 1041–1047.

Roelofs, W., Glover, T., Tang, X.-H., Sreng, I., Robbins, P., Eckenrode, C., Löfstedt, C., Hansson, B. S. & Bengtsson, B. O. (1987). Sex pheromone production and perception in European corn borer moths is determined by both autosomal and sex-linked genes. *Proceedings of the National Academy of Sciences of the United States of America* **84**, 7585–7589.

Roelofs, W. L., Du, J.-W., Linn, C., Glover, T. J. & Bjostad, L. B. (1986). The potential for genetic manipulation of the redbanded leafroller moth sex pheromone blend. In *Evolutionary Genetics of Invertegrate Behavior-progress and Prospects* (ed. M. D. Huettel), pp. 263–272. Plenum Press, New York.

Roff, D. A. (1997). *Evolutionary Quantitative Genetics*. Chapman & Hall, New York.

Roff, D. A. & Fairbairn, D. J. (2014). The evolution of phenotypes and genetic parameters under preferential mating. *Ecology and Evolution* **4**, 2759–2776.

Rowe, L. & Houle, D. (1996). The lek paradox and the capture of genetic variance by condition dependent traits. *Proceedings of the Royal Society of London Series B: Biological Sciences* **263**, 1415–1421.

Sæther, S. A., Sætre, G. P., Borge, T., Wiley, C., Svedin, N., Andersson, G., Veen, T., Haavie, J., Servedio, M. R., Bureš, S., Král, M., Hjernquist, M. B., Gustafsson, L., Träf, J. & Qvarnström, A. (2007). Sex chromosome-linked species recognition and evolution of reproductive isolation in Flycatchers. *Science* **318**, 95–97.

von Schantz, T., Tufvesson, M., Göransson, G., Grahn, M., Wilhelmson, M. & Wittzell, H. (1995). Artificial selection for increased comb size and its effects on other sexual characters and viability in *Gallus domesticus* (the domestic chicken). *Heredity* **75**, 518–529.

Schärer, L., Littlewood, D. T. J., Waeschenbach, A., Yoshida, W. & Vizoso, D. B. (2011). Mating behavior and the evolution of sperm design. *Proceedings of the National Academy of Sciences of the United States of America* **108**, 1490–1495.

Servedio, M. R. & Bürger, R. (2014). The counterintuitive role of sexual selection in species maintenance and speciation. *Proceedings of the National Academy of Sciences of the United States of America*, **111**(22), 8113–8118 (doi: 10.1073).

Sgrò, C. M. & Hoffmann, A. A. (2004). Genetic correlations, tradeoffs and environmental variation. *Heredity* **93**, 241–248.

van der Sluijs, I., Seehausen, O., Van Dooren, T. J. M. & Alphen, J. J. M. (2010). No evidence for a genetic association between female mating preference and male secondary sexual trait in a Lake Victoria cichlid fish. *Current Zoology* **56**, 57–64.

Shaw, K. L. & Lesnick, S. C. (2009). Genomic linkage of male song and female acoustic preference QTL underlying a rapid species radiation. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 9737–9742.

Simmons, L. W. & Kotiaho, J. S. (2007). Quantitative genetic correlation between trait and preference supports a sexually selected sperm process. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 16604–16608.

van der Sluijs, I., Dijkstra, P. D., Lindeyer, C. M., Visser, B., Smith, A. M., Groothuis, T. G. G., van Alphen, J. J. M. & Seehausen, O. (2013). A test of genetic association among male nuptial coloration, female mating preference, and male aggression bias within a polymorphic population of cichlid fish. *Current Zoology* **59**, 221–229.

Thüler, K., Bussiere, L. F., Postma, E., Ward, P. I. & Blanckenhorn, W. U. (2011). Genetic and environmental sources of covariance among internal reproductive traits in the yellow dung fly. *Journal of Evolutionary Biology* **24**, 1477–1486.

West-Eberhard, M. J. (1983). Sexual selection, social competition, and speciation. *The Quarterly Review of Biology* **58**, 155–183.

West-Eberhard, M. J. (2014). Darwin's forgotten idea: the social essence of sexual selection. *Neuroscience and Biobehavioral Reviews* **46**, 501–508.

Wiley, C., Ellison, C. K. & Shaw, K. A. (2012). Widespread genetic linkage of mating signals and preferences in the Hawaiian cricket *Laupala*. *Proceedings of the Royal Society of London Series B: Biological Sciences* **279**, 1203–1209.

Wiley, C. & Shaw, K. L. (2010). Multiple genetic linkages between female preference and male signal in rapidly seciating Hawaiian crickets. *Evolution* **64**, 2238–2245.

Wilkinson, G. S. & Reillo, P. R. (1994). Female choice response to artificial selection on an exaggerated male trait in a stalk-eyed fly. *Proceedings of the Royal Society of London Series B: Biological Sciences* **255**, 1–6.

Zhou, Y., Kelly, J. K. & Greenfield, M. D. (2011). Testing the fisherian mechanism: examining the genetic correlation between male song and female response in waxmoths. *Evolutionary Ecology* **25**, 307–329.