

Supporting Information

ARE WE UNDERESTIMATING THE GENETIC VARIANCES OF DIMORPHIC TRAITS?

Wolak, M.E.* , D.A. Roff, and D.J. Fairbairn

*Corresponding author: Matthew Wolak; Address: School of Biological Sciences, Zoology Building, University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TZ, UK. E-mail: matthew.wolak@abdn.ac.uk. Phone: +44 1224 273255.

S1 Univariate and bivariate animal models

Univariate model

A univariate animal model of a trait expressed in two morphs within the population can be specified as:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_a\mathbf{a} + \mathbf{e} \quad (\text{S1.1})$$

When every individual has only one measurement, \mathbf{y} is a $nx1$ vector of phenotypes in a population of n individuals and \mathbf{X} is a $nx f$ design matrix (i.e., contains 0s and 1s), where f is the number of levels of fixed effects in the model, and contains 1s in rows occupied by observations with a particular level of the fixed effect in the f th column. The matrix \mathbf{X} relates the observation in \mathbf{y} to the appropriate fixed effect (mean) in $\boldsymbol{\beta}$. If morph is included as a fixed effect to account for differences in mean phenotype, then \mathbf{X} contains 1s in the first column at rows occupied by morph M1 (corresponding to rows in \mathbf{y}) and 1s in the second column at rows occupied by morph M2. The matrix \mathbf{Z}_a is an nxn design matrix which associates the phenotypic observation in \mathbf{y} to the breeding value in \mathbf{a} . The variables \mathbf{a} and \mathbf{e} are the $nx1$ vectors of additive genetic effects and environmental effects, respectively. The random variables \mathbf{a}

Wolak et al., Are we underestimating genetic variances?

and \mathbf{e} are assumed normally distributed with means of zero and variances of $Var(\mathbf{a})=\mathbf{G}_a \otimes \mathbf{A}$, where \mathbf{A} is the additive genetic relationship matrix (\otimes symbolizes the direct product between two matrices), and $Var(\mathbf{e})=\mathbf{R} \otimes \mathbf{I}$, where \mathbf{I} is an identity matrix ($n \times n$, with 1s along the diagonal). In this model, $\mathbf{G}_a = \sigma_a^2$ where σ_a^2 is the additive genetic variance in the base population and $\mathbf{R} = \sigma_e^2$, the environmental variance.

Bivariate model

A bivariate model of a trait expressed in two morphs within the population can be specified as:

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_2 \end{bmatrix} \begin{bmatrix} \boldsymbol{\beta}_1 \\ \boldsymbol{\beta}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{a1} & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_{a2} \end{bmatrix} \begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix} \quad (\text{S1.2})$$

In equation S1.2, \mathbf{a} (the bivariate distribution of \mathbf{a}_1 and \mathbf{a}_2) and \mathbf{e} (the bivariate distribution of \mathbf{e}_1 and \mathbf{e}_2) are assumed to represent random effects described by multivariate normal distributions. The $Var(\mathbf{a})=\mathbf{G}_a \otimes \mathbf{A}$, where \mathbf{G}_a is a 2x2 matrix (see equation 3 in main text).

S2 Literature search

To evaluate the extent to which morph-specific estimates of additive genetic variances are estimated in the literature, we sampled four journals that present the majority of estimates of additive genetic variances in evolutionary ecology: *Evolution*, *the American Naturalist*, *Journal of Evolutionary Biology*, and *Heredity*. For each journal we included the issues for January through December 2013 and January through October 2014 (22 months). We read the title, abstract, and keywords of every paper published in this sample to determine if genetic variances or heritabilities were estimated. If yes, we read the full paper and categorized it according to: (1) the type of trait studied (monomorphic, dimorphic, or polymorphic), (2) whether morph was included in the statistical analysis, (3) whether morph was included as a fixed effect, (4) whether a bivariate model of both morphs (or multivariate in the case of a polymorphism) was used to estimate morph-specific genetic variances, and (5) whether morphs were analyzed in separate statistical models (regardless of how the study was categorized in 4).

We considered morph was included as a fixed effect (3) if it was either entered directly in the statistical model as a fixed effect or if the raw phenotypic data were mean centered across morphs before analyses (effectively the same as including fixed effect in the model). Similarly, we considered the morph to be modeled using a bivariate model (4) if the morphs were entered as separate traits or if a random interaction with morph was included (e.g., morph-by-sire family in a sire variance component model or morph-by-identity in an animal model). Finally, we did not include papers that either estimated additive genetic variances and heritabilities from simulated data or estimated mutational genetic variances.

Table S2.1 Results from the literature sample

Ref.	Organism	Trait(s)	1-Morph	2-Morph in analysis	3-Fixed effect	4-Bivariate model	5-Separate morph models
1	<i>Hyla versicolor</i>	advertisement call	Dimorphic	yes	yes	no	no
2	<i>Agalychnis callidryas</i>	risk-induced hatching timing & morphology	Dimorphic	yes	yes	yes	no
3	<i>Tyto alba</i>	color spots	Dimorphic	yes	yes	no	no
4	<i>Tyto alba</i>	nestling vocalizations	Dimorphic	yes	yes	no	no
5	<i>Hirundo rustica</i>	flight initiation distance	Polymorphic	no	no	no	no
6	<i>Cyanistes caeruleus</i>	egg characteristics	Polymorphic	yes	yes	yes	no
7	<i>Cyanistes caeruleus</i>	body mass	Polymorphic	yes	yes	yes	no
8	<i>Ficedula albicollis</i>	tail, tarsus, wing, & mass	Dimorphic	yes	yes	no	no
9	<i>Ficedula albicollis</i> and <i>Taeniopygia guttata</i>	morphology & sexually selected traits	Dimorphic	yes	yes	no	no
10	<i>Falco tinnunculus</i>	coloration, body mass, & immunity	Dimorphic & Polymorphic	yes	yes	no	no (age) yes (sex)
11	<i>Acrocephalus arundinaceus</i>	wing tarsus length	Dimorphic	yes	yes	yes	yes
12	<i>Parus major</i>	oxidative damage & resistance to oxidative stress	Dimorphic	yes	yes	yes	yes
13	<i>Parus major</i>	clutch size	Monomorphic	NA	NA	NA	NA
14	<i>Parus major</i>	gonad size	Polymorphic	yes	yes	yes	yes
15	<i>Parus major</i>	egg-laying dates (female)	Dimorphic	yes	yes	yes	no
16	<i>Parus major</i> and <i>Taeniopygia guttata</i>	plumage & beak color	Dimorphic	yes	yes	no	no
17	<i>Anser anser</i>	dominance rank & aggression	Dimorphic	yes	yes	yes	yes
18	<i>Perisoreus infaustus</i>	body mass	Dimorphic	yes	yes	no	no
19	<i>Melospiza melodia</i>	female extra-pair reproduction and male paternity success	Monomorphic	NA	NA	NA	NA
20	<i>Melospiza melodia</i>	male reproductive success	Monomorphic	NA	NA	NA	NA
21	<i>Larus michahellis</i>	antioxidant defence, endocrine signal, & body mass	Dimorphic	yes	yes	yes	yes
22	<i>Taeniopygia guttata</i>	neural traits associated with song morphology, male sexual activity	Dimorphic	yes	yes (resources) no (sex)	yes (resources) no (sex)	no
23	<i>Taeniopygia guttata</i>	& basal metabolic rate	Dimorphic & Polymorphic	yes	yes	yes	no
24	<i>Hippopodina iririkiensis</i>	fitness	Polymorphic	yes	yes	yes	yes
25	<i>Heliocidaris erythrogramma armigera</i>	fertilization & hatching success	Dimorphic	yes	yes	yes	no

26	<i>Gasterosteus aculeatus</i>	survival & body size	Polymorphic	yes	yes	yes	no
27	<i>Salmo salar</i>	fitness	Dimorphic	yes	yes	no	yes
28	<i>Salmo salar</i>	morphology	Dimorphic	yes	yes	yes	no
29	<i>Gasterosteus aculeatus</i>	body size & shape	Dimorphic & Polymorphic	yes	yes	(environment) (sex) no	no
30	<i>Lasius niger</i>	cuticular hydrocarbons, fertility, & head size	Dimorphic	yes	no	no	yes
31	<i>Grylloides sigillatus</i>	oxidative damage, antioxidant protection, reproductive effort, lifespan, & ageing	Dimorphic	yes	?	yes	no
32	<i>Grylloides sigillatus</i>	female spermatophylax feeding behavior & amino acid composition	Monomorphic	NA	NA	NA	NA
33	<i>Teleogryllus commodus</i>	mate choice	Dimorphic	yes	yes	yes	no
34	<i>Gnatocerus cornutus</i>	mandable size & locomotor activity	Dimorphic	yes	no	no	yes
35	<i>Sepsis punctum</i>	development rate	Dimorphic & Polymorphic	yes	yes	yes	no
36	<i>Drosophila melanogaster</i>	macronutrient preferences	Dimorphic	yes	?	yes	no
37	<i>Drosophila simulans</i>	cuticular hydrocarbons	Dimorphic	yes	yes	no	yes
38	<i>Drosophila yakuba</i> and <i>santomea</i>	pigmentation	Dimorphic	yes	yes	no	yes
39	<i>Drosophila melanogaster</i>	egg-to-adult viability	Dimorphic	yes	yes	yes	no
40	<i>Drosophila melanogaster</i>	lifespan	Dimorphic	yes	yes	yes	no
41	<i>Drosophila melanogaster</i>	cuticular hydrocarbons	Dimorphic	yes	yes	yes	no
42	<i>Drosophila serrata</i>	mating preferences	Dimorphic	yes	yes	yes	no
43	<i>Drosophila simulans</i>	cuticular hydrocarbons	Dimorphic	yes	yes	yes	yes
44	<i>Drosophila serrata</i>	fitness	Dimorphic & Polymorphic	yes	yes	yes	yes
45	<i>Drosophila serrata</i>	contact pheromones	Dimorphic & Polymorphic	yes	yes	yes	no
46	<i>Drosophila melanogaster</i>	fecundity & copula duration	Monomorphic	NA	NA	NA	NA
47	<i>Drosophila serrata</i>	cuticular hydrocarbons	Monomorphic	NA	NA	NA	NA
48	<i>Drosophila simulans</i>	heat tolerance	Monomorphic	NA	NA	NA	NA
49	<i>Drosophila serrata</i>	cuticular hydrocarbons	Polymorphic	yes	yes	no	yes
50	<i>Drosophila simulans</i>	cuticular hydrocarbons	Polymorphic	yes	yes	yes	no
51	<i>Melitaea cinxia</i>	metabolic rates	Dimorphic	yes	yes	no	yes
52	<i>Tenebrio molitor</i>	immune response, melanisation, & morphology	Dimorphic & Polymorphic	yes	?	yes	no

53	<i>Tribolium castaneum</i>	external immune defences	Monomorphic	NA	NA	NA	NA
54	<i>Tribolium castaneum</i>	growth & life history	Polymorphic	yes	yes	yes	no
55	<i>Gryllus firmus</i>	melanization, ovary/testis mass & DLM mass	Dimorphic & Polymorphic	yes	yes	yes	yes
56	<i>Callosobruchus maculatus</i>	fitness	Dimorphic	yes	no	yes	no
57	<i>Nauphoeta cinerea</i>	discontinuous gas exchange, metabolic rate, & body mass	Dimorphic	yes	yes	no	yes
58	<i>Enchenopa binotata</i>	female mate preference	Monomorphic	NA	NA	NA	NA
59	<i>Enchenopa binotata</i>	mate preferences	Monomorphic	NA	NA	NA	NA
60	<i>Bemisia tabaci</i>	survival & fecundity	Dimorphic	yes	yes	no	yes
61	<i>Bos taurus</i>	social dominance	Monomorphic	NA	NA	NA	NA
62	<i>Homo sapiens</i>	ages at first & last reproduction	Dimorphic	yes	?	yes	yes
63	<i>Homo sapiens</i>	metabolic profiles	Monomorphic	NA	NA	NA	NA
64	laboratory house mice	wheel running behavior	Dimorphic	yes	yes	yes	yes
65	<i>Suricata suricatta</i>	growth & size	Dimorphic	yes	yes	yes	yes
66	<i>Ovis aries</i>	antibody titer & body weight	Polymorphic	yes	yes	yes	no
67	<i>Saimiri boliviensis</i>	neonate mass	Dimorphic	yes	yes	yes	no
68	<i>Ipomoea purpurea</i>	fitness & tolerance to competition	Dimorphic	yes	yes	yes	no
69	<i>Plantago coronopus</i>	reproductive & vegetative traits	Dimorphic & Polymorphic	yes	yes	yes	no
70	<i>Solanum carolinense</i>	resistance to herbivory	Monomorphic	NA	NA	NA	NA
71	<i>Pinus pinaster</i>	early seedling performance	Dimorphic	yes	yes	yes	no
72	<i>Ipomoea hederacea</i>	size, flowering time, & seed number	Monomorphic	NA	NA	NA	NA
73	<i>Arabidopsis lyrata</i>	seed size	Monomorphic	NA	NA	NA	NA
74	<i>Geranium carolinianum</i>	competitive ability	Polymorphic	yes	no	yes	no
75	<i>Arabidopsis lyrata</i>	plant performance & coping with drought	Polymorphic	yes	yes	no	yes
76	<i>Arabidopsis thaliana</i>	13 varied traits	Polymorphic	yes	yes	yes	yes
77	<i>Pinus radiata</i>	resistance to herbivores	Dimorphic	yes	yes	yes	no
78	<i>Eucalyptus globulus</i>	disease resistance	Polymorphic	yes	yes	yes	no
79	<i>Schistocephalus solidus</i>	fitness	Monomorphic	NA	NA	NA	NA

Literature Cited for Table S2.1

1. Welch, A. M., Smith, M. J., & Gerhardt, H. C. (2014). A multivariate analysis of genetic variation in the advertisement call of the gray treefrog, *Hyla versicolor*. *Evolution*, *68*(6), 1629–39. doi:10.1111/evo.12397
2. Gomez-Mestre, I., & Warkentin, K. M. (2013). Risk-induced hatching timing shows low heritability and evolves independently of spontaneous hatching in red-eyed treefrogs. *Journal of Evolutionary Biology*, *26*(5), 1079–1089. doi:10.1111/jeb.12121
3. Steinsland, I., Larsen, C. T., Roulin, A., & Jensen, H. (2014). Quantitative genetic modeling and inference in the presence of nonignorable missing data. *Evolution*, *68*(6), 1735–1747. doi:10.1111/evo.12380
4. Dreiss, A.N., Ruppli, C.A., & Roulin, A. (2013). Individual vocal signatures in barn owl nestlings: does individual recognition have an adaptive role in sibling vocal competition? *Journal of Evolutionary Biology*, *27*, 63–75. doi:10.1111/jeb.12277
5. Møller, A. P. (2014). Life history, predation and flight initiation distance in a migratory bird. *Journal of Evolutionary Biology*, *27*(6), 1105–1113. doi:10.1111/jeb.12399
6. Hadfield, J. D., Heap, E.A., Bayer, F., Mittell, E.A., & Crouch, N.M.A. (2013b). Intraclutch differences in egg characteristics mitigate the consequences of age-related hierarchies in a wild passerine. *Evolution*, *67*(9), 2688–2700. doi:10.1111/evo.12143
7. Hadfield, J. D., Heap, E.A., Bayer, F., Mittell, E.A., & Crouch, N. M.A. (2013a). Disentangling genetic and prenatal sources of familial resemblance across ontogeny in a wild passerine. *Evolution*, *67*(9), 2701–2713. doi:10.1111/evo.12144
8. Bjorklund, M., Husby, A., & Gustafsson, L. (2013). Rapid and unpredictable changes of the G-matrix in a natural bird population over 25 years. *Journal of Evolutionary Biology*, *26*, 1–13. doi:10.1111/jeb.12044
9. Husby, A., Schielzeth, H., Forstmeier, W., Gustafsson, L., & Qvarnstrom, A. (2013). Sex chromosome linked genetic variance and the evolution of sexual dimorphism of quantitative traits. *Evolution*, *67*(3), 609–619. doi:10.5061/dryad.3hq60
10. Kim, S.-Y., Fargallo, J. A., Vergara, P., & Martinez-Padilla, J. (2013). Multivariate heredity of melanin-based coloration, body mass and immunity. *Heredity*, *111*(2), 139–146. doi:10.1038/hdy.2013.29
11. Tarka, M., Akesson, M., Hasselquist, D., & Hansson, B. (2014). Intralocus sexual conflict over wing length in a wild migratory bird. *The American Naturalist*, *183*(1), 62–73. doi:10.1086/674072
12. Losdat, S., Helfenstein, F., Blount, J. D., & Richner, H. (2014). Resistance to oxidative stress shows low heritability and high common environmental variance in a wild bird. *Journal of Evolutionary Biology*, *27*, 1990–2000. doi:10.1111/jeb.12454
13. Nicolaus, M., Brommer, J. E., Ubels, R., Tinbergen, J. M., & Dingemanse, N. J. (2013). Exploring patterns of variation in clutch size-density reaction norms in a wild passerine bird. *Journal of Evolutionary Biology*, *26*(9), 2031–2043. doi:10.1111/jeb.12210
14. Schaper, S. V., Gienapp, P., Dawson, A., & Visser, M. E. (2013). Heritability of gonad size varies across season in a wild songbird. *Journal of Evolutionary Biology*, *26*(12), 2739–2745. doi:10.1111/jeb.12249

15. Gienapp, P., van Noordwijk, A.J., & Visser, M. E. (2013). Genetic background, and not ontogenetic effects, affects avian seasonal timing of reproduction. *Journal of Evolutionary Biology*, *26*(10), 2147–2153. doi:10.1111/jeb.12205
16. Evans, S. R., Schielzeth, H., Forstmeier, W., Sheldon, B. C., & Husby, A. (2014). Nonautosomal genetic variation in carotenoid coloration. *The American Naturalist*, *184*(3), 374–383. doi:10.1086/677397
17. Weiß, B. M., & Foerster, K. (2013). Age and sex affect quantitative genetic parameters for dominance rank and aggression in free-living greylag geese. *Journal of Evolutionary Biology*, *26*(2), 299–310. doi:10.1111/jeb.12042
18. Gienapp, P., & Merilä, J. (2014). Disentangling plastic and genetic changes in body mass of Siberian jays. *Journal of Evolutionary Biology*, *27*, 1849–1858. doi:10.1111/jeb.12438
19. Reid, J. M., Arcese, P., Keller, L. F., & Losdat, S. (2014). Female and male genetic effects on offspring paternity: additive genetic (co)variances in female extra-pair reproduction and male paternity success in song sparrows (*Melospiza melodia*). *Evolution*, *68*(8), 2357–2370. doi:10.1111/evo.12424
20. Reid, J. M., Arcese, P., & Losdat, S. (2014). Genetic covariance between components of male reproductive success: within-pair vs. extra-pair paternity in song sparrows. *Journal of Evolutionary Biology*, *27*(10), 2046–56. doi:10.1111/jeb.12445
21. Kim, S.-Y., Noguera, J. C., Tato, A., & Velando, A. (2013). Vitamins, stress and growth: the availability of antioxidants in early life influences the expression of cryptic genetic variation. *Journal of Evolutionary Biology*, *26*(6), 1341–1352. doi:10.1111/jeb.12136
22. Woodgate, J. L., Buchanan, K. L., Bennett, A. T. D., Catchpole, C. K., Brighton, R., & Leitner, S. (2014). Environmental and genetic control of brain and song structure in the zebra finch. *Evolution*, *68*(1), 230–240. doi:10.1111/evo.12261
23. Mathot, K. J., Martin, K., Kempenaers, B., & Forstmeier, W. (2013). Basal metabolic rate can evolve independently of morphological and behavioural traits. *Heredity*, *111*(3), 175–81. doi:10.1038/hdy.2013.35
24. Monro, K., & Marshall, D. J. (2013). Evolutionary constraints and the maintenance of individual specialization throughout succession. *Evolution*, *67*(12), 3636–3644. doi:10.1111/evo.12220
25. Lymbery, R. a, & Evans, J. P. (2013). Genetic variation underlies temperature tolerance of embryos in the sea urchin *Heliocidaris erythrogramma armigera*. *Journal of Evolutionary Biology*, *26*(10), 2271–2282. doi:10.1111/jeb.12225
26. DeFaveri, J., & Merilä, J. (2014). Local adaptation to salinity in the three-spined stickleback? *Journal of Evolutionary Biology*, *27*(2), 290–302. doi:10.1111/jeb.12289
27. Houde, A.L., Wilson, C. C., & Neff, B. D. (2013). Genetic architecture of survival and fitness-related traits in two populations of Atlantic salmon. *Heredity*, *111*(6), 513–9. doi:10.1038/hdy.2013.74
28. Debes, P. V, Fraser, D. J., McBride, M. C., & Hutchings, J.A. (2013). Multigenerational hybridisation and its consequences for maternal effects in Atlantic salmon. *Heredity*, *111*(3), 238–47. doi:10.1038/hdy.2013.43
29. Ramler, D., Mitteroecker, P., Shama, L. N. S., Wegner, K. M., & Ahnelt, H. (2014). Nonlinear effects of temperature on body form and developmental canalization in the threespine stickleback. *Journal of Evolutionary Biology*, *27*, 497–507. doi:10.1111/jeb.12311

30. Holman, L., Linksvayer, T. A., & D'Ettoire, P. (2013). Genetic constraints on dishonesty and caste dimorphism in an ant. *The American Naturalist*, *181*(2), 161–170. doi:10.1086/668828
31. Archer, C. R., Sakaluk, S. K., Selman, C., Royle, N. J., & Hunt, J. (2013). Oxidative stress and the evolution of sex differences in life span and ageing in the decorated cricket, *Gryllobates sigillatus*. *Evolution*, *67*(3), 620–634. doi:10.5061/dryad.cs16k
32. Gershman, S. N., Hunt, J., & Sakaluk, S. K. (2013). Food fight: sexual conflict over free amino acids in the nuptial gifts of male decorated crickets. *Journal of Evolutionary Biology*, *26*(4), 693–704. doi:10.1111/jeb.12078
33. Hall, M. D., Lailvaux, S. P., & Brooks, R. C. (2013). Sex-specific evolutionary potential of pre- and postcopulatory reproductive interactions in the field cricket, *Teleogryllus commodus*. *Evolution*, *67*(6), 1831–1837. doi:10.1111/evo.12067
34. Fuchikawa, T., & Okada, K. (2013). Inter- and intrasexual genetic correlations of exaggerated traits and locomotor activity. *Journal of Evolutionary Biology*, *26*(9), 1979–1987. doi:10.1111/jeb.12197
35. Berger, D., Postma, E., Blanckenhorn, W. U., & Walters, R. J. (2013). Quantitative genetic divergence and standing genetic (co)variance in thermal reaction norms along latitude. *Evolution*, *67*(8), 2385–2399. doi:10.1111/evo.12138
36. Reddiex, A. J., Gosden, T. P., Bonduriansky, R., & Chenoweth, S. F. (2013). Sex-specific fitness consequences of nutrient intake and the evolvability of diet preferences. *The American Naturalist*, *182*(1), 91–102. doi:10.1086/670649
37. Ingleby, F. C., Hunt, J., & Hosken, D. J. (2013). Heritability of male attractiveness persists despite evidence for unreliable sexual signals in *Drosophila simulans*. *Journal of Evolutionary Biology*, *26*(2), 311–324. doi:10.1111/jeb.12045
38. Matute, D. R., & Harris, A. (2013). The influence of abdominal pigmentation on desiccation and ultraviolet resistance in two species of *Drosophila*. *Evolution*, *67*(8), 2451–2460. doi:10.1111/evo.12122
39. Ketola, T., Kellermann, V. M., Loeschke, V., López-Sepulcre, A., & Kristensen, T. N. (2014). Does environmental robustness play a role in fluctuating environments? *Evolution*, *68*(2), 587–594. doi:10.1111/evo.12285
40. Lehtovaara, A., Schielzeth, H., Flis, I., & Friberg, U. (2013). Heritability of life span is largely sex limited in *Drosophila*. *The American Naturalist*, *182*(5), 653–665. doi:10.1086/673296
41. Ingleby, F. C., Innocenti, P., Rundle, H. D., & Morrow, E. H. (2014). Between-sex genetic covariance constrains the evolution of sexual dimorphism in *Drosophila melanogaster*. *Journal of Evolutionary Biology*, *27*(8), 1721–1732. doi:10.1111/jeb.12429
42. Gosden, T. P., & Chenoweth, S. F. (2014). The evolutionary stability of cross-sex, cross-trait genetic covariances. *Evolution*, *68*(6), 1687–1697. doi:10.1111/evo.12398
43. Ingleby, F. C., Hosken, D. J., Flowers, K., Hawkes, M. F., Lane, S. M., Rapkin, J., Dworkin, I., & Hunt, J. (2013). Genotype-by-environment interactions for cuticular hydrocarbon expression in *Drosophila simulans*. *Journal of Evolutionary Biology*, *26*(1), 94–107. doi:10.1111/jeb.12030

44. Punzalan, D., Delcourt, M., & Rundle, H. D. (2014). Comparing the intersex genetic correlation for fitness across novel environments in the fruit fly, *Drosophila serrata*. *Heredity*, *112*(2), 143–148. doi:10.1038/hdy.2013.85
45. Gosden, T. P., Rundle, H. D., & Chenoweth, S. F. (2014). Testing the correlated response hypothesis for the evolution and maintenance of male mating preferences in *Drosophila serrata*. *Journal of Evolutionary Biology*, *27*(10), 2106–12. doi:10.1111/jeb.12461
46. Edward, D. A., Poissant, J., Wilson, A. J., & Chapman, T. (2014). Sexual conflict and interacting phenotypes: a quantitative genetic analysis of fecundity and copula duration in *Drosophila melanogaster*. *Evolution*, *68*(6), 1651–1660. doi:10.1111/evo.12376
47. Hine, E., McGuigan, K., & Blows, M. W. (2014). Evolutionary constraints in high-dimensional trait sets. *The American Naturalist*, *184*(1), 119–131. doi:10.1086/676504
48. Van Heerwaarden, B., & Sgrò, C. M. (2013). Multivariate analysis of adaptive capacity for upper thermal limits in *Drosophila simulans*. *Journal of Evolutionary Biology*, *26*(4), 800–809. doi:10.1111/jeb.12090
49. Aguirre, J. D., Hine, E., Mcguigan, K., & Blows, M. W. (2014). Comparing G : multivariate analysis of genetic variation in multiple populations. *Heredity*, *112*(1), 21–29. doi:10.1038/hdy.2013.12
50. Ingleby, F. C., Hosken, D. J., Flowers, K., Hawkes, M. F., Lane, S. M., Rapkin, J., House, C. M., Sharma, M. D., & Hunt, J. (2014). Environmental heterogeneity, multivariate sexual selection and genetic constraints on cuticular hydrocarbons in *Drosophila simulans*. *Journal of Evolutionary Biology*, *27*(4), 700–713. doi:10.1111/jeb.12338
51. Mattila, a L. K., & Hanski, I. (2014). Heritability of flight and resting metabolic rates in the Glanville fritillary butterfly. *Journal of Evolutionary Biology*, *27*(8), 1733–1743. doi:10.1111/jeb.12426
52. Prokkola, J., Roff, D., Kärkkäinen, T., Krams, I., & Rantala, M. J. (2013). Genetic and phenotypic relationships between immune defense, melanism and life-history traits at different temperatures and sexes in *Tenebrio molitor*. *Heredity*, *111*(2), 89–96. doi:10.1038/hdy.2013.20
53. Joop, G., Roth, O., Schmid-Hempel, P., & Kurtz, J. (2014). Experimental evolution of external immune defences in the red flour beetle. *Journal of Evolutionary Biology*, *27*(8), 1562–1571. doi:10.1111/jeb.12406
54. Irwin, K. K., & Carter, P. A. (2013). Constraints on the evolution of function-valued traits: a study of growth in *Tribolium castaneum*. *Journal of Evolutionary Biology*, *26*(12), 2633–2643. doi:10.1111/jeb.12257
55. Roff, D. A., & Fairbairn, D. J. (2013). The costs of being dark: the genetic basis of melanism and its association with fitness-related traits in the sand cricket. *Journal of Evolutionary Biology*, *26*(7), 1406–1416. doi:10.1111/jeb.12150
56. Berger, D., Grieshop, K., Lind, M. I., Goenaga, J., Maklakov, A. A., & Arnqvist, G. (2014). Intralocus sexual conflict and environmental stress. *Evolution*, *68*(8), 2184–2196. doi:10.1111/evo.12439
57. Schimpf, N. G., Matthews, P. G. D., & White, C. R. (2013). Discontinuous gas exchange exhibition is a heritable trait in speckled cockroaches *Nauphoeta cinerea*. *Journal of Evolutionary Biology*, *26*(7), 158815–97. doi:10.1111/jeb.12093
58. Rodríguez, R. L., Hallett, A. C., Kilmer, J. T., & Fowler-Finn, K. D. (2013). Curves as traits: genetic and environmental variation in mate preference functions. *Journal of Evolutionary Biology*, *26*(2), 434–442. doi:10.1111/jeb.12061

59. Rebar, D., & Rodríguez, R. L. (2014). Genetic variation in host plants influences the mate preferences of a plant-feeding insect. *The American Naturalist*, *184*(4), 489–99. doi:10.1086/677751
60. Díaz, F., Muñoz-Valencia, V., Juvinao-Quintero, D. L., Manzano-Martínez, M. R., Toro-Perea, N., Cárdenas-Henao, H., & Hoffmann, A. A. (2014). Evidence for adaptive divergence of thermal responses among *Bemisia tabaci* populations from tropical Colombia following a recent invasion. *Journal of Evolutionary Biology*, *27*(6), 1160–1171. doi:10.1111/jeb.12387
61. Sartori, C., & Mantovani, R. (2013). Indirect genetic effects and the genetic bases of social dominance : evidence from cattle. *Heredity*, *110*(1), 3–9. doi:10.1038/hdy.2012.56
62. Bürkli, A., & Postma, E. (2014). Genetic constraints underlying human reproductive timing in a premodern Swiss village. *Evolution*, *68*(2), 526–537. doi:10.1111/evo.12287
63. Alul, F. Y., Cook, D. E., Shchelochkov, O. A., Fleener, L. G., Berberich, S. L., Murray, J. C., & Ryckman, K. K. (2013). The heritability of metabolic profiles in newborn twins. *Heredity*, *110*(3), 253–8. doi:10.1038/hdy.2012.75
64. Careau, V., Wolak, M. E., Carter, P. A., & Garland, T. J. (2013). Limits to behavioral evolution: the quantitative genetics of a complex trait under directional selection. *Evolution*, *67*(11), 3102–19. doi:10.1111/evo.12200
65. Huchard, E., Charmantier, A., English, S., Bateman, A., Nielsen, J. F., & Clutton-Brock, T. (2014). Additive genetic variance and developmental plasticity in growth trajectories in a wild cooperative mammal. *Journal of Evolutionary Biology*, *27*(9), 1893–1904. doi:10.1111/jeb.12440
66. Hayward, A. D., Garnier, R., Watt, K. A., Pilkington, J. G., Grenfell, B. T., Matthews, J. B., Pemberton, J.M., Nussey, D. H., & Graham, A. L. (2014). Heritable, heterogeneous, and costly resistance of sheep against nematodes and potential feedbacks to epidemiological dynamics. *The American Naturalist*, *184*(Suppl), S58–76. doi:10.1086/676929
67. Blomquist, G. E., & Williams, L. E. (2013). Quantitative genetics of costly neonatal sexual size dimorphism in squirrel monkeys (*Saimiri boliviensis*). *Journal of Evolutionary Biology*, *26*(4), 756–765. doi:10.1111/jeb.12096
68. Chaney, L., & Baucom, R. S. (2014). The costs and benefits of tolerance to competition in *ipomoea purpurea*, the common morning glory. *Evolution*, *68*(6), 1698–16709. doi:10.1111/evo.12383
69. Hansen, C. F., García, M. B., & Ehlers, B. K. (2013). Water availability and population origin affect the expression of the tradeoff between reproduction and growth in *Plantago coronopus*. *Journal of Evolutionary Biology*, *26*(5), 993–1002. doi:10.1111/jeb.12114
70. Wise, M. J., & Rausher, M. D. (2013). Evolution of resistance to a multiple-herbivore community: genetic correlations, diffuse coevolution, and constraints on the plant’s response to selection. *Evolution*, *67*(6), 1767–1779. doi:10.1111/evo.12061
71. Zas, R., Cendán, C., & Sampedro, L. (2013). Mediation of seed provisioning in the transmission of environmental maternal effects in Maritime pine (*Pinus pinaster* Aiton). *Heredity*, *111*(3), 248–55. doi:10.1038/hdy.2013.44
72. Stinchcombe, J. R., Simonsen, A. K., & Blows, M. W. (2013). Estimating uncertainty in multivariate responses to selection. *Evolution*, *68*(4), 1188–1196. doi:10.1111/evo.12321

73. Willi, Y. (2013). The battle of the sexes over seed size: support for both kinship genomic imprinting and interlocus contest evolution. *The American Naturalist*, *181*(6), 787–798. doi:10.1086/670196
74. Shirk, R. Y., & Hamrick, J. L. (2014). Multivariate adaptation but no increase in competitive ability in invasive geranium carolinianum L. (Geraniaceae). *Evolution*, *68*(10), 2945–59. doi:10.1111/evo.12474
75. Paccard, A., Vance, M., & Willi, Y. (2013). Weak impact of fine-scale landscape heterogeneity on evolutionary potential in *Arabidopsis lyrata*. *Journal of Evolutionary Biology*, *26*(11), 2331–2340. doi:10.1111/jeb.12220
76. Tonsor, S. J., Elnaccash, T. W., & Scheiner, S. M. (2013). Developmental instability is genetically correlated with phenotypic plasticity, constraining heritability, and fitness. *Evolution*, *67*(10), 2923–2935. doi:10.1111/evo.12175
77. Moreira, X., Zas, R., & Sampedro, L. (2013). Additive genetic variation in resistance traits of an exotic pine species: little evidence for constraints on evolution of resistance against native herbivores. *Heredity*, *110*(5), 449–56. doi:10.1038/hdy.2012.108
78. Hamilton, M. G., Williams, D. R., Tilyard, P. A., Pinkard, E. A., Wardlaw, T. J., Glen, M., Vaillancourt, M. E., & Potts, B. M. (2013). A latitudinal cline in disease resistance of a host tree. *Heredity*, *110*(4), 372–9. doi:10.1038/hdy.2012.106
79. Benesh, D. P. (2013). Parental effects on the larval performance of a tapeworm in its copepod first host. *Journal of Evolutionary Biology*, *26*(8), 1625–1633. doi:10.1111/jeb.12165