Supporting information:
Worked examples

This is supporting information for the article:

First, we describe how the dataset was constructed for the worked example 'Fat, sexy and fecund' in the main text. Second, we provide a worked example ('Cheating vs caring') for our quantitative genetic model, based on simulated data. Datasets and R code for all worked examples are provided at https://doi.org/10.5061/dryad.1fp7830.

1 Construction of dataset for the worked example 'Fat, sexy and fecund'

We simulated body size Z, mating success M and reproductive success R in a sample of 1000 females. We assumed that Z follows a normal distribution, standardised to have a mean of zero and variance of one. Reproductive success increases with female size, but is not influenced by mating success: we assumed that $R = 10 + 3(Z + \varepsilon_R)$, where $\varepsilon_R \sim \mathcal{N}(0,1)$ is a standard normal variable that is independent of body size. Mating success also increases with female size, because males prefer larger females: we assumed $M = 5 + 2(Z + \varepsilon_M)$, where $\varepsilon_M \sim \mathcal{N}(0,1)$ is independent of body size. We rounded values of R and M to the nearest integer. We then converted any negative values of R to zero (as the number of offspring must be non-negative). Values of M that were less than one were converted to one (i.e. we assumed that each female mates at least once).

Results for 'Fat, sexy and fecund' are given in Table 2 in the main text.

2 Cheating vs caring: a worked example of the quantitative genetic model

Here we construct and analyse a dataset based loosely on socially monogamous birds. We simulate both trait values and a pedigree, which allows us to apply the quantitative genetic model of sexual selection from the main text.

2.1 Construction of dataset

We assumed that all males have a social mate, whose offspring they invest in. They also seek copulations with extra-pair females, whom they advertise to using an ornament. Extra-pair mating success M increases with ornament expression O, and reproductive success R increases with both care effort C and extra-pair mating success M. We assumed that care effort is negatively correlated with ornament expression at the genetic level, due to inherent resource trade-offs. However, they are positively correlated at the phenotypic level because the total resources available to a male are influenced by unmeasured environmental effects.

We simulated care effort C, ornament expression O, mating success M and reproductive success R for a sample of 10 000 males of known parentage. Our simulation consists of two generations – the parent generation and the offspring generation, with the measured males belonging to the latter. Each individual has quantitative genetic traits G_C, G_O, G_M and G_R. These are not breeding values, but contribute to breeding values via the causal process described below. Values for all genetic traits were assumed to be multivariate normal. Values for care effort and ornament expression have an additive genetic correlation of $\text{cor}(G_C, G_O) = -0.4$ due to resource trade-offs. All other pairs of genetic traits are independent. For convenience, we standardised the variables (G_C, G_O, G_M, G_R) to have mean zero and covariance matrix given by:

$$\Sigma_G = \begin{bmatrix} 1 & -0.4 & 0 & 0 \\ -0.4 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix} \tag{S1}$$

This is similar to the matrix G_ϵ in Morrissey (2014), in that it represents additive genetic (co)variances beyond those attributable to causal effects among the measured traits. The overall additive genetic variance-covariance matrix among the traits, which includes all causal effects, depends on both Σ_G and the assumed causal relationships given in equations (S3) through (S5) below (cf. the results in Figure S2b).

The parent generation consists of 20 000 individuals with an even sex ratio. We simulated genetic trait values for the parent generation according to the above covariance structure using Cholesky decomposition (Asmussen & Glynn 2007). We then defined a set of possible parent pairs by assigning two potential mates to each female at random (yielding 10 000 females × 2 mates = 20 000 parent pairs). The parents of each male offspring were drawn from the possible parent pairs at random with replacement (we ignored female offspring). Offspring genetic trait values were simulated as the mean values of their parents, plus a multivariate normal random variable with mean zero and covariance matrix $\frac{1}{2}\Sigma_G$. This ensures that offspring values of the genetic traits are normally distributed with variance-covariance matrix Σ_G, which is consistent with an infinitesimal model of inheritance with no selection (Bulmer 1980; Barton et al. 2017).

For the 10 000 males of the offspring generation, we simulated phenotypic trait values, mating success and reproductive success. We assumed that environmental effects on care effort E_C and ornament expression E_O were multivariate normal with a strong correlation of $\mathrm{cor}(E_C, E_O) = 0.8$, reflecting environmental variance in resources needed by both traits. We standardised these environmental effects to have mean zero and covariance matrix

$$\Sigma_E = \begin{bmatrix} 1 & 0.8 \\ 0.8 & 1 \end{bmatrix} \tag{S2}$$

Care effort and ornament expression were modelled as the sum of genetic and environmental effects, with each contributing equally:

$$C = \frac{1}{\sqrt{2}}\left(G_C + E_C\right), \quad O = \frac{1}{\sqrt{2}}\left(G_O + E_O\right) \tag{S3}$$

The factor of $1/\sqrt{2}$ ensures that these traits are standard normal random variables. The overall phenotypic correlation between care effort and ornament expression is $\mathrm{cor}(C, O) = 0.2$.

We modelled each male's extra-pair mating success as

$$M = 2 + \frac{1}{4}\left(3O + G_M + 4E_M\right) \tag{S4}$$

where $E_M \sim \mathcal{N}(0, 1)$ is an independent environmental effect. We rounded values of M to the nearest integer and converted negative values to zero.

Reproductive success is the sum of within-pair reproductive success R_0 and extra-pair reproductive success R_i with each extra-pair mate i:

$$R = R_0 + \sum_{i=1}^{M} R_i \tag{S5}$$

3

Within-pair reproductive success was modelled as $R_0 = 4 + \frac{1}{2}(3C + G_R + 4E_0)$. Extra-pair reproductive success with the ith mate was $R_i = 1 + \frac{1}{2}E_i$. In both cases the $E_i \sim \mathcal{N}(0,1)$ are independent environmental effects. We rounded each of the variables $R_0, R_1, \ldots, R_M$ to the nearest integer and then converted negative values to zero. Under these assumptions, care effort directly affects within-pair reproductive success, but ornament expression affects extra-pair reproductive success indirectly via mating success (Figure S1). Males typically achieve higher reproductive success with their social mates than with any particular extra-pair mate.

2.2 Analysis of dataset

We estimated the additive genetic variances and covariances of the traits (C, O, M, R) using ASReml-R, assuming an unstructured variance-covariance matrix (see R code in Supporting Information). Care effort and ornament expression were standardised so that $\sigma_C^2 = \sigma_O^2 = 1$. Mating success and reproductive success were relativised by dividing by their respective means. We modelled the relationships as $\mathbf{y} = \boldsymbol{\mu} + \mathbf{AX} + \boldsymbol{\varepsilon}$, where:

   i. $\mathbf{y}$ is an $n \times 4$ matrix of trait values with rows (C_i, O_i, M_i, R_i),

  ii. $\boldsymbol{\mu}$ is a matrix of fixed mean values (i.e. $\boldsymbol{\mu}_i = \boldsymbol{\mu}_j$ for all i, j),

 iii. $\mathbf{A}$ is the relatedness matrix of dimensions $n \times n$ derived from the pedigree,

  iv. $\mathbf{X}$ is an $n \times 4$ matrix of estimated additive genetic effects, and

   v. $\boldsymbol{\varepsilon}$ is a matrix of normally distributed errors with mean zero.

We then estimated path coefficients for the phenotypic model using equations (5) and (6) and for the genetic model using equations (12) and (13) from the main text, based on the path diagram in Figure S1.

2.3 Results

At the phenotypic level, both care effort and ornament expression were under strong positive selection ($s_C = 0.26$ and $s_O = 0.16$; Figure S2). Our model attributes this mainly to direct remaining selection on C (i.e. care effort affects reproductive success directly), and to direct sexual selection on O (i.e. ornament expression affects mating success, which then affects reproductive success). This pattern of direct selection was reinforced by indirect sexual selection on C and indirect remaining selection on O, which arose from the positive phenotypic covariance between these two traits (Table S1).
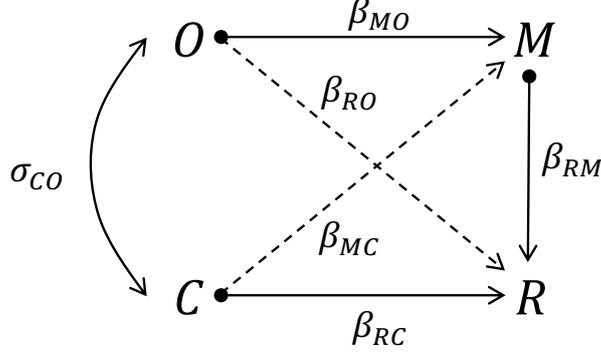
4

Figure S1: Path diagram for the worked example 'Cheating vs caring', shown with care effort C, ornament expression O, mating success M, and reproductive success R. Single-headed arrows indicate potential causal effects that are included in the model, shown as solid arrows if there is a true causal effect, and as dashed arrows if there is no true causal effect. The double-headed arrow indicates a covariance that is not analysed causally. Path coefficients from A to B are written β_{AB} and covariances are written σ_{AB}.

(a) Phenotypic variance-covariance matrix:

$$
\begin{bmatrix} \mathbf{P}_{ZM} & \mathbf{s} \\ \mathbf{s}^T & \sigma_R^T \end{bmatrix} = \begin{bmatrix} \sigma_C^2 & \sigma_{CO} & m_C & s_C \\ & \sigma_O^2 & m_O & s_O \\ & & I_s = \sigma_M^2 & s_M \\ & & & \sigma_R^2 \end{bmatrix} = \begin{bmatrix} 1 & 0.19 & 0.07 & 0.26 \\ & 1 & 0.36 & 0.16 \\ & & 0.39 & 0.15 \\ & & & 0.24 \end{bmatrix}
$$

(b) Additive genetic variance-covariance matrix:

$$
\begin{bmatrix} \mathbf{G}_{ZM} & \mathbf{s}_g \\ \mathbf{s}_g^T & \sigma_{gR}^T \end{bmatrix} = \begin{bmatrix} \sigma_{gC}^2 & \sigma_{gCO} & m_{gC} & s_{gC} \\ & \sigma_{gO}^2 & m_{gO} & s_{gO} \\ & & \sigma_{gM}^2 & s_{gM} \\ & & & \sigma_{gR}^2 \end{bmatrix} = \begin{bmatrix} 0.50 & -0.21 & -0.09 & 0.08 \\ & 0.53 & 0.19 & 0.01 \\ & & 0.09 & 0.01 \\ & & & 0.02 \end{bmatrix}
$$

Figure S2: Estimated phenotypic and additive genetic variance-covariance matrices for the worked example 'Cheating vs caring'

	Parameter		Formula	Value
Phenotypic path coefficients	Mating gradients	C	β_{MC}	0.00
		O	β_{MO}	0.36
	Selection gradients	C	β_{RC}	0.24
		O	β_{RO}	0.00
	Partial Bateman gradient		β_{RM}	0.34
	Partial Jones index		$x'_{\max} = \beta_{RM}\sigma_M$	0.21
Sexual selection	Direct	C	$\sigma_C^2 \beta_{RM}\beta_{MC}$	0.00
		O	$\sigma_O^2 \beta_{RM}\beta_{MO}$	0.12
	Indirect	C	$\sigma_{CO}\beta_{RM}\beta_{MO}$	0.02
		O	$\sigma_{CO}\beta_{RM}\beta_{MC}$	0.00
	Total	C	$x_C = m_C\beta_{RM}$ $= \sigma_C^2\beta_{RM}\beta_{MC} + \sigma_{CO}\beta_{RM}\beta_{MO}$	0.02
		O	$x_O = m_O\beta_{RM}$ $= \sigma_O^2\beta_{RM}\beta_{MO} + \sigma_{CO}\beta_{RM}\beta_{MC}$	0.12
Remaining selection	Direct	C	$\sigma_C^2\beta_{RC}$	0.24
		O	$\sigma_O^2\beta_{RO}$	0.00
	Indirect	C	$\sigma_{CO}\beta_{RO}$	0.00
		O	$\sigma_{CO}\beta_{RC}$	0.05
	Total	C	$r_C = \sigma_C^2\beta_{RC} + \sigma_{CO}\beta_{RO}$	0.24
		O	$r_O = \sigma_O^2\beta_{RO} + \sigma_{CO}\beta_{RC}$	0.04
Total selection	Selection differentials	C	$s_C = \sigma_{CR} = x_C + r_C$	0.26
		O	$s_O = \sigma_{OR} = x_O + r_O$	0.16

Table S1: Results of 'Cheating vs caring', showing phenotypic path coefficients and estimates of sexual, remaining and total selection on care effort C and ornament expression O. All non-zero parameter values are statistically significant.

	Parameter		Formula	Value
Genetic path coefficients	Mating gradients	C	β_{gMC}	-0.03
		O	β_{gMO}	0.34
	Selection gradients	C	β_{gRC}	0.21
		O	β_{gRO}	0.03
	Partial Bateman gradient		β_{gRM}	0.19
	Genetic partial Jones index		$x'_{g\max} = \beta_{gRM}\sigma_{gM}$	0.06
Response to sexual selection	Direct	C	$\sigma_{gC}^2\beta_{gRM}\beta_{gMC}$	0.00
		O	$\sigma_{gO}^2\beta_{gRM}\beta_{gMO}$	0.03
	Indirect	C	$\sigma_{gCO}\beta_{gRM}\beta_{gMO}$	-0.01
		O	$\sigma_{gCO}\beta_{gRM}\beta_{gMC}$	0.00
	Total	C	$\begin{aligned}x_{gC} &= m_{gC}\beta_{gRM} \\ &= \sigma_{gC}^2\beta_{gRM}\beta_{gMC} + \sigma_{gCO}\beta_{gRM}\beta_{gMO}\end{aligned}$	-0.02
		O	$\begin{aligned}x_{gO} &= m_{gO}\beta_{gRM} \\ &= \sigma_{gO}^2\beta_{gRM}\beta_{gMO} + \sigma_{gCO}\beta_{gRM}\beta_{gMC}\end{aligned}$	0.04
Response to remaining selection	Direct	C	$\sigma_{gC}^2\beta_{gRC}$	0.11
		O	$\sigma_{gO}^2\beta_{gRO}$	0.02
	Indirect	C	$\sigma_{gCO}\beta_{gRO}$	-0.01
		O	$\sigma_{gCO}\beta_{gRC}$	-0.04
	Total	C	$r_{gC} = \sigma_{gC}^2\beta_{gRC} + \sigma_{gCO}\beta_{gRO}$	0.10
		O	$r_{gO} = \sigma_{gO}^2\beta_{gRO} + \sigma_{gCO}\beta_{gRC}$	-0.03
Total response to selection	Genetic selection differentials	C	$s_{gC} = \sigma_{gCR} = x_{gC} + r_{gC}$	0.08
		O	$s_{gO} = \sigma_{gOR} = x_{gO} + r_{gO}$	0.01

Table S2: Results of 'Cheating vs caring', showing genetic path coefficients and the estimated evolutionary response to sexual, remaining and total selection on care effort C and ornament expression O.

The estimated response to selection at the genetic level was much smaller than the phenotypic selection differentials ($s_{gC} = 0.08$ and $s_{gO} = 0.01$; Figure S2). There are two reasons for this. First, since both genes and the environment contribute to trait expression, all traits had smaller additive genetic variance than phenotypic variance (Figure S2). This constrains the additive genetic covariance between traits and reproductive success, by which we estimate the response to selection. Second, care effort and ornament expression covaried negatively at the genetic level. This genetic trade-off resulted in negative indirect selection on breeding values for both traits. Direct and indirect selection consequently pulled in different directions, which reduced the overall response to selection (Table S2).

Our model controls for care effort and ornament expression when estimating the relationship between mating success and reproductive success (i.e. the partial Bateman gradient $\beta_{RM} = 0.34$ and genetic partial Bateman gradient $\beta_{gRM} = 0.19$). At the phenotypic level, the simple Bateman gradient ($\beta_{ss} = 0.37$) modestly overestimated this relationship by failing to account for the positive covariance between care effort (which affects reproductive success) and ornament expression (which affects mating success). The opposite happened at the genetic level, where the negative covariance between C and O led the genetic simple Bateman gradient ($\beta_{gss} = 0.06$) to drastically underestimate the causal effect of mating success on reproductive success.

References

Asmussen, S., and P. W. Glynn. 2007. Stochastic Simulation: Algorithms and Analysis. Springer, New York.

Barton, N. H., A. M. Etheridge, and A. Véber. 2017. The infinitesimal model: Definition, derivation, and implications. Theor Popul Biol 118:50–73.

Bulmer, M.G. 1980. The Mathematical Theory of Quantitative Genetics. Clarendon Press, Oxford.

Morrissey, M. B. 2014. Selection and evolution of causally covarying traits. Evolution 68:1748–1761.