



# THE UNIVERSITY *of* EDINBURGH

## Edinburgh Research Explorer

### Measuring Selection when Parents and Offspring Interact

**Citation for published version:**

Thomson, CE & Hadfield, J 2017, 'Measuring Selection when Parents and Offspring Interact', *Methods in ecology and evolution*, vol. 8, pp. 678. <https://doi.org/10.1111/2041-210X.12795>

**Digital Object Identifier (DOI):**

[10.1111/2041-210X.12795](https://doi.org/10.1111/2041-210X.12795)

**Link:**

[Link to publication record in Edinburgh Research Explorer](#)

**Document Version:**

Peer reviewed version

**Published In:**

Methods in ecology and evolution

**General rights**

Copyright for the publications made accessible via the Edinburgh Research Explorer is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

**Take down policy**

The University of Edinburgh has made every reasonable effort to ensure that Edinburgh Research Explorer content complies with UK legislation. If you believe that the public display of this file breaches copyright please contact [openaccess@ed.ac.uk](mailto:openaccess@ed.ac.uk) providing details, and we will remove access to the work immediately and investigate your claim.



# Measuring Selection when Parents and Offspring Interact

Caroline E. Thomson

Department of Zoology, Edward Grey Institute, University of Oxford, Oxford,

OX1 3PS, United Kingdom

Evolution Diversit  Biologique, B timent 4R1, Universit  de Toulouse Paul

Sabatier, 118 Route de Narbonne, 31062 Toulouse Cedex 09, France

caroline.thomson@univ-tlse3.fr

Jarrod D. Hadfield

Institute of Evolutionary Biology, University of Edinburgh, UK

j.hadfield@ed.ac.uk

1 Non-social and social selection gradients are key evolutionary parameters  
14 in systems where individuals interact. They are most easily obtained by  
regressing an individual's fitness on the trait values of the individual and  
16 its social partner.

2 In the context of parental care it is more common to regress the trait value  
18 of the parents (ie. the social partner) on a 'mixed' fitness measure that is a  
function of the parent's and offspring's fitness (for example the number of  
20 recruits, which equals parental fecundity multiplied by offspring survival).

3 For such an approach to yield correct estimates of net-selection, the trait  
22 must be sex-limited and not affect the parents' own survival.

4 When a trait is not sex-limited, the non-social selection should be weighted  
24 by one (because all individuals express the trait) and social selection  
should be weighted by a half (because the relatedness between parents  
26 and the offspring they care for is a half, usually). The ‘mixed’ fitness  
approach does not give estimates of both components of selection and so  
28 they cannot be weighted appropriately.

5 We show that mixed fitness components are frequently used in place of di-  
30 rect fitness measures in the literature (37% of fecundity selection estimates  
use a mixed fitness approach), but that the frequency is much higher in  
32 some taxa, such as birds and mammals.

6 We suggest alternative methods that could be used to estimate both social  
34 and non-social selection gradients, while at the same time assessing the  
importance of unmeasured traits.

36 When measuring evolutionary change, the time points between which change  
is measured must be stipulated. In species with discrete generations the most  
38 natural time point is at conception such that evolutionary change is due to se-  
lection *within* a generation followed by the inheritance of that change *across*  
40 generations (Falconer, 1983). In species with overlapping generations all indi-  
viduals are not conceived at a single point in time, but evolutionary change  
42 can still be measured as the difference in breeding value of newly conceived  
individuals born one unit of time apart (Hill, 1974; Charlesworth, 1994).

44 In many taxa, parents directly affect the attributes of their offspring ei-  
ther through the properties of their eggs/seeds or through extended post-natal  
46 care (Mousseau & Fox, 1998; Clutton-Brock, 1991; Royle *et al.*, 2012). These  
non-genetic cross-generational effects complicate the study of natural selection  
48 and evolutionary change, but Kirkpatrick & Lande (1989) developed a body  
of theory by which they could be understood. They took a direct fitness ap-  
50 proach whereby the fitness of an individual is measured from its conception

and is defined as the number of zygotes it produces. However, the fitness of  
52 the individual can depend on its parents, either because parental phenotype  
has a direct effect on the individual’s fitness, or indirectly because the fitness  
54 of an individual depends on its own phenotype, which is partly determined by  
parental phenotype. This model by Kirkpatrick & Lande (1989) (henceforth  
56 the K-L model) is most easily understood when selection on the traits is weak  
and constant, rather than strong and fluctuating. Then, the change in breeding  
58 values between newly conceived individuals of successive generations is:

$$\Delta \mathbf{a}^{(I)} = COV(\mathbf{a}^{(I)}, \mathbf{z}^{\top(I)}) (\boldsymbol{\delta} \circ \boldsymbol{\beta}^{(I)}) + COV(\mathbf{a}^{(I)}, \mathbf{z}^{\top(S)}) \boldsymbol{\beta}^{(S)} \quad (1)$$

where  $\mathbf{a}^{(I)}$  and  $\mathbf{z}^{(I)}$  are the vectors of breeding values and phenotypes, respec-  
60 tively, in an individual and  $\mathbf{z}^{(S)}$  is the vector of phenotypes in that individual’s  
mother (the social partner of the focal offspring). The  $\top$  superscript denotes the  
vector transpose.  $\boldsymbol{\beta}^{(I)}$  is the *direct* effect of the individual’s own traits on the  
62 individual’s fitness, and this is multiplied element wise by  $\boldsymbol{\delta}$  (as indicated by  $\circ$ )  
64 which has elements equal to a half if the trait is sex-limited (Lande, 1982) and  
one otherwise. We refer to  $\boldsymbol{\beta}^{(I)}$  throughout as the non-social selection gradient  
66 (Wolf *et al.*, 1999), although it has also been called a direct selection gradient  
(Kirkpatrick & Lande, 1989; Hadfield, 2012).  $\boldsymbol{\beta}^{(S)}$  is the *direct* effect of the  
68 individual’s mother’s traits on the individual’s fitness. It is not multiplied by  
a half because all individuals, both male and female, have a mother, and we  
70 assume that the maternal effect is not sex-specific. We call  $\boldsymbol{\beta}^{(S)}$  the social se-  
lection gradient (Wolf *et al.*, 1999), although it has also been called a parental  
72 selection gradient (Kirkpatrick & Lande, 1989; Hadfield, 2012). The first term  
in Equation 1 can be thought of as the correlated response of breeding values to  
74 selection on the individual’s own traits, and the second term as the correlated  
response of breeding values to selection on the individual’s parent’s traits. The  
76 covariance between breeding value and phenotype is complicated when mothers

and offspring interact because maternal effects contribute to the covariance in  
78 addition to the direct effect of (inherited) genes. However, as with standard  
patterns of inheritance  $COV(\mathbf{a}^{(I)}, \mathbf{z}^{\top(S)}) = \frac{1}{2}COV(\mathbf{a}^{(I)}, \mathbf{z}^{\top(I)})$  and so Equation  
80 1 is often expressed as

$$\Delta \mathbf{a}^{(I)} = COV(\mathbf{a}^{(I)}, \mathbf{z}^{\top(I)}) \left( \boldsymbol{\delta} \circ \boldsymbol{\beta}^{(I)} + \frac{1}{2}\boldsymbol{\beta}^{(S)} \right) \quad (2)$$

where the selection term in brackets is called the net selection gradient. It  
82 should be emphasised, however, that the factor of half associated with social  
selection is due to inheritance: a different value would be used if mothers were  
84 not related to the individuals they care for by half (for example if there was egg  
dumping (Andersson *et al.*, 2017), or extra-pair paternity in paternal/biparental  
86 care models (Thomson *et al.*, 2017)).

Although the K-L model employs a direct fitness approach (where fitness is  
88 measured from conception as the number of zygotes produced), it is possible  
- and useful - to interpret it from an inclusive-fitness perspective (Hadfield &  
90 Thomson, 2017). Indeed, the two approaches yield the same results, but from a  
mathematical perspective the direct fitness approach is often simpler when con-  
92 structing theoretical models (Taylor *et al.*, 2007) and, we argue, when applying  
statistical models to data. However, in many empirical studies of natural selec-  
94 tion, the number of *recruits* an individual leaves is often advocated as a fitness  
measure (Clutton-Brock, 1988; Moran & Clark, 2012), which we call a ‘mixed’  
96 fitness measure, as it combines both parental fitness (fecundity) and offspring  
fitness (survival). This is neither a direct fitness nor inclusive fitness approach  
98 (Grafen, 1982), and the resulting selection estimates have no easy evolution-  
ary interpretation. Because of this, there have been repeated calls, primarily  
100 from evolutionary geneticists, to measure fitness from conception (Arnold, 1985;  
Cheverud & Moore, 1994; Hadfield, 2012; Smiseth *et al.*, 2012). In contrast, the  
102 most thorough theoretical work exploring the consequences of using a mixed

fitness measure seems to suggest that both the direct fitness approach and the  
104 mixed fitness approach have shortcomings (Wolf & Wade, 2001). Here we reap-  
praise the value of the mixed fitness approach and show that, in general, it will  
106 give the wrong answer. The conditions under which it gives the right answer are  
quite restrictive, in contrast to the direct fitness approach that, if used correctly,  
108 can be applied in a wide range of circumstances.

As in Wolf & Wade (2001), our immediate criterion for correctness is whether  
110 the estimated selection gradient multiplied by the genetic variance correctly pre-  
dicts the amount of evolutionary change. However, this is probably a secondary  
112 aim of most biologists, who are often more interested in quantifying selection  
to understand the adaptive significance of the traits they study (Grafen, 1988).  
114 In these instances the ‘mixed’ fitness approach usually obscures the underlying  
biology by conflating inheritance and selection, and the fitness of parents and  
116 their offspring. This conflation prevents the clean assessment of patterns of  
natural selection and makes the study of ideas such as parent-offspring conflict  
118 exceptionally difficult (Smiseth *et al.*, 2012; Hadfield, 2012).

## 120 **Theory**

The most general model in Wolf & Wade (2001) follows that of Cheverud’s  
122 (1984) extension of the Willham (1972) model. Two traits are considered where  
trait 1 maternally affects trait 2, with maternal effect coefficient  $\psi_{2,1}$ . Non-  
124 social selection acts on both traits, but social selection only acts on trait 1.  
Social selection on trait 1 is assumed to affect fitness through juvenile survival  
126 only, and Wolf & Wade (2001) also assume that non-social selection on trait 1  
is limited to fecundity, and non-social selection on trait 2 is limited to juvenile  
128 survival. Here we relax these assumptions and allow non-social selection on both  
traits to operate through both fitness components. The two fitness components  
130 are given by:

$$w^{(I:J)} = \mu^{(J)} + \beta_1^{(I:J)} z_1^{(I)} + \beta_1^{(S:J)} z_1^{(S)} + \beta_2^{(I:J)} z_2^{(I)} \quad (3)$$

and

$$w^{(I:F)} = \mu^{(F)} + \beta_1^{(I:F)} z_1^{(I)} + \beta_2^{(I:F)} z_2^{(I)} \quad (4)$$

132 where  $w$  is relative fitness and we use the notation  $:J$  or  $:F$  to denote quan-  
 133 tities that relate to juvenile survival and adult fecundity respectively, and  $I$ : or  
 134  $S$ : to indicate that the trait is expressed in the individual or its social partner,  
 respectively. Assuming our organisms are semelparous total absolute fitness  
 136  $W^{(I)}$  is simply  $W^{(I:J)}W^{(I:F)}$ . In Figure 1 a graph of the causal relationships  
 between traits, and traits and fitness components is given.

138 *Figure 1 here*

However, in many studies the fitness measure is not the survival and fe-  
 140 cundity of a single individual, but often the fecundity of an individual multi-  
 plied by the survival of that individual's offspring (e.g. number of recruits):  
 142  $W^{(M)} = W^{(I:J)}W^{(S:F)}$  where the superscript  $M$  stands for mixed. Arnold &  
 Wade (1984a,b) show that when selection is weak and the total lifetime fitness  
 144 of individuals can be divided into multiplicative episodes, then selection gra-  
 dients can be obtained by regressing the relative fitness at each episode on trait  
 146 values, and then summing the gradients across episodes. Wolf & Wade (2001)  
 consider two approaches for obtaining an estimated selection gradient for trait  
 148 1: *Direct*: the univariate regression of direct relative fitness ( $w^{(I)}$ ) on trait 1 of  
 the individual ( $z_1^{(I)}$ ) and *Mixed*: the univariate regression of the relative number  
 150 of recruits ( $w^{(M)}$ ) on trait 1 of the parent ( $z_1^{(S)}$ ). In what follows we will also  
 deviate from Wolf & Wade (2001) and relax the assumption that trait 1 has to  
 152 be sex-limited and allow environmental covariances between the two traits as  
 well as genetic covariances.

154 Assuming that trait 1 is variance standardised, the estimated selection gra-  
 dient using mixed fitness is (Robertson, 1966; Lande & Arnold, 1983; Arnold &  
 156 Wade, 1984a):

$$\begin{aligned}
 \beta_{1,M} &= \delta COV(w^{(I:J)} + w^{(S:F)}, z_1^{(S)}) \\
 &= \delta \frac{1}{2} \beta_1^{(I:J)} g_1 + \delta \beta_1^{(S:J)} + \delta (\beta_2^{(I:J)} + \beta_2^{(I:F)}) (\frac{1}{2} g_{1,2} + \psi_{2,1}) + \delta \beta_1^{(I:F)}
 \end{aligned} \tag{5}$$

which is equivalent to Equation A8 in Wolf & Wade (2001) if  $\beta_1^{(I:J)} =$   
 158  $\beta_2^{(I:F)} = 0$  and  $\delta = 1/2$ . In the results section we consider a number of special  
 cases of this general equation and discuss how, or even if, the resulting mixed  
 160 selection gradients can be interpreted.

162 Using direct fitness in the univariate approach the estimated selection gra-  
 dient is

$$\begin{aligned}
 \beta_{1,D} &= COV(w^{(I:J)} + w^{(I:F)}, z_1^{(I)}) \\
 &= \beta_1^{(I:J)} + \frac{1}{2} \beta_1^{(S:J)} g_1 + (\beta_2^{(I:J)} + \beta_2^{(I:F)}) (g_{1,2} + e_{1,2} + \frac{1}{2} \psi_{2,1} g_1)
 \end{aligned} \tag{6}$$

164 which is Equation A7 in Wolf & Wade (2001) when  $\beta_1^{(I:J)} = \beta_2^{(I:F)} = 0$ ,  
 $e_{1,2} = 0$  and  $\delta = 1/2$ . However, although direct fitness is used, the method does  
 166 not include both offspring and parental traits as predictors of an individual's  
 fitness and therefore is not appropriate for estimating social selection gradients  
 168 (Kirkpatrick & Lande, 1989). Because of this, we do not discuss this approach  
 further, and instead spend time discussing simple methods for estimating social  
 170 and non-social selection gradients using a direct fitness approach.

The measure of validity used by Wolf & Wade (2001) was whether the esti-  
 172 mated selection gradients multiplied by the genetic variance will correctly pre-  
 dict the amount of evolutionary change in trait 1. From Equation 2 we can see  
 that this will be the case when the estimated selection gradient is equal to what  
 174 Kirkpatrick & Lande (1989) call the net selection gradient:



$$\beta_{1,M} = \delta_1 \beta_1^{(I)} + \frac{1}{2} \beta_1^{(S)} \quad (7)$$

176 and the covariance between the breeding value for trait 1 and the phenotype  
for trait 2 is zero (or net selection on trait 2 is zero):

$$\text{COV}(a_1^{(I)}, z_2^{(I)}) = \text{COV}(a_1^{(I)}, z_2^{(S)}) = 0 \quad \text{or} \quad \delta_2 \beta_2^{(I)} + \frac{1}{2} \beta_2^{(S)} = 0 \quad (8)$$

178 In cases where relatedness between parents and the offspring they care for is  
not a half, the factor of a half can be replaced by relatedness in the preceding  
180 (and following) equations.

To evaluate when these two conditions will be met, and why, we work through  
182 a series of examples that have different patterns of selection and maternal ef-  
fects. In all cases, we assume that selection has been measured through the  
184 effect of trait 1 ( $z_1$ ) on a mixed fitness measure (number of offspring surviving  
to some point past conception). First, we consider the case where trait 2 is  
186 absent, and trait 1 alone affects the individual's fecundity and the individual's  
offspring's survival (Figure 2); the case which the mixed fitness approach seems  
188 to be most suited to. Then we consider more complicated scenarios where the  
mixed fitness approach would appear less suited (Figure 3).

190

*If the causal model motivating the mixed fitness approach is true*

192

*Figure 2 here*

In the first instance, we will assume that the causal model that appears to  
194 motivate the mixed fitness approach is true (Figure 2): trait 1 can affect its  
bearer's own fitness via fecundity and that of its offspring via survival. All  
196 other routes by which trait 1 could affect the fitness of either party are assumed  
absent, and a second (unmeasured) trait is assumed not to exist. In this case

198 fitness via survival is simply  $w^{(I:J)} = \mu^{(J)} + \beta_1^{(S:J)} z_1^S$  and the mixed selection  
 gradient is therefore:

$$\beta_{1,M} = \delta_1 \beta_1^{(I:F)} + \delta_1 \beta_1^{(S:J)} \quad (9)$$

200 i.e. the sum of non-social selection through the effects of trait 1 on fecundity  
 ( $\beta_1^{(I:F)}$ ), and social selection through effects of the social partner's trait 1 on  
 202 survival ( $\beta_1^{(S:J)}$ ). Under these conditions Wolf & Wade (2001) state that the  
 mixed fitness approach is a valid way of estimating net-selection, but we see  
 204 here that this relies on the assumption that the trait is sex-limited, i.e.  $\delta_1 = \frac{1}{2}$   
 (as acknowledged by Wolf & Wade, 2001) and that the relatedness of parents  
 206 and the offspring they care for is a half. In addition the mixed fitness approach  
 does not allow the researcher to get individual estimates of social and non-social  
 208 selection. However, if the trait does not affect the parent's own fecundity then  
 $\beta_{1,M} = \delta_1 \beta_1^{(S:J)}$  is a valid social selection gradient (although halved if it is  
 210 assumed trait 1 is sex-limited). Alternatively, if the trait does not affect the  
 offspring's survival then  $\beta_{1,M} = \delta_1 \beta_1^{(I:F)}$  and is a valid non-social selection gra-  
 212 dient.

214 *If the causal model motivating the mixed fitness approach is not true*

The case presented above assumes that the underlying model is that for  
 216 which the mixed fitness approach is most suited. However, one can envision  
 many situations where the biology is more complicated (Figure 3). Below we  
 218 add additional fitness and maternal effects to the basic model described above,  
 and illustrate the model with a *possible* example from the literature. Similar sce-  
 220 narios to ii) and iii) are also covered in Wolf & Wade (2001) with sex-limitation.

*Figure 3 here*

222 (i) Juvenile survival is affected by the individual's own trait 1 ( $\beta_1^{(I:J)} \neq 0$ ).

In this case, the trait is simultaneously expressed in both parents and their  
 224 offspring. A possible example of such a scenario is provided by Bouteiller-Reuter  
 & Perrin (2005) who estimated selection on female body mass in greater white-  
 226 toothed shrews (*Crocidura russula*) using the number of weaned offspring per  
 litter as a fitness measure. Body mass is evidently expressed in both parents and  
 228 their offspring simultaneously, and so juvenile survival may be influenced by the  
 individual's own trait value rather than (or in addition to) that of the parent.  
 230 Consequently, juvenile survival is determined by both its own trait value ( $z_1^{(I)}$ )  
 and that of the mother ( $z_1^{(S)}$ ), and becomes  $w^{(I:J)} = \mu^{(J)} + \beta_1^{(I:J)} z_1^{(I)} + \beta_1^{(S:J)} z_1^{(S)}$   
 232 and

$$\beta_{1,M} = \delta_1 \beta_1^{(I:F)} + \delta_1 \beta_1^{(S:J)} + \delta_1 \frac{1}{2} g_1 \beta_1^{(I:J)} \quad (10)$$

Where, as before,  $\beta_1^{(I:J)}$  is the non-social selection acting through juvenile  
 234 survival, and  $\beta_1^{(S:J)}$  is the social selection gradient acting through juvenile sur-  
 vival. Here the mixed fitness approach cannot give the correct answer even when  
 236 the trait is sex-limited, because direct (non-social) selection operating through  
 juvenile survival is underestimated by a factor equal to half the heritability  
 238 ( $g_1 = h_1^2$  because the trait has been variance standardised). Similarly, in cases  
 where parental traits have no direct effect on offspring fitness, after conditioning  
 240 on offspring traits (there is no social selection;  $\beta_1^{(S:J)} = 0$ ) then:

$$\beta_{1,M} = \delta_1 \beta_1^{(I:F)} + \delta_1 \frac{1}{2} g_1 \beta_1^{(I:J)} \quad (11)$$

If non-social selection on a trait via fecundity was antagonistic to that on  
 242 juvenile survival (i.e.  $\beta_1^{(I:F)}$  and  $\beta_1^{(I:J)}$  have opposing signs), such that there was  
 no overall effect of the trait on fitness, then using a mixed fitness measure would  
 244 incorrectly provide evidence of selection for trait values that favour fecundity.

246 (ii) *Fitness is affected by a second (non-sex-limited) trait expressed in the*

individual ( $\beta_2^{(I:J)} + \beta_2^{(I:F)} \neq 0$ ).

248 Whilst the preceding considerations are likely to be important when selection is  
measured on a trait that is expressed concurrently in two generations (such as  
250 body size), many studies estimate selection on traits only expressed in adults.  
For example, selection on phenological traits has been estimated through their  
252 effects on offspring fitness, including the effects of laying date (Charmantier  
*et al.*, 2006), parturition date (McAdam & Boutin, 2003), and arrival date (Sea-  
254 mons *et al.*, 2007). As the trait is not expressed during juvenile life stages  
 $\beta_1^{(I:J)} = 0$  by definition. However, a second trait ( $z_2$ ) expressed at juvenile,  
256 and possibly adult stages (such as body mass), may be genetically correlated  
with the focal trait ( $g_{1,2} \neq 0$ ). This is illustrated well by Sheldon *et al.* (2003),  
258 where a significant genetic correlation exists between laying date and tail length  
in collared flycatchers, and both are shown to be under significant directional  
260 selection through a measure of mixed fitness. In such cases, where trait 1 is  
only expressed in adults but is genetically correlated with trait 2, then selection  
262 measured on trait 1 becomes

$$\beta_{1,M} = \delta_1 \beta_1^{(I:F)} + \delta_1 \beta_1^{(S:J)} + \delta_1 (\beta_2^{(I:J)} + \beta_2^{(I:F)}) \frac{1}{2} g_{1,2} \quad (12)$$

Where  $\beta_2^{(I:J)}$  and  $\beta_2^{(I:F)}$  are the non-social selection gradients on the second  
264 trait acting through effects on juvenile survival and adult fecundity, respectively.  
Only when the genetic correlation between the traits is zero ( $g_{1,2} = 0$ ), and trait  
266 1 is sex-limited ( $\delta_1 = \frac{1}{2}$ ), does the mixed fitness approach give the correct an-  
swer. More generally, selection on trait 1 will be biased towards the correlated  
268 response to selection on trait 2 ( $g_{1,2} \beta_2^{(I)}$ ) although this will be multiplied by a  
half, or a quarter if trait 1 is assumed to be sex-limited (see Cheverud, 1984,  
270 also).

272 (iii) *Fitness is affected by a second (non-sex-limited) trait expressed in the*

individual that is maternally affected by trait 1 ( $\psi_{2,1} \neq 0$  and  $\beta_2^{(I:J)} + \beta_2^{(I:F)} \neq 0$ ).

274 In the above example, trait 1 in the mother and trait 2 in the offspring are  
assumed to be correlated because of shared genes. However, a correlation may  
276 also exist if trait 1 in the parents directly affects the value of the second trait in  
the offspring, through maternal (or paternal) effects. For example, in Thomson  
278 *et al.* (2017) we show how parental performance for offspring mass (a trait of  
the parents that captures all effects they have on their offspring's mass) directly  
280 affects the parent's own fecundity and indirectly affects their offspring's survival  
via an effect on body mass. Under scenarios like this,

$$\beta_{1,M} = \delta_1 \beta_1^{(I:F)} + \delta_1 \beta_1^{(S:J)} + \delta_1 (\beta_2^{(I:J)} + \beta_2^{(I:F)}) (\frac{1}{2} g_{1,2} + \psi_{2,1}) \quad (13)$$

282 which is equivalent to scenario ii) but the term  $\psi_{2,1}$  (the maternal effect  
coefficient) contributes to the covariance between the traits. As a consequence,  
284 the mixed fitness approach fails when the trait maternally affects other traits  
under selection even when the traits are not genetically correlated.

286

## Empirical Patterns

288

### *Methods*

To assess the frequency with which direct and mixed fitness approaches are  
290 used in the literature, we went through the papers from which Kingsolver &  
Diamond (2011) had collated estimates of selection from wild populations. For  
292 each paper we assessed which of the two approaches the authors had used when  
estimating linear selection gradients. These papers are a combination of those  
294 from Kingsolver *et al.* (2001) and Siepielski *et al.* (2009), and inclusion criteria  
are explained explicitly in those papers. Broadly, the papers report all studies  
296 of selection on quantitative phenotypic traits from wild unmanipulated popula-  
tions from 1984 to 2001 (Kingsolver *et al.*, 2001), and all studies with temporally

298 replicated estimates from 2002 to 2009 (Siepielski *et al.*, 2009). In total there  
are 2819 estimates of linear selection gradients from 97 studies across 89 species.  
300 The fitness measures used in these studies had already been broadly categorised  
as fecundity, mating success, survival, and total (lifetime) selection, but there  
302 was often heterogeneity within a category with regard to which fitness com-  
ponents had actually been measured, and whether the fitness components were  
304 measured on the same individual or different individuals. In particular, the origi-  
nal ‘fecundity’ category often included measures of the number of zygotes/eggs,  
306 but also the number of surviving offspring. Thus, we explicitly recategorised  
the measures used in these studies as Adult survival (A), Juvenile Survival (J;  
308 any survival pre-recruitment was considered juvenile), Mating Success (M), and  
Fecundity (F; the number of zygotes) and studies using fitness measures that  
310 were a composite were recorded as such. In addition, for those studies where  
the fitness measure could not be truly classified into one of these categories,  
312 we recorded it as ‘other’ (using a proxy for fitness, or the true measure could  
not be determined from the paper). We also recorded whether the trait was  
314 measured in the same individual for which the fitness component was defined,  
or on the individual’s parent. For example, a study that looked at selection on a  
316 parental trait where the fitness measure was how many offspring that individual  
recruited into the population would be denoted as  $F^{(S,S)} + J^{(I,S)}$  where the first  
318 letter in the superscript designates whose fitness was measured and the second  
letter whose trait was measured.

320

### *Results*

322 Of the 2819 estimated linear selection gradients in Kingsolver & Diamond  
(2011), the fitness measure used could be classified according to our system for  
324 2556 estimates from 95 papers. Reclassification of the fitness measures showed  
that there was considerable disparity between studies classified under the same

326 original broad fitness measure categories, and in total 637 selection gradients  
from 22 studies used either a mixed fitness approach or had measured social  
328 selection gradients rather than non-social selection gradients. Originally, 681  
selection gradients had been classed as measuring selection using fecundity as  
330 a fitness measure. From our reclassification, 351 truly measured fecundity as  
the number of zygotes, with a further 66 as some measure of mating success  
332 (generally pollen grains removed). 252 selection gradients were estimated us-  
ing a mixed fitness approach (106 of which considered offspring survival pre-  
334 independence, and the others post-independence from the parent). Of the 602  
selection gradients classed as measuring fitness as mating success, 185 used a  
336 mixed fitness approach (of which 84 included pre-independence offspring sur-  
vival, and and the other 101 used a post-independence time point).

338 Furthermore, there are 1263 measures of survival selection, of which 94 used  
mixed fitness. In addition, 74 social selection gradients were measured - 28  
340 used a measure of survival to independence, 36 used survival to a point post-  
independence, and 10 used offspring survival from a point post-independence  
342 to another time point (recruitment, or pupation). Finally, of the 52 selection  
gradients reporting ‘total’ fitness, 20 used a mixed fitness approach.

344 The distribution of the different fitness measures across taxonomic groups  
can be seen in Table 2. This makes it clear that there are differences between  
346 researchers working in different taxonomic domains in how fitness is measured;  
whilst true fecundity (as the number of zygotes, or some proxy for this) is often  
348 measured in Angiosperms and insects, a mixed fitness measure of fecundity is  
more frequently measured in birds.

350

*Table 2 here*

## 352 **Statistical Solutions**

*Methods*

354 We propose a statistical method that simultaneously models both survival  
and fecundity, and allows both non-social and social selection gradients to be  
356 estimated. The advantage of modelling survival and fecundity simultaneously,  
rather than in separate analyses, is that it allows any remaining covariance  
358 (after conditioning on measured traits) between the parent’s fecundity and the  
offspring’s survival to be estimated. For analysing data from the full model  
360 described above we imagine two statistical models:

$$f_i = b_0^{(F)} + z_{1i}b_1^{(I:F)} + z_{2i}b_2^{(I:F)} + e_i^{(F)} \quad (14)$$

where  $f_i$  is the linear predictor for the fecundity of individual  $i$ ,  $b_0^{(F)}$  is the  
362 intercept,  $b_1^{(I:F)}$  the regression coefficient associated with the individuals’ own  
trait 1 values and  $e_i$  the residual. In what follows we will assume that the  
364 fecundity of an individual is Poisson distributed with rate  $\exp(f_i)$ .  $s_{ij}$  is the  
linear predictor for survival of offspring  $j$  from individual  $i$ :

$$s_{ij} = b_0^{(J)} + z_{1i}b_1^{(S:J)} + z_{1ij}b_1^{(I:J)} + z_{2ij}b_2^{(I:J)} + u_i^{(J)} \quad (15)$$

366 where  $u_i^{(J)}$  is a random effect that allows the survival of offspring from the  
same parent to be correlated after conditioning on the traits and their associ-  
368 ated regression coefficients  $b$ . We will assume that the survival probability of  
individual  $ij$  is  $F_N(s_{ij})$  where  $F_N$  is the Gaussian cumulative density function  
370 (i.e a probit or threshold model Pearson, 1900). We allow  $e_i^{(F)}$  (the residual  
parental fecundity) and  $u_i^{(J)}$  (the parental effect on offspring survival) to be  
372 correlated. Allowing a covariance between the a residual and a random effect  
is non-standard, but Thomson *et al.* (2017) provides a Markov chain Monte  
374 Carlo (MCMC) strategy for estimating such covariances. In this context, the  
covariance could be due to unmeasured traits that a) have a non-social effect on  
376 fecundity and a social effect on survival b) have a non-social effect on fecundity  
and are phenotypically correlated with other unmeasured traits that have social



378 effects on survival or c) have a non-social effect on fecundity and survival and are  
heritable (due to genes and/or maternal effects) or d) have a cross-generation  
380 correlation with other unmeasured traits that have a non-social effect on sur-  
vival. With sufficient data the contribution of a) and b) versus c) and d) could  
382 be assessed by including a genetic and/or maternal genetic terms for both fitness  
components, using cross-fostering or a multigenerational pedigree.

384 In summary we run a bivariate mixed model with the two responses being  
fecundity and survival. The individual's own trait values are fitted as fixed  
386 effects for each response (non-social selection), and parental trait 1 is included  
as a fixed effect for juvenile survival (social selection). It should be noted that  
388 a social selection effect for trait 2 has not been fitted; it could be fitted, but we  
prefer to omit a trait so that the code presented in the Supplementary Materials  
390 can be more easily tailored to situations where all traits are not fitted as both  
social and non-social predictors of fitness. This approach for estimating selection  
392 is consistent with the K-L approach and has some similarities to contextual  
analysis (Heisler & Damuth, 1987; Goodnight *et al.*, 1992) and particularly  
394 neighbourhood models (Nunney, 1985).

1000 data-sets were simulated according to the model for 200 adults and their  
396 offspring. The genetic and environmental variances for  $z_1$  and  $z_2$  were both 1,  
with genetic covariance  $g_{1,2} = 0.25$ , random-residual covariance  $COV(e^{(F)}, u^{(J)}) =$   
398  $-0.25$  and maternal effect  $\psi_{2,1} = 0$ . The remaining parameters were all esti-  
mated in the model and the values used in the simulation are reported in Table  
400 1. Model parameters were estimated using MCMCglmm (Hadfield, 2010) with  
flat improper priors, a chain length of 13000, a burn-in of 3000 and a thinning  
402 interval of 10. The posterior means and 95% credible intervals for all parameters  
were stored for each analysis.

404 The selection gradient is defined as (Lande, 1979; Lande & Arnold, 1983):

$$\boldsymbol{\beta} = \frac{E[\partial W/\partial \mathbf{z}]}{E[W]} \quad (16)$$

where  $W$  is absolute fitness and  $\mathbf{z}$  are all traits, both those of the mother and the individual itself. The expectation is taken over individuals with respect to all variables (in this case the traits and random effects). An element  $k$  of the vector of selection gradients ( $\boldsymbol{\beta}$ ) therefore represents the average effect on fitness of perturbing trait  $k$  whilst holding the other traits constant. Conditional on the fixed effects and random effects (including the fecundity residual), survival and fecundity are independent such that the expected absolute fitness of an individual is  $W_i = F_N(s_i)\exp(f_i)$ . Consequently, the  $k^{th}$  element of the selection gradient is given as:

$$\boldsymbol{\beta} = \frac{E\left[\exp(f)\left(f_N(s)b_k^{(J)} + F_N(s)b_k^{(F)}\right)\right]}{E[F_N(s)\exp(f)]} \quad (17)$$

where  $f_N$  is the probability density function of the Gaussian. The six dimensional integral required to obtain the expectation is not analytically tractable, and so we simply sample the variables from their distribution, evaluate the numerator and denominator in Equation 17 for each sample, and take their averages. If selection is weak, the distribution is

$$\begin{bmatrix} e^{(F)} \\ u^{(J)} \\ \mathbf{z}^{(I)} \\ \mathbf{z}^{(S)} \end{bmatrix} \sim N \left( \begin{bmatrix} 0 \\ 0 \\ \boldsymbol{\mu}_z \\ \boldsymbol{\mu}_z \end{bmatrix}, \begin{bmatrix} \text{VAR}(e^{(F)}) & \text{COV}(e^{(F)}, u^{(J)}) & 0 & 0 \\ \text{COV}(u^{(J)}, e^{(F)}) & \text{VAR}(u^{(F)}) & 0 & 0 \\ 0 & 0 & \mathbf{G} + \mathbf{E} & \frac{1}{2}\mathbf{G} \\ 0 & 0 & \frac{1}{2}\mathbf{G} & \mathbf{G} + \mathbf{E} \end{bmatrix} \right) \quad (18)$$

where  $\boldsymbol{\mu}_z$  is vector of trait means, and  $\mathbf{G}$  and  $\mathbf{E}$  are their genetic and environmental covariance matrices. Since the traits are not modelled (they just appear as fixed predictors of survival and/or fecundity)  $\boldsymbol{\mu}_z$ ,  $\mathbf{G}$  and  $\mathbf{E}$  are not estimated as part of the model. It would be possible to jointly model the distri-

bution of these traits (Thomson *et al.*, 2017) but an easier solution is to assume  
424 that the means and (co)variance structure of the four traits (individual and  
parental) are identical to those actually sampled (i.e. the empirical mean and  
426 covariance of the predictors  $z_1^{(I)}$ ,  $z_2^{(I)}$ ,  $z_1^{(S)}$  and  $z_2^{(S)}$ ). Such a strategy may also  
be more robust to strong selection, given it would measure the distribution of  
428 the parental traits post-selection, as required (Kirkpatrick & Lande, 1989). In  
short, we take a draw from Equation 18 and evaluate the two expressions in  
430 Equation 17 that lie within the square brackets. We repeat this 1000 times and  
then take the average of the evaluation for each expression to obtain the selec-  
432 tion gradient in Equation 17. This procedure can be repeated for each MCMC  
iteration to get a posterior distribution for the selection gradient. The code to  
434 simulate the data, fit the model and obtain the selection gradients can be found  
in the supplementary material.

436 It should be stressed that in this example we do not have the complete  
life-history for any individual; we have fecundity data from one generation and  
438 survival data from the following generation. We therefore have to assume that  
patterns of fecundity and survival selection are the same in the two generations.  
440 With more complete data then this assumption could be relaxed.

### *Results*

442 The results of the simulation are reported in Table 1. For all parameters, the  
mean of the posterior means were close to their true values with location terms  
444 generally differing by less than  $\pm 0.01$ . The mean of the posterior mean variances  
( $\text{VAR}(e^{(F)})$  and  $\text{VAR}(u^{(J)})$ ) were slightly higher than their true values, as would  
446 be expected given their skewed distributions, but the means of the posterior  
modes were closer ( $0.997 \pm 0.005$  for  $\text{VAR}(e^{(F)})$  and  $1.011 \pm 0.008$  for  $\text{VAR}(u^{(J)})$ ).  
448 The covariance between  $e^{(F)}$  and  $u^{(J)}$  was close to its true value. Coverage  
seemed reasonable: on average the lower 95% credible interval was above the  
450 true parameter value in 26.2/1000 cases and the upper 95% credible interval

was below the true parameter value in 25.7/1000 cases, roughly in-line with the  
452 expectation of 25/1000. Under this particular set of parameters the selection  
gradients are close to the sum of the two (survival and fecundity) regression  
454 coefficients ( $\beta_1^{(I)} = -0.199$ ,  $\beta_2^{(I)} = 0.298$ ,  $\beta_1^{(S)} = 0.397$  and  $\beta_2^{(S)} = 0$ ) although  
in general this won't be the case.

456 *Table 1 here*

## 458 **Discussion**

In many taxa, parents can affect the survival, and even fecundity, of their  
460 offspring. Because of this, phenotypic selection is often measured using the num-  
ber of recruits an individual leaves as a fitness measure (Clutton-Brock, 1988).  
462 This fitness measure, which we call a mixed fitness measure, is a combination of  
parental fecundity and offspring survival and is generally inappropriate for esti-  
464 mating phenotypic selection. Our conclusion is largely in agreement with Wolf  
& Wade (2001) although they suggest that when offspring survival is solely a  
466 function of parental traits (Grafen's (1988) 'independence of control') the mixed  
fitness approach can be appropriate. However, we show that this will only be  
468 true when the parental trait can be assumed to be sex-limited. Under this  
condition we do not need to separate the effect of the trait on the individual's  
470 own fecundity (non-social selection) from that on the individual's offspring's  
survival (social selection) because both components are weighted by a half; the  
472 first because the trait is only expressed in half the parents (Lande, 1982), and  
the second because parents are usually related to the offspring they care for by  
474 a half (Kirkpatrick & Lande, 1989). When the trait is not sex limited these  
components have to be weighted by one and half, respectively, and this cannot  
476 be done unless the social and non-social selection are estimated separately. In  
addition, Wolf & Wade (2001) assume that the trait is only expressed at the  
478 adult stage and so cannot directly affect the juvenile survival of the individual

itself. If this condition of ‘independence of control’ is not met, then the contri-  
480 bution of non-social selection acting via juvenile survival is undervalued by half  
the heritability, and the net selection gradient will be biased towards selection  
482 on fecundity.

At face value, the assumption that a trait is sex-limited and is only expressed  
484 at the adult stage seems reasonable; other than in birds, uniparental care is the  
norm, and by definition parental care is only expressed in adults. However,  
486 although the parental effect of a trait may only be manifest in adults of one  
sex, this does not imply that the trait itself needs to be sex-limited and only  
488 expressed at maturity (e.g. body-size; Bouteiller-Reuter & Perrin, 2005). For  
example, of the 19 bird studies in Kingsolver & Diamond (2011) that included  
490 selection via juvenile survival, 11 used a mixed fitness approach, 6 of which in-  
volved traits that were not sex-limited and 3 involved traits that were expressed  
492 at the juvenile stage. Only one study considered the implications of using the  
number of recruits as a fitness measure (Sheldon *et al.*, 2003) despite more than  
494 half using a fitness measure that was inappropriate for the traits studied.

Wolf & Wade (2001) also suggest that the direct fitness approach has its  
496 own shortcomings, and because of this the mixed fitness approach still has some  
utility. However, it is important to realise that the direct fitness approach  
498 analysed by Wolf & Wade (2001) is not the appropriate direct fitness approach  
for the problem at hand; only the trait value of the individual is used to predict  
500 fitness. Faced with the option of using a mixed fitness approach, or using a  
direct fitness approach that ignores the effect of parental traits on offspring  
502 fitness, it is only natural that many researchers advocate the former (Clutton-  
Brock, 1988; Moran & Clark, 2012). However the direct fitness approach used  
504 in the K-L model explicitly requires the trait values of both the individual  
and its mother be used as predictors of an individuals fitness (Kirkpatrick &  
506 Lande, 1989; Hadfield, 2012). Doing so is relatively straightforward, and here  
we suggest a simple statistical model that directly estimates the social and non-

508 social selection gradients separately, while accounting for the covariance between  
parental fecundity and offspring survival that is not accounted for by the traits  
510 that are the object of the selection analysis.

Throughout, we have presented the problem of mixed fitness in the con-  
512 text of studies that make assumptions about the action of a parental trait on  
offspring fitness. However, in some cases, mixed fitness may be used without  
514 the explicit assumption that the parental trait is directly affecting offspring fit-  
ness. For example, even when parents do not explicitly affect their offspring's  
516 fitness, a second argument sometimes given for using mixed fitness is that only  
offspring that survive to breed are able to contribute to the continuation of  
518 the focal individual's germ line. This logic has even been extended to suggest  
that grand-offspring, or more distant descendants, should be counted as fitness  
520 (Hunt *et al.*, 2004; Bolund & Lummaa, 2016). However, doing so will exacer-  
bate the problems we highlight because an individual's trait value will be ever  
522 more weakly correlated with those of their more distant descendants and so the  
force of selection will be underestimated. In addition, the fitnesses of relatives  
524 will be correlated, even in the absence of genetic variation, as they are calcu-  
lated from the same numbers, making the interpretation of inheritance difficult.  
526 Given these arguments we find mixed fitness approaches that include the sur-  
vival and fecundity of distant descendants even more hard to justify than the  
528 usual two-generational approach.

It has also been suggested that the use of mixed fitness measures in behav-  
530 ioral ecology stems from the fact that behavioral ecologists are more interested  
in optimality and adaptation than in predicting evolutionary dynamics (Wolf  
532 & Wade, 2001). While we agree that the focus of many behavioural ecologists  
is comparative statics, and that because of this they may be able to ignore the  
534 genetic basis of the traits they study (the Phenotypic gambit: Grafen, 1988),  
we disagree that this focus justifies the use of the mixed fitness approach. For  
536 example, evolutionary conflict over parental care traits (Trivers, 1974), due to

antagonistic effects on the fitness of both parents and their offspring (Williams,  
538 1966; Stearns, 1992), are a central topic in behavioral ecology (Davies *et al.*,  
2012). In this context the optimal trait value is a compromise between the cost  
540 it directly imposes on the parent and the indirect benefits it provides through  
increased offspring survival (Cheverud, 1984). The net selection gradient will  
542 be zero under these circumstances, yet the mixed fitness approach will only pro-  
vide evidence of this under the restrictive assumptions outlined above. More-  
544 over, even if these assumptions are met, the mixed fitness approach does not  
allow researchers to quantify the effect of a trait on each component of inclu-  
546 sive fitness. Consequently, when the net selection gradient is zero it would be  
impossible to determine whether a trait has important but opposing effects on  
548 the fitness of parents and their offspring, or simply has no effect on the fitness  
of either party. The direct fitness approach of the K-L model allows us to say  
550 whether the traits are optimal under a broader range of conditions, and also  
gives us some insight into why they are optimal.

552 Here we have shown that the common use of ‘mixed’ fitness approaches to  
measuring selection are likely to generate misleading results about the strength  
554 and direction of selection, and the evolutionary response to that selection. We  
acknowledge that, in reality, unless the number of offspring can be counted at  
556 the point of conception, all fecundity measures are likely to be a mixed fitness  
to some extent due to early mortality. Nevertheless, the extent to which fitness  
558 measures are mixed can be minimised (e.g. count of the number of offspring at  
birth rather than at the age of ten days). Thus, we suggest that the widespread  
560 use of mixed fitness approaches should be replaced by direct fitness approaches  
unless a valid case can be made that they work for the particular system under  
562 study.

## 564 **Acknowledgements**

566 We thank Jacob Moorad and Per Smiseth for useful discussions regarding  
this work, and Joel McGlothlin and two anonymous reviewers for their com-  
568 ments. CET was supported by EPSRC, The Clarendon Fund and Magdalen  
College and JDH by a Royal Society Fellowship.

570

### Data Accessibility

572

Data in this paper is available from Data Dryad doi:10.5061/dryad.k1r87.

574

### Author contributions

576

CET re-evaluated the selection measures shown in the empirical results; JDH  
578 simulated and developed the statistical analysis; CET and JDH developed the  
theory and wrote the paper.

580

## References

582 Andersson, M., Taylor, P.D. & Michalakis, Y. (2017) Helping relatives survive  
and reproduce: Inclusive fitness and reproductive value in brood parasitism.

584 *The American Naturalist*, **189**, 138–152.

Arnold, S.J. & Wade, M.J. (1984a) On the measurement of natural and sexual  
586 selection - applications. *Evolution*, **38**, 720–734.

Arnold, S.J. & Wade, M.J. (1984b) On the measurement of natural and sexual  
588 selection - theory. *Evolution*, **38**, 709–719.

Arnold, S. (1985) Quantitative genetic models of sexual selection. *Experientia*,  
590 **41**, 1296–1310.



- 592 Bolund, E. & Lummaa, V. (2016) The effects of resource availability and the  
demographic transition on the genetic correlation between number of children  
and grandchildren in humans. *Heredity*, **118**, 186–192.
- 594 Bouteiller-Reuter, C. & Perrin, N. (2005) Sex-specific selective pressures on  
body mass in the greater white-toothed shrew, *Crocidura russula*. *Journal of*  
596 *evolutionary biology*, **18**, 290–300.
- Charlesworth, B. (1994) *Evolution in age-structured populations*. Cambridge  
598 University Press Cambridge.
- Charmantier, A., Perrins, C., McCleery, R.H. & Sheldon, B.C. (2006) Evolu-  
600 tionary response to selection on clutch size in a long-term study of the mute  
swan. *The American Naturalist*, **167**, 453–465.
- 602 Cheverud, J.M. (1984) Evolution by kin selection - a quantitative genetic model  
illustrated by maternal performance in mice. *Evolution*, **38**, 766–777.
- 604 Cheverud, J. & Moore, A. (1994) Quantitative genetics and the role of the  
environment provided by relatives in behavioral evolution. C.R.B. Boake, ed.,  
606 *Quantitative Genetic Studies of Behavioral Evolution*, pp. 67–100. University  
of Chicago Press, Chicago and London.
- 608 Clutton-Brock, T.H., ed. (1988) *Reproductive success*. Univeristy of Chicago  
Press, Chicago.
- 610 Clutton-Brock, T.H. (1991) *The Evolution of Parental Care*. Princeton Univer-  
sity Press, Princeton, NJ.
- 612 Davies, N.B., Krebs, J.R. & West, S.A. (2012) *An introduction to behavioural*  
*ecology*. John Wiley & Sons.
- 614 Falconer, D.S. (1983) *Introduction to Quantitative genetics*. Longman Group.

- Goodnight, C.J., Schwartz, J.M. & Stevens, L. (1992) Contextual analysis of  
616 models of group selection, soft selection, hard selection, and the evolution of  
altruism. *American Naturalist*, **140**, 743–761.
- 618 Grafen, A. (1988) On the uses of data on lifetime reproductive success. T.H.  
Clutton-Brock, ed., *Reproductive success*, pp. 454–471. Univeristy of Chicago  
620 Press, Chicago.
- Grafen, A. (1982) How not to measure inclusive fitness. *Nature*, **298**, 425–426.
- 622 Hadfield, J.D. & Thomson, C.E. (2017) Interpreting selection when individuals  
interact. *Methods in Ecology & Evolution*, **submitted**.
- 624 Hadfield, J.D. (2010) MCMC methods for multi-response generalized linear  
mixed models: the MCMCglmm R package. *Journal of Statistical Software*,  
626 **33**, 1–22.
- Hadfield, J. (2012) The quantitative genetic theory of parental effects. N.J.  
628 Royle, P.T. Smiseth & M. Kölliker, eds., *The Evolution of Parental Care*, pp.  
267–284. Oxford University Press, Oxford, UK.
- 630 Heisler, I.L. & Damuth, J. (1987) A method for analyzing selection in hierar-  
chically structured populations. *American Naturalist*, **130**, 582–602.
- 632 Hill, W.G. (1974) Prediction and evaluation of response to selection with over-  
lapping generations. *Animal Production*, **18**, 1.
- 634 Hunt, J., Bussiere, L.F., Jennions, M.D. & Brooks, R. (2004) What is genetic  
quality? *Trends in Ecology & Evolution*, **19**, 329–333.
- 636 Kingsolver, J.G. & Diamond, S.E. (2011) Phenotypic selection in natural pop-  
ulations: What limits directional selection? *American Naturalist*, **177**, 346–  
638 357.

- Kingsolver, J.G., Hoekstra, H.E., Hoekstra, J.M., Berrigan, D., Vignieri, S.N.,  
640 Hill, C.E., Hoang, A., Gibert, P. & Beerli, P. (2001) The strength of phenotypic selection in natural populations. *American Naturalist*, **157**, 245–261.
- 642 Kirkpatrick, M. & Lande, R. (1989) The evolution of maternal characters. *Evolution*, **43**, 485–503.
- 644 Lande, R. (1979) Quantitative genetic analysis of multivariate evolution, applied to the brain:body size allometry. *Evolution*, **33**, 402–416.
- 646 Lande, R. (1982) Rapid origin of sexual isolation and character divergence in a cline. *Evolution*, **36**, 213–223.
- 648 Lande, R. & Arnold, S.J. (1983) The measurement of selection on correlated characters. *Evolution*, **37**, 1210–1226.
- 650 McAdam, A.G. & Boutin, S. (2003) Variation in viability selection among cohorts of juvenile red squirrels (*Tamiasciurus hudsonicus*). *Evolution*, **57**,  
652 1689–1697.
- Moran, E.V. & Clark, J.S. (2012) Causes and consequences of unequal seedling  
654 production in forest trees: a case study in red oaks. *Ecology*, **93**, 1082–1094.
- Mousseau, T.A. & Fox, C.W. (1998) The adaptive significance of maternal effects. *Trends in Ecology & Evolution*, **13**, 403–407.  
656
- Nunney, L. (1985) Group selection, altruism, and structured-deme models. *The*  
658 *American Naturalist*, **126**, 212–230.
- Pearson, K. (1900) Mathematical contributions to the theory of evolution. VII.  
660 on the correlation of characters not quantitatively measurable. *Philosophical Transactions of the Royal Society A*, **195**, 1–47.
- 662 Robertson, A. (1966) A mathematical model of culling process in dairy cattle. *Animal Production*, **8**, 95–108.

- 664 Royle, N.J., Smiseth, P.T. & Kölliker, M. (2012) *The evolution of parental care*.  
Oxford University Press.
- 666 Seamons, T.R., Bentzen, P. & Quinn, T.P. (2007) DNA parentage analysis  
reveals inter-annual variation in selection: results from 19 consecutive brood  
668 years in steelhead trout. *Evolutionary Ecology Research*, **9**, 409–431.
- Sheldon, B.C., Kruuk, L.E.B. & Merila, J. (2003) Natural selection and inher-  
670 itance of breeding time and clutch size in the collared flycatcher. *Evolution*,  
**57**, 406–420.
- 672 Siepielski, A.M., DiBattista, J.D. & Carlson, S.M. (2009) It’s about time: the  
temporal dynamics of phenotypic selection in the wild. *Ecology Letters*, **12**,  
674 1261–1276.
- Smiseth, P.T., Kölliker, M. & Royle, N.J. (2012) What is parental care? N.J.  
676 Royle, P.T. Smiseth & M. Kölliker, eds., *The Evolution of Parental Care*, pp.  
1–14. Oxford University Press, Oxford, UK.
- 678 Stearns, S. (1992) *The Evolution of Life Histories*. Oxford University Press,  
Oxford, UK.
- 680 Taylor, P., Wild, G. & Gardner, A. (2007) Direct fitness or inclusive fitness: how  
shall we model kin selection? *Journal of evolutionary biology*, **20**, 301–309.
- 682 Thomson, C.E., Bayer, F., Farrell, S., Crouch, M., Mittell, E.A., Heap, E. A.  
Zurita-Cassinello, M. & Hadfield, J.D. (2017) Selection on parental perfor-  
684 mance opposes selection for larger body size in a wild population of blue tits.  
*Evolution*, **71**, 716–732.
- 686 Trivers, R.L. (1974) Parent-offspring conflict. *American Zoologist*, **14**, 249–264.
- Willham, R.L. (1972) The role of maternal effects in animal breeding: III. Bio-  
688 metrical aspects of maternal effects in animals. *Journal of Animal Science*,  
**35**, 1288–1293.

690 Williams, G.C. (1966) Natural selection, the costs of reproduction, and a refine-  
ment of Lack's principle. *American Naturalist*, **100**, 687–690.

692 Wolf, J.B., Brodie, E.D. & Moore, A.J. (1999) Interacting phenotypes and the  
evolutionary process: II. Selection resulting from social interactions. *Ameri-  
694 can Naturalist*, **153**, 254–266.

Wolf, J.B. & Wade, M.J. (2001) On the assignment of fitness to parents and  
696 offspring: whose fitness is it and when does it matter? *Journal of Evolutionary  
Biology*, **14**, 347–356.

### 698 **Supporting Information**

700 *Simulation and analysis code* : R script for carrying out the simulation and  
analysis shown in the statistical solution section.

702

Parameter	True Value	Mean Estimate	<l-95%	>u-95%
$b_0^{(F)}$	1.00	$0.987 \pm 0.003$	22	30
$b_0^{(J)}$	0.00	$0.000 \pm 0.004$	22	25
$b_1^{(I:F)}$	-0.10	$-0.100 \pm 0.002$	32	27
$b_2^{(I:F)}$	0.00	$0.002 \pm 0.002$	40	22
$b_1^{(S:J)}$	0.40	$0.412 \pm 0.003$	31	27
$b_1^{(I:J)}$	-0.10	$-0.103 \pm 0.001$	21	20
$b_2^{(I:J)}$	0.30	$0.302 \pm 0.001$	31	22
$\text{VAR}(e^{(F)})$	1.00	$1.032 \pm 0.005$	22	32
$\text{VAR}(u^{(J)})$	1.00	$1.104 \pm 0.009$	18	30
$\text{COV}(e^{(F)}, u^{(J)})$	-0.25	$-0.264 \pm 0.005$	23	22

Table 1: Table of model parameters and their true values used in the simulations. The Mean Estimate is the mean of the posterior means followed by the standard error of the mean. <l-95% and >u-95% are the number of simulations in which the true value is less than the lower 95% credible interval or greater than the upper 95% credible interval, respectively. If the method has good coverage we expect this to be the case in 25 out of the 1000 simulations for each parameter.

	Amphibian	Angiosperm	Arachnid	Bird	Crustacean	Fish	Gymnosperm	Insect	Mammal	Reptile
$J^{(I,I)}$	0	18	0	164	0	110	0	8	33	24
		(4)		(3)		(10)		(2)	(3)	(8)
$A^{(I,I)}$	0	15	0	465	0	55	0	123	40	40
		(6)		(60)		(9)		(37)	(8)	(4)
$F^{(I,I)}$	19	458	0	17	14	0	0	326	0	6
	(7)	(137)		(9)	(4)			(61)		(6)
$F^{(I,I)}M^{(I,I)}+A^{(I,I)}$	0	0	0	0	0	0	0	6	0	0
								(3)		
$J^{(I,I)}+F^{(I,I)}M^{(I,I)}+A^{(I,I)}$	0	0	0	0	0	0	0	20	0	0
								(5)		
$J^{(I,S)}$	0	0	0	32	0	0	12	6	26	10
				(11)			(6)	(1)	(2)	(5)
$F^{(S,S)}+J^{(I,S)}$	0	12	2	429	0	0	0	0	24	12
		(6)	(2)	(32)					(6)	(6)
$F^{(S,S)}M^{(S,S)}+A^{(S,S)}+J^{(I,S)}$	0	0	0	2	0	64	0	0	6	0
				(2)		(4)			(1)	

Table 2: The number of linear selection gradients reported in Kingsolver & Diamond (2011) for each taxonomic group (columns) and fitness measure (rows). The number in brackets is the number of trait/species combinations, such that a study that reports multiple gradients for a trait over time is only counted once. F is fecundity measured as the number of zygotes, M is mating success, A is adult survival, and J is juvenile survival. Superscripts indicate the individual upon whom the fitness and trait have been measured - where the first superscript indicates the fitness and the second the trait. Thus (I,I) indicates the trait and fitness were measured upon the same individual in a direct approach, and (S,S) in the mixed fitness approach, and (I,S) indicates that the fitness and trait were measured in different individuals (the offspring and parent, respectively).

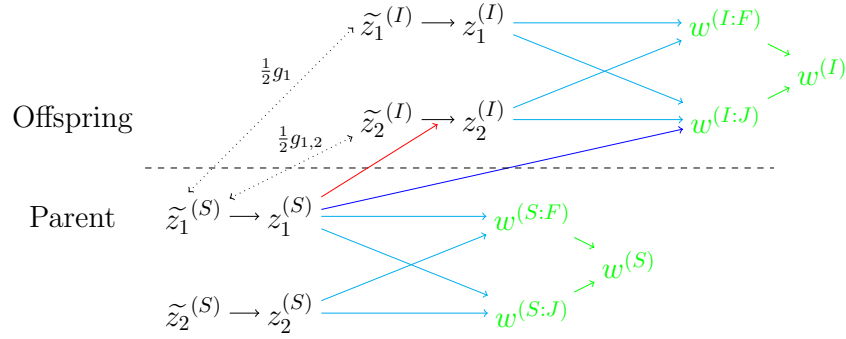


Figure 1: Schematic of the most complex causal model analysed. As in Hadfield & Thomson (2017) we denote the traits prior to the action of maternal effects as  $\tilde{z}_2^{(I)} = a_2^{(I)} + e_2^{(I)}$  and the traits after the action of maternal effects as  $z_2^{(I)} = \tilde{z}_2^{(I)} + \psi_{2,1}z_1^{(S)}$ , where  $a$  and  $e$  are breeding value and environmental value respectively. The red arrow represents the maternal effect of trait 1 on trait 2 and has coefficient  $\psi_{2,1}$ . Light blue arrows represent non-social selection, and the dark blue arrow represents social selection (on trait 1). The dashed double-headed arrows represent the covariances between the  $\tilde{z}$ 's measured in parents and offspring, and are a direct function of the genetic (co)variances. It should be noted that in the presence of maternal effects, the covariance between the  $z$ 's are not equal to the covariance between the  $\tilde{z}$ 's.



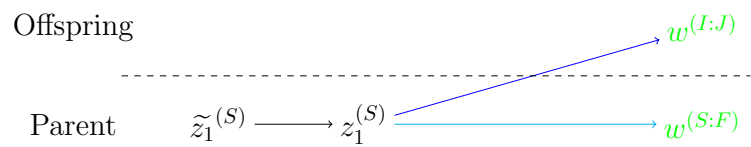


Figure 2: Schematic of the causal model that motivates the use of mixed fitness approach (Equation 9); only trait 1 is considered, which has a direct effect on the fitness of both the parent (S) and the offspring (I) when expressed in the parent. The dark blue arrow represents social selection and the light blue arrow represents non-social selection.

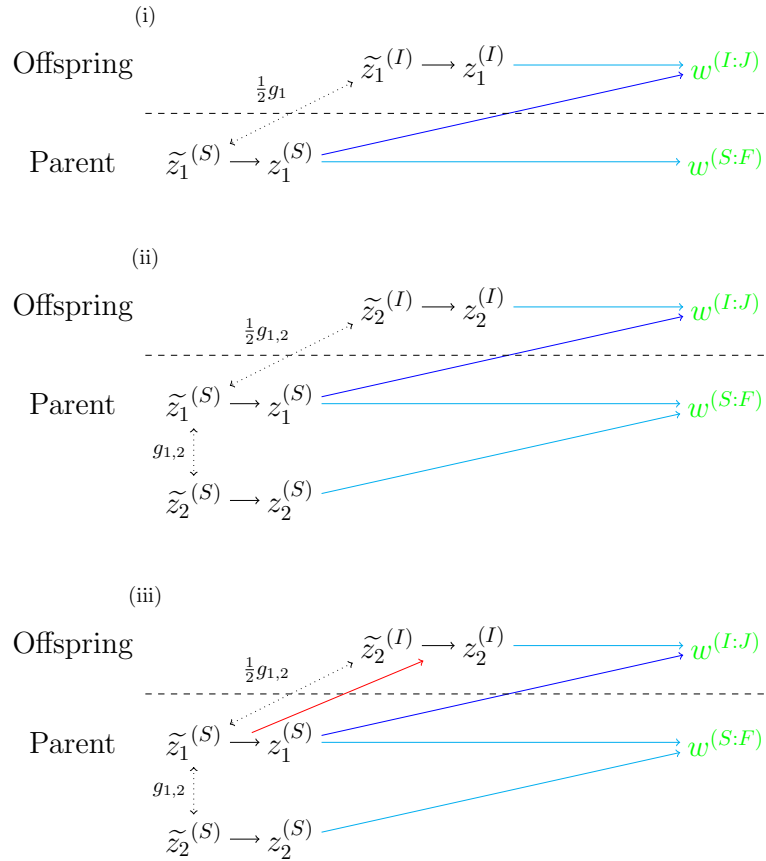


Figure 3: Schematic of the what is measured using a mixed fitness approach when the causal model that motivates its use is not true. (i) the case where trait  $z_1$  affects both the juvenile survival and fecundity of the bearer, and can have a social effect on the juvenile survival of the bearer's offspring (dark blue arrow). (ii) where a second trait ( $z_2$ ) affects the juvenile survival and fecundity of the bearer and is genetically correlated with  $z_1$ . (iii) where a second trait ( $z_2$ ) affects the juvenile survival and fecundity of the bearer and is maternally affected by  $z_1$ .