

Sex-specific demography and generalization of the Trivers–Willard theory

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The Trivers–Willard theory¹ proposes that the sex ratio of offspring should vary with maternal condition when it has sex-specific influences on offspring fitness. In particular, mothers in good condition in polygynous and dimorphic species are predicted to produce an excess of sons, whereas mothers in poor condition should do the opposite. Despite the elegance of the theory, support for it has been limited^{2,3}. Here we extend and generalize the Trivers–Willard theory to explain the disparity between predictions and observations of offspring sex ratio. In polygynous species, males typically have higher mortality rates⁴, different age-specific reproductive schedules and more risk-prone life history tactics than females; however, these differences are not currently incorporated into the Trivers–Willard theory. Using two-sex models parameterized with data from free-living mammal populations with contrasting levels of sex differences in demography, we demonstrate how sex differences in life history traits over the entire lifespan can lead to a wide range of sex allocation tactics, and show that correlations between maternal condition and offspring sex ratio alone are insufficient to conclude that mothers adaptively adjust offspring sex ratio.

Trivers and Willard¹ proposed that when the fitness benefit to a mother of producing sons increases faster with her own condition than the benefit of producing a daughter, good-condition mothers should produce more male than female offspring. Trivers and Willard hypothesized that these fitness benefits should be observed when (1) maternal condition determines offspring condition, (2) the condition of offspring at independence correlates with condition at adulthood, (3) good-condition males produce more offspring than poor-condition ones, and (4) there is greater variation in lifetime reproductive success among males than females^{1,2}. The original theory focused on monogamous species with non-overlapping generations, but has been extended to polygynous populations⁵, and to overlapping generations⁶. The theory has been investigated in a wide range of birds⁷ and mammal³ species, including humans⁸, but has received mixed support^{2,9}, with many species expected to adhere to Trivers and Willard's predictions often failing to do so^{2,9}. The discrepancy between theoretical predictions and empirical observations has led to much debate, with explanations falling into three broad categories: first, it may be physiologically impossible for a female to determine the sex of her offspring⁵; second, tests of the theory are often inadequate as systems have not been shown to conform to the assumptions of the theory^{9,10}; and third, data quality is poor³. The consensus seems to be that adaptive sex ratio production of offspring often does not occur when expected^{2,3}. Modelling work has been performed to examine why this is the case. In a notable article, Leimar¹¹ demonstrated that appropriate tests of the Trivers–Willard theory¹ require a comparison of the reproductive values (RV) of sons and daughters rather than a comparison of lifetime reproductive success, as reproductive value is the appropriate measure of fitness¹¹. The lifetime reproductive success of an individual

measures the number of offspring produced over its lifetime, whereas RV describes the fraction of a future population that has descended from it¹². Leimar¹¹ went on to show that if maternal condition influences the RV of offspring in one sex more than in the other, then life histories in which good-condition mothers produce an excess of daughters could be adaptive. However, to our knowledge, no one has calculated the RV of females and males for naturally occurring systems. Leimar's model¹¹ consequently remains an elegant, but abstract, demonstration of theoretical scenarios where species, which otherwise conform to Trivers and Willard's assumptions, do not follow the predicted sex allocation tactic. Here we extend and generalize the insights of Leimar¹¹ and demonstrate that, contrary to Fisher's theory of parental investment¹³, sex differences in life history at both pre- and post-independence determine optimal offspring sex ratio as a function of maternal condition, and apply this new approach to two empirical data sets.

Where adaptive sex ratio variation has been expected, for instance in polygynous and sexually dimorphic species, males often have higher mortality rates than females at all stages of life^{4,14} as a consequence of their more risk-prone life history tactic which, in many species, involves reproducing at a later age and fighting more with conspecifics than females^{15,16}. Fisher's theory¹³ of sex allocation predicts higher investment in the rarer sex, or the sex experiencing higher mortality during the period of dependency, such that the sex ratio at independence is unity. However, this conclusion holds at the population level only under the assumption that all same-sex individuals have equal chances of reproducing. Trivers and Willard¹ refined Fisher's theory¹³ by demonstrating that, for a given individual, it might be optimal to invest more into the sex with higher fitness benefits if these vary with maternal condition. Remarkably, Trivers and Willard did not explicitly list sex differences in mortality or growth between independence and adulthood, or age differences in reproductive output as an adult, when identifying conditions in which their predictions should be observed. Sex differences in demographic rates have never been incorporated into models predicting the RV of female and male offspring of mothers in varying conditions^{6,11,17}. Although Fisher¹³ stated that the period after offspring independence should not influence the optimal sex ratio, the RV factors in information on mortality and reproductive rates at all ages. This means that when examining the relative RV of sons and daughters to a mother of a given condition, it is necessary to consider offspring mortality rates both pre- and post-independence, and reproductive rates at all ages.

Estimating RV from two-sex models is challenging as standard approaches to estimate RV for one-sex models do not easily extend to two sexes. Therefore, we first developed an approach to calculate RV for realistic two-sex models (see Methods). Next, we incorporated sex-specific mortality and other sex-specific life history traits into two-sex integral projection models¹⁸ (IPMs) and explored how the RV of male and female offspring born to mothers of a given condition vary as the

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level of sex differences in a life history trait is altered (see Methods). Specifically, we took a published model for Columbian ground squirrels (*Urocitellus columbianus*)¹⁸, a system where we neither expect nor observe females skewing offspring sex ratio as a function of body weight¹⁹, and examined under what circumstances we could generate optimal offspring sex ratios varying with maternal weight. We next adapted a published two-sex IPM for bighorn sheep (*Ovis canadensis*)²⁰, a species where adaptive sex ratio variation is expected but empirical evidence is inconclusive^{21–23}, and predicted optimal offspring sex allocation.

Using an IPM to explore adaptive sex ratio variation allowed us to alter a range of demographic rates in ways that are not possible in naturally occurring systems. For instance, we altered the strength of size selection in a mating system, differential male and female mortality schedules, assumptions about correlations between weight at independence and at maturity, and between parental and offspring weight. We calculated the expected RV of male and female offspring born to mothers of a given weight (a surrogate for condition widely used in empirical tests of the Trivers–Willard theory^{2,3,7,19,21,24,25}; see Methods). We then calculated the difference between the RV of male and female offspring at each maternal weight and the slope of this difference in relation to maternal weight (Fig. 1; Methods). A positive slope represents support for the prediction of Trivers and Willard¹ that large mothers should produce an excess of sons and small mothers an excess of daughters; we call this a ‘Trivers–Willard effect’ (Fig. 1a). A negative slope represents a reverse sex allocation tactic that we call a ‘reversed Trivers–Willard effect’ because large females gain a fitness advantage by producing daughters rather than sons (Fig. 1d). A slope not differing from zero indicates that offspring of both sexes provide equivalent fitness benefits to all mothers. We also identified two further sex allocation tactics in which the difference between male and female RV is u-shaped or n-shaped. In the first of these tactics (a ‘Trivers–Willard effect type 3’), mothers in poor or exceptional condition should produce sons, while all others should produce daughters (Fig. 1e). Likewise, we called the tactic in which only the lightest and heaviest mothers should produce daughters the ‘Trivers–Willard effect type 4’ (Fig. 1f). Next, we altered parameters in the model that determine the level of sex differences in life history traits and recalculated the slope. The difference between the slopes from the perturbed and the unperturbed model represents the sensitivity of adaptive sex ratio variation to altering aspects of the survival, fertility, growth, inheritance and mating functions that constitute the IPM. A positive value in the difference between the slopes implies an increase in the strength of the Trivers–Willard effect (Fig. 1b). A negative slope difference suggests a decrease in the strength of the Trivers–Willard effect (Fig. 1c), leading to a possible reversal of the prediction if the difference is sufficiently negative (Fig. 1d). A parameter change can also cause the difference between male and female RV to be u-shaped or n-shaped (Fig. 1e, f), which might apply to systems with two alternative reproductive morphs (‘sneakers’ and ‘fighters’). Our framework allowed us to assess how changing the level of sex differences in life history tactics, and consequently the level of sex differences in demographic rates, affects the direction of selection on sex ratio variation for a given maternal condition.

For this, we used a recently published two-sex IPM of Columbian ground squirrels¹⁸—a species that is polytocous²⁶, polygynandrous²⁷, and has greater variance in reproductive success among males than females²⁶. Differences in male and female mortality schedules are less pronounced than in most species where Trivers–Willard effects are expected²⁸. We therefore treated their demographic rates as identical (Supplementary Table 1). We predicted a small reversed Trivers–Willard effect: a small deviation from a sex ratio of unity as maternal weight increases (Fig. 2; solid black line). The difference in RV is small because we assumed identical survival and growth rates for females and males. The reason a reverse Trivers–Willard effect occurs is that, although males and females have identical growth and survival rates in our model, males need to reach a greater age before achieving good

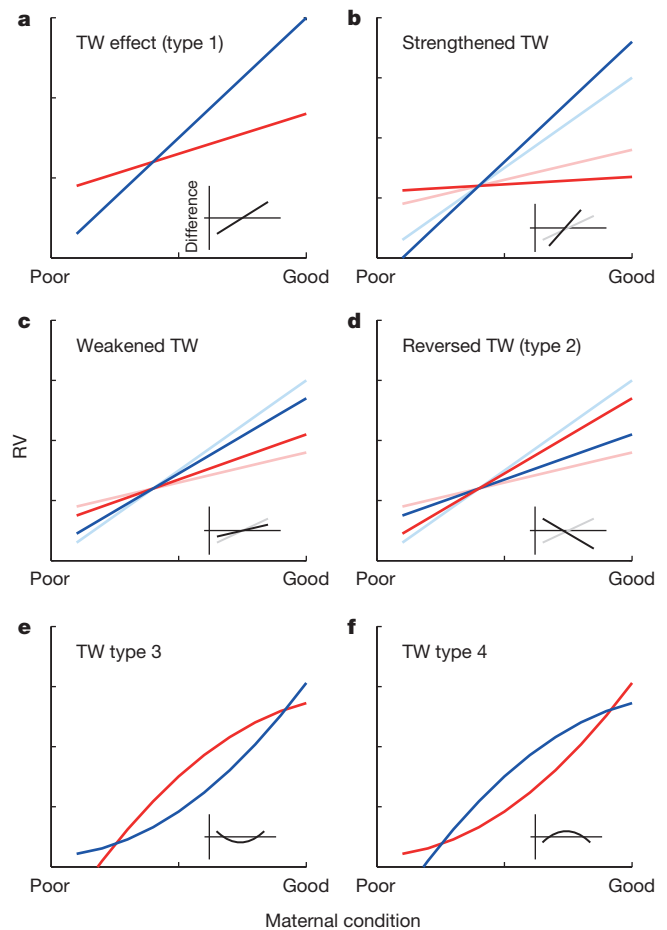


Figure 1 | Female reproductive value (RV, red line) and male RV (blue) depend on maternal condition. Differences between male and female RV are shown as insets (black and grey lines). **a**, Trivers–Willard (TW) effect: for good-condition mothers, sons have higher RV than daughters. For poor-condition mothers, daughters have higher RV than sons. **b–d**, Changes in demographic parameters can result in a more pronounced Trivers–Willard effect (**b**), a smaller difference between female and male RV (**c**), or a reversal of a Trivers–Willard effect (**d**). Original RV and difference in RV before demographic rates have been changed are shown in light red (females), light blue (males) and grey (difference in RV in insets) in **b–d**. **e, f**, The difference between male and female RV can be u-shaped (type 3 Trivers–Willard effect) (**e**), or n-shaped (type 4 Trivers–Willard effect) (**f**).

chances of reproductive success compared to females because male mating success is size-selective. Large females maximize their RV, when litter size is fixed, by producing females that breed at a younger age instead of producing males. We can see this by altering the mean age of reproduction among females; as this increases, the reversed Trivers–Willard effect is reduced until it eventually disappears completely (Extended Data Fig. 1a, b).

When we increased mortality of pre-reproductive males (that is, squirrels below an estimated size threshold of 279 g) to be 3% greater than female mortality, we predict that the reversed effect is replaced with a Trivers–Willard effect (Fig. 2; dotted line). As male mortality increases, fewer males make it to reproductive age, but those that do (that is, those born to larger mothers) have increased reproductive success. Mothers that can produce large males with a reasonable chance of growing to reproductive age can gain substantial RV because males are rare, even though males may have to wait longer to achieve reproductive success. In other words, as we alter differential mortality between the sexes and the variance in reproductive success amongst males, we alter the optimal tactic that mothers of a given body size should follow (Extended Data Fig. 2, solid line; see Extended Data Fig. 3 for a trade-off between mortality and mating chances).

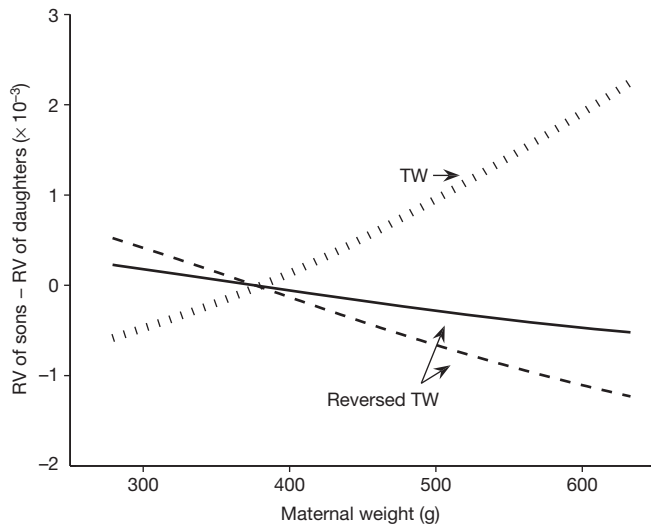


Figure 2 | Reproductive value differs with maternal condition and offspring sex in Columbian ground squirrels. The graph shows RV of sons minus RV of daughters when male mating success increases with body weight. Solid line, females and males have the same mortality rate; dotted line, survival rates of pre-breeding males (weight below 279 g) are 3% lower than female survival rates; dashed line, increased size selection in male mating success (parameter ρ raised from 0.1 to 0.25, see Supplementary Table 1). We scaled the RV of females and males such that the female RV of the smallest reproductive size class is 1.

However, these results are context-dependent. In our initial model, the population growth rate was greater than one and the population increased in size with time. If we increased female mortality such that the population growth rate fell below one, the advantage of reproducing early disappeared, and females could gain reproductive value by producing males that mate at a later age compared to females.

These results show that because RV is a complex function of condition-dependent mortality and reproductive rates, and these rates generate a growing or shrinking population, the optimal sex allocation tactic can change over a relatively small range of parameter values. Despite this, it is valuable to analyse our baseline model parameterized for squirrels. As parameter values are altered, we find that those parameters generating a differential between male and female mortality (survival function), and those that influence the correlation between weight at independence and weight at adulthood (the growth function) strongly influence the expected bias in offspring sex ratio for a given maternal condition (Extended Data Figs 4 and 5). In contrast, altering age-independent female reproductive success (fecundity function) and the correlation between mean parental weight at time t and offspring mass when they recruit to the population at $t + 1$ (the inheritance function) have relatively small effects on the direction or magnitude of the Trivers–Willard effect (Extended Data Figs 4 and 5). However, the results are surprisingly nuanced. We find that increasing male mortality at all ages on the logit-scale by reducing the survival intercept generates a type 3 Trivers–Willard effect. In contrast, if we reduce the body-mass survival slope for males such that larger males have rates of mortality that are elevated to a greater extent than those that are smaller, we weaken the strength of the reversed Trivers–Willard effect. Despite this complexity, we identified a general pattern that holds for the first two types of sex allocation tactics (Trivers–Willard effect and reversed Trivers–Willard effect): if a perturbation to a parameter increases the variance in male RV at birth relative to the variance in female RV at birth, the strength of the predicted Trivers–Willard effect increases, and vice versa (Extended Data Fig. 5). This pattern holds for the bighorn sheep model.

Bighorn sheep are a monotonous, polygynous species with strong sexual size-dimorphism, and are expected to exhibit a Trivers–Willard

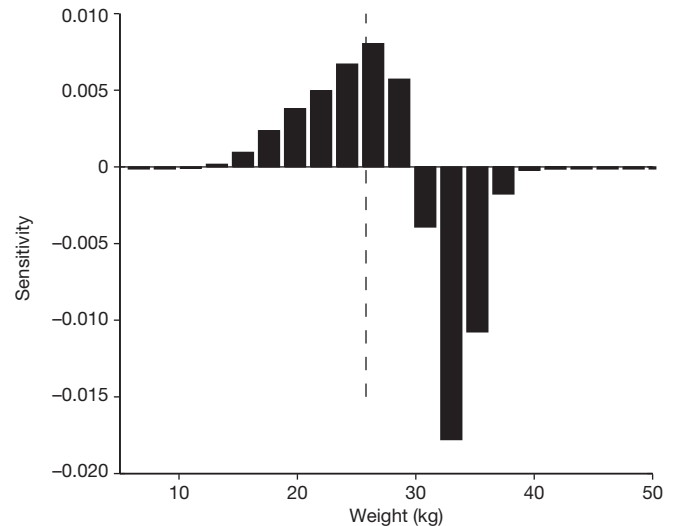


Figure 3 | Size-specific sensitivity of the Trivers–Willard effect to a 1% increase in male mortality in bighorn sheep lambs. The probability of mortality has been independently increased by 1% in each size class and the change of the slope of the Trivers–Willard effect plotted. The vertical dashed line denotes mean male lamb weight. Increasing mortality for male lambs below average weight strengthens the Trivers–Willard effect (bars are above zero), whereas increasing mortality for male lambs of above average weight weakens the Trivers–Willard effect (bars are predominantly below zero). Size-specific sensitivities of all stages (lamb, yearling, adult, and senescent) are provided in Extended Data Fig. 8. The y-axis plots $\partial \Delta v_a / \partial s_i \times s_i \varepsilon$, where $\partial \Delta v_a / \partial s_i$ is the sensitivity of difference between male and female reproductive value (Δv_a) to a perturbation in parameter s_i by ε (see Methods). The index a denotes age, shown here at birth (that is, $a = 0$); i denotes the parameter, running from 1–69 for the bighorn sheep model.

effect; empirically, however, they do not^{21,22}. In contrast to Columbian ground squirrels, female and male mortality schedules differ markedly throughout life¹⁴. We used a two-sex IPM including age structure²⁰ (see parameters in Supplementary Tables 2 and 3) because demographic rates depend on both weight and age in bighorn sheep²⁹. For this species, our model predicts a Trivers–Willard effect (Extended Data Fig. 6). The overall size of the Trivers–Willard effect in sheep is larger than for squirrels because there are marked sex differences in life history at all ages. However, as with squirrels, sex differences in mortality rates before age at first breeding had the same effects on the predicted Trivers–Willard effect: increasing mortality rates of male lambs and yearlings increased the strength of the Trivers–Willard effect, and increasing male mortality and male growth rates had the largest effects on the sex allocation tactic (Extended Data Fig. 7). In addition, within each life stage, increasing mortality rates of small males increased the strength of the Trivers–Willard effect, whereas increasing mortality of large rams had the opposite effect (Fig. 3 and Extended Data Fig. 8). This reveals that sex differences in size-specific mortality can trade-off against one another at different ages to influence the optimal behaviour of a mother of a given size. In spite of the similarities between squirrels and sheep, there are also differences. In sheep, parameters of the inheritance functions (which determine the correlation between parental and offspring size) also influence the magnitude of the effect (Extended Data Fig. 7). Taken together, these results reveal two things: first, there is a need to consider the entire life history when assessing whether a mother in a specific condition should produce male or female offspring; and second, sex differences in life history traits, especially before the age at first breeding and often beyond the age of dependency, can affect the RV of male and female offspring of a mother in a given condition.

Our results show that in order to conclude that females are behaving adaptively from a regression of maternal condition against offspring sex ratio, it is necessary to show (1) that offspring sex ratio is equivalent

to the ratio of male to female RV at birth, and (2) that the slope or shape of the association between maternal condition and difference in the RV of sons and daughters (Fig. 1) is of the same sign or form as the slope or shape of the regression of maternal condition against birth sex ratio. Offspring sex ratio alone may not be a good predictor of whether females are behaving adaptively because it does not necessarily strongly correlate with the relative RV of sons and daughters. This is because the RV is a complex function of age- and condition-specific survival, fertility, development trajectories and phenotypic inheritance. The calculation of RV for females and males is challenging and we have been unable to identify shortcuts to its calculation. Without this, it will be necessary to construct two-sex models of the population dynamics of species of interest and calculate the RV of sons and daughters born to mothers in different conditions. We are hopeful that application of our approach to multiple systems will reveal a shortcut to RV calculation. Until that time, we cannot conclude that females are, or are not, behaving adaptively by correlating offspring sex ratio with maternal condition alone.

We have extended Trivers and Willard's original theory¹ to incorporate differential demographic rates between the sexes. We show that currently the only way to examine how sex differences in mortality in a specific system influence optimal sex allocation tactic as a function of maternal condition is to calculate the RV for male and female offspring born to mothers in different conditions, and we have provided a method for doing so. As further research utilizing data to construct two-sex IPMs for different systems is carried out, we expect to gain a better understanding of the frequency with which females adaptively adjust the sex ratio of their offspring. As it is currently difficult to interpret the vast empirical literature testing this theory, calculating the RV of males and females born to mothers in different conditions for many systems will reveal whether Trivers and Willard's important insight that mothers should manipulate the sex ratio of their offspring to maximise their fitness is supported or not. However, the context-dependent nature of relative RV of sons and daughters to a mother suggests that an appropriate empirical test of the Trivers–Willard theory would be to observe mothers altering their sex allocation tactic across a range of conditions that affect the optimal sex allocation tactic.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Supplementary Information is available in the online version of the paper.

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Author Contributions S.S., J.M.G. and T.C. conceived and designed the study. S.S. developed the models and, with S.T., derived the formulas. S.S. and T.C. wrote the manuscript. S.S., A.G. and S.T. contributed to the mathematical formulation of the model. P.N. collated data on Columbian ground squirrels. L.T. parameterized data for bighorn sheep. T.C. parameterized data for squirrels. All authors edited the manuscript.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to S.S. (Susanne.Schindler@zoo.ox.ac.uk).

METHODS

Data reporting. No statistical methods were used to predetermine sample size.

Summary. We use deterministic two-sex integral projection models (IPMs), that is, stochastic effects are excluded, because demographic rates of males and females typically fluctuate together with the environment. To calculate the RV for two sexes in an age- and size-structured population model we construct a sex-, age-, and size-structured generation/cohort projection matrix. The left eigenvector of this generation matrix gives the RV at birth for females and males, $v^{\circ}(s_0)$ and $v^{\sigma}(s_0)$, as a function of birth weight s_0 . Maternal body weight is a cue for maternal condition because it strongly affects survival^{30,31} and breeding success^{32,33}. We therefore weight the RV with the offspring distribution conditioned on maternal weight and age to obtain the RV of daughters (d) and sons (s) to a mother of weight s_f and age a , $v_a^d(s_f)$ and $v_a^s(s_f)$. The difference between the RV of male and female offspring is $\Delta v_a(s_f) = v_a^s(s_f) - v_a^d(s_f)$; it is a function of maternal weight and age, and if $\Delta v_a(s_f)$ is nearly linear then the slope determines whether there is a Trivers–Willard effect (type 1, positive slope) or a reversed Trivers–Willard effect (type 2, negative slope). In some instances, the association is nonlinear, leading us to identify type-3 and -4 Trivers–Willard effects (see main text).

The Model. The integral projection model uses four functions: first, the age-specific survival (superscript s) probability $p_a^s(s)$ as a function of weight s ; second, the age-specific probability distribution $p_a^g(s_2|s_1)$ of weight at next time-step s_2 as a function of current weight s_1 conditioned on survival (superscript g, growth); third, the offspring number $R_a(s)$ as a function of maternal age a and weight s ; and fourth, the offspring weight distribution $f(s|s_f, s_m)$ as a function of maternal, s_f and paternal weight s_m at conception. Mating behaviour is described by the set of mating probabilities between every parental weight and age combination $m(a_f, s_f; a_m, s_m)$. We use models applied to Columbian ground squirrels¹⁸ and big-horn sheep²⁰. For both species, we assume that male mating probability increases with male body weight; we assume, in contrast, that female mating probability is independent of body weight once it is above a size (squirrels) or age (sheep) threshold. For sheep, we assume that male mating probability is zero for rams below 80 kg and then increases linearly with the weight of the ram. The population level offspring sex ratio at birth is unity in both models (although the observed sex ratio in the squirrel population is extremely flexible). The IPM projects a population structured along a continuous trait (here, body weight) from one time-step to the next. There are no stochastic or density effects, and the numerical iteration of the projection converges quickly. Model outputs are the population growth rate λ and asymptotic age- and weight-distribution of the female and male components of the population, $n^{\circ}(a, s)$ and $n^{\sigma}(a, s)$.

Construction of a cohort projection matrix. Age-structured models readily generalize to age- and stage-structured models³⁴. We use the asymptotic population distributions, $n^{\circ}(a, s)$ and $n^{\sigma}(a, s)$, to calculate the age- and size-specific fertility functions ($M_a^{\circ}(s)$ and $M_a^{\sigma}(s)$), the age- and size-specific inheritance functions ($D_a^{\circ}(s_0|s)$ and $D_a^{\sigma}(s_0|s)$), and the age- and birth-size-specific survivorship functions ($L_a^{\circ}(s, s_0)$ and $L_a^{\sigma}(s, s_0)$). The exact calculation of $M_a^{\circ}(s)$, $M_a^{\sigma}(s)$, $D_a^{\circ}(s_0|s)$, $D_a^{\sigma}(s_0|s)$, $L_a^{\circ}(s, s_0)$, and $L_a^{\sigma}(s, s_0)$ is given in detail below. Here we provide definitions of these terms and outline how we use them to construct a generation projection matrix.

The total number of offspring (both sexes) produced by a female (or male) of age a and weight s is $M_a^{\circ}(s)$ (and $M_a^{\sigma}(s)$ for males). The fraction of these offspring that start life with birth weight s_0 is given by $D_a^{\circ}(s_0|s)$ (and $D_a^{\sigma}(s_0|s)$ for males). Among the $M_a^{\circ}(s)$ offspring that a mother produces are $M_a^{\circ\circ}(s)$ daughters and $M_a^{\circ\sigma}(s)$ sons. Similarly, the daughters ($M_a^{\sigma\circ}(s)$) and sons ($M_a^{\sigma\sigma}(s)$) of a father sum to $M_a^{\sigma}(s)$. We assume that mothers and fathers produce sons and daughters at an even ratio, therefore $M_a^{\circ\circ}(s) = M_a^{\circ\sigma}(s) = \frac{1}{2}M_a^{\circ}(s)$ and $M_a^{\sigma\circ}(s) = M_a^{\sigma\sigma}(s) = \frac{1}{2}M_a^{\sigma}(s)$. The probability that a newborn male (or female) of age 1 and birth weight s_0 is alive with weight s at age a is $L_a^{\sigma}(s, s_0)$ (and $L_a^{\circ}(s, s_0)$ for females).

We assume that the inheritance of body weight is independent of offspring sex, that is, $D_a^{\circ\circ}(s_0|s) = D_a^{\circ\sigma}(s_0|s) = D_a^{\sigma\circ}(s_0|s)$ and $D_a^{\sigma\sigma}(s_0|s) = D_a^{\circ\sigma}(s_0|s) = D_a^{\sigma\circ}(s_0|s)$. With $r = \ln \lambda$, the stable population growth rate, we define the operators:

$$A_r^{\circ\circ}(s_1, s_0) = \sum_a \int e^{-ra} \frac{1}{2} D_a^{\circ}(s_1|s) M_a^{\circ\circ}(s) L_a^{\circ}(s, s_0) ds \quad (1)$$

$$A_r^{\circ\sigma}(s_1, s_0) = \sum_a \int e^{-ra} \frac{1}{2} D_a^{\circ}(s_1|s) M_a^{\circ\sigma}(s) L_a^{\circ}(s, s_0) ds \quad (2)$$

$$A_r^{\sigma\circ}(s_1, s_0) = \sum_a \int e^{-ra} \frac{1}{2} D_a^{\sigma}(s_1|s) M_a^{\sigma\circ}(s) L_a^{\sigma}(s, s_0) ds \quad (3)$$

$$A_r^{\sigma\sigma}(s_1, s_0) = \sum_a \int e^{-ra} \frac{1}{2} D_a^{\sigma}(s_1|s) M_a^{\sigma\sigma}(s) L_a^{\sigma}(s, s_0) ds \quad (4)$$

where $A_r^{\circ\circ}(s_1, s_0)$, for example, gives the fraction of male progenies with birth weight s_1 that are produced by a female of birth weight s_0 during the course of her life. We construct the generation/cohort projection matrix A :

$$A = \begin{pmatrix} A_r^{\circ\circ} & A_r^{\circ\sigma} \\ A_r^{\sigma\circ} & A_r^{\sigma\sigma} \end{pmatrix} \quad (5)$$

which projects one cohort to the next. Let $u^{\circ}(s_0)$ be the female newborn distribution and $u^{\sigma}(s_0)$ the male newborn distribution. Matrix A maps the cohort distribution of newborns of generation t to the offspring distribution produced by this cohort in generation $t + 1$. That is for a population with growth rate r :

$$\begin{pmatrix} u_{t+1}^{\circ} \\ u_{t+1}^{\sigma} \end{pmatrix} = A \begin{pmatrix} u_t^{\circ} \\ u_t^{\sigma} \end{pmatrix} \quad (6)$$

Matrix A has a dominant eigenvalue of unity, a right eigenvector that gives the stable newborn distribution, that is, $(u^{\circ}, u^{\sigma})^T$, and a left eigenvector that gives the RV, that is, (v°, v^{σ}) , of newborns of each size and sex.

Calculation of RV as a function of maternal weight. We are interested in optimal sex allocation, an optimization task conducted by mothers. Males can influence primary sex ratio, for instance, by transmitting an unequal share of male or female gametes³⁵, but the female is in principle able to render her partner’s preference of offspring sex ineffective. She can do so by cryptic gamete choice or, if females are the heterogametic sex, by producing more gametes of one sex than the other.

We use the left eigenvector of matrix A which gives the female and male RV for each birth weight, $v^{\circ}(s_0)$ and $v^{\sigma}(s_0)$, and weight it with the offspring distribution of a mother of age a and weight s , $D_a^{\circ}(s_0|s)$:

$$v_a^s(s_f) = \int v^{\sigma}(s_0) D_a^{\sigma}(s_0|s_f) ds_0 \quad \text{and} \quad v_a^d(s_f) = \int v^{\circ}(s_0) D_a^{\circ}(s_0|s_f) ds_0 \quad (7)$$

to obtain the RV of a son and a daughter as a function of maternal weight.

Trivers–Willard effect, reversed Trivers–Willard effect, and other sex allocation tactics. We study the difference between male and female RV as a function of maternal weight: $\Delta v_a(s_f) = v_a^s(s_f) - v_a^d(s_f)$, where s_f is maternal weight. If $\Delta v_a(s)$ is approximately linear then the sign of the approximate slope of $\Delta v_a(s)$ determines whether the species is predicted to show a Trivers–Willard effect or a reversed Trivers–Willard effect. Positive slope, that is, female RV exceeds male RV at low maternal body weight and male RV exceeds female RV at high maternal body weight, means there is a Trivers–Willard effect (Fig. 1a). A negative slope of $\Delta v_a(s)$ implies a reversed Trivers–Willard effect (Fig. 1d):

$$\Delta v_a(s_{\max}) - \Delta v_a(s_{\min}) \begin{cases} > 0 & \text{Trivers – Willard effect (type 1),} \\ < 0 & \text{reversed Trivers – Willard effect (type 2)} \end{cases} \quad (8)$$

where s_{\max} and s_{\min} denote the midpoint of the largest and smallest reproductive weight-class, respectively.

If $\Delta v_a(s)$ is strongly nonlinear such that a linear approximation would be inappropriate, then the shape of $\Delta v_a(s)$ defines the optimal sex allocation tactic. For example, a u-shape implies that intermediate-sized mothers should produce daughters, while mothers at the extreme ends of the weight scale should produce sons; we name this tactic a type 3 Trivers–Willard effect (Fig. 1e). An n-shape implies that intermediate mothers should produce sons, while mothers at the extreme ends of the weight scale should produce daughters; we name this tactic a type 4 Trivers–Willard effect (Fig. 1f).

Sensitivity analysis. We approximate the sensitivity of Δv_a to an upward perturbation ε of any parameter p by:

$$\frac{\partial \Delta v_a}{\partial p}(s) \approx \frac{\Delta v_a(s, p(1 + \varepsilon)) - \Delta v_a(s, p)}{p\varepsilon} \quad (9)$$

We perturb survival parameters by 1% downwards and all other parameters by 1% upwards, which means that any perturbation results in increased mortality, growth, or inheritance probabilities. If $\Delta v_a(s)$ and $\frac{\partial \Delta v_a(s)}{\partial p}$ are reasonably linear then a change in the slope implies either a strengthening or weakening effect. If $\frac{\partial \Delta v_a(s)}{\partial p}$ has a steeper slope of the same positive (or negative) sign as $\Delta v_a(s)$ then we say that a parameter perturbation strengthens a Trivers–Willard effect (Fig. 1b; or reversed Trivers–Willard effect). If the slope of $\frac{\partial \Delta v_a(s)}{\partial p}$ is shallower than that of $\Delta v_a(s)$, then we speak of weakening the effect (Fig. 1c). If the slope of $\frac{\partial \Delta v_a(s)}{\partial p}$ is negative in contrast to a positive slope of $\Delta v_a(s)$, then a Trivers–Willard effect has been reversed (Fig. 1d). However, neither $\Delta v_a(s)$ nor $\frac{\partial \Delta v_a(s)}{\partial p}$ have to be linear.

For example, when we perturb the male survival intercept in the squirrel model, a reversed Trivers–Willard effect changes into a type 3 effect (u-shape). The results of the sensitivity analyses for squirrels in are shown in Extended Data Figs 4 and 5, and for sheep in Extended Data Figs 7 and 8.

Mean and variance in RV. To calculate the properties of the distribution of offspring’s RV we use the stable population distribution $n^\circ(a, s)$ and $n^\sigma(a, s)$ from iterating the two-sex IPM. We denote the mean and variance of the RV distribution with $\mathbb{E}(v)$ and $\text{Var}(v)$ and calculate it by

$$\mathbb{E}(v_a^d) = \frac{\int_0^\infty v_a^d(s) n^\circ(a, s) ds}{\int_0^\infty n^\circ(a, s) ds} \quad \text{and} \quad \mathbb{E}(v_a^s) = \frac{\int_0^\infty v_a^s(s) n^\sigma(a, s) ds}{\int_0^\infty n^\sigma(a, s) ds} \quad (10)$$

$$\text{Var}(v_a^d) = \mathbb{E}((v_a^d)^2) - (\mathbb{E}(v_a^d))^2 \quad \text{and} \quad \text{Var}(v_a^s) = \mathbb{E}((v_a^s)^2) - (\mathbb{E}(v_a^s))^2 \quad (11)$$

Calculation of D_a . The term $D_a^\sigma(s_0|s)$ (or $D_a^\circ(s_0|s)$) denotes the probability that an offspring produced by a father (or a mother, respectively) of age a and weight s is born with birth weight s_0 . The terms $D_a^\sigma(s_0|s)$ and $D_a^\circ(s_0|s)$ are conditional probabilities, that is, $\int D_a^\sigma(s_0|s) ds_0 = \int D_a^\circ(s_0|s) ds_0 = 1$. They are calculated using the mating function $m(a_f, s_f; a_m, s_m)$ and fertility function $R_{a_f}(s_f)$ of the two-sex IPM, as well as the stable female and male distributions $n^\circ(a_f, s_f)$ and $n^\sigma(a_m, s_m)$, which are obtained by iteration. The D_a functions are calculated by:

$$D_{a_f}^\circ(s_0|s_f) = \begin{cases} \frac{\sum_{a_m} \int f(s_0|s_f, s_m) m(a_f, s_f; a_m, s_m) R_{a_f}(s_f) n^\sigma(a_m, s_m) ds_m}{\sum_{a_m} \int m(a_f, s_f; a_m, s_m) R_{a_f}(s_f) n^\sigma(a_m, s_m) ds_m} & \text{if } \sum_{a_m} \int m(a_f, s_f; a_m, s_m) R_{a_f}(s_f) n^\sigma(a_m, s_m) ds_m > 0 \\ 0 & \text{otherwise} \end{cases} \quad (12)$$

$$D_{a_m}^\sigma(s_0|s_m) = \begin{cases} \frac{\sum_{a_f} \int f(s_0|s_f, s_m) m(a_f, s_f; a_m, s_m) R_{a_f}(s_f) n^\circ(a_f, s_f) ds_f}{\sum_{a_f} \int m(a_f, s_f; a_m, s_m) R_{a_f}(s_f) n^\circ(a_f, s_f) ds_f} & \text{if } \sum_{a_f} \int m(a_f, s_f; a_m, s_m) R_{a_f}(s_f) n^\circ(a_f, s_f) ds_f > 0 \\ 0 & \text{otherwise} \end{cases} \quad (13)$$

Calculation of M_a . The term $M_a^{\circ\circ}(s)$ denotes the total number of daughters produced by a mother of weight s and age a . Similarly, $M_a^{\sigma\sigma}(s)$ gives the number of sons to a mother, $M_a^{\circ\sigma}(s)$ gives the number of daughters to a father, and $M_a^{\sigma\circ}(s)$ gives the number of sons to a father of age a and weight s . The terms are calculated using the mating function $m(a_f, s_f; a_m, s_m)$ and fertility function $R_{a_f}(s_f)$ of the two-sex IPM, as well as the stable female and male distributions $n^\circ(a_f, s_f)$

and $n^\sigma(a_m, s_m)$, which are obtained by iteration. The M_a° and M_a^σ functions are calculated by:

$$M_{a_f}^\circ(s_f) = C \sum_{a_m} \int m(a_f, s_f; a_m, s_m) R_{a_f}(s_f) n^\sigma(a_m, s_m) ds_m \quad (14)$$

$$M_{a_m}^\sigma(s_m) = C \sum_{a_f} \int m(a_f, s_f; a_m, s_m) R_{a_f}(s_f) n^\circ(a_f, s_f) ds_f \quad (15)$$

with the normalization constant

$$C = \frac{\sum_{a_f > a_{\min}} \int_{s_{\min}} n^\circ(a_f, s_f) ds_f}{\sum_{a_f, a_m} \int m(a_f, s_f; a_m, s_m) n^\circ(a_f, s_f) n^\sigma(a_m, s_m) ds_f ds_m} \quad (16)$$

where a_{\min} and s_{\min} are the minimum age and weight necessary to start reproducing.

Calculation of L_a . The term $L_a^\circ(s, s_0)$ (or $L_a^\sigma(s, s_0)$) gives the probability that a newborn female (or a newborn male, respectively) born with weight s_0 will be alive at age a and weigh s weight units. The L_a terms are calculated recursively using the combined and age-specific survival and growth function p_a^{sg} (see refs 18 and 20 for more detail on p_a^{sg}) by

$$L_1^\circ(s, s_0) = L_1^\sigma(s, s_0) = \begin{cases} 1 & \text{if } s = s_0 \\ 0 & \text{otherwise} \end{cases} \quad (17)$$

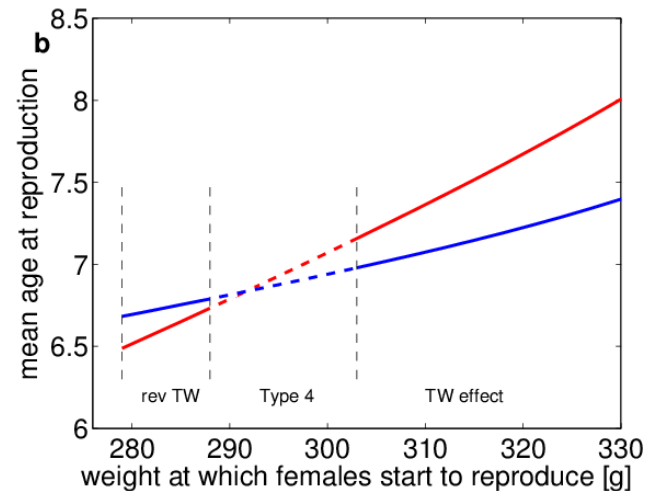
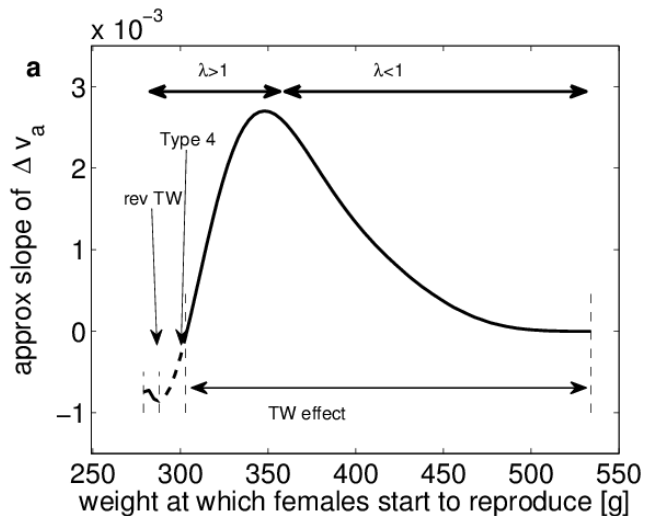
$$L_{a_f}^\circ(s, s_0) = \int p_{a_f-1}^{\text{sg}, \circ}(s, s_1) L_{a_f-1}^\circ(s_1, s_0) ds_1 \quad \text{for } a_f \geq 2 \quad (18)$$

$$L_{a_m}^\sigma(s, s_0) = \int p_{a_m-1}^{\text{sg}, \sigma}(s, s_1) L_{a_m-1}^\sigma(s_1, s_0) ds_1 \quad \text{for } a_m \geq 2 \quad (19)$$

where $p_{a_f}^{\text{sg}, \circ}(s, s_1)$ and $p_{a_m}^{\text{sg}, \sigma}(s, s_1)$ give the probability of a female or male, respectively, of age a and weight s_1 to survive and attain weight s in the next time step.

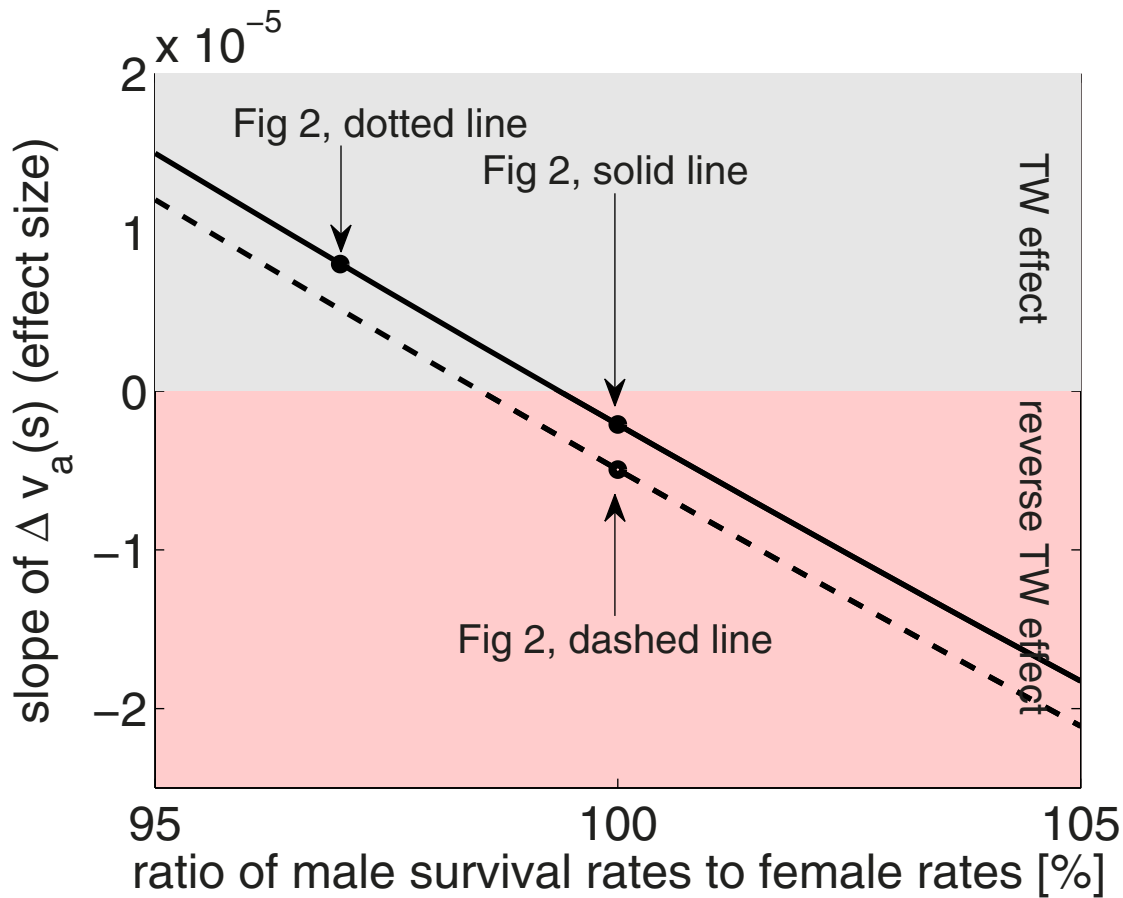
Code availability. A Matlab script for calculating RV as left eigenvectors from the cohort projection matrix is given in Supplementary Information, appendix B. The script covers calculations in equations (1–5, 7, and 12–19) and does not include the two IPM models described elsewhere^{18,20}.

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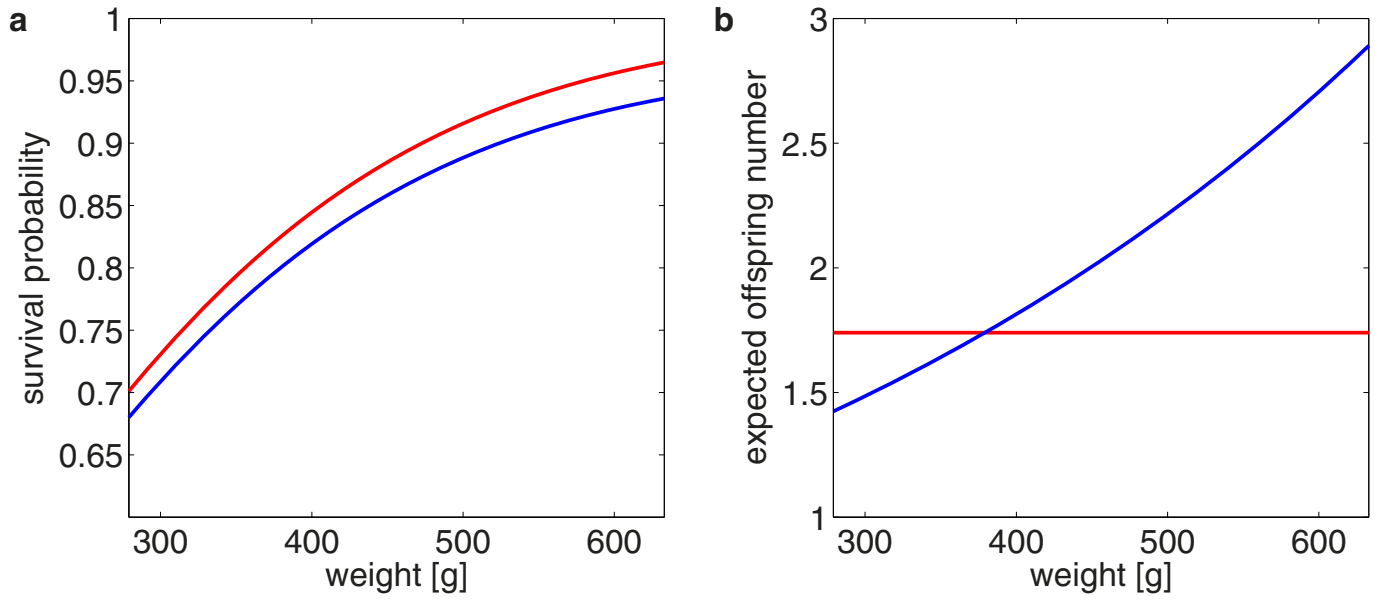
Extended Data Figure 1 | Mean female age at reproduction affects optimal sex allocation. **a**, Slope of the difference between male and female RV as a function of the size threshold above which females reproduce. The male size threshold is fixed at 279 g. Negative values indicate a reversed Trivers–Willard effect, positive values a Trivers–Willard effect. Dashed lines indicate a type 4 effect. When the population growth rate λ is greater than 1 (growing population), increasing female age at reproduction selects towards a Trivers–

Willard effect. In contrast, when the population is shrinking ($\lambda < 1$), reproducing at a later age increases fitness³⁶ and selects towards a reversed Trivers–Willard effect with increasing female age at reproduction. **b**, Mean maternal (red) and paternal (blue) age at reproduction as a function of the size threshold at which females reproduce. Dashed lines indicate the range of size thresholds that cause a type 4 effect.

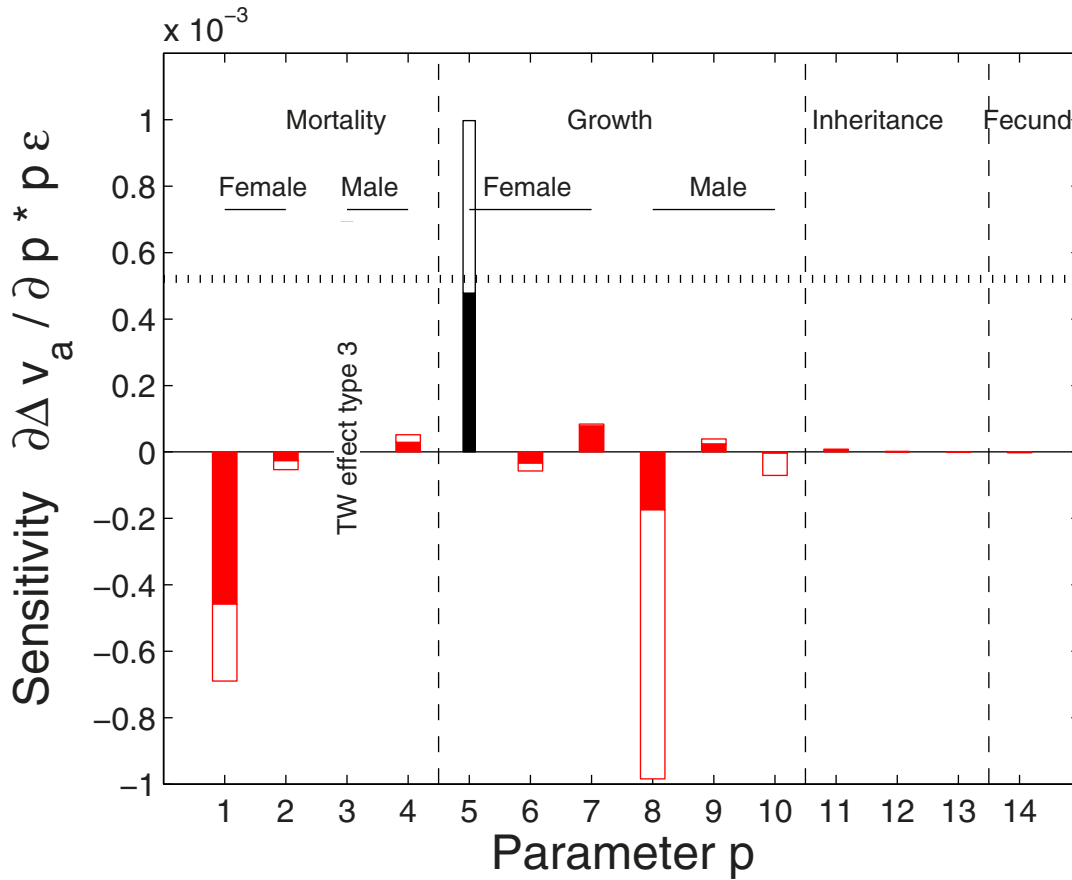


Extended Data Figure 2 | Strength of Trivers–Willard and reversed Trivers–Willard effects in squirrels as a function of the male to female survival ratio. The x -axis plots the ratio of male to female survival rate (independent of size and age) to the slope of the difference between male and female reproductive value, $\Delta v_a(s)$. Positive values indicate a Trivers–Willard effect (grey background), negative values a reversed Trivers–Willard effect (red

background). The more positive (or negative) the slope of $\Delta v_a(s)$ the more the expected sex ratio in offspring to good-condition mothers is biased towards males (or females). Solid line, no sex differences in mortality; dashed line, strength of mate selection has been increased from $\rho = 0.1$ to $\rho = 0.25$ (see Supplementary Table 1). Points highlighted with arrows indicate the settings that are used in Fig. 2 to plot $\Delta v_a(s)$ against maternal size s .

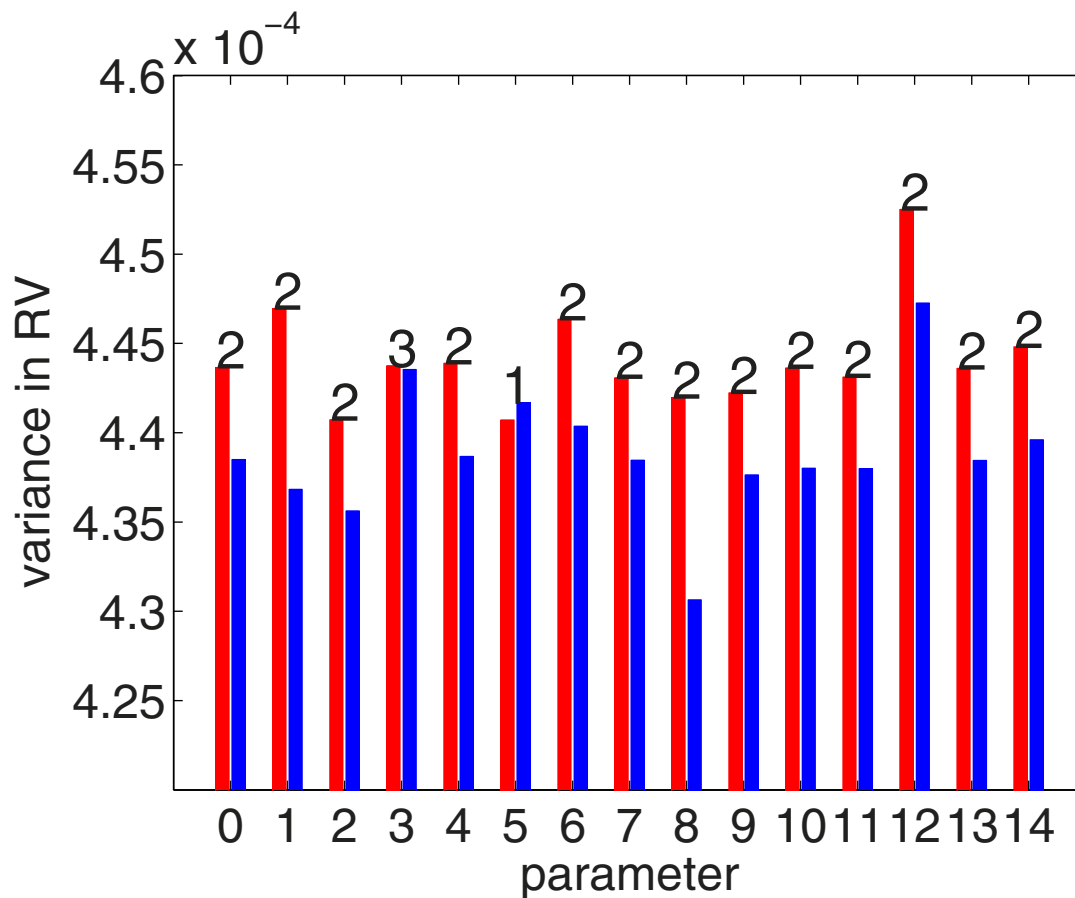


Extended Data Figure 3 | Trade-off between survival and reproduction in squirrels. a, Females (red) have higher survival rates than males (blue) at all ages. b, Small females are expected to produce more offspring than small males, while large females produce less offspring than large males.



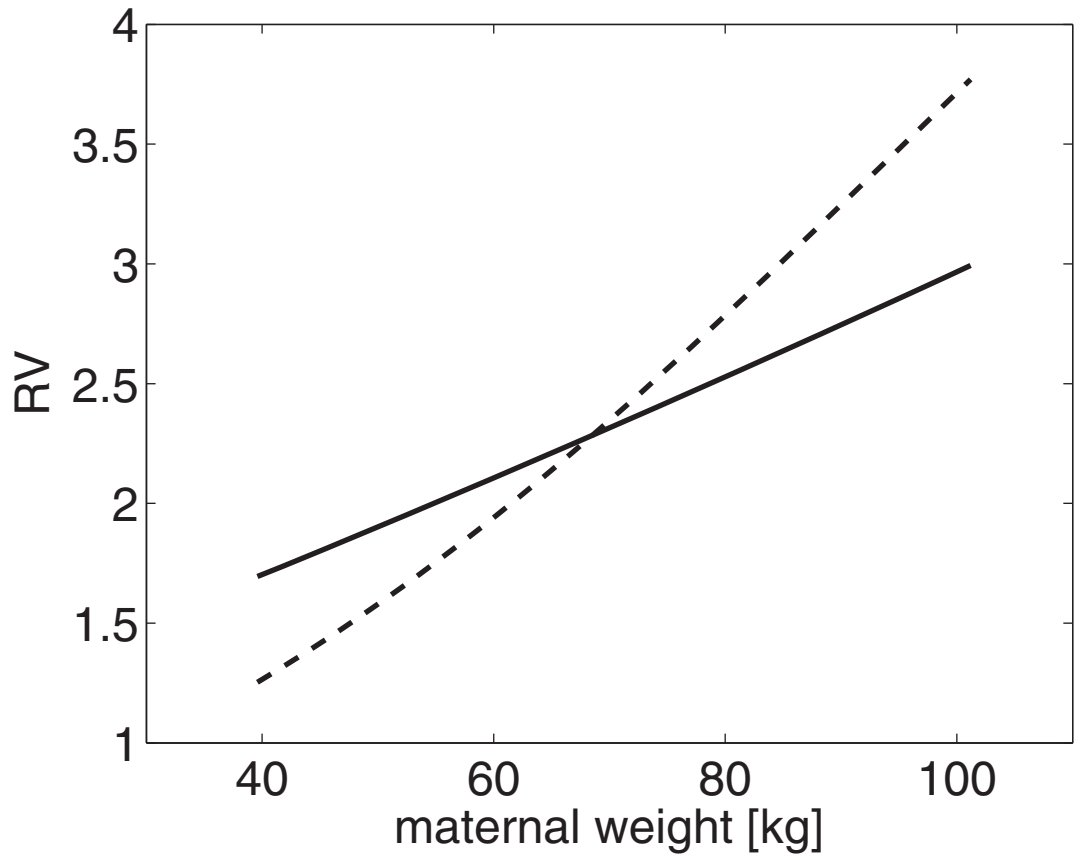
Extended Data Figure 4 | Sensitivity of the reversed Trivers-Willard effect to parameter perturbations in squirrels. When bars lie in the positive (or negative) range, then a change in parameters works towards a Trivers-Willard effect (or strengthening the reversed Trivers-Willard effect). The horizontal dashed line shows the difference in slope needed to neutralise the reversed Trivers-Willard effect. The bar above the dashed line indicates a Trivers-Willard effect (black); bars below indicate a reversed Trivers-Willard effect (red). Filled fractions of the bars indicate the contribution of change caused by parameter perturbation owing to change of female RV, and, in the white fractions, to change in male RV (see also Extended Data Fig. 5). Bars 1 to 4 show the sensitivity of the Trivers-Willard effect in squirrels to perturbations of the following parameters by 1% downwards (which corresponds to higher

mortality in the sex affected): (1) female survival intercept; (2) female survival slope; (3) male survival intercept, parameter change resulted in curved Δv_a which we indicate with 'TW effect type 3' and omit the bar; (4) male survival slope. Bars from 5 to 14 show the sensitivity of the Trivers-Willard effect in squirrels to perturbations of the following parameters by 1% upwards (which corresponds to higher rates in the affected sex): (5) female growth (mean intercept); (6) female growth (mean slope); (7) female growth variance; (8) male growth (mean intercept); (9) male growth (mean slope); (10) male growth variance; (11) inheritance (mean intercept); (12) inheritance (mean slope); (13) inheritance variance; (14) expected offspring number. All parameters are listed in Supplementary Table 1.



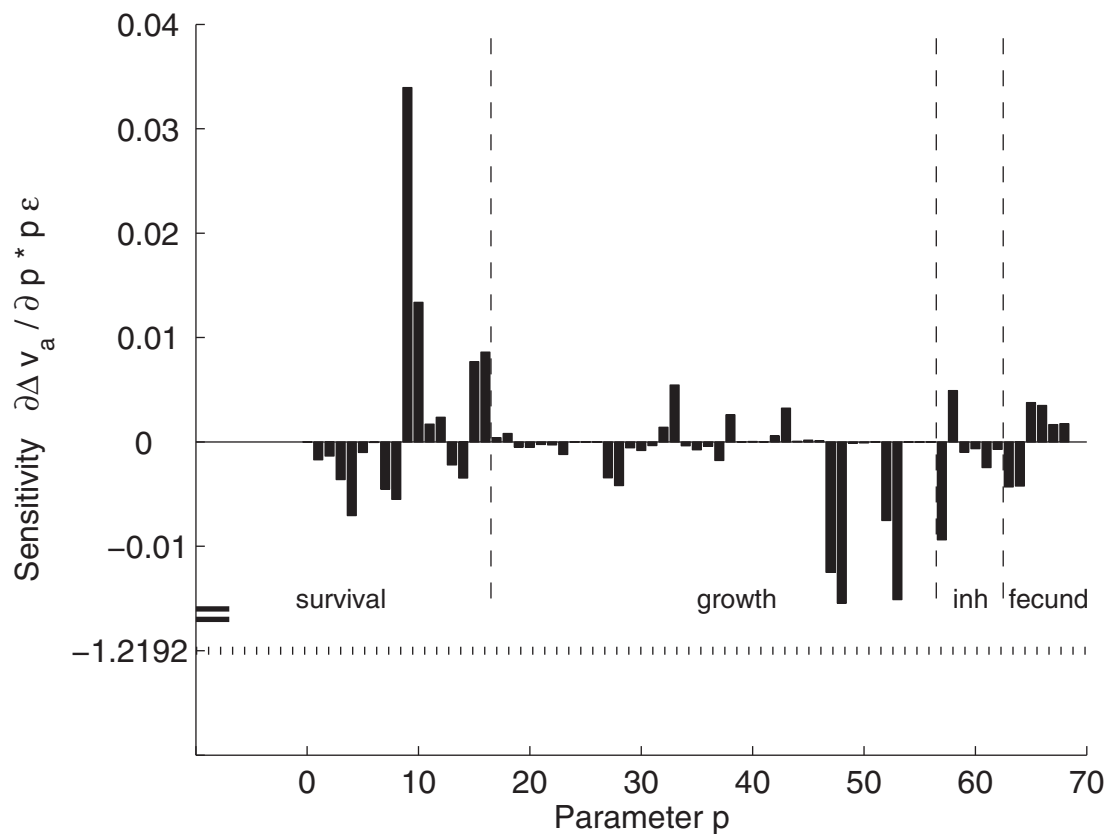
Extended Data Figure 5 | Female (red) and male (blue) variance in RV in original model (bar 0) and when parameters are perturbed (bars 1–14) in squirrels. Number 1 above bars indicates a Trivers–Willard effect, number 2 a reversed Trivers–Willard effect, and number 3 a type 3 Trivers–Willard effect. Bars 1 to 4 show variances in RV when the survival parameters are perturbed by 1% downwards (which corresponds to higher mortality in the affected sex): (1) female survival intercept; (2) female survival slope; (3) male survival intercept; and (4) male survival slope. Bars 5 to 14 show variances in RV when

the following parameters are perturbed by 1% upwards (which corresponds to higher rates in the affected sex): (5) female growth (mean intercept); (6) female growth (mean slope); (7) female growth variance; (8) male growth (mean intercept); (9) male growth (mean slope); (10) male growth variance; (11) inheritance (mean intercept); (12) inheritance (mean slope); (13) inheritance variance; and (14) expected offspring number. All parameters are listed in Supplementary Table 1.



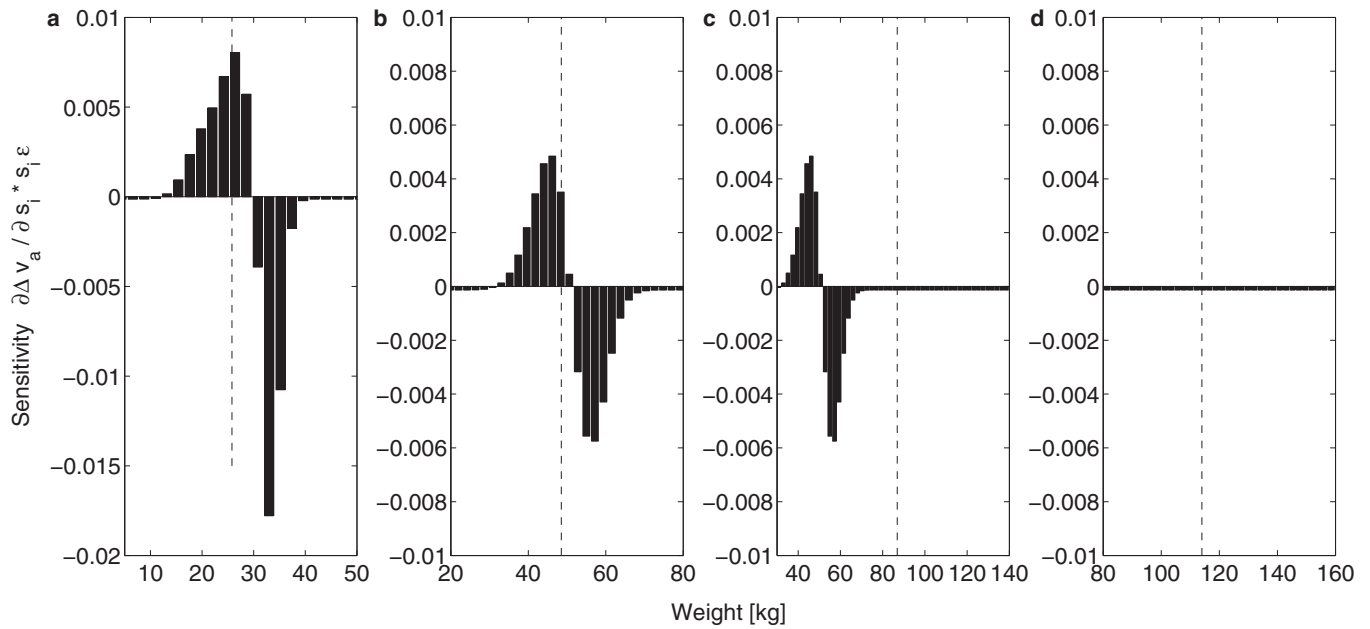
Extended Data Figure 6 | Reproductive value (RV) of female (solid line) and male (dashed line) offspring in bighorn sheep. For small mothers, daughters have higher RV than sons. For large mothers, sons have higher RV

than daughters. We scaled the RV of females and males such that the female RV of the smallest reproductive size class is 1.



Extended Data Figure 7 | Sensitivity of the Trivers–Willard effect to parameter perturbations in sheep. Bars in the positive range indicate that the Trivers–Willard effect is strengthened; bars in the negative range indicate a weakened Trivers–Willard effect. The horizontal dotted line marks the sensitivity needed to reverse the Trivers–Willard effect. The parameters are: 1–8 female survival (2 parameters each for the stages lamb, yearling, adult,

and senescent); 9–16 male survival (2 parameters for each stage); 17–36 female growth (5 parameters for each stage); 37–56 male growth (5 parameters for each stage); 57–60 female inheritance (inh) (2 intercepts for mean and variance, 2 slopes for female contribution to mean and variance); 61–62 male inheritance (male contributions to mean and variance); and 63–68 fecundity (fecund). All parameters are listed in Supplementary Tables 2 and 3.



Extended Data Figure 8 | Sensitivity of Trivers-Willard effect to size-specific male mortality increases of 1% in sheep. **a–d**, The survival probability of each size class in each stage (lamb (**a**), yearling (**b**), adult (**c**), and senescent (**d**)) has been independently lowered by 1%. The vertical dashed black line denotes the mean body weight of male sheep in the corresponding stage. In the early stages (**a** and **b**, lamb and yearling) we find that male-mortality

increases in small size classes strengthen the Trivers-Willard effect, whereas male-mortality increases in heavy size classes weaken the Trivers-Willard effect. In the later stages (**c** and **d**, adult and senescent), mortality increases hardly affect the Trivers-Willard effect (note that adult rams usually weigh above 60 kg).