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Resource Transfers and Evolution: Helpful Offspring and Sex Allocation

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Abstract

In some vertebrates, offspring help their parents produce additional offspring. Often individuals of only one sex become “helpers at the nest”. We analyze how such sex-biased offspring helping can influence sex ratio evolution. It is essential to account for age-structure because the sex ratios of early broods influence how much help is available for later broods; previous authors have not correctly accounted for this fact. When each female produces the same sex ratio in all broods (as assumed in all previous analyses of sex-biased helping), the optimal investment strategy is biased towards the more-helpful sex. When a female has facultative control over the sex ratio in each brood and each helper of a given sex increases the resource available for offspring production by a fixed amount, the optimal strategy is to produce only the more-helpful sex in early broods and only the less-helpful sex in later broods. When there are nonlinear returns from helping, i.e., each helper increases the amount of resource available for reproduction by an amount dependent upon the number of helpers, the optimal strategy is to maximize resource accrual from helping in early broods (which may involve the production of both sexes) and then switch to the exclusive production of the less-helpful sex in later broods. The population sex ratio is biased towards the more helpful sex regardless of whether the sex ratio is fixed or age-dependent. When fitness returns from helping exhibit environmental patchiness, females are selected to produce only males on some patches and only females on others, and the population sex ratio may be biased in either direction. We discuss our results in light of empirical information on offspring helping, and we show via meta-analysis that there is no support for the claim of that parents produce more of the helpful sex when that sex is rare or absent.

Keywords

sex allocation; optimality; offspring helping; intergenerational transfers; demography

1. Introduction

1.1. The biology of offspring helping

Offspring assist their parents in rearing offspring in some birds (Brown 1987, Skutch 1987, Stacey and Koenig 1990, Koenig and Dickinson 2004, Cockburn 2006) and a few mammals (Solomon and French 1997). Offspring of one sex are often more helpful than those of the other sex, and it is reasonable to ask if such sex-biased helping favors the evolution of

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biased sex ratios in order to maximize the gain from helping. This question has attracted much interest, especially after the discovery of striking sex-ratio biases in some species with helping (Komdeur 2004, West 2009).

Two aspects of sex-biased offspring helping are of critical importance in understanding its consequences for sex-ratio evolution. The first is that increased production of the more-helpful sex in early broods ensures that more help will be available for later broods. The second is that helpers produced early in life are more valuable than those produced later, since there are more subsequent broods in which the benefits of helping can be gained. It is therefore necessary to account for age structure when analyzing the consequences of sex-biased offspring helping. Since the sex ratios of early broods influence the size of later broods, the evolutionary consequences of the sex ratio of a brood can only be evaluated by assessing its effect on lifetime fitness (not only its effect on a single brood).

Previous authors have modeled sex-ratio evolution with sex-biased helping in two different ways. In the first, the environment is uniform and parents are assumed to always produce the same sex ratio, and in the second, the environment is patchy with respect to the gains from helping and parents are assumed to adjust their sex ratios to local conditions. The first scenario has been a focus of all theoretical analyses from Emlen et al. (1986a, b) to Pen and Weissing (2000); only the latter authors have also considered the second scenario. We develop models of both scenarios and extend the analysis in two important ways. First, we allow a female to adjust her sex ratio according to her age. Second, we allow helpers to interfere or cooperate with each other. We begin with a review of previous theoretical work.

1.2 Helping in a Uniform Environment

Building on a comment by Trivers and Hare (1976, note 63), Malcolm and Marten (1982, p. 12) suggested that sex-biased offspring helping could favor biased sex ratios: “By helping to raise more of their parents’ subsequent offspring, males [in the African Wild Dog] effectively pay back more of the effort initially invested in raising them than females. It is therefore overall less costly to produce a son than a daughter, which would explain the [male-] biased sex ratio.” Their idea is that the more-helpful sex is effectively cheaper to produce and therefore, it should be produced in greater numbers in accordance with the equal investment result of Fisher (1930). However, Fisher’s result does not apply in this case and selection favors excess investment in the more-helpful sex when there is sex-biased offspring helping (see below).

Emlen et al.(1986a) provided the first analysis of this “repayment model” give the assumption that a female always produces the same sex ratio. They also assumed that only sons help, that each helper augments the brood by a fixed amount, and that a fixed fraction of sons in one brood become helpers for the next. These assumptions imply that each successive brood is larger and produces more helpers than its predecessor, since there are more resources to invest in offspring. As Emlen et al. stated (p. 2), their “formulation deals only with expected values for the population and ignores changes in successive broods of a single female”. They cited Maynard Smith as having developed a model that accounted for these changes; apparently, the model was never published. Emlen et al. focused on a female producing a brood with “average” numbers of male and female offspring; they were apparently thinking of the average brood across the whole population. However, the evolutionarily relevant average is over all broods produced by a given female (see below).

Emlen et al.’s model is undermined by the further assumption that a female producing an average brood also has an average number of helpers. This cannot be true because the helpers for the average brood were produced in the previous brood, which had a less than average number of potential helpers. Nonetheless, Emlen et al. suggested correctly that the optimal sex ratio is biased toward the more helpful sex when each female produces the same sex ratio in all broods.

Emlen et al. were the first to recognize the potential importance of sibling interactions in the context of offspring helping. They suggested that offspring helping can be subject to diminishing returns because helpers tend to compete with each other, and they argued that such returns reduce the expected bias toward the more-helpful sex. Such effects have been ignored by subsequent authors. Our treatment includes the effects of both competition and cooperation among helpers.

Lessells and Avery (1987) extended the repayment model by including helping by daughters as well as sons, by allowing helpers to be other than full sibs of the additional offspring, and by allowing helpers to influence maternal survival. They made the important point that any decrease in the influence of early sex ratio decisions on later maternal fitness (e.g., because help is available from unrelated individuals) reduces the sex ratio bias.

Koenig and Walters (1999) criticized the model of Emlen et al. on both empirical and theoretical grounds. Their central theoretical concern was that double counting of fitness increments limited the applicability of the model. As noted by Pen and Weissing (2000), however, there was no such double counting since the benefits of helping were correctly assigned only to parents.

Frank (1998, p. 235) analyzed a model in which each daughter produced from parental resources (but not from helper resources) increased the size of the following brood. However, his model has no explicit age structure and is based on the assumption that brood size is the same for all females, which contradicts the assumed effect of helpers.

Pen and Weissing’s (2000) analysis of sex-biased offspring helping is based on a two-stage demographic model in which individuals are either juvenile non-reproductives, which can become helpers, or adult reproductives, which benefit from helpers. In any given time period, a juvenile remains a juvenile, becomes an adult, or dies, while an adult either reproduces or dies. The probabilities of these events are allowed to differ between the sexes. Pen and Weissing (p. 539-540) claimed that their analysis applied to “a general class of life histories,” although their model lacks explicit age structure and has the assumption that life expectancy is independent of age. They were the first to account for the increasing help provided to parents as they age. However, they assumed that a female must produce a fixed sex ratio during her lifetime and that the sex ratio in any given brood has no influence on the reproductive value of any future brood (see their Eqn. 4). The “powerful result of Taylor (1996)” they cited is not relevant to the repayment model because it is based on the assumption that the sex ratio employed in one brood has no consequences for the reproductive value of later broods. The sex-ratio equilibrium they present involves only the average number of helpers of a given sex and the amount of help provided by an offspring of that sex. Although elegant in its simplicity, this result is not correct, as we show below.

Gowaty and Lennartz (1985) were the first to argue that parents should respond to the absence of helpers by producing the more-helpful sex. (Other authors endorsing this claim include Creel 1998, West and Sheldon 2002, Allaine 2004, Doutrelont et al. 2004, West et al. 2005, Griffin et al. 2005, and West 2009.) At present, there is no theoretical analysis that supports this claim. Some authors cite Pen and Weissing (2000) as showing that natural selection favors such a facultative response, but in fact, they argued that females on helping-favored patches should produce the more-helpful sex and females on helping-not-favored patches should produce the less-helpful sex, regardless of whether helpers are present.

Sex-biased helping often involves differential dispersal with the more-helpful sex more likely to remain with its parents. Most models of sex-ratio evolution with sex-biased offspring helping, including those presented here, do not explicitly account for such differential dispersal. Only Wild (2006) has addressed the consequences of differential dispersal in a model with sex-biased helping. Unlike the models developed here, he assumed that helping increases parental survival rather than the resource available for parental reproduction. To our knowledge, there is no analysis that includes differential dispersal and helping that increases the amount of reproductive resource.

1.3 Helping in a Patchy Environment

Conditional sex ratio strategies can be favored if individuals face local circumstances that differentially affect the fitness of males and females. Conditional or facultative adustment of the sex ratio has been studied for more than a century (see Appendix A), but only Pen and Weissing (2000) have analyzed a model of conditional sex allocation in the context of sex-biased helping. Their model was motivated by the association between highly biased sex ratios in the Seychelles Warbler and differences in environmental quality (Komdeur 1996, Komdeur et al. 1997). They assumed that parents occupy fixed positions along an environmental gradient that affects the sexspecific gains from offspring helpers. Age structure was not addressed and evolutionary success was measured in terms of the contribution to the next time period rather than lifetime offspring production. Pen and Weissing stated correctly that parents are selected to produce all females or all males, depending on their position along the environmental gradient, and that the population sex ratio may be biased toward either sex. However, their analysis is flawed, and we provide a reanalysis framed in terms of lifetime fitness.

2. Model Formulation

2.1. Demographic Framework

We assume that each female can produce a brood at each age from α, the age of first reproduction, to ω, the age of last reproduction. Individuals are born (age 0) and become available to help at age 1. Pre-reproductive individuals (ages 1 to $\alpha - 1$) are potential helpers. Let n_{sx} be the number of individuals of sex $s = m$ (male) or f (female) and age $x = 0, 1, \ldots, \alpha, \ldots, \omega$, and define the vector $n^T = (n_{f0}, \cdots, n_{f\omega}, n_{m0}, \cdots, n_{m\omega})$, where T denotes transpose. The change of n from time t to $t + 1$ is described by $n(t+1) = An(t)$, where the matrix A is

$$\begin{array}{cccccccccc}
0 & 0 & \frac{1}{2}f_f & \frac{1}{2}f_{f\;\;1} & \frac{1}{2}f_f & 0 & 0 & \frac{1}{2}f_m & \frac{1}{2}f_{m\;\;1} & \frac{1}{2}f_m \\
P_{f0} & & & & & & & & & \\
 & P_{f\;\;1} & & & & & & & & \\
 & & P_f & & & & & & & \\
 & & & P_{f\;\;1} & 0 & & & & & \\
0 & 0 & \frac{1}{2}m_f & \frac{1}{2}m_{f\;\;1} & \frac{1}{2}m_f & 0 & 0 & \frac{1}{2}m_m & \frac{1}{2}m_{m\;\;1} & \frac{1}{2}m_m \\
 & & & & & P_{m0} & & & & \\
 & & & & & & P_{m\;\;1} & & & \\
 & & & & & & & P_m & & \\
 & & & & & & & & P_{m\;\;1} & 0
\end{array}$$

in which the unspecified elements are 0, and P_{sx} is the probability that an individual of sex s survives from age x to $x+1$. An individual of sex s and age x produces f_{sx} females and m_{sx} males. α and ω are assumed to be the same for both sexes, but the following analysis holds if they differ. The population is censused at the end of each time period during which mating occurs and offspring are born and reared to independence. Thus, f_{sx} and m_{sx} are each a product of the number of conceptions and the rate of survival to independence. Helpers produced at an early age x increase the resource available for reproduction at a later age $x + \Delta x$ and thereby increase the number of offspring reared at that age ($f_{sx+\Delta x}$, $m_{sx+\Delta x}$).

We assume that both sexes are diploid. Half of the genes in a female's offspring come from her and the other half from her mates, which may be of any age. The numbers of female and male offspring in the next time period are

$$n_{f0}(t+1) = \frac{1}{2}\sum_{x=\alpha}^{\omega} f_{fx} n_{fx}(t) + \frac{1}{2}\sum_{x=\alpha}^{\omega} f_{mx} n_{mx}(t)$$

$$n_{m0}(t+1) = \frac{1}{2}\sum_{x=\alpha}^{\omega} m_{fx} n_{fx}(t) + \frac{1}{2}\sum_{x=\alpha}^{\omega} m_{mx} n_{mx}(t)$$

where the first sum in each equation is the contribution of females and the second sum is the contribution of males to the same offspring. Since every offspring has a mother and a father,

$$F(t) = \sum_{x=\alpha}^{\omega} f_{fx} n_{fx}(t) = \sum_{x=\alpha}^{\omega} f_{mx} n_{mx}(t) \quad [1]$$

$$M(t) = \sum_{x=\alpha}^{\omega} m_{fx} n_{fx}(t) = \sum_{x=\alpha}^{\omega} m_{mx} n_{mx}(t) \quad [2]$$

where $F(t)$ and $M(t)$ denote the number of females and the number of males produced at time t. We assume that the sex ratio is controlled by the female parent and that the population growth rate depends only on the number of reproductive females. Under mild assumptions, such a population converges to a stable age distribution determined by the elements of A (Keyfitz 1968). (Caswell and Weeks 1986 reported that two-sex models with mating competition among individuals of different ages can exhibit complex dynamics and even chaos. In their model, however, the number of offspring produced by females does not equal the number of offspring produced by males, and therefore cannot apply to any population where each offspring has a mother and a father. Whether there are more biologically plausible models of mate competition that give rise to chaotic dynamics is not known.)

2.2. Measuring Fitness

We evaluate the evolutionary consequences of different sex ratios in terms of the reproductive value of females producing them, following Taylor (1996), Frank (1998), and Pen and Weissing (2000, 2002). At demographic equilibrium, formula, where v is the left eigenvector of A and λ is the dominant eigenvalue of A. Therefore, v_{sx}, the xth element for sex s in v (which gives the reproductive value of an individual of age x and sex s) is

$$\begin{aligned} v_{sx} &= \tfrac{1}{\lambda}\left(P_{sx} v_{s(x+1)}\right) \quad \text{for} \quad 0 \le x \le \alpha - 1 \\ v_{sx} &= \tfrac{1}{\lambda}\left[\tfrac{1}{2}\left(f_{sx} v_{f0} + m_{sx} v_{m0}\right) + P_{sx} v_{sx+1}\right] \quad \text{for} \quad 0 \le x \le \omega - 1 \end{aligned} \quad [3]$$

and

$$\nu_{s\omega}=\frac{1}{2\lambda}\left(f_{s\omega}\nu_{f0}+m_{s\omega}\nu_{m0}\right)\quad \text{for}\quad x=\omega.$$

Consider a population fixed for a sex-ratio strategy ($\widehat{f}_{sx}, \widehat{m}_{sx}$), and introduce a rare mutation that produces a sex ratio (f_{sx}, m_{sx}), that differs only at age x from the resident strategy. The reproductive value of a mutant female of age x is

$$\nu_{fx}=\frac{1}{\lambda}\left[\frac{1}{2}\left(f_{fx}\nu_{f0}+m_{fx}\nu_{m0}\right)+P_{fx}\nu_{fx+1}\right]$$

by substitution into Eqn. 3. Reproductive value is proportional to the sum of current reproduction $f_{fx}\nu_{f0}+m_{fx}\nu_{m0}$, and future reproduction $p_{fx}\nu_{fx+1}$. Future reproduction can be ignored if a sex ratio at a given age does not influence the probability of surviving to some later age or the reproductive value of a brood produced at that later age (e.g. Taylor 1996, Pen and Weissing 2000), but this is not the case for the helping scenario considered here because the choice of a sex ratio at one age influences the amount of resource available for later broods.

Accordingly, we express the reproductive value of an offspring at age 0 in terms of the offspring it can expect to produce over its lifetime. Repeated substitution for reproductive value in the expressions for ν_{f0} and ν_{m0} yields

$$\nu_{f0}=\frac{\nu_{f0}}{2}\sum_{x=\alpha}^{\omega}\frac{l_{fx}f_{fx}}{\lambda^{x}}+\frac{\nu_{m0}}{2}\sum_{x=\alpha}^{\omega}\frac{l_{fx}m_{fx}}{\lambda^{x}}\qquad[4]$$

$$\nu_{m0}=\frac{\nu_{f0}}{2}\sum_{x=\alpha}^{\omega}\frac{l_{mx}f_{mx}}{\lambda^{x}}+\frac{\nu_{m0}}{2}\sum_{x=\alpha}^{\omega}\frac{l_{mx}m_{mx}}{\lambda^{x}}\qquad[5]$$

where $l_{sx}=\sum_{x=0}^{x-1}P_{sx}$. As shown in Appendix B,

$$\frac{\nu_{f0}}{\nu_{m0}}=\frac{M}{F},$$

where M/F is the ratio of the total number of males and the total number of females produced in the population as a whole each cycle at demographic equilibrium. We can now write the lifetime fitness of a female producing f_{fx} female and m_{fx} male offspring for each age x as

$$\phi_{f}=\nu_{f0}=\frac{\nu_{m0}M}{2}\left(\frac{r_{f}\sum_{x=1}^{\omega}l_{fx}f_{fx}}{F}+\frac{r_{m}\sum_{x=1}^{\omega}l_{fx}f_{fx}}{M}\right)\qquad[6]$$

where the relatedness parameters $r_f = r_m = 1/2$. (This result is independent of the value of λ). As with many other problems in sex allocation (see Charnov 1982), the fitness function (Eqn. 6) is a variant of the equation derived by Shaw and Mohler (1953) for the discrete generation case.

It is convenient to rewrite γ_f in terms of brood number. Consider a female producing her n^{th} brood (f_n, m_n) with $1 \leq n \leq z$ where 1 corresponds to age α and z corresponds to age ω. Taking l_n as the probability a female survives to produce her n^{th} brood, we have

$$\phi_f = \frac{\nu_{m0} M}{4} \left(\frac{\sum_{n=1}^{Z} l_n f_n}{F} + \frac{r_m \sum_{n=1}^{Z} l_n f_n}{M} \right) = \frac{\nu_{m0} M}{4} \left(\frac{F_L}{F} + \frac{M_L}{M} \right) \quad [7]$$

where F_L and M_L are the expected lifetime production of female and male offspring, respectively. We refer to a given sequence of broods (f_n, m_n) for $n = 1$ to z as a *lifetime strategy*. For given constraints on offspring production and returns from helping, we seek an evolutionarily stable lifetime strategy such that if all females employ that strategy no other strategy can invade. We assume that the population is so large that the choice of a sex ratio by a given female at any age has no effect on the overall production of F females and M males in each time period or on the dominant eigenvalue λ and the associated eigenvectors.

Some features of the geometry of lifetime fitness will prove useful. By implicit differentiation, one can show that any fixed value of γ_f defines a line in the (F_L, M_L) plane with slope

$$\frac{dM_L}{dF_L} = -\frac{M}{F},$$

The segment of this line in the positive quadrant is a *fitness isocline* since all lifetime strategies corresponding to points on such a line segment share the same fitness. A given population sex ratio M/F defines a family of parallel fitness isoclines, each of which runs from the M_L axis to the F_L axis. A line from the origin with slope M/F passes through the midpoint of each fitness isocline. This *fitness bisector* has two convenient properties. First, it summarizes all fitness isoclines corresponding to a given population sex ratio. If the population sex ratio changes, the slope of the fitness bisector changes, reflecting the changing slope of all fitness isoclines. Second, if all females employ a given lifetime strategy (F_L, M_L), then the fitness bisector passes through that point. These properties are illustrated below.

We can now assess the fitness consequences of any lifetime sequence of sex ratios, given specified constraints on offspring production.

2.3. Constraints on Offspring Production

We assume that offspring production is constrained at the level of the individual brood and is linear in terms of current offspring. Thus, the constraint for brood n is

$$\pi_n = f_n c_f + m_n c_m - E_n = 0$$

where c_s is the cost of producing an offspring of sex s measured in units of the resource limiting reproduction, and E_n is the amount of resource available to produce brood n. E_n is the sum of E_p, the amount of limiting resource available to a female from her own efforts (and perhaps those of her mate), and E_{hn}, the amount provided by helpers assisting with the production of brood n. E_p is assumed to be independent of n, but E_{hn} depends on the numbers of males and females produced in previous broods and on their effectiveness as helpers. There are no previous offspring to help with brood 1, so $E_1 = E_p$ but the offspring in this brood (f_1, m_1) may help with the second brood, and we have

$$E_2=E_p+f_1l_{f1}\gamma_f\tau_f+m_1l_{m1}\gamma_m\tau_m$$

where l_{s1} is the probability that an offspring of sex s survives to age 1 (when a surviving mother produces her next brood), γ_s is the probability that a previous offspring of sex s becomes a current helper, and τ_s is the amount of resource added by each helper of sex s. We assume that E_p, l_{s1}, γ_s, and τ_s are temporally-invariant. For any brood after the second, helpers may be recruited from more than one previous brood, and for brood n we have

$$E_n=E_p+\gamma_f\tau_f\sum_{i=1}^{u}l_{fi}f_{n-i}+\gamma_m\tau_m\sum_{i=1}^{u}l_{mi}m_{n-i}, \quad [8]$$

where $u = a-1$ if $a-1 \leq z-n$ and $u = z-n$ otherwise. We assume that helpers are recruited from all earlier offspring of suitable age regardless of their history of helping. (Pen and Weissing 2000 assumed that helpers for a given brood are recruited only from offspring that were either helpers or newborns in the previous brood.)

If offspring are available for only a single bout of helping ($a = 2$), Eqn. 8 becomes

$$E_n=E_p+l_{f1}\gamma_f\tau_ff_{n-1}+l_{m1}\gamma_m\tau_mm_{n-1}$$

This is equivalent to

$$E_n=E_p+\left[(1-k_n)R_{f1}+k_nR_{m1}\right]E_{n-1}$$

where $k_n = m_nc_m/(f_nc_f + m_nc_m)$ is the proportion of resource invested in males in brood n, and $R_{s1}=l_{s1}\gamma_s\tau_s/c_s$ is the contribution per unit cost of a helper of sex s produced in brood n −1. If a female is constrained to produce a fixed k, it follows that

$$E_n=E_p\left(\frac{1-X_1^n}{1-X_1}\right)$$

where $X_1=(1-k)R_{f1}+kR_{m1}$ is the average per capita contribution per unit cost of helpers of the two sexes (see Appendix C). The constraint on offspring production in each brood is linear, but the amount of resource available to invest grows nonlinearly from brood to brood if there is sex-biased helping ($R_{f1}\neq R_{m1}$). If the two sexes are equally helpful $X_1 = R_{f1} = R_{m1}$, and E_n is independent of the sex ratio in previous broods.

A critical feature of the repayment model is that the sex ratios of earlier broods determine the amount of resource available for the production of later broods. Consider a case where only two broods are produced ($z = 2$) and males are the more helpful sex (see Fig. 1). The choice of a given first brood (f_1, m_1) subject to $\pi_1 = f_1c_f + m_1c_m - E_p = 0$ determines the number of helpers for the second brood, and thereby determines E_2, the amount of resource available to produce that brood. E_2 is maximized when only males are produced in the first brood (the resulting constraint on the second brood is $\widehat{\pi}_2=f_2c_f+m_2c_m-\left(E_p+m_1l_{m1}\gamma_m\tau_m\right)=0$) and E_2 is minimized when only females are produced in the first brood (the resulting constraint on the second brood is $\dot{\pi}_2 = f_2 c_f + m_2 c_m - \left(E_p + f_1 l_{f1} \gamma_f \tau_f\right) = 0$) An intermediate sex ratio in the first brood generates an intermediate constraint on the second brood. The lifetime output of female offspring is $F_L = l_1 f_1 + l_2 f_2$ and that of male offspring is $M_L = l_1 m_1 + l_2 m_2$. Strategies corresponding to points on the outer boundary between MM (males only in both broods) and MF (males only in first, females only in second) produce the more-helpful sex (males) in the first brood and an intermediate sex ratio in the second brood. Strategies corresponding to points on the inner boundary between FF (females only in both) and MF (males only in first, females only in second) produce the less-helpful sex in the first brood and an intermediate sex ratio in the second brood. Strategies corresponding to points in the interior of the accessible set produce intermediate sex ratios in both broods. The set of accessible strategies lies in a region bounded by two lines with slope $-c_f/c_m$; the inner one corresponds to the exclusive production of the less-helpful sex (FF) and the outer one to the exclusive production of the more helpful sex (MM).

We have assumed that each helper provides the same amount of resource regardless of how many helpers are present. Alternatively, there may be competition or cooperation among helpers such that the contribution of each helper depends on the number of helpers. To account for such interactions, we write

$$E_n = E_p + g_m\left(h_{fn}, h_{mn}\right) + g_f\left(h_{fn}, h_{mn}\right), \quad [9]$$

where $g_s(h_{fn}, h_{mn})$ is a function describing the amount of resource provided by helpers of sex s, given the number of female helpers, h_{fn}, and of male helpers, h_{mn}, present in brood n. For illustration, we use the exponential form

$$E_n = E_p + h_{fn}^a \tau_f + h_{mn}^b \tau_m = E_p + \left(\sum_{i=1}^{u} l_{fi} \gamma_f f_{n-1}\right)^a \tau_f + \left(\sum_{i=1}^{u} l_{mi} \gamma_m m_{n-1}\right)^b \tau_m \quad [10]$$

where τ_s is the amount of resource provided by a helper of sex s when alone, and $n-u$ is the earliest brood contributing helpers to brood n. Eqn. 10 is based on the assumption that competition and cooperation occur only among helpers of the same sex. If there is competition among females (males), $a < 1$ ($b < 1$), and there are diminishing returns from helping. If there is cooperation among females (males), $a > 1$ ($b > 1$), and there are increasing returns from helping. The consequences for sex allocation of differential nonlinear gains through male and female gametes or offspring have been analyzed previously (e.g., Charnov et al. 1976, Clark 1978, Charnov 1979, Bawa 1980, Givnish 1980, Seger and Charnov 1980, Taylor 1981, Toro 1982, Godfray 1986, and Uller 2006.)

We next analyze sex-ratio evolution in cases where the sex ratio is fixed, i.e., each female is constrained to employ the same sex ratio in each brood she produces. We then analyze cases of facultative sex ratio adjustment where a female can alter her sex ratio from brood to brood.

3. Results

3.1. Evolutionary Equilibrium with a Fixed Sex Ratio

Previous treatments of the repayment model (Emlen 1986a, Lessells and Avery 1987, Frank 1998, Pen and Weissing 2000) had the assumption that each female produces a fixed sex ratio. We begin with this case. Assume that $k_n = k$ for all n, i.e., a fixed fraction of resource is invested in the males of each brood. We derive the evolutionarily stable value of k, say $\widehat{k}$, such that if all females employ $\widehat{k}$, no mutation causing a different value of k can invade.

Given a constraint on each brood n with E_n given by Eqn. 9, lifetime production of each sex as functions of k are given by

$$\begin{aligned} F_L(k) &= \tfrac{(1-k)}{c_f} \sum_{n=1}^{z} l_n E_n = \tfrac{(1-k)}{c_f} E_L(k) \\ M_L(k) &= \tfrac{k}{c_m} \sum_{n=1}^{z} l_n E_n = \tfrac{k}{c_m} E_L(k) \end{aligned} \qquad [11]$$

where we write $E_L(k)$ to indicate that the lifetime amount of resource is a function of k. $E_L(k)$ also depends on parental survival, i.e., l_i for $i = 1$ to z, which are assumed to be independent of k. Substitution into Eqn. 7 gives lifetime fitness as a function of k,

$$\phi_f(k) = \frac{\nu_{m0} M}{4} \left(\frac{(1-k)\, E_L(k)}{F c_f} + \frac{k E_l(k)}{M c_m} \right).$$

A necessary condition for $\phi_f\left(\widehat{k}\right)$ to be a maximum is

$$\frac{d\phi_f}{dk} = E_L\left(\widehat{k}\right) \left(\frac{1}{M c_m} - \frac{1}{F c_f} \right) + \frac{dE_L\left(\widehat{k}\right)}{dk} \left(\frac{1-\widehat{k}}{F c_f} + \frac{\widehat{k}}{M c_m} \right) = 0.$$

Since $\widehat{k} = M c_m / \left(F c_f + M c_m \right)$ in a stationary population where all females employ $\widehat{k}$, we have

$$E_L\left(\widehat{k}\right) \left(\frac{1-2\widehat{k}}{2\widehat{k}\left(1-\widehat{k}\right)} \right) + \frac{dE_L\left(\widehat{k}\right)}{d\widehat{k}} = 0, \qquad [12]$$

which holds only if the two terms on the left hand side are of opposite sign. If males are the more-helpful sex, $E_L(k)$ increases with k and the marginal “resource return”, $dE_L(k)/dk$, is positive. In this case, the equality is satisfied for some $\widehat{k} > 1/2$. Similarly, if females are the more-helpful sex, $E_L(k)$ decreases with k, $dE_L(k)/dk$ is negative, and the equality is satisfied for some $\widehat{k} < 1/2$. Consequently, a necessary condition for $\phi_f\left(\widehat{k}\right)$ to be a maximum is that each female biases her investment toward the more-helpful sex. In the absence of helping, or if the two sexes are equally helpful, $dE_L(k)/dk$ vanishes, and we recover equal investment in the two sexes, $\widehat{k} = 1/2$.

Whether a given $\widehat{k}$ satisfying Eqn. 11 is a maximum depends on the sign of the second derivative of $\phi_f(k)$ evaluated at $\widehat{k}$. We have

$$\frac{d^2\phi_f}{dk^2} = 2\frac{dE_L(k)}{dk} \left(\frac{1}{M c_m} - \frac{1}{F c_f} \right) + \frac{d^2 E_L(k)}{dk^2} \left(\frac{1-k}{F c_f} + \frac{k}{M c_m} \right),$$

which is equivalent to

$$\frac{d^2\phi_f}{dk^2} = \frac{dE_L(k)}{dk} \left(\frac{1-2\widehat{k}}{\widehat{k}\left(1-\widehat{k}\right)} \right) + \frac{d^2 E_L(k)}{dk^2}$$

when all females employ $\hat{k}$. The first term is always negative since $dE_L(k)/dk$ and $1-2\hat{k}$ have opposite signs at equilibrium (see above). The second derivative is negative, and $\hat{k}$ is evolutionarily stable if $d^2E_L(k)/dk^2$ is zero or negative, i.e., there are constant or diminishing returns to further investment in the more-helpful sex. It is also possible for $\hat{k}$ to be evolutionarily stable if $d^2E_L(k)/dk^2$ is positive but smaller than the first term, i.e., if there are only weakly increasing returns to helping. If the second derivative is positive and sufficiently large, such that there are strongly increasing returns from helping, is evolutionarily unstable, and the population can be invaded by a mixture of females, some of which always produce males while the others always produce females.

For illustration, we assume that there is only a single bout of helping ($\alpha = 2$), in which case the constraint on an arbitrary brood n (Eqn. 10) is

$$E_n(k) = E_p + \left(\gamma_f l_{f1} c_f^{-1} (1-k) E_{n-1}\right)^a \tau_f + \left(\gamma_m l_{m1} c_s^{-1} k E_{n-1}\right)^b \tau_m.$$

Iterating this expression yields all E_n. The lifetime amount of resources, $E_L(k)$ is a weighted sum of these values (Eqn. 10), and the constraint on lifetime offspring production is $\pi_L(k) = F_L(k)c_f + M_L(k)c_m - E_L(k) = 0$. $\pi_L(k)$ is shown in Fig. 2 (with no competition or cooperation) and in Fig. 3 (with competition or cooperation.)

If there is no competition or cooperation ($a = b = 1$) and one sex is more helpful than the other, $\pi_L(k)$ is convex (bowed out from the origin) and the evolutionarily stable equilibrium is monomorphic, with k biased toward the sex that is more helpful per unit cost (the slope of $\hat{\beta}$ is greater than the slope of ϵ in Fig. 2). This shows that equal investment need not occur in cases with sex-biased offspring helping. (Fisher's 1930 "equal investment" result is based on the assumption that offspring do not influence the reproductive output of their parents.) If the two sexes are equally helpful, $\pi_L(k)$ is a straight line, and we recover equal investment, $\hat{k} = 1/2$, at equilibrium.

Fig. 3 illustrates cases with competition or cooperation among helpers of the same sex. If there is competition (diminishing returns, $a = b < 1.0$), there is a unique interior that is evolutionarily stable ($\hat{\beta}=\epsilon$ is stable in Fig. 3A). If there is cooperation (increasing returns, $a = b > 1.0$), any fixed k can be invaded by a mixture of females that always produce a single sex ($k = 1.0$ or $k = 0$) ($\hat{\beta}=\epsilon$ is unstable in Fig. 3B). If there is competition in one sex and cooperation in the other, the evolutionarily stable equilibrium can be polymorphic (Fig. 3C) or monomorphic (Fig. 3D), depending on how much the sex-specific exponents differ from 1.0.

The qualitative geometry illustrated in Fig. 3 holds if the returns from helping differ between the sexes in ways other than the exponents a and b, but the transition between convex and concave is displaced from $a = b = 1$. In all cases where the two sexes differ, the sex ratio at equilibrium is biased toward the sex with the greater contribution to lifetime production of offspring per unit cost. This implies that $\hat{\beta} \neq \epsilon$, i.e., equal investment in the two sexes does not hold at equilibrium.

Pen and Weissing (2000) presented an expression for the optimal fixed intermediate k given linear returns from helping (see their Eqn. 8). Their result can be expressed as

$$\frac{\widehat{k}}{1-\widehat{k}}=\frac{\widehat{M}c_m}{\widehat{F}c_f}=\frac{E_p+\tau_m\bar{h}_m}{E_p+\tau_f\bar{h}_f}, \quad [13]$$

where $\bar{h}_s$ is the average number of helpers of sex s per brood. They expressed Eqn. 12 in terms of $b_s=\tau_s/E_p$ for each sex s. (There is an erroneous factor of 2 in their helping terms because the equilibrium condition given by their Eqn. 6, which has an extraneous factor of 1/2 in the first term, does not follow from their Eqn. 5.) The result of Emlen et al. (1986a), $\widehat{k}/\left(1-\widehat{k}\right)=\left(E_p+\tau_m\bar{h}_m\right)/E_p$, is a special case of Eqn. 12 when only males help (this follows from their Eqns. 6b and 9a.) By focusing on a single brood subject to a linear constraint, these authors in effect assumed that lifetime offspring production is likewise subject to a linear constraint, but this is not true given their assumptions. Eqn. 12 correctly describes the equilibrium investment ratio *only* for a mixture of females, each of which always produces all females or all males (contradicting the assumption that each female uses the same sex ratio at equilibrium). To see this, note that the lifetime output of a mixture of lifetime specialists employing $k = 0$ or $k = 1$ corresponds to a point on the line segment between $M_L(1)$ and $F_L(0)$, which has slope $-M_L(1)/F_L(0)$. At equilibrium, the fitness bisector passes through the midpoint of this line segment, and we have $\widehat{M}/\widehat{F}=M_L(1)/F_L(0)$. For any value of k, lifetime resource is $E_L(k)=\bar{B}(E_p+\tau_f\bar{h}_f+\tau_m\bar{h}_m)$, where $\bar{B}$ is the average number of broods per lifetime. Eqn. 12 follows because the lifetime output of a female producing only males is $M_L(1)=E_L(0)/c_m=\bar{B}(E_p+\tau_m\bar{h}_m)/c_m$ and that of a female producing only females is $F_L(1)=E_L(0)/c_f=\bar{B}(E_p+\tau_f\bar{h}_f)/c_f$.

3.2. Evolutionary Equilibrium with Conditional Sex Ratios and Linear Returns to Helping

We show that an evolutionarily stable sequence of sex ratios, (f_n, m_n), for $n = 1$ to z, consists of the exclusive production of the more-helpful sex in early broods, say from brood 1 to brood t−1, followed by a transition brood t which can include both sexes, and then the exclusive production of the less-helpful sex in broods $t + 1$ to z.

Consider a population in which females produce a maximum of three broods ($z = 3$). The set of accessible strategies is shown in Figure 4A. Suppose that every female produces only males in the first two broods and a given mixture of both sexes in the third. The effective fitness isocline then passes through the set of accessible strategies (Fig. 4B), and any strategy in the lightly shaded area has greater fitness than the resident strategy and can invade. Any mutant strategy that produces sequences closer to MMF increases in frequency, and the slope of the fitness bisector shifts as shown by the arrow.

Now suppose that each female produces only females in the first brood, both sexes in the second brood, and only males in the third brood. As before, the effective fitness isocline passes through the set of accessible strategies (Fig. 4C), and any strategy in the lightly shaded area has greater fitness than the resident strategy and can invade. Any mutant strategy that produces sequences closer to MMF increase in frequency and the slope of the fitness bisector shifts as shown by the arrow. At equilibrium, all females produce MMF and the fitness bisector passes through MMF (Fig. 4D). The slope of $\widehat{\beta}$, $\widehat{M}/\widehat{F}$ is greater than the slope of ε, c_f/c_m. Therefore, $\widehat{M}c_m/\widehat{F}c_f$, and investment at equilibrium is biased towards males (the more helpful sex). Since the effective fitness isocline does not pass through the set of accessible strategies, no other strategy can invade, and the strategy $(\widehat{F}_L, \widehat{M}_L)$ is a global ESS, and since it can invade any population fixed for a different strategy, it is also convergence stable (see Apaloo 2009).

It is possible that the fitness bisector at equilibrium passes through an edge rather than a corner on the outer boundary of the accessible set, in which case the effective fitness isocline is coincident with an outer line segment and all lifetime strategies that correspond to points on that line segment are equally fit. Such an equilibrium can be monomorphic or polymorphic (if a mixture producing $\widehat{M}/\widehat{F}$ is genetically self-sustaining.)

As the maximum number of broods, z, becomes large, the set of accessible strategies takes on a smooth shape (Fig. 5). At equilibrium with very large z, the fitness bisector passes through a point on the outer boundary, and the effective fitness isocline is tangent at that point. Investment at equilibrium is biased toward the more helpful sex.

In the case where there is a single bout of helping (α = 2) and there is an intermediate sex ratio that is optimal in the transition brood $\widehat{t}$, the evolutionarily stable investment ratios are

$$\frac{\widehat{M}c_m}{\widehat{F}c_f}=l_{\hat{i}}\left[l_{\hat{i}}+\left(R_{f1}-R_{m1}\right)\sum_{i=1}^{z-\widehat{t}}l_{\widehat{t}+i}R_{f1}^{i-1}\right]^{-1}\quad \text{for}\quad R_{m1}>R_{f1}$$

$$\frac{\widehat{M}c_m}{\widehat{F}c_f}=l_{\hat{i}}\left[l_{\hat{i}}+\left(R_{m1}-R_{f1}\right)\sum_{n=1}^{z-\widehat{t}}l_{\widehat{t}+n}R_{m1}^{n-1}\right]^{-1}\quad \text{for}\quad R_{m1}<R_{f1}$$

(see Appendix D). The equilibrium ratio is biased toward the sex that is more helpful per unit cost (i.e., the sex s with the greater value of $R_{si}=l_{fn-i}\gamma_s\tau_s C_s^{-1}$). Only the more-helpful sex is produced before the transition brood $\widehat{t}$, and only the less-helpful sex thereafter. When the two sexes are equally helpful, equal investment holds ($\widehat{F}c_f=\widehat{M}c_m$) and there is no advantage to producing different sex ratios in different broods.

3.3. Evolutionary Equilibrium with Conditional Sex Ratios and Nonlinear Returns to Helping

We now consider cases where females have the ability to alter their sex ratios from brood to brood and there are nonlinear resource returns from helping. For simplicity, we analyze cases with a single bout of helping (α = 2) in which case the amount of resource in the next brood is

$$E_{n+1}=E_p+g_f\left(f_n,m_n\right)+g_m\left(f_n,m_n\right) \quad [14]$$

from Eqn. 9. We assume that males are more helpful per unit cost when alone, i.e., $l_{m1}\gamma_m\tau_m c_m^{-1}>l_{f1}\gamma_f\tau_f c_f^{-1}$ but equivalent results apply if females are more helpful per unit cost.

We begin with the special case in which only males help, i.e., $g_f(f_n, m_n) = 0$ and $g_m(f_n, m_n) > 0$ for all n. If female offspring have no positive influence on the effectiveness of male helpers, i.e., $dg_m/df_n \le 0$, total lifetime resource and total lifetime male production both take their maximal values, say $\tilde{E}_L$ and $\tilde{M}_L$, if only males are produced in every brood:

$$\tilde{E}_L=\sum_{n=1}^{z}l_{fn}\tilde{E}_n \quad \text{and} \quad \tilde{M}_L=\sum_{n=1}^{z}l_{fn}\tilde{E}_n/c_m=\tilde{E}_L/c_m,$$

where $\tilde{E}_n$ is the maximal amount of resource in brood n from producing only males in brood $n-1$. Now consider a "bang-bang" strategy such that only males are produced in every brood $n<t$, a possible mixture in brood t, and only females in broods $n>t$. Such a strategy devotes an amount

$$E_f = l_{ft}\,(1-k_t)\,E_t + \sum_{n=t+1}^{z} l_{fn} E_n\,(k_t)$$

to female production where k_t is the fraction invested in males in brood t and $E_n(k_t)$ is the resource available in brood n given k_t and the exclusive production of females in each brood $n>t$. The lifetime amount of resource devoted to male production by such a strategy is $\tilde{E}_L - E_f$. Now consider any other strategy with some lifetime amount of resource E_L that devotes the same amount to female production. Such a strategy produces the same number of females as the bang-bang strategy but devotes less total lifetime resource to male production, $E_L - E_f$, since E_L is necessarily less than. The bang-bang strategy produces more males for any value of E_f and must comprise the outer boundary of the set of accessible strategies. Consequently, if only a single sex helps, the optimal strategy is the same bang-bang strategy as in the case of linear returns except for transition brood, in which an intermediate sex ratio may be favored. If so, the optimal strategy in the transition brood consists of a mixture of extreme sex ratios if there are increasing returns and a single intermediate sex ratio if there are diminishing returns.

If offspring of both sexes provide help, a variation on the bang-bang strategy between extreme brood sex ratios is optimal: increase resource availability as quickly as possible in early broods (which may involve the production of both sexes) and then switch to the exclusive production of the less-helpful sex. To see this, we first find the constrained values of $\tilde{f}_n$ and $\tilde{m}_n$ that maximize E_{n+1}. The Lagrangian function for this problem is

$$\Lambda\,(f_n, m_n) = E_{n+1} - \Psi \pi_n = 0$$

where ψ is an undetermined coefficient, E_{n+1} is given by Eqn. 14, $\pi_n = f_n c_f + m_n c_m - E_n = 0$ and. The necessary conditions for $\tilde{E}_{n+1}(\tilde{f}_n, \tilde{m}_n)$ to be a constrained maximum are:

$$\frac{\partial \Lambda}{\partial f_n} = \frac{\partial g_f}{\partial f_n} + \frac{\partial g_m}{\partial f_n} - \Psi c_f = 0$$

$$\frac{\partial \Lambda}{\partial m_n} = \frac{\partial g_f}{\partial m_n} + \frac{\partial g_m}{\partial m_n} - \Psi c_m = 0$$

$$\frac{\partial \Lambda}{\partial \Psi} = f_n c_f + m_n c_m - E_n = 0$$

evaluated at $(\tilde{f}_n, \tilde{m}_n)$. From the first two equations, we see that an intermediate sex ratio in brood n maximizes E_{n+1} only if

$$\frac{1}{c_f}\left(\frac{\partial g_f}{\partial f_n}+\frac{\partial g_m}{\partial f_n}\right)=\frac{1}{c_m}\left(\frac{\partial g_f}{\partial m_n}+\frac{\partial g_m}{\partial m_n}\right), \quad [15]$$

i.e., only if the resource returns per unit cost are the same for the two sexes. Given a linear constraint on each brood, an extreme value of E_{n+1} typically requires an extreme sex ratio in brood n if there is sex-biased helping. A given female can produce from 1 to E_n/c_m males in brood n. Suppose she has already produced m_n males and no females. If she still has sufficient resource to produce another offspring, she should produce her first female if $g_f(1, m_n) > g_m(0, m_n+1)-g_m(0, m_n)$ and another male if the inequality is reversed. Even if male helpers face diminishing returns, a female may go through her entire life before the resource provided by the next male falls below that of the first female, especially if brood sizes and the lifetime number of broods are both small.

If there is a global maximum value of $\tilde{E}_{n+1}(\tilde{f}_n, \tilde{m}_n)$ for each brood n, the maximal lifetime amount of resource $\tilde{E}_L$ corresponds to producing $(\tilde{f}_n, \tilde{m}_n)$ as appropriate for each brood n. In such a case, the relevant portion of the outer boundary of the set of accessible strategies corresponds to taking the lifetime strategy that produces $\tilde{E}_L$ and successively converting earlier broods to female production beginning with the terminal brood z. Consequently, the optimal lifetime strategy is a modified bang-bang strategy such that $\tilde{E}_{n+1}(\tilde{f}_n, \tilde{m}_n)$ is maximized in earlier broods followed by the exclusive production of the less-helpful sex in later broods. In contrast to the linear case, the strategy that maximizes $\tilde{E}_L$ may differ from the exclusive production of the initially more-helpful sex.

It is helpful to consider E_n given by Eqn. 10, which assumes exponential gains within each sex. We have

$$\frac{\tilde{m}_n^{b-1}}{\tilde{f}_n^{a-1}}=\left[\frac{a\left(l_{f1}\gamma\right)^a\tau_f c_m}{b(l_{m1}\gamma)^b\tau_m c_f}\right]$$

as a necessary condition from Eqn. 15. This condition is difficult to satisfy, and extreme sex ratios are often favored. In the special case where $a = b$, we have

$$\frac{\tilde{m}_n}{\tilde{f}_n}=\left[\frac{\left(l_{f1}\gamma\right)^a\tau_f c_m}{(l_{m1}\gamma)^a\tau_m c_f}\right]^{\frac{1}{a-1}},$$

which is the same for all n, and a strategy that maximizes E_L is a fixed-k strategy as illustrated in Fig. 3. Figs. 3A and 3B illustrate special cases with all helping parameters identical in the two sexes; equal investment is favored in every brood and there is no selection for facultative adjustment. A fixed intermediate sex ratio is favored in every brood in the case of diminishing returns (Fig. 3A), and the same result is achieved as a mixture of extreme sex ratios in the case of increasing returns (Fig. 3B). If females have the ability to alter their sex ratios from brood to brood and the two sexes have different helping parameters, however, the lifetime output constraints based on employing a fixed k in every brood as shown in Fig. 3 do not correspond to the outer boundary of the set of accessible strategies. The fixed-k strategy that maximizes E_L corresponds to a point on the lifetime output constraint that is tangent to a line with a slope $-c_f/c_m$. The outer boundary between $\tilde{E}_L$ and the F_L axis lies beyond the fixed-k curve and corresponds to bang-bang strategies such that E_L is maximized in early broods and only the less-helpful sex is produced thereafter. In general, sex-biased helping favors the bang-bang strategy that maximizes resource accrual in early broods and then switches to exclusive production of the less-helpful sex.

The sufficient conditions such that $\tilde{E}_{n+1}$ is a local maximum depend on the signs of the principal minors of the bordered Hessian, i.e.,

$$|H_1|=\det\begin{pmatrix} 0 & c_f \\ c_f & \Lambda_{ff} \end{pmatrix} \quad \text{and} \quad |H_2|=\det\begin{pmatrix} 0 & c_f & c_m \\ c_f & \Lambda_{ff} & \lambda_{fm} \\ c_m & \Lambda_{mf} & \Lambda_{mm} \end{pmatrix},$$

where $\Lambda_{xy}=\partial^2\lambda/\partial x\partial y$ with $x, y = f_n$ or m. If $|H_1| < 0$ and $|H_2| > 0$, $\tilde{E}_{n+1}$ is a local maximum. $|H_1|= - c_f^2$ is always negative, while the sign of $|H_2|$ depends on the second partials of Γ. If E_n is given by Eqn. 10, $\Lambda_{mm}=\Lambda_{mf}=0$, $\Lambda_{ff}=a\,(a-1)\,f_n^{a-2}\left(l_{f1}\gamma_f\right)^a\tau_f$, Γ_{mm} $=b(b-1_{mn}b-2l_{f1}\gamma_f b\tau_m$, and $H_2 =-c_m 2\Gamma_{ff}-c_f 2\Gamma_{mm}$. If both sexes are subject to diminishing returns (i.e., $a, b>1$), $|H_2|$ is positive and $\tilde{E}_{n+1}$ is a maximum. In the event that a and b are of opposite sign, whether a given $\tilde{E}_{n+1}$ is a maximum depends on the values of Γ_{ff} and Γ_{mm} evaluated at $\tilde{f}, \tilde{m}_n$.

3.4. Evolutionary Equilibrium in a Patchy Environment

Pen and Weissing (2000) analyzed a model of conditional sex ratio adjustment in which the benefits from helpful offspring vary along an environmental gradient. They were motivated by Komdeur's (1996) report that Seychelles Warblers on high-quality patches produce mostly females (the more helpful sex) while those on low-quality patches produce mostly males. Their analysis considered fitness differences over a single time period. We analyze a model based on lifetime fitness, ϕ_f, given by Eqn. 7.

Following Pen and Weissing, we define $p(e)$ as the probability that a female reproduces on a patch of type e, where e is an environmental variable defined over the interval [0,1]. We assume that $p(e)$ applies to each female regardless of her patch of origin and that she occupies the same patch throughout her reproductive life. We further assume that population dynamics are described by the transition matrix A with suitable definitions of its elements to account for variation across patches. In particular, the survival probabilities, P_{ij}, do not vary among patches and the offspring terms f_{ij} and m_{ij} represent averages over all patches. (This kind of "mean-field" approximation to the analysis of evolutionary dynamics given environmental or spatial heterogeneity can be incorrect, cf., Durrett and Levin 1994; an analysis explicitly accounting for such heterogeneity is needed.) We evaluate the fitness of a female against this background given that she produces $F_L(e)$ and $M_L(e)$ over her lifespan on a patch of type e.

From Eqn. 7, the lifetime fitness of a female on a patch of type e is

$$\phi_f=\frac{\nu_{m0}M}{4}\left(\frac{F_L\,(e)}{F}+\frac{M_L\,(e)}{M}\right), \quad [16]$$

where F and M are the total number of offspring produced by the population. Assuming linear returns from helping, $F_L(e)$ and $M_L(e)$ are maximized when only a single sex is produced throughout life. A female can maximize her fitness by producing only females if $F_L(e)/F > M_L(e)/M$ and only males if the inequality is reversed. As females producing these extreme sex ratios increase in frequency, F and M shift until there is some value of $e = \hat{e}$ below which only one sex is favored and above which only the other sex is favored. If the lifetime output of females producing only females increases more rapidly with e than that of females producing only males, selection favors producing only males when $e < \hat{e}$ and only females when. In this case, all females produce unisexual broods, and the average lifetime production of male and female offspring are

$$\bar{M}_L=\int_0^{\hat{e}} M_L(e)\,p(e)\,de$$

$$\bar{F}_L=\int_{\hat{e}}^1 F_L(e)\,p(e)\,de,$$

A female reproducing on a patch at the transition point formula gains the same amount of fitness through the exclusive production of females as through the exclusive production of males, and from Eqn. 16,

$$\frac{F_L(\hat{e})}{F}=\frac{M_L(\hat{e})}{M}.$$

This can be written as

$$F_L(\hat{e})\,\bar{M}_L=\int_0^{\hat{e}} p(e)\,de=M_L(\hat{e})\,\bar{F}_L=\int_{\hat{e}}^1 p(e)\,de \qquad [17]$$

since M is proportional to $\frac{N_M}{N_T}=\int_0^{\hat{e}} p(e)\,de$ and F is proportional to $\frac{N_F}{N_T}=\int_{\hat{e}}^1 p(e)\,de$, where N_M is the number of male-only patches, N_F is the number of female-only patches, and N_T is the total number of patches with reproducing females. (Eqn. 17 can be compared to similar expressions in Pen and Weissing 2000 who incorrectly divide by N_M/N_T and N_F/N_T.) Since we assume that both $M_L(e)$ and $F_L(e)$ increase with e, $M_L(e)$ takes its maximal value and $F_L(e)$ takes its minimal value at $e = \hat{e}$ and thus $M_L(\hat{e}) > \bar{M}_L$ and $F_L(\hat{e}) < \bar{F}_L$. It follows from Eqn. 14 that

$$\int_0^{\hat{e}} p(e)\,de>\int_{\hat{e}}^1 p(e)\,de,$$

so there are more male-only patches than female-only patches at equilibrium. The argument is symmetrical, and if $M_L(e)$ increases more rapidly with e than $F_L(e)$, there are more female-only patches than male-only patches at equilibrium. In either case, there is a greater number of less-productive patches at equilibrium as compared to the number of more-productive patches.

At equilibrium, the total number of males, M, may be less than or greater than the total number of females, F, depending on the distribution of patch types and how $M_L(e)$ and $F_L(e)$ vary with e. In the special case where $\bar{M}_L=\bar{F}_L$ or nearly so, the population sex ratio is biased toward the sex produced on the less productive patches.

4. Discussion

4.1. Our results in the context of previous theoretical results

The original idea underlying the repayment model was that the more-helpful sex is effectively less expensive to produce because of its greater contribution to later broods

(Malcolm and Marten 1982). Accordingly, it seemed plausible that natural selection would favor excess production of this sex. However, it is misleading to say that the more-helpful sex is less expensive to produce. Instead, the value of the more-helpful sex is that it increases the amount of limiting resource available for offspring production in later broods by a greater amount than does the other sex. This advantage declines with age since there are fewer later broods to benefit from the additional resource, and the way to take maximal advantage of the greater rate of resource accrual is to produce the more-helpful sex in early broods and then convert the accumulated capital to the production of the less-helpful sex in later broods. It is remarkable that this has not been previously noted.

A fundamental flaw in previous theoretical treatments of the repayment model is their focus on the fitness associated with a single brood rather than on the fitness associated with the sequence of broods produced over the lifetime. Analysis of lifetime fitness is required to account for the consequences of early sex ratio decisions on later reproductive opportunities. Earlier work was further limited by the assumption that females employ a fixed sex ratio throughout their lives. This assumption precluded facultative adjustment from brood to brood, which we find to be a common feature of optimal strategies when there is sex-biased helping.

If females have the ability to adjust their sex ratios from brood to brood, our central result is that the optimal sex-ratio strategy consists of maximizing the amount of resource available for offspring production in early broods (which can involve the exclusive production of the more-helpful sex) followed by the exclusive production of the less-helpful sex. Similar bang-bang strategies are optimal in other situations involving a tradeoff between investment in productive capacity and investment in reproduction. For example, Cohen (1971) showed that seed production in an annual plant is maximized by first investing in vegetative growth, which increases photosynthetic capacity, and then using this capacity to produce seeds. Similarly, Macevicz and Oster (1976) and Oster and Wilson (1978) showed that the number of reproductives produced by an annual colony of social insects is maximized by producing only workers (thereby increasing the rate of resource harvesting) and then using this enhanced productive capacity to produce only reproductives. In all of these cases, the optimal strategy consists of an early phase devoted to expanding productive capacity and a later phase devoted to converting that capacity to fitness.

We note that sex-biased offspring helping engenders a fundamental tension between natural selection for excess production of the more-helpful sex (so as to maximize the gain from offspring helping) and natural selection for equal investment in the two sexes (because both sexes contribute equally to future generations). The investment optima we have identified in the context of the repayment model represent “compromises” between these selective pressures. In a uniform environment, the compromise is greater investment in the more-helpful sex in the population as a whole, whereas when the returns from helping vary because of local circumstances, investment in the population as a whole can be biased towards the less-helpful sex.

4.2. Our results and sex ratios in natural populations

4.2.1. Why are extreme sex ratios rare?—Extreme sex ratios are a component of most of the optimal facultative strategies we derive, but such sex ratios appear to be rare in natural populations of vertebrates. We note that sex-ratio biases in vertebrates such as the Seychelles Warbler and the African Wild Dog demonstrate that chromosomal sex determination provides no necessary barrier to strongly-biased sex ratios. In as much as few data on the sequence of brood sex ratios produced by individual females are available, it is possible that strongly-biased sex ratios are more common than now believed.

If such sex ratios are truly rare, there are several possible non-exclusive reasons.

First, intermediate sex ratios are favored under the assumption that the same sex ratio is produced throughout life. However, such an equilibrium can be invaded by a conditional strategy producing the more-helpful sex in early broods and the less-helpful sex in later broods.

Second, biased sex ratios are expected only if male and female helpers differ in their helping ability; such differences may not be common. If offspring of both sexes are similarly effective as helpers, there is no selective pressure to bias the sex ratio. Unfortunately, present data on sex differences are limited and even some well-studied species lack adequate information on such differences (see Table 1).

Environmental stochasticity may also cause intermediate sex ratios to be optimal when there is sex-biased helping. At present, there are no analyses of stochasticity that include offspring helping. However, Bull (1981) analyzed a sex ratio model with two patch types having different consequences for sex-specific fitness. He showed that extreme sex ratios are favored for sufficiently large differences in sex-specific fitness, but intermediate sex ratios are favored in both patches if the ratio of sex-specific fitnesses is sufficiently close to 1.0. Results from the analysis of other life history phenomena also indicate that stochasticity can lead to the evolution of a graded response, although this is not universal (see Kozlowski 1992, Perrin and Sibly 1993, and Mitesser et al. 2007). For example, Cohen (1971) showed that an optimal annual plant should first grow and then reproduce. But King and Roughgarden (1982) and Amir and Cohen (1990) showed that if the probability of survival varies over time, natural selection can favor a graded response such that growth and reproduction occur simultaneously over a portion of the season. These results underscore the need for analyses of helping models that account for the consequences of temporal variation of survival probabilities and of resource provided per helper. Also worth exploring are the consequences of noisy perception (e.g., females can only crudely determine brood number or patch type) and noisy control (e.g., females can only adjust the mean of a conditional sex ratio).

Another important theoretical endeavor is analysis of the influence of the number of helpers on parental survival. Previous analyses of the influence of offspring on parental survival but without helping (Charlesworth 1977, Charnov 1982, p. 96, and Frank 1998, p. 221) indicate that natural selection favors postponing production of the sex that has a larger negative influence on parental survival. We expect that the joint influence of helping on parental reproduction and on survival is such that conditional sex ratios are favored. This will be true if the more helpful sex (in terms of resource accrual) also increases the survival rate of the parent. However, helping a female produce more offspring could decrease her survival rate more than if she were unaided. Explicit analyses given plausible assumptions as well as data on the influence of helping on parental survival are needed.

4.2.2. A reanalysis of the relationship between offspring helping and sex allocation—We now address empirical studies of offspring helping and sex allocation in birds and mammals and how they may relate to our theoretical results. West's (2009) summary of such empirical studies is based upon West and Sheldon (2002), Griffin and West (2003), West et al. (2005), and Griffin et al. (2005). The premise of these analyses is that females produce a sex ratio that is conditional upon the number of helpers present. For example, West and Sheldon (2002, p. 1685) stated that they are "restricting their meta-analyses to cases in which there is a clear theoretical prediction as to the direction of an effect" and that "in cooperatively breeding species where one sex helps (in the rearing of subsequent offspring) more than the other, it is predicted that when an individual (or group) lacks helping individuals, they should bias their offspring sex ratio toward the sex that provides greater help." (see also West et al. 2005, p. 1213). Gowaty and Lennartz (1985) were the first to make this claim that females should respond conditionally to the presence and absence of helpers. However, there is no current theoretical support for such a claim.

West et al. cited Pen and Weissing (2000) as having demonstrated this claim, but their analyses assume either a fixed sex ratio or one dependent upon patch quality if the returns to helping vary across patches. In the latter case, assuming linear returns to helping, females are selected to produce only the more-helpful or the less-helpful sex depending on patch quality, regardless of whether helpers are present. Similar mistaken confounding of an optimal conditional sex allocation behavior with a range of unconditional sex allocation behaviors are well known. For example, Werren (1983) incorrectly interpreted the range of optimal unconditional sex ratios across foundress number (as predicted by Hamilton's 1967 model of local mate competition in which foundress number is a fixed constant) as a prediction of the conditional set of sex ratios produced by a female when she encounters variable foundress number during her lifetime.

The data set analyzed by West (2009) contains species that appear to differ in their response to the benefits of helping (based on the incorrect belief that females should respond conditionally to the number of helpers present, see above). These differences were interpreted by Griffin et al. (2005) as supporting the adaptive claim that the magnitude of the evolved sex ratio adjustment in response to the presence or absence of helpers is proportional to the magnitude of the benefit the helpers provide.

The treatment and interpretation by West and colleagues of the data concerning conditional sex ratios and helping are problematic for several reasons.

First, they assume that the reproductive ecology of the species is broadly consistent with the assumptions of the repayment model. However, this is not credible for some of the species. For example, the Bell Miner (*Manorina melanophrys*) has colonies that often include hundreds of birds and are comprised of smaller groups (coteries) with one to three reproducing females (Ewen et al. 2003). Coteries also include multiple non-reproductives, which are usually male. Related and unrelated individuals of both sexes help but females disperse early, apparently joining other coteries (Wright et al. 2010). Ewen et al. reported a male bias in the population and that broods produced in the first year of a new territory are female-biased while all subsequent broods are male-biased. Males help rear offspring of all females in the group, but there is no evidence that an increase in the number of male helpers results in an increase in the number of offspring produced. Additional males may have value in ensuring a sizable group to hold new territory, and excluding competitors.

This reproductive ecology is very different from that embodied in the repayment model, and it is misleading to include the Bell Miner case as an apparently unambiguous example of offspring helping. At minimum, a suitable model for this species would include coterie dynamics. The repayment model has the assumption that females start out with no helpers and produce all helpers themselves. In Bell Miners, however, helpers are always present and much of their benefit may accrue solely from their ability to increase resource availability for the coterie as a whole.

Other species included by West and colleagues that have substantive discrepancies between their reproductive biology and the repayment model are the Seychelles Warbler, the Acorn Woodpecker, and the Red-cockaded Woodpecker.

Second, West and colleagues ignored some contrary results presented by the authors of the studies they included. For example, they presented Gowaty and Lennartz's (1985) finding in the Red-cockaded Woodpecker of a sex ratio bias among offspring of females that were new arrivals to a breeding group (interpreted by Gowaty and Lennartz as an adaptive response to avoid mate competition among sons, see pp. 350-351). However, West and colleagues did not include Gowaty and Lennartz's test of the hypothesis that parents adjust their sex ratios in response to the number of helpers present. These authors stated (p. 350)

> The nestling and fledgling sex ratios for unassisted pairs (48 males to 26 females, 65% males) differed significantly from 50, 50 ($G = 6.6394$, df = 1, $P < .01$), whereas pairs with auxiliaries [helpers] produced sex ratios among nestlings (51 males to 43 females, 54% males) and fledglings (50 males to 42 females, 54%) that were not significantly different from 50, 50. Despite the interesting apparent disparity in the sex ratios for the two clan types, no statistical dependence of sex on clan type is apparent ($G = 1.6$, df = 1, $P > .10$).

Third, we cannot replicate all of the meta-analytic results reported by West and Sheldon (2002), West et al. (2005), and Griffin et al. (2005) based on the information provided in the original papers (see Table 1).

Fourth, the analysis of Griffin et al. (2005) contained some effect sizes for conditional sex ratio adjustment that were based on comparing brood sex ratios and others based on comparing the aggregated offspring produced by pairs with helpers with the aggregated offspring produced without helpers (for Acorn Woodpecker and Harris's Hawk). West et al. (2005, p. 1214) claimed that effect sizes must be calculated using the number of pairs or broods in a study. The assumption underlying this approach is that a single decision on the part of the female or parental pair determines the sex ratio of the entire brood given the helping environment. In fact, it is arguable that the sex of each offspring is determined independently for most if not all of the vertebrate species analyzed here (and for vertebrates in general; few, if any, studies suggest that vertebrate sex ratios are overdispersed, as would be expected if the sex of siblings is positively correlated). Regardless of one's decision about the best choice of effect size estimate from a biological point of view, it is clear that the two types of estimates should not be mingled in the same analysis.

In light of the above considerations, we reanalyzed the association reported by Griffin et al. We have included all species, including those whose reproductive ecology is only very loosely consistent with the repayment model (see above and related discussion in Koenig and Walters 1999). We provide new sex ratio and helping effect size estimates for various species, based on the information provided in the original papers, the original data, or recent more complete data (see Table 1).

We did two separate analyses of the data, one based on sex ratio effect sizes calculated at the brood level and one based on sex ratio effect sizes calculated at the individual level (see Figure 6). In the former case, the Pearson correlation between effect size estimates for helping and effect size estimates for the sex ratio is 0.084 ($n = 7$, $P = 0.858$, 95% CI: −0.714 - 0.787). In the latter case, the Pearson correlation is 0.337 ($n = 8$, $P = 0.415$, 95% CI: −0.482 - 0.842). (For both cases, estimates of rank correlations have P values similar to those shown for the Pearson correlation).

We conclude that there is no current evidence of an association between sex ratio adjustment and the benefits of helping. These results underscore the *lack* of resolution (cf. West 2009, p. 42) of "the debate of over the generality of sex ratio adjustment in response to [local resource enhancement] in vertebrates." Even if there were evidence for such an association, present theory does not predict a conditional sex ratio adjustment to the presence and absence of helpers, and so the evolutionary basis of the association would be unclear. It would be premature to interpret such an association as a consequence of natural selection.

Of course, further theoretical work may reveal circumstances under which females are selected to conditionally adjust their sex ratios to the presence and absence of helpers in individual broods. If so, what would remain to be determined is whether the biological assumptions of models that predict such a conditional adjustment are consistent with the biology of the species analyzed here.

Finally, we emphasize that our models of helping in a uniform environment all predict that the equilibrium *population* sex ratio is biased towards the more helpful sex (if there is one). It is incorrect to conclude *in general* that population sex ratios when sex-biased helping is present are too “hard to predict” (cf., West 2009, p. 39) (although this is correct in some circumstances). To this extent, we suspect that many instances of unbiased population sex ratios in the presence of sex-biased helping reflect a true lack of response to natural selection favoring biased investment.

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Appendix A. Historical overview of wor k on conditional sex allocation

It has long been recognized that parents in some species produce different sex ratios depending on the conditions they experience. Düsing (1884) presented many examples of what he interpreted as sex ratios changing in response to changes in nutritional status of parents. Fabre (1886) showed that females of some solitary wasps and bees could influence the sex of their offspring and that they provided more food for female offspring than for male offspring. He also argued that females benefit more from being larger than do males. Fabre noted that the behavior made efficient use of scarce resources, but he never suggested that this was a consequence of natural selection (Fabre never accepted Darwinism, see Favret 1999.) Chewyreuv (1913) showed that ichneumonid parasites of lepidopteran pupae produce mostly males on small hosts and mostly females on large hosts, but he also offered no adaptive explanation.

Sex can also be a conditional response by offspring rather than by their parents. For example, Baltzer (1914) showed that if a planktonic larva of the echiuroid worm *Bonellia viridis* settles in an area without conspecifics it develops as a female and if it settles on an adult female it develops into a dwarf male. In this case, individuals shift their investment entirely to the production of ova or of sperm. Williams (1966, pp. 154-155) judged this conditional sex determination to be an adaptation.

Ghiselin (1969, p. 190) provided a description of adaptive facultative sex allocation in his work on sequential hermphroditism, “Suppose that the reproductive functions of one sex were better discharged by a small animal, or those of the other sex by a large one. An animal which, as it grew, assumed the sex advantageous to its current size would thereby increase it reproductive potential. The model could be extended to cover other advantages of membership in a particular sex at a given period of life…” This is equivalent to facultative adjustment of the sex ratio by parents when they face different conditions with different consequences for the expected reproductive potential of male and female offspring. Trivers and Willard (1973) suggested that such facultative adjustment according to maternal condition could be an important source of biased brood sex ratios in mammals.

These early authors arguing for the adaptive value of conditional sex allocation were analyzing different situations: environmental sex determination (Williams 1966), sequential hermaphroditism (Ghiselin 1969), and the sex-specific consequences of differences in maternal condition (Trivers and Willard 1973). Nonetheless, a common logic underlies these cases. If individuals face different conditions such that the relative reproductive potential of being a female differs from that of being a male, they can increase their contribution to future generations by becoming the locally-favored sex or by changing to that sex or by producing offspring of that sex. The requirements for adaptive adjustment to local conditions were discussed by Charnov and Bull (1977) in the context of environmental sex determination.

These early verbal arguments were followed by mathematical treatments of conditional sex allocation. Among the first were the simulation results of Warner (1975) and the analytical work of Warner et al. (1975) and Leigh et al.(1976), all of which dealt with sequential hermaphroditism. In these models, the relative fitness associated with being male or female changes with age or size, and it is necessary to consider lifetime fitness in populations with age or size structure and overlapping generations. The simpler case of a randomly mating population with discrete generations in which individuals randomly encounter “patches” in which the relative value of the two sexes differ was explored by Charnov (1979a, b), Charnov et al. (1981), Bull (1981), and Green (1982). Patches may be defined geographically or in other ways such as when parasitic wasps encounter hosts of different sizes.

Models vary in terms of the kind of patches considered and how sex is determined (e.g., by parents or offspring), but two conclusions apply across all current deterministic “patchy condition“ models. The first is that extreme sex ratios are favored, all males or all females in each patch with the possible exception of a single patch type where a mixture may be favored. If we order the set of patches by the relative fitness of the two sexes, say V_{mi}/V_{fi}, where V_{mi} is the fitness of a male in patch type i measured relative to other males and V_{fi} is the same for females measured relative to other females, then there is some value of V_{mi}/V_{fi} below which only one sex is favored and above which the other sex is favored. The second conclusion is that the population sex ratio depends on the distribution of patch types and generally does not reflect equal investment in the two sexes, as repeatedly emphasized by Frank (1987, 1990, 1995) but contrary to Trivers and Willard (1973).

Appendix B. Reproductive value and investment ratio at demographic equilibrium

We show that the total reproductive value through female offspring equals that through male offspring at demographic equilibrium. The right eigenvector u associated with the dominant eigenvalue λ describes the stable age distribution determined by the vital rates in A. At equilibrium, we have

$$u_{f0}=\frac{1}{2\lambda}\left(f_{f\alpha}u_{f\alpha}+\cdots+f_{f\omega}u_{f\omega}+f_{m\alpha}u_{m\alpha}+\cdots+f_{m\omega}u_{m\omega}\right)=\frac{F}{\lambda} \quad \text{[B.1]}$$

$$u_{m0}=\frac{1}{2\lambda}\left(m_{f\alpha}u_{f\alpha}+\cdots+m_{f\omega}u_{f\omega}+m_{m\alpha}u_{m\alpha}+\cdots+m_{m\omega}u_{m\omega}\right)=\frac{M}{\lambda} \quad \text{[B.2]}$$

(up to a common multiple). The expression in parentheses in each equation is equal to $2F$ ($2M$) because the total number of females (males) produced by females must equal the total number of females (males) produced by males (see Eqns. 1 and 2, which describe F and M at time t). The remaining elements of u are given by

$$u_{fx}=\frac{P_{fx}}{\lambda}u_{fx-1}=\frac{l_{fx}}{\lambda^{x}}u_{f0}\quad \text{for}\quad 1\le x\le \text{to}\quad \omega\quad [\text{B.3}]$$

$$u_{mx}=\frac{P_{mx}}{\lambda}u_{mx-1}=\frac{l_{mx}}{\lambda^{x}}u_{m0}\quad \text{for}\quad 1\le x\le \text{to}\quad \omega\quad [\text{B.4}]$$

where $l_{sx}=\sum_{x=0}^{x-1}P_{ix}$ is the probability an individual of sex s survives to age x.

Since $l_{fx}/\lambda^{x}=u_{fx}/u_{f0}$ and $l_{mx}/\lambda^{x}=u_{mx}/u_{m0}$, from Eqns. B.3 and B.4, we have

$$v_{f0}=\frac{v_{f0}}{2u_{f0}}\sum_{x=1}^{\omega}u_{fx}f_{fx}+\frac{v_{m0}}{2u_{f0}}\sum_{x-1}^{\omega}u_{fx}m_{fx}=\frac{1}{2u_{f0}}\left(v_{f0}F+v_{m0}M\right)$$

$$v_{m0}=\frac{v_{f0}}{2u_{m0}}\sum_{x=1}^{\omega}u_{mx}f_{mx}+\frac{v_{m0}}{2u_{m0}}\sum_{x-1}^{\omega}u_{mx}m_{mx}=\frac{1}{2u_{m0}}\left(v_{f0}F+v_{m0}M\right)$$

by substitution into Eqns. 4 and 5. Since formula from Eqns. B.1 and B.2, we have

$$\frac{v_{f0}}{v_{m0}}=\frac{u_{m0}}{u_{f0}}+\frac{M}{F},$$

Appendix C. Resource available for reproduction in the nth brood

We derive the amount of resource available to a female producing her n^{th} brood given that she produced the same sex ratio in each preceding brood and that each brood is subject to a linear constraint. We assume that a juvenile may become a helper at any age from 1 to $\alpha-1$ with probability σ_s before attempting to reproduce on its own at age α. The constraint on each brood n is given by

$$E_n=E_p+\sum_{i=1}^{u}\left(f_{n-i}l_{f1}\gamma_f\tau_f+m_{n-i}l_{m1}\gamma_m\tau_m\right),$$

where $u=\alpha-1$ if $\alpha-1\le z-n$ and $u=z-n$ otherwise. Taking $k=m_ic_m/(f_ic_f+m_ic_m)$ as the fixed investment ratio in each brood i, we have

$$E_n=E_p+\sum_{i=1}^{u}E_{n-i}\left[(1-k)\,c_f^{-1}l_{fi}\gamma_f\tau_f+kc_m^{-1}l_{mi}\gamma_m\tau_m\right].$$

The resource contribution to brood n by offspring of sex s produced in brood $n-i$ is

$$R_{si}=l_{si}\gamma_s\tau_sc_s^{-1}$$

and we can write

$$E_n=E_p+\sum_{i=1}^{u}E_{n-i}\left[(1-k)R_{fi}+kR_{mi}\right]=E_p+\sum_{i=1}^{u}E_{n-i}\left[X_i\right],$$

where $X_i=(1-k)R_{fi}+kR_{mi}$. When $\alpha = 2$, offspring are available for only a single bout of helping, and we have only X_1. In this case, the amounts of resource available for the first few broods are

$$E_1=E$$

$$E_2=E_p+E_pX_i=E_p(1+X_1)$$

$$E_3=E_p+E_p(1+X_1)X_i=E_p\left[1+X_1+X_1^2\right],$$

and so

$$E_n=E_p\left[\frac{1-X_1^n}{1-X_1}\right] \quad \text{[C.1]}$$

from the standard result for the sum of a geometric series.

Appendix D. Investment ratio with conditional behavior and linear returns from helping

We derive lifetime offspring production given a switch from exclusive production of one sex to the exclusive production of the other when there is a single bout of helping ($\alpha = 2$), and then use this result to obtain the evolutionarily stable investment ratio. Assume that males are the more-helpful sex ($R_{m1}>R_{f1}$) and that a female produces only males in broods 1 through $t-1$, a mixture in brood t, and only females in broods $t+1$ to z. Analogous results apply if females are the more-helpful sex and the transition is from females in early broods to males in later broods.

For the transition brood t,

$$E_t=E_p+E_{t-1}R_{m1},$$

where $E_{t-1}R_{m1}$is the contribution from helpers from the last all-male brood. The constraint on offspring production is

$$\pi_t=f_tc_f+m_tc_m-E_t$$

with slope $-c_f/c_m$. Taking $k_t = m_tc_m/E_t$, the proportion invested in malesin the transition brood t, we have $f_t=(1-k_t)E_t/c_f$ and $m_t=k_tE_t/c_f$. The lifetime output of males by a female with proportion formula in the transition brood t is

$$M_L\left(t,k_t\right)=\frac{E_p}{c_m}\sum_{n=1}^{t-1} l_n\left[\frac{1-R_{m1}^n}{1-R_{m1}}\right]+l_t k_t\frac{E_t}{c_m},$$

where the first term follows from Eqn. C.1 with $k = 1$. The lifetime production of females is

$$F_L\left(t,k_t\right)=\frac{l_t\left(1-k_t\right)E_t}{c_f}+\frac{1}{c_f}\sum_{i=1}^{z-t} l_{t+i}E_{t+i}, \quad \text{[D.1]}$$

and it remains to show how the amount of resource available in each subsequent brood, E_{t+i}, depends on k_t.

For the first brood after switching to female production,

$$E_{t+1}+E_p+E_tX_{t1},$$

where $X_{t1}=(1-k_t)R_{f1}+k_tR_{m1}$ accounts for the possibility of both male and female helpers from brood t. Only female helpers are available in subsequent broods so that

$$E_{t+2}=E_p\left(1+R_{f1}\right)+E_tX_{t1}R_{f1},$$

$$E_{t+3}=E_p\left(1+R_{f1}+R_{f1}^2\right)+E_tX_{t1}R_{f1}^2,$$

$$E_{t+4}=E_p\left(1+R_{f1}+R_{f1}^2+R_{f1}^3\right)+E_tX_{t1}R_{f1}^3$$

and for an arbitrary brood $t + i$, we have

$$E_{t+i}=E_p\left(\frac{1-R_{f1}^i}{1-R_{f1}}\right)+E_tX_{t1}R_{f1}^{i-1}, \quad \text{[D.2]}$$

where the first term on the right includes the resources in brood $t + i$ derived from parental resources (E_p) in brood $t + 1$, while the second term includes the resources in brood $t + i$ derived from helper-provided resources (E_tX_{t1}) in brood $t + 1$, all of which were produced in brood t and may have been of both sexes. Finally, substitution from Eqn. D.2 into Eqn. D.1 yields

$$F_L\left(t,k_t\right)=\frac{E_t}{c_f}\left[l_t\left(1-k_t\right)+X_{t1}\sum_{i=1}^{z-t} l_{t+i}R_{f1}^{i-1}\right]+\frac{E_p}{c_f}\sum_{i=1}^{z-t} l_{t+i}\left(\frac{1-R_{f1}^i}{1-R_{f1}}\right),$$

The set of possible sex ratios in the transition brood t corresponds to a line segment on the outer boundary of the set of accessible strategies with slope

$$\frac{\Delta M_L}{\Delta F_L}=\frac{M_L(t,1)-M_L(t,0)}{F_L(t,1)-F_L(t,0)}=-\frac{c_f}{c_m}l_t\left[l_t+\left(R_{f1}-R_{m1}\right)\sum_{n=1}^{z-t}l_{t+n}R_{f1}^{n-1}\right]^{-1}. \quad \text{[D.3]}$$

If is the optimal transition brood and $\widehat{k_t}$ is the optimal investment ratio in that brood, the sex ratio of lifetime output $M_L\left(\widehat{t,\widehat{k_t}}\right)/F_L\left(\widehat{t,k}\right)$ equals *M/F*, the sex ratio of the joint output of all females. The slope of the fitness function at such an equilibrium, say $-\widehat{M}/\widehat{F}$, must be equal to the slope of given by Eqn. D.3, and thus

$$\frac{\widehat{M}c_m}{\widehat{F}c_f}l_{\widehat{i}}\left[l_{\widehat{i}}+\left(R_{f1}-R_{m1}\right)\sum_{i=1}^{z-\widehat{t}}l_{\widehat{t}+i}R_{f1}^{i-1}\right]^{-1}.$$

An equivalent argument assuming that females are the more-helpful sex yields

$$\frac{\widehat{M}c_m}{\widehat{F}c_f}l_{\widehat{i}}\left[l_{\widehat{i}}+\left(R_{m1}-R_{f1}\right)\sum_{i=1}^{z-\widehat{t}}l_{\widehat{t}+i}R_{m1}^{i-1}\right]^{-1}.$$

In both cases, the equilibrium investment ratio is biased toward the sex that is more helpful per unit cost (i.e., the sex s with the greater value of $R_{s1}=l_{s1}\gamma_s\tau_s c_s^{-1}$).

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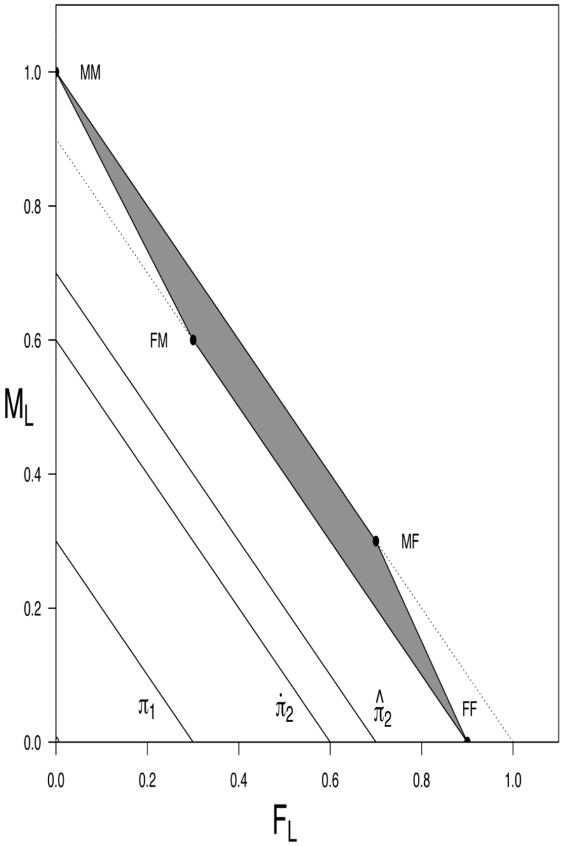


Figure 1.

Lifetime output with linear returns from helping and two broods ($z = 2$).Males are more helpful than females (τ_m=1.0, τ_f=0.5), and c_f=c_m=γ_m=γ_f=l_{f1}=l_{m1}=1. The constraints π_1, the maximal $\widehat{\pi}_2$, and the minimal $\dot{\pi}_2$ are shown as solid lines. Accessible combinations of F_L and M_L are shaded and are bounded by (dotted) lines with slope $-c_f/c_m$. Strategy MM produces only males in both broods, FF produces only females in both broods, MF produces only males in the first brood and only females in the second, and FM produces only females in the first brood and only males in the second.

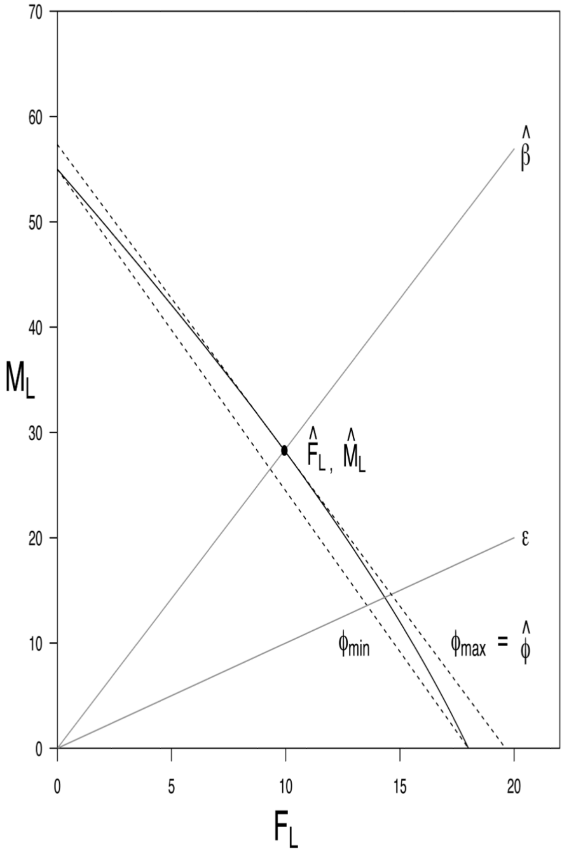
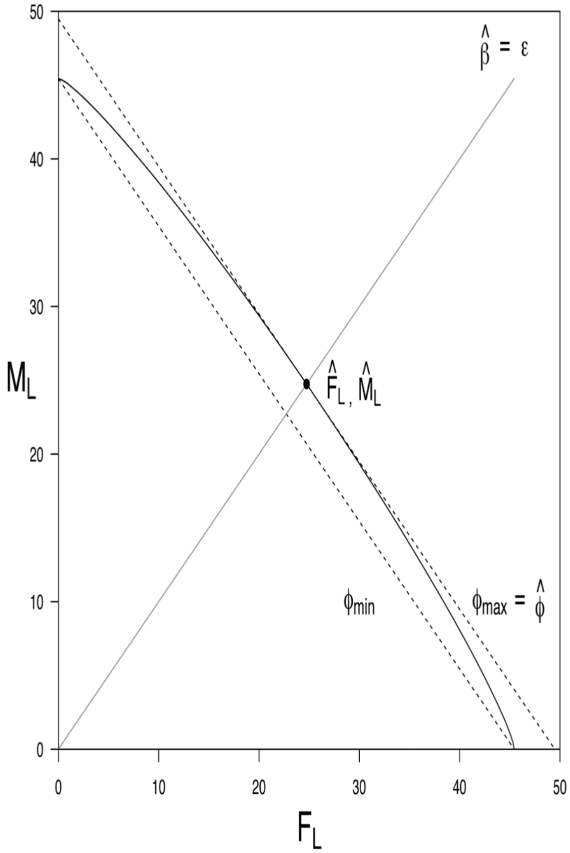


Figure 2.

Lifetime output with a fixed investment ratio *k* and linear returns from helping. Males are more helpful than females (τ_m=1.0, τ_f=0.5), and c_f=c_m=γ_m=γ_f=l_{f1}=l_{m1}=1. There is a single bout of helping (α = 2) and a maximum of ten broods (z = 10). π_L is the constraint on lifetime output (solid curve). ϕ_{min} and ϕ_{max} are the minimum and maximum fitness isoclines (dashed). $\widehat{\beta}$ is the equilibrium fitness bisector and is the equal investment line. The point formula is a global ESS and is convergence stable.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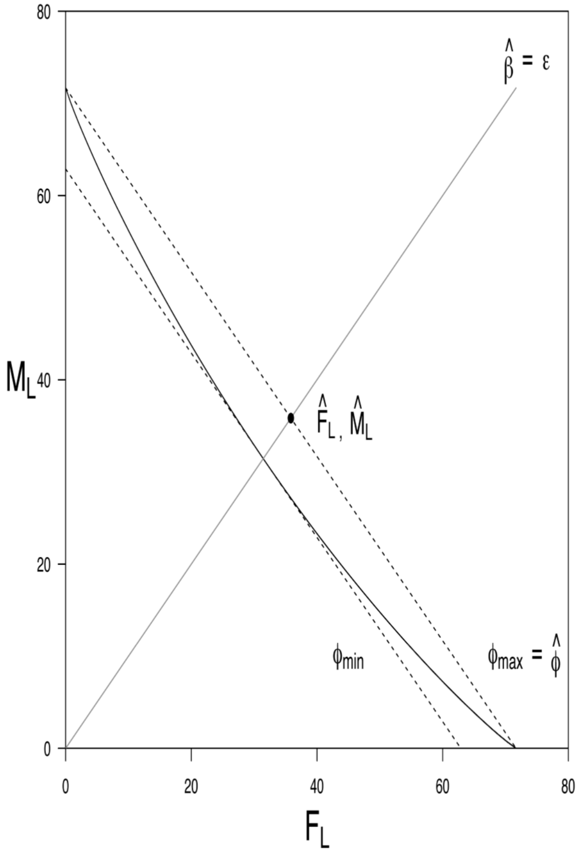

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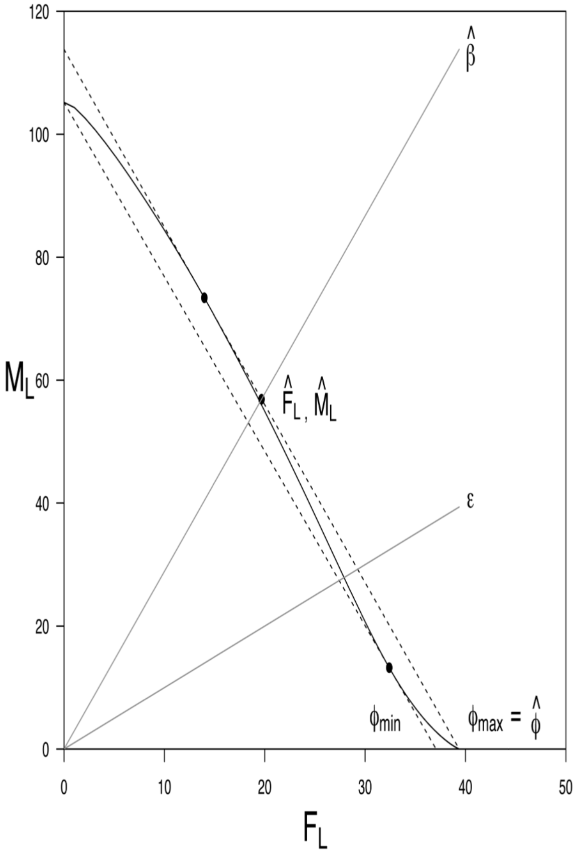

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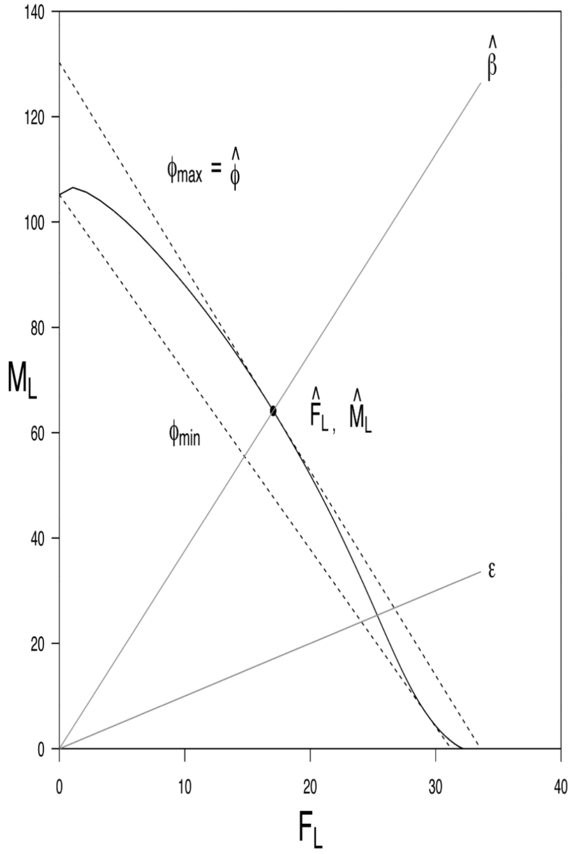


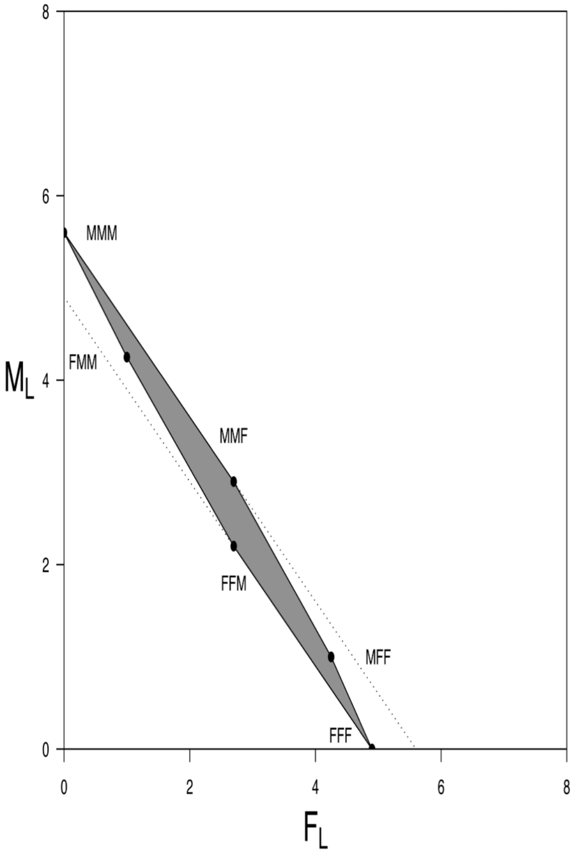
Figure 3.

(A). Lifetime output with a fixed investment ratio k and nonlinear linear returns from helping. There is a single bout of helping ($\alpha = 2$), a maximum of 10 broods ($z = 10$), and c_f=c_m=γ_m=γ_f=l_{f1}=l_{m1}=1. π_L is the constraint on lifetime output (solid curve). ϕ_{min} and ϕ_{max} are the minimum and maximum fitness isoclines (dashed). $\widehat{\beta}$ is the equilibrium fitness bisector and ε is the equal investment line. There are diminishing returns in both sexes, $a = b = 0.95$.

(B). Lifetime output with a fixed investment ratio k and nonlinear linear returns from helping. Assumptions as in 3(A) except that there are increasing returns in both sexes, $a = b = 1.02$.

(C) Lifetime output with a fixed investment ratio k and nonlinear linear returns from helping. Assumptions as in 3(A) except that there are diminishing returns in females, $a = 0.99$, and increasing returns in males, $b = 1.03$.

(D). Lifetime output with a fixed investment ratio k and nonlinear linear returns from helping. Assumptions as in 3(A) except that there are diminishing returns in females, $a = 0.98$, and increasing returns in males, $b = 1.03$.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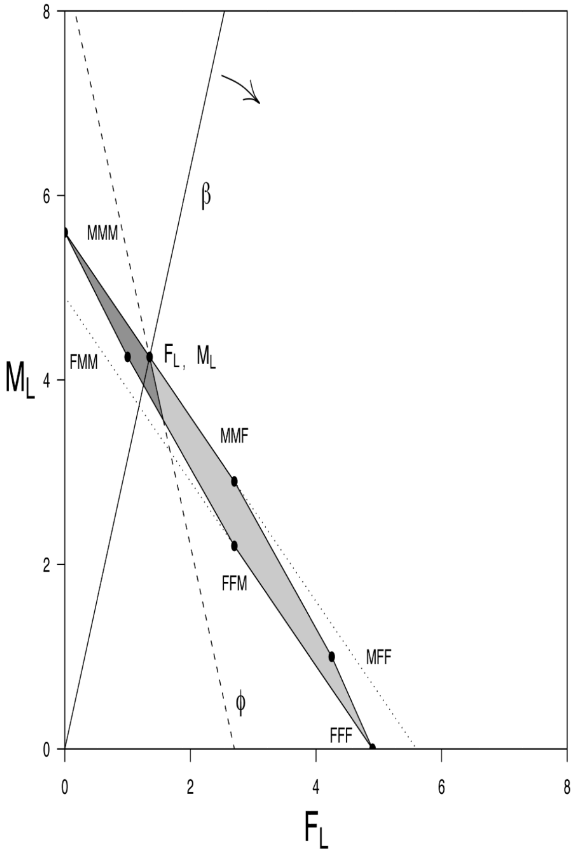
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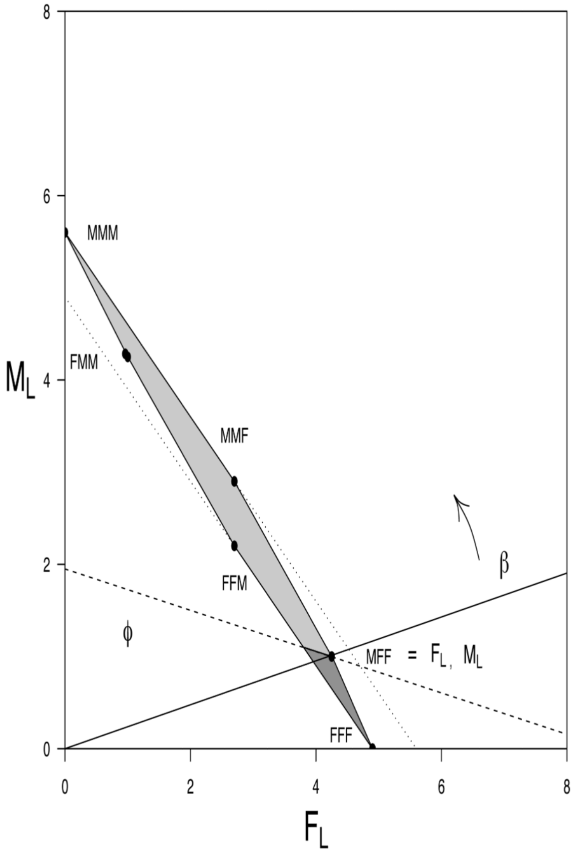
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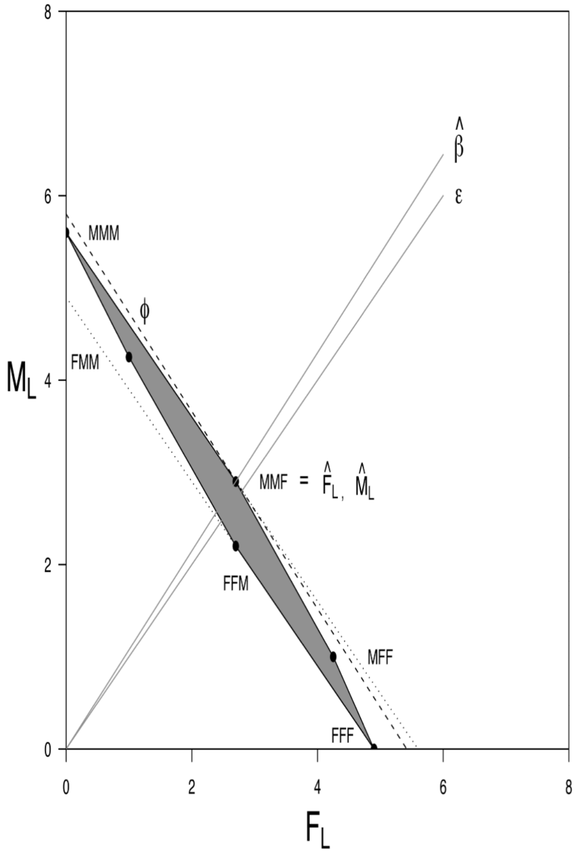

Figure 4.

(A) Lifetime output with linear returns from helping and conditional sex ratios. Males are more helpful than females (τ_m=1.0, τ_f=0.5), and c_f=c_m=γ_m=γ_f=l_{f1}=l_{m1}=1. Points on the boundary follow the same labeling convention as Fig. 1. Lifetime output is M_L, F_L. β is the fitness bisector and ϕ is the effective fitness isocline (dashed). (A) Accessible combinations of F_L and M_L are shaded and are bounded by dotted lines with slope $-c_f/c_m$.

(B). Lifetime output with linear returns from helping and conditional sex ratios. Assumptions as in 4(A) except that each female produces only males in the first two broods and mixture in the third brood.

(C). Lifetime output with linear returns from helping and conditional sex ratios. Assumptions as in 4(A) except that each female produces only females in the first brood, both sexes in the second brood, and only males in the third brood.

(D). Lifetime output with linear returns from helping and conditional sex ratios. Assumptions as in 4(A). At equilibrium, all females produce only males in the first two broods and only females in the third (MMF).The equilibrium fitness bisector $\widehat{\beta}$ passes through this point, and the equilibrium fitness isocline $\widehat{\phi}$ intersects the set of accessible strategies only at this point. is the equal-investment line.

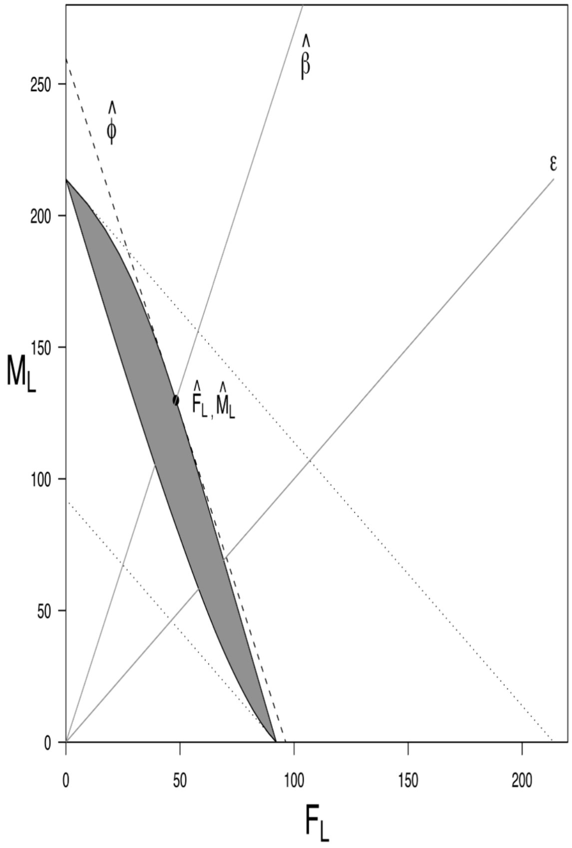

Figure 5.

Lifetime output with many broods and linear returns from helping. There is a single bout of helping ($\alpha = 2$), the maximum number of broods is $z = 30$, and $a = b = 1$.Males are more helpful than females (τ_m=1.0, τ_f=0.5), and c_f=c_m=γ_m=γ_f=l_{f1}=l_{m1}=1. The set of accessible lifetime strategies is shaded, and the optimal lifetime strategy is ($\widehat{M_L}, \widehat{F_L}$). $\widehat{\beta}$ is the equilibrium fitness bisector, and $\widehat{\phi}$ is the equilibrium fitness isocline (dashed). ε is the equal-investment line.

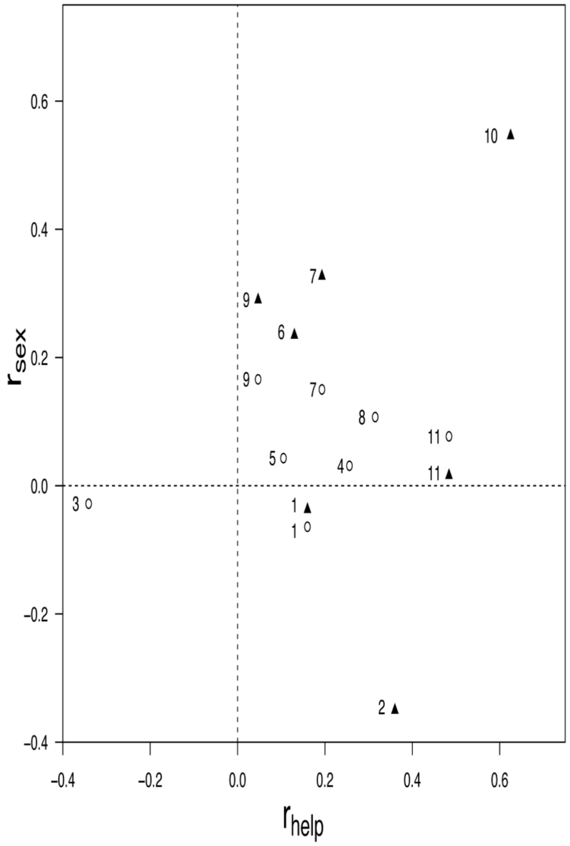

Figure 6.

The relationship between the effect size for helping (r_{help}) and the effect size for change of sex ratio (r_{sex}). Circles denote r_{sex} "offspring" estimates based on comparing the aggregate of offspring produced by pairs with helpers and the aggregate of offspring produced by pairs without helpers. Triangles denote r_{sex} "brood" estimates based on comparing sex ratios produced by pairs with helpers and sex ratios produced by pairs without helpers. Numbers denote species as listed in Table 1.

Table 1

Effect sizes r_{sex} and r_{help}. B denotes a “brood” estimate based on comparing sex ratios produced by pairs with helpers and sex ratios produced by pairs without helpers, O denotes an “offspring” estimate based on comparing the aggregate of offspring produced by pairs with helpers and the aggregate of offspring produced by pairs without helpers. *n* denotes sample size. Original estimates from Griffin et al. (2005). * denotes an original estimate that we cannot replicate. NA denotes not calculable from published data. Number after species name denotes point in Figure 6. Effect size estimates were calculated using standard formulae in Rosenthal (1991).

Species	r_{sex} original	*n*	r_{sex} B	n	r_{sex} O	*n*	r_{help} original	n	r_{help} revised	*n*
Seychelles Warbler[a] (10)	0.546 B	178	0.546	178	NA	NA	0.662	15	0.625	15
Laughing Kookaburra[b] (1)	−0.239* B	38	−0.037	75	−0.064	187	−0.187	24	0.160	119
Bell Miner[c] (9)	0.233 B	59	0.290	59	0.166	105	0.635	12	0.047	33
Acorn Woodpecker[d] (4)	0.031 O	837	NA	NA	0.031	837	0.093*	160	0.256	160
Harris’s Hawk[e] (3)	−0.028 O	261	NA	NA	−0.028	261	0.039	60	−0.341	60
Sociable Weaver[f] (2)	−0.316 B	58	−0.350	54	NA	NA	0.268	77	0.360	77
Green Woodhoopoe[g] (5)	0.113* B	128	NA	NA	0.043	233	0.102	144	0.105	144
Red-cockaded Woodpecker[h] (8)	0.364* B	41	NA	NA	0.107	168	0.314	93	0.315	93
Western Bluebird[i] (6)	0.235 B	153	0.235	153	NA	NA	0.143	613	0.130	741
African Wild Dog[j] (11)	0.720 B	16	0.016	84	0.077	800	0.491	47	0.484	84
Alpine Marmot[k] (7)	0.327 B	82	0.327	82	0.150	302	0.193	134	0.193	134

[a] r_{sex}: Brood estimate based on Komdeur (1996, Fig. 3) who reported 53.13 for the change in deviance between logistic regression models with and without territory quality as a continuous predictor of offspring sex ratio produced by first young (no helpers).

r_{help}: Original estimate based on measuring Fig. 9B in Komdeur (1994, p. 182) showing results from a helper-removal experiment. This estimate is incorrect (A. Griffin, pers. comm.) Revised estimate based on the average number of yearlings produced when helpers were removed (0.17 ± 0.37 SD, $n = 6$, Table 2, p. 183) and when helpers were present (0.94 ± 0.66 SD, $n = 9$, J. Komdeur, pers. comm.), which yields $t = 2.89$. Females were judged more helpful because 87.5% of helpers are female (Komdeur 1996, Table 1).

[b] r_{sex}: Original brood-based estimate based on Legge et al.(2001, p. 526) who reported “Group size vs. sex ratio; $\chi^2_3 = 6.2$”. The sample size of 38 given by Griffin et al. is incorrect; 66 is the correct sample size (= the number of broods produced by 38 persistent groups). We are unable to replicate the reported estimate from the χ^2 value. Revised brood estimate based on 0.105, the change in deviance between logistic regression models with and without group type as a factor (original data on clutch sex ratios produced by unassisted pairs and larger groups supplied by S. Legge). Offspring estimate based on 21 males and 31 females produced by pairs and 66 males and 69 females produced by groups, yielding $\chi^2_1 = 0.776$ (S. Legge, original data).

r_{help}: Original estimate based on Legge (2000, p. 720) who reported the effect of group size on fledging success using Wilcoxon's paired sample by rank test yield $T = -25.5$, $p < 0.18$, $n = 24$. The estimate was calculated from $p = 0.18$ assuming a normal distribution ($z = -0.916$). Revised estimate based on 3.05, the change in deviance between Poisson log-linear regression models of the number of fledglings with and without the number of male helpers as a predictor variable (original data on fledgling number supplied by S. Legge). Males were judged more helpful because step-wise analysis (based on change of AIC) of a Poisson log-linear regression model with the number of female helpers and number of male helpers as predictor variables indicates that males increase the number of fledglings and females reduce the number of fledglings.

[c] r_{sex}: Original brood estimate based on Ewen et al. (2003, p. 161) who reported Wald $\chi^2_1 = 3.2$ derived from logistic regression models with and without major helpers. Revised brood estimate based on 4.961, the change in deviance between logistic regression models with and without group type as a factor (original data on clutch sex ratios produced by pairs with and without major helpers supplied by J. Ewen). Offspring estimate based on 9 males and 1 female produced by pairs without major helpers and 54 males and 41 females produced by pairs with major helpers, yielding $\chi^2_1 = 2.878$ (J. Ewen, original data).

r_{help}: Original estimate based on Clarke (1989, p. 298) who reported the number of fledglings produced by pairs with 6 or fewer helpers and those with 7 or more (Mann-Whitney U test, $z = -2.2$, $n = 12$). Revised estimate based on 0.072, the change in deviance between Poisson log-linear regression models of the number of nestlings produced with male and female helpers and with female helpers only (original data from McDonald et al. 2008, 2009 supplied by P. McDonald) Males were judged more helpful because 85% of helpers are male ($n = 261$, original data from McDonald et al. 2008, 2009).

[d] r_{sex}: Offspring estimate based on Koenig et al. (2001, Table 3) who reported that groups without helpers produced 194 males and 178 females and that groups with helpers produced 227 males and 237 females, which yields $\chi^2_1 = 0.79$. Only offspring of nests from which all offspring survived to the post-juvenile molt (and the end of parental care) are included.

r_{help}: Estimate based on Koenig and Mumme (1987, Table 6.5) who reported “$\chi^2_1 = 1.0$”. We are unable to replicate this estimate. There two columns with $\chi^2 = 1$ in Table 6.5 but both have $df = 2$ and neither sample size equals 160. Revised estimate based on Koenig and Mumme (1987, Table 6.7) who reported the average number of young alive in February produced by groups with no helpers (0.88 ± 1.35 SD, n = 93) and by groups with helpers of both sexes (1.66 ± 1.56 SD, $n = 67$), which yields $t = 3.30$. Males were judged 6.3% more helpful by Koenig et al. (2001, p. 360) based on assessments of dispersal and feeding rates.

[e] r_{sex}: Offspring estimate based on Bednarz and Hayden (1991, p. 122) who reported that groups without helpers produced a sex ratio of 0.56 (85 males and 67 females) and that groups with helpers produced a sex ratio of 0.59 (64 males and 45 females), which yields $\chi^2_1 = 0.202$, $n = 261$.

r_{help}: Original estimate based on Bednarz (1987, Table 2) (not Table 1 as reported) who reported average number of eggs produced by pairs with no helpers (1.90 ± 0.92 SD, $n = 30$) and by pairs with helpers (1.97 ± 0.76 SD, $n = 30$) per “succesful nest attempt,” which yields $t = 0.321$. Revised estimate based on Bednarz (1987, Table 5) who reported the average number of fledglings produced by pairs with no helpers (0.93 ± 0.52 SD, $n = 29$)and by pairs with helpers (0.60 ± 0.47 SD, $n = 30$) regardless of nest success, which yields $t = -2.55$. Males were judged more helpful because “most auxiliaries are males” (p. 402).

[f] r_{sex}: Original brood estimate based on Doutrelont et al. (2004, p. 2) who reported sex ratios for broods (sexed on day 9) with and without helpers ($F_{1,52} = 7.24$, $p = 0.008$). The estimate was calculated from $p = 0.008$ assuming a normal distribution ($z = -2.409$) and a sample size of 58 (as shown in their Figure 2). Revised brood estimate was calculated from $F_{1,52}$ and a sample size of 54 (as implied by the subscript on the F-statistic.)

r_{help}: Original estimage based on “R. Covas, personal communication, from manuscript in preparation” with no further details. Revised estimate was calculated from $F_{1,56}$ based on Covas et al. (2008, p. 108) who reported that “the number of young fledged increased significantly with group size ($F_{1,56} = 8.34$, p% = 0.0006; 0.27 ± 0.09”. Males were judged more helpful because Doutrelant et al. (2004, p. 151) reported that all 12 older helpers (> 1 yr) and 26 of 39 yearling helpers were males and because males tended to have higher feeding rates

[g] r_{sex}: Original brood estimate based on a “comparison of small and large flock sex ratios” from Ligon and Ligon (1990, p. 767). We are unable to replicate this estimate. Revised offspring estimate is based on Ligon and Ligon (Table 1, p. 767) who reported 43 males and 57 females from 55 “small flocks” and 63 males and 70 females from 73 “large flocks”, which yields $\chi^2_1 = 0.4393$.

r_{help}: Estimate based on Du Plessis (1993, Table 3) who reported average number of fledglings produced by pairs with no helpers (0.71 ± 0.92 SD, $n = 60$) and by pairs with helpers (0.93 ± 1.17 SD, $n = 84$). Griffin et al. reported $t = 1.22$; our recalculation generates $t = 1.26$. Du Plessis also reported that the number of young surviving to 6 months does not differ between pairs with and without helpers. Females were judged more helpful because Ligon and Ligon (1990, p. 766) reported that females make significantly more feeding visits than males

[h] r_{sex}: Original brood estimate based on Gowaty and Lennartz (1985). We are unable to replicate this estimate. The reported sample size (41.49 in West and Sheldon 2002, suppl. material) was apparently obtained by dividing the total number of males and females (82) produced by all “clan” types (Gowaty and Lennartz 1985, Table 2) by the average number of nestlings per brood (1.976 = 168 offspring/85 broods, Table 1). Revised offspring estimate based on Gowaty and Lennartz (1985, Table 1) who reported 48 males and 26 females produced by unassisted pairs and 51 males and 43 females produced by pairs with auxiliaries, which yields $\chi^2_1 = 1.926$

r_{help}: Estimate based on Lennartz et al. (1987, p. 77) who reported the average number of fledglings produced by pairs with helpers (2.05 ± 0.97 SD, $n = 43$) and by unassisted pairs (1.40 ± 1.01 SD, $n = 50$), which yields $t = 3.161$. Males were judged more helpful because 95% of helpers of known sex were male ($n = 40$).

[i] r_{sex}: Brood estimate based on Dickinson (2004, Table 2) who reported the average sex ratio produced by mothers with breeding-age sons that were “breeding, not helping” (50 ± 2% SE, $n = 21$), which yields $t = 2.97$.

r_{help}: Original estimate based on Dickinson et al. (1996, p. 174) (not Dickinson 2004 as reported), who reported the average number of fledglings produced by first nests with helpers (3.87 ± 0.30 SE) and without helpers (2.75 ± 0.09 SE), which yields $t = 3.58$. Dickinson et al. noted that these estimates include the effects of helpers on both nest success or failure as well as the number of young fledged from successful nests. As recognized by Griffin and West (2002), the reported sample size ($n = 613$) refers only to nests that fledged at least one offspring. Revised estimate based on $t = 3.58$ and the corrected sample size of $n = 741$ (= 38 nests with helpers + 703 nests without helpers, Fig. 4, p. 172). Males were judged more helpful because all helpers at first nests of the year were adults males, but helping is “occasional“; 7% of nests had helpers.

[j] r_{sex}: Original brood estimate based on Creel et al. (1998, p. 317) who reported the average sex ratio produced by primiparous mothers (with few helpers) (0.63 ± 0.06 SE, $n = 12$) and by multiparous mothers (with more helpers) (0.36 ± 0.06 SE, $n = 6$). Creel et al. reported $Z_{16} = 2.88$ for this comparison; treating this value as a standard normal deviate and $n = 16$ yields the reported estimate, but 18 is the correct sample size. Revised brood estimate based on 0.020, the change in deviance between logistic regression models with and without the number of helper males as a predictor variable (original data from McNutt and Silk 2008 supplied by authors). Offspring estimate based on 63 males and 34 females produced by young mothers (ages 1 – 2) and 370 males and 333 females produced by older mothers (age 3 - 10), which yields $\chi^2_1 = 4.74$.

r_{help}: Original estimate is a weighted average of an estimate, 0.518, derived from 4.56, the change in deviance between Poisson log-linear regression models with and without the number of helpers as a predictor variable (analysis of the data in Malcolm and Marten 1982, Figure 6) and an estimate, 0.484, derived from 0.234, the amount of variance explained by a least-squares regression with pack size as a predictor variable (analysis of the data in Creel et al. 1998, Figure 1, p. 317). The weighted average is $((0.5179)(17) + (0.4837)(30))/47 = 0.496$. Revised estimate based on 19.682, the change in deviance between Poisson log-linear regression models of the number of pups produced with and without the number of male helpers as a predictor variable (original data supplied by McNutt and Silk). Males were judged more helpful because step-wise analysis (based on change of AIC) of a model with the number of female helpers and number of male helpers as predictor variables indicates that males increase the number of pups and females reduce the number of pups.

[k] r_{sex}: Original brood estimate based on Allainé (2004, Table 1) who reported a Wald $\chi^2_1 = 8.74$ based on the change in deviance between logistic regression models with and without the presence of male helpers. Revised offspring estimate based on Allainé (2004, p. 999) who reported that mothers without helpers produced a sex ratio of 0.66 (54 males and 28 females) and that mothers with helpers produced a sex ratio of 0.49 (108 males and 112 females), which yields $\chi^2_1 = 6.750$.

r_{help}: Estimate based on Allainé et al. (2000, Figure 2A) who reported 5.01, the change in deviance between logistic regression models of the proportion of juveniles surviving the winter with and without the number of nonparental male adults in the hibernating group. Males were judged more helpful because juvenile winter survival increases with the number of male helpers present and decreases with the number of female helpers present (Allainé et al. 2000, p. 510)