

Sex-ratio optimization with helpers at the nest

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In many cooperatively breeding animals, offspring produced earlier in life assist their parents in raising subsequent broods. Such helping behaviour is often confined to offspring of one sex. Sex-allocation theory predicts that parents overproduce offspring of the helping sex, but the expected degree of sex-ratio bias was thought to depend on specific details of female and male life histories, hampering empirical tests of the theory. Here we demonstrate the following two theories. (i) If all parents produce the same sex ratio, the evolutionarily stable sex ratio obeys a very simple rule that is valid for a general class of life histories. The rule predicts that the expected sex-ratio bias depends on the product of only two parameters which are relatively easily measured: the average number of helping offspring per nest and the relative contribution to offspring production per helper. (ii) If the benefit of helping varies between parents, and parents facultatively adjust the sex ratio accordingly, then the population sex ratio is not necessarily biased towards the helping sex. For example, in line with empirical evidence, if helpers are produced under favourable conditions and parents do not adjust their clutch size to the number of helpers, then a surplus of the non-helping sex is expected.

Keywords: sex allocation; life history; kin selection; reproductive value; clutch size; social behaviour

1. INTRODUCTION

In adult populations of many cooperatively breeding birds, females are outnumbered by males (Brown 1987). It has been argued that the 'marriage squeeze' resulting from this sex-ratio skew might be a causal agent in the evolution of helping by sons (Rowley 1965; Maynard Smith & Ridpath 1972; Reyer 1980). However, the argument works the other way around as well, helping by sons selecting parents to produce more sons than daughters ultimately causing a skewed sex ratio. According to this so-called repayment model (Emlen *et al.* 1986; Lessells & Avery 1987; Koenig & Walters 1999), the helping sex, all else being equal, is the cheaper sex because it repays part of the costs the parents have incurred in raising it. Fisher's (1930) principle of equal investment in the sexes then predicts that parents produce an excess of the helping sex.

The repayment models have the desirable property that they express the predicted sex ratio in terms of three measurable parameters: brood size, the proportion of males born the previous year that act as helpers this year, and the effectiveness of such helpers relative to their parents. The first empirical tests of the models were based on a study of the red-cockaded woodpecker, *Picoides borealis*, by Gowaty & Lennartz (1985). In this species the vast majority of helpers are sons, and the observed male-biased brood sex ratio fitted the model predictions reasonably well (Emlen *et al.* 1986; Lessells & Avery 1987). However, a later study on red-cockaded woodpeckers, based on a much larger sample size (Walters 1990), failed to find any sex-ratio bias at all. Moreover, in another bird species, the Seychelles warbler *Acrocephalus sechellensis*, it was found that the brood sex ratio at the population level was biased towards the non-helping sex (Komdeur *et al.* 1997).

The failure of the repayment models to correctly predict the average brood sex ratio might be because a number of

model assumptions are violated in most species (Koenig & Walters 1999). First, the models tacitly assume that helpers help during one season only and that sons and daughters do not differ in any life-history traits other than helping behaviour. Second, the models assume that all parents produce the same sex ratio, that is, the sex ratio is not adjusted facultatively according to some factor that differentially affects the benefits of having helpers around.

In this paper we relax these assumptions and we reach the following conclusions. (i) If all parents produce the same sex ratio, an overproduction of the helping sex is to be expected. The evolutionarily stable (ESS) sex ratio is quite robust and does not depend on differences in life history between sons and daughters. Moreover, it depends on just two parameters that are relatively easily measured in the field: the average number of helpers per nest and the relative contribution to offspring production per helper. (ii) If parents facultatively adjust the sex ratio according to the expected benefit of having helpers, the population sex ratio is not necessarily biased towards the helping sex. In the case where the parents do not adjust the clutch size to the presence of helpers, a clear-cut prediction can be made: an excess of the non-helping sex is expected if helpers are produced under favourable circumstances, contrary to the predictions of the classic repayment models and in line with the results of Komdeur *et al.* (1997). In contrast, if helpers are produced under unfavourable circumstances, an excess of the helping sex is expected. In the case where the parents increase their clutch size in the presence of helpers, the prediction of the population sex ratio is less straightforward. The population sex ratio may be biased in either direction, independent of the circumstances in which helpers are produced, and dependent on specific life-history details.

2. UNIFORM SEX-RATIO ADJUSTMENT

(a) Life history

We assume that the model organism lives in a seasonal environment and reproduces once per season. Without

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any helpers around, breeding females produce on average m sons and f daughters, where

$$m = sc\mu \quad \text{and} \quad f = (1 - s)c\phi. \quad (1)$$

Here s denotes the proportion of sons in a clutch of size c , and μ and ϕ denote the probabilities of survival of sons and daughters to the next season, respectively. We assume that the sex ratio, s , is under maternal control, but identical results are obtained in the case of paternal control. Sons and daughters have an arbitrary sex-specific tendency to become a helper, starting one season after birth. Sons and daughters also have an arbitrary sex-specific tendency to stop helping, and they may differ in other life-history parameters as well, such as mortality and age at maturity. Let b_m and b_f measure the contributions to offspring production of a helping son and a helping daughter, respectively, relative to the parents' contribution. That is, if a mother has h_m helping sons and h_f helping daughters, then she produces $(1 + b_m h_m + b_f h_f)f$ daughters and $(1 + b_m h_m + b_f h_f)m$ sons. In other words, following the earlier repayment models (Emlen *et al.* 1986; Lessells & Avery 1987), we assume that the number of helpers has an additive effect on the number of extra offspring produced. This should be a reasonable approximation for species with either a small number of helpers or very many. Let \bar{h}_m and \bar{h}_f be the average number of helping sons and daughters, and let $H = 1 + b_m \bar{h}_m + b_f \bar{h}_f$. Then mothers produce on average Hm sons and Hf daughters. The probability P that reproducing females survive from one season to the next is assumed to be independent of the sex ratio they produce, and therefore independent of the number of helpers.

(b) *The product maximization criterion*

An ESS (Maynard Smith & Price 1973) sex ratio s^* , if adopted by most mothers in the population, cannot be successfully invaded by any rare mutant sex ratio $s \neq s^*$. In other words, the reproductive value $v(s, s^*)$ of a mutant mother with sex ratio s in a population with ESS sex ratio s^* is maximal with respect to s when $s = s^*$. If \bar{v}_m and \bar{v}_f are the average reproductive values of sons and daughters, respectively, then the reproductive value of a mutant mother is given by

$$v(s, s^*) = Pv(s, s^*) + r_f H(s) f(s) \bar{v}_f(s, s^*) + r_m H(s) m(s) \bar{v}_m(s, s^*), \quad (2)$$

where r_f and r_m denote the mother's genetic relatedness to her daughters and sons, respectively. We assume $r_f = r_m = r$. Equation (2) follows the usual recursive definition of reproductive value (Taylor 1996; Frank 1998; Pen *et al.* 1999), which states that the present reproductive value of a mother is the sum of the reproductive values of individuals (including herself) she contributes to the next time-unit, weighted according to genetic relatedness. Due to a powerful result by Taylor (1996; see also Pen & Weissing 2000), the ESS sex ratio s^* can be found by replacing on the right-hand side of equation (2) the reproductive values of the mutant (i.e. $v(s, s^*)$, $\bar{v}_f(s, s^*)$ and $\bar{v}_m(s, s^*)$) by the corresponding values of the resident ($v(s^*, s^*)$, $\bar{v}_f(s^*, s^*)$ and $\bar{v}_m(s^*, s^*)$, respectively). In other words, we need not maximize these quantities to find an ESS. Equation (2) is quite general, because the average reproductive values of sons and daughters can be regarded as averaged

over an arbitrary number of life-history stages (Caswell 1989). The number of life-history stages and their relative abundances are irrelevant to our calculations, because, as Fisher (1930) noted, the total reproductive value of all daughters equals the total reproductive value of all sons, that is,

$$H(s^*)f(s^*)\bar{v}_f(s^*) = H(s^*)m(s^*)\bar{v}_m(s^*). \quad (3)$$

A mutant mother's reproductive value can therefore be rescaled as

$$v(s, s^*) = \frac{Pv(s^*, s^*)}{H(s^*)f(s^*)\bar{v}_f(s^*)} + r \frac{H(s)}{H(s^*)} \left[\frac{f(s)}{f(s^*)} + \frac{m(s)}{m(s^*)} \right]. \quad (4)$$

Assuming that a mother's survival P is independent of her brood sex ratio s , maximizing $v(s, s^*)$ with respect to s requires

$$\frac{\partial v}{\partial s} = r \frac{d}{ds} \frac{H(s)}{H(s^*)} \left[\frac{f(s)}{f(s^*)} + \frac{m(s)}{m(s^*)} \right] = 0, \quad (5)$$

evaluated at $s = s^*$, or equivalently

$$\frac{1}{2} \left[\frac{1}{f(s^*)} \frac{df(s^*)}{ds} + \frac{1}{m(s^*)} \frac{dm(s^*)}{ds} \right] + \frac{1}{H(s^*)} \frac{dH(s^*)}{ds} = 0. \quad (6)$$

This condition is equivalent to maximization of the product $Hf \times Hm$ with respect to s^* . Such product-maximization properties of an ESS are common in evolutionary models in general (Charnov 1997), and in models of sex allocation in particular (Charnov 1982; Lessard 1989; but see Pen & Weissing 2000). Condition (6) separates the effect of the sex ratio on reproductive output, the term between brackets, and the effect of the sex ratio on the amount of help received, the second term on the left.

(c) *Evolutionarily stable sex ratio*

From equation (1) we get $(1/m)dm/ds = 1/s$ and $(1/f)df/ds = -1/(1-s)$; hence in the absence of a sex-ratio effect on the amount of help ($dH/ds = 0$), the ESS sex ratio equals $s^* = 1/2$, as expected. In order to calculate dH/ds we need to know how the average number of helping sons \bar{h}_m and helping daughters \bar{h}_f depend on the sex ratio s . In appendix A it is shown that \bar{h}_m and \bar{h}_f depend in a rather complicated way on several life-history parameters (equation (A2)), but the derivative dH/ds has a simple form

$$\frac{dH}{ds} = H \left(\frac{b_m \bar{h}_m}{s} - \frac{b_f \bar{h}_f}{1-s} \right). \quad (7)$$

Substitution in the ESS condition (6) yields the result

$$\frac{s^*}{1-s^*} = \frac{1 + 2b_m \bar{h}_m}{1 + 2b_f \bar{h}_f}. \quad (8)$$

For the special case where only one sex helps,

$$\frac{\text{number of helping sex}}{\text{number of non-helping sex}} = 1 + 2b\bar{h}, \quad (9)$$

where b is the contribution per helper relative to that of the parents and \bar{h} is the average number of helpers. This is our first result.

Result 1. The evolutionarily stable ratio of the helping sex to the non-helping sex deviates from unity by an amount equal to twice the product of two parameters—the average number of helpers per nest and the relative contribution per helper.

Note that the same value of $b\bar{h}$ can be obtained for many combinations of \bar{h} and b , that is, the expected sex ratio is the same for two species where one species compared to the other species has twice the number of helpers but which are only half as effective. Results (8) and (9) make intuitive sense, because they say that the expected degree of sex-ratio bias depends only on the relative amounts of help offered by sons and daughters. These relative amounts depend strongly on differences in life history between sons and daughters (see equation (A2)), such as differences in mortality and dispersal, but direct knowledge of such differences is not required to test the theory.

3. FACULTATIVE SEX-RATIO ADJUSTMENT

Now suppose that the benefit of helping varies with some continuous environmental variable t , such as territory quality (Komdeur 1992). For simplicity we assume that members of only one sex, say the daughters, have a tendency to help. The environmental variable t takes values in the normalized range $[0, 1]$, according to some arbitrary probability distribution $p(t)$, and the benefit of help increases with t . Then the parents' ESS sex-ratio strategy is to produce the non-helping sex (sons) up to a point $t = \tau^*$, and switch to the production of the helping sex (daughters) as t becomes larger than τ^* . Parents in environment $t \leq \tau^*$ who produce only sons have a clutch size $c_m(t)$ and sons survive with probability $\mu(t)$. Likewise, parents in environment $t > \tau^*$ who produce only daughters have a clutch size $c_f(t)$ and daughters survive with probability $\phi(t)$, which includes the effect of helping on survival. The population primary sex ratio (sons/daughters) is given by $M_1(\tau^*)/F_1(\tau^*)$ where

$$M_1(\tau^*) = \frac{\int_0^{\tau^*} c_m(t)p(t)dt}{\int_0^{\tau^*} p(t)dt}, \quad (10b)$$

$$F_1(\tau^*) = \frac{\int_{\tau^*}^1 c_f(t)p(t)dt}{\int_{\tau^*}^1 p(t)dt}.$$

The sex ratio of surviving offspring, or the secondary sex ratio, is given by $M_2(\tau^*)/F_2(\tau^*)$, where

$$M_2(\tau^*) = \frac{\int_0^{\tau^*} c_m(t)\mu(t)p(t)dt}{\int_0^{\tau^*} p(t)dt}, \quad (11a)$$

$$F_2(\tau^*) = \frac{\int_{\tau^*}^1 c_f(t)\phi(t)p(t)dt}{\int_{\tau^*}^1 p(t)dt}. \quad (11b)$$

The reproductive value $v_m(t)$ of a son relative to the reproductive value $v_f(t)$ of a daughter born in environment t equals a son's relative survival probability $\mu(t)/\phi(t)$ multiplied by the ratio of surviving daughters to sons. That is,

$$\frac{v_m(t)}{v_f(t)} = \frac{\mu(t) F_2(\tau^*)}{\phi(t) M_2(\tau^*)}. \quad (12)$$

The ESS switch point τ^* is such that parents who produce sons at τ^* have the same reproductive value as parents that produce daughters at τ^* . In other words, we have the ESS condition

$$c_m(\tau^*)v_m(\tau^*) = c_f(\tau^*)v_f(\tau^*). \quad (13)$$

Now suppose that parents with helpers have the same clutch size as parents without helpers in a given environment t , that is, $c_m(t) = c_f(t)$. If parents produce the helping sex under favourable circumstances, that is, $\mu(t)$ and $\phi(t)$ are increasing with t , then equation (13) implies that $M_1(\tau^*) > F_1(\tau^*)$. If, on the other hand, parents produce the helping sex under unfavourable circumstances ($\mu(t)$ and $\phi(t)$ decrease with t), then equation (13) implies that $M_1(\tau^*) < F_1(\tau^*)$. Following a proof by Frank & Swingland (1988), this can be seen as follows. If $\mu(t)$ and $\phi(t)$ increase with t , then

$$M_2(\tau^*) < \mu(\tau^*) \frac{\int_0^{\tau^*} c_m(t)p(t)dt}{\int_0^{\tau^*} p(t)dt} = \mu(\tau^*)M_1(\tau^*) \quad (14)$$

and similarly $F_2(\tau^*) > \phi(\tau^*)F_1(\tau^*)$. By equation (12) and the ESS condition $v_m(\tau^*) = v_f(\tau^*)$, this implies that $M_1(\tau^*) > F_1(\tau^*)$. If $\mu(t)$ and $\phi(t)$ decrease with t , the inequality signs are reversed and we obtain $M_1(\tau^*) < F_1(\tau^*)$. In other words, we have shown result 2.

Result 2. If parents facultatively adjust the sex ratio according to the expected benefits of help, and parents do not adjust the clutch size to the presence of helpers, then the average sex ratio is biased towards the non-helping sex if helpers are produced under favourable circumstances and towards the helping sex if helpers are produced under unfavourable circumstances.

If parents increase their clutch size when helpers are present, $c_f(\tau^*) > c_m(\tau^*)$, then the population sex ratio may be biased in either direction, irrespective of helpers being produced under favourable or unfavourable conditions. If, for example, $\mu(t) = \phi(t) = \text{constant}$, then $v_m(\tau^*) = 1/M_1(\tau^*)$ and $v_f(\tau^*) = 1/F_1(\tau^*)$, and it follows from equation (13) that $M_1(\tau^*) < F_1(\tau^*)$. However, if $\mu(t)$ and $\phi(t)$ increase sufficiently steeply and $c_f(\tau^*)/c_m(\tau^*)$ is sufficiently small, then the proof of result 2 applies again and we have $M_1(\tau^*) > F_1(\tau^*)$. This implies result 3.

Result 3. If parents facultatively adjust the sex ratio according to the expected benefits of help, and parents adjust the clutch size to the presence of helpers, then the average sex ratio can be biased towards either sex, depending on details of male and female life histories.

4. DISCUSSION

Whether selection should favour a sex ratio biased towards the sex that yields the greatest helping benefits to the parents depends on what scale the observations are made. If the benefit of help varies predictably according to some environmental factor, then parents are expected to adjust the sex ratio such that parents who stand to gain the most from help produce the helping sex. Parents that expect to gain less, but perhaps still a positive, benefit are expected to produce the non-helping sex. At the population level this may lead to an excess production of the non-helping sex, in particular if the parents do not adjust their clutch size to the presence of helpers (result 2). If parents with helpers increase their clutch size, then the average sex ratio may be biased in either direction (result 3). These predictions are in agreement with results from a study on the Seychelles warbler. In this species females are the helpers, but whether the parents actually benefit from having helpers depends strongly on territory quality, as measured by insect prey availability (Komdeur 1992). On good territories helpers increase the survival probability of the chicks they help raise, but on bad territories helpers reduce the parents' reproductive success. As expected, parents on good territories produce daughters, parents on bad territories produce sons. Clutch sizes do not vary according to territory quality or number of helpers, because nearly all birds lay a single egg per breeding attempt. As expected, the brood sex ratio averaged over all territories is biased towards sons, the non-helping sex (Komdeur 1996; Komdeur *et al.* 1997). Perhaps the lack of a sex-ratio bias at the population level in the red-cockaded woodpecker (Walters 1990) can also be explained by variation in the benefits of helping.

If the benefit of helping does not vary strongly between parents, then the expectation is that all parents produce an excess of the sex that helps the most, and consequently the population sex ratio will also be biased towards that sex (result 1). Our model generalizes the earlier repayment models of Emlen *et al.* (1986) and Lessells & Avery (1987). These models apply to a less general class of life histories than considered here, but despite being more general, our result (equations (8) and (9)) is much simpler. We have shown that the sex-ratio bias depends only on the average number of helpers of each sex and the relative contributions to offspring production per helper. The results of the earlier models were more complicated because they did not consider the dynamics of the number of helpers over time and they did not express the sex ratio in terms of the number of helpers but in terms of various life-history parameters (see also Frank 1998). The number of helpers of each sex depends strongly on several life-history parameters (see equation (A2)), but knowledge of these parameters is not required to predict the sex ratio. It is simpler just to count the number of helpers. For this reason, our result holds true regardless of any life-history differences between the sexes. In this sense

our result can be regarded as a 'life-history invariant' rule (Charnov 1993, 1997). The earlier repayment models were recently criticized for their disregard of life-history differences between the sexes (Koenig & Walters 1999). It was argued that life-history differences between the helping and the non-helping sex might explain why a sex-ratio bias towards the helping sex at the population level is not always observed. However, our result shows that as long as parents do not facultatively adjust the sex ratio, such a bias is always expected.

We stress that neither our models, nor the earlier models of Emlen *et al.* (1986) and Lessells & Avery (1987) suffer from the 'double accounting error' (Grafen 1984), that is, crediting the benefits of help to both helpers and recipients of help, as claimed by Koenig & Walters (1999). In our models and the earlier models, credit is given solely to the parents. Moreover, Koenig & Walters use a method described by Lucas *et al.* (1996) to correct the 'error', a method which was shown to be flawed by Queller (1996).

There are a number of complicating factors that we have disregarded in our models. A potentially important one concerns the spatial structure and viscosity of the population (Taylor 1992; Pen 2000). If related helpers compete for the inheritance of their parents' territory or locally around their parents' territory (local resource competition, LRC; Clark 1978), then the benefits of help (local resource enhancement, LRE) will be exported less efficiently, and the overall benefit of producing a biased sex ratio is diminished. It remains a challenge to incorporate into a single framework the simultaneous LRE and LRC effects of having helpers.

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APPENDIX A: HELPER DYNAMICS

Suppose a fraction y_0 of sons born last year become helpers this year, and a fraction y_1 of males helping last year are still helpers this year. Likewise, a fraction z_0 of newborn daughters become helpers and a fraction z_1 remain helpers. Let the vector $\mathbf{h} = (h_m, h_f)$ keep track of the number of male and female helpers. For an individual female, these numbers change from the $(j-1)$ th breeding attempt to the next according to $\mathbf{h}_j = \mathbf{A}\mathbf{h}_{j-1} + \mathbf{g}$, where

$$\mathbf{A} = \begin{pmatrix} y_1 + b_m y_0 m & b_f y_0 m \\ b_m z_0 f & z_1 + b_f z_0 f \end{pmatrix} \quad \text{and} \quad \mathbf{g} = \begin{pmatrix} y_0 m \\ z_0 f \end{pmatrix}. \quad (\text{A1})$$

Here b_f and b_m are the number of additional offspring produced per female and male helper, respectively. Given that there are no helpers in the first breeding attempt ($\mathbf{h}_1 = 0$), the solution of the recurrence relation is given by $\mathbf{h}_j = (\mathbf{I} - \mathbf{A}^{j-1})(\mathbf{I} - \mathbf{A})^{-1}\mathbf{g}$, where \mathbf{I} denotes the identity matrix. In a stationary population the distribution of females breeding for the j th time is given by $(1 - P)P^{j-1}$; hence the average number of helpers is

$$\begin{aligned}\bar{\mathbf{h}} &= \sum_{j=1}^{\infty} (1-P)P^{j-1}\mathbf{h}_j = P(\mathbf{I} - P\mathbf{A})^{-1}\mathbf{g} \\ &= \frac{P}{D} \begin{pmatrix} (1 - Pz_1)y_0m \\ (1 - Py_1)z_0f \end{pmatrix},\end{aligned}\quad (\text{A2})$$

where $D = (1 - Py_1)(1 - Pz_1) - P(1 - Pz_1)b_my_0m - P(1 - Py_1)b_fz_0f$. Then $H = 1 + b_m\bar{h}_m + b_f\bar{h}_f = (1 - Py_1) \times (1 - Pz_1)/D$ and we find that

$$\frac{dH}{ds} = H \left(\frac{b_m\bar{h}_m}{s} - \frac{b_f\bar{h}_f}{1-s} \right).\quad (\text{A3})$$

REFERENCES

- Brown, J. L. 1987 *Helping and communal breeding in birds: ecology and evolution*. Princeton University Press.
- Caswell, H. 1989 *Matrix population models*. Sunderland, MA: Sinauer.
- Charnov, E. L. 1982 *The theory of sex allocation*. Princeton University Press.
- Charnov, E. L. 1993 *Life history invariants*. Oxford University Press.
- Charnov, E. L. 1997 Trade-off-invariant rules for evolutionarily stable life histories. *Nature* **387**, 393–394.
- Clark, A. B. 1978 Sex ratio and local resource competition in a prosimian primate. *Science* **201**, 163–165.
- Emlen, S. T., Emlen, M. & Levin, S. A. 1986 Sex ratio selection in species with helpers-at-the-nest. *Am. Nat.* **127**, 1–8.
- Fisher, R. A. 1930 *The genetical theory of natural selection*. Oxford, UK: Clarendon.
- Frank, S. A. 1998 *Foundations of social evolution*. Princeton University Press.
- Frank, S. A. & Swingland, I. R. 1988 Sex ratio under conditional sex expression. *J. Theor. Biol.* **135**, 415–418.
- Gowaty, P. A. & Lennartz, M. R. 1985 Sex ratios of nestling and fledgling redcockaded woodpeckers (*Picoides borealis*) favor males. *Am. Nat.* **126**, 347–353.
- Grafen, A. 1984 Natural selection, kin selection, and group selection. In *Behavioural ecology: an evolutionary approach* (ed. J. R. Krebs & N. B. Davies), pp. 62–84. Oxford, UK: Blackwell Scientific.
- Koenig, W. D. & Walters, J. R. 1999 Sex-ratio selection in species with helpers at the nest: the repayment model revisited. *Am. Nat.* **153**, 124–130.
- Komdeur, J. 1992 Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature* **358**, 493–495.
- Komdeur, J. 1996 Facultative sex ratio bias in the offspring of Seychelles warblers. *Proc. R. Soc. Lond. B* **263**, 661–666.
- Komdeur, J., Daan, S., Tinbergen, J. & Mateman, C. 1997 Extreme adaptive modification in sex ratio of the Seychelles warbler's eggs. *Nature* **385**, 522–525.
- Lessard, S. 1989 Resource allocation in Mendelian populations: further in ESS theory. In *Mathematical evolutionary theory* (ed. M. Feldman), pp. 207–246. Princeton University Press.
- Lessells, C. M. & Avery, M. I. 1987 Sex-ratio selection in species with helpers at the nest: some extensions of the repayment model. *Am. Nat.* **129**, 610–620.
- Lucas, J. R., Creel, S. R. & Waser, P. M. 1996 How to measure inclusive fitness, revisited. *Anim. Behav.* **51**, 225–228.
- Maynard Smith, J. & Price, G. R. 1973 The logic of animal conflict. *Nature* **246**, 15–18.
- Maynard Smith, J. & Ridpath, M. G. 1972 Wife sharing in the Tasmanian native hen, *Tribonyx mortierii*: a case of kin selection? *Am. Nat.* **106**, 447–452.
- Pen, I. 2000 Reproductive effort in viscous populations. *Evolution* (In the press.)
- Pen, I. & Weissing, F. J. 2000 Optimal sex allocation: steps towards a mechanistic theory. In *The sex ratio handbook* (ed. I. Hardy). Cambridge University Press (In the press.)
- Pen, I., Weissing, F. J. & Daan, S. 1999 Seasonal sex ratio trend in the European kestrel: an ESS analysis. *Am. Nat.* **153**, 384–397.
- Queller, D. C. 1996 The measurement and meaning of inclusive fitness. *Anim. Behav.* **51**, 229–232.
- Reyer, H. U. 1980 Flexible helper structure as an ecological adaptation in the pied kingfisher (*Ceryle rudis rudis* L.). *Behav. Ecol. Sociobiol.* **6**, 219–227.
- Rowley, I. 1965 The life history of the superb blue wren, *Malurus cyaneus*. *Emu* **64**, 251–297.
- Taylor, P. D. 1992 Altruism in viscous populations—an inclusive fitness model. *Evol. Ecol.* **6**, 352–356.
- Taylor, P. D. 1996 Inclusive fitness arguments in genetic models of behaviour. *J. Math. Biol.* **34**, 654–674.
- Walters, J. R. 1990 Red-cockaded woodpeckers: a 'primitive' cooperative breeder. In *Cooperative breeding in birds* (ed. P. B. Stacey & W. D. Koenig), pp. 67–101. Cambridge University Press.