Size and the Not-So-Single Sex: Disentangling the Effects of Size and Budget on Sex Allocation in Hermaphrodites

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Size and the Not-So-Single Sex: Disentangling the Effects of Size and Budget on Sex Allocation in Hermaphrodites

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No. 30 van Dooren TJM: *The Evolutionary Ecology of Dominance-Recessivity.* IIASA Interim Report IR-98-096 (1998). Journal of Theoretical Biology 198:519-532 (1999).

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No. 37 Gyllenberg M, Metz JAJ: *On Fitness in Structured Metapopulations.* IIASA Interim Report IR-99-037 (1999). Journal of Mathematical Biology 43:545-560 (2001).

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No. 41 Nowak MA, Sigmund K: *Games on Grids.* IIASA Interim Report IR-99-038 (1999). Dieckmann U, Law R, Metz JAJ (eds): The Geometry of Ecological Interactions: Simplifying Spatial Complexity, Cambridge University Press, Cambridge, UK, pp. 135-150 (2000).

No. 42 Ferrière R, Michod RE: *Wave Patterns in Spatial Games and the Evolution of Cooperation.* IIASA Interim Report IR-99-041 (1999). Dieckmann U, Law R, Metz JAJ (eds): The Geometry of Ecological Interactions: Simplifying Spatial Complexity, Cambridge University Press, Cambridge, UK, pp. 318-332 (2000).

No. 43 Kisdi É, Jacobs FJA, Geritz SAH: *Red Queen Evolution by Cycles of Evolutionary Branching and Extinction.* IIASA Interim Report IR-00-030 (2000). Selection 2:161-176 (2001).

No. 44 Meszéna G, Kisdi É, Dieckmann U, Geritz SAH, Metz JAJ: *Evolutionary Optimisation Models and Matrix Games in the Unified Perspective of Adaptive Dynamics.* IIASA Interim Report IR-00-039 (2000). Selection 2:193-210 (2001).

No. 45 Parvinen K, Dieckmann U, Gyllenberg M, Metz JAJ: *Evolution of Dispersal in Metapopulations with Local Density Dependence and Demographic Stochasticity.* IIASA Interim Report IR-00-035 (2000). Journal of Evolutionary Biology 16:143-153 (2003).

No. 46 Doebeli M, Dieckmann U: *Evolutionary Branching and Sympatric Speciation Caused by Different Types of Ecological Interactions.* IIASA Interim Report IR-00-040 (2000). The American Naturalist 156:S77-S101 (2000).

No. 47 Heino M, Hanski I: *Evolution of Migration Rate in a Spatially Realistic Metapopulation Model.* IIASA Interim Report IR-00-044 (2000). The American Naturalist 157:495-511 (2001).

No. 48 Gyllenberg M, Parvinen K, Dieckmann U: *Evolutionary Suicide and Evolution of Dispersal in Structured Metapopulations.* IIASA Interim Report IR-00-056 (2000). Journal of Mathematical Biology 45:79-105 (2002).

No. 49 van Dooren TJM: *The Evolutionary Dynamics of Direct Phenotypic Overdominance: Emergence Possible, Loss Probable.* IIASA Interim Report IR-00-048 (2000). Evolution 54: 1899-1914 (2000).

No. 50 Nowak MA, Page KM, Sigmund K: *Fairness Versus Reason in the Ultimatum Game.* IIASA Interim Report IR-00-57 (2000). Science 289:1773-1775 (2000).

No. 51 de Feo O, Ferrière R: *Bifurcation Analysis of Population Invasion: On-Off Intermittency and Basin Riddling.* IIASA Interim Report IR-00-074 (2000). International Journal of Bifurcation and Chaos 10:443-452 (2000).

No. 52 Heino M, Laaka-Lindberg S: *Clonal Dynamics and Evolution of Dormancy in the Leafy Hepatic Lophozia Silvicola.* IIASA Interim Report IR-01-018 (2001). Oikos 94:525-532 (2001).

No. 53 Sigmund K, Hauert C, Nowak MA: *Reward and Punishment in Minigames.* IIASA Interim Report IR-01-031 (2001). Proceedings of the National Academy of Sciences of the USA 98:10757-10762 (2001).

No. 54 Hauert C, De Monte S, Sigmund K, Hofbauer J: *Oscillations in Optional Public Good Games.* IIASA Interim Report IR-01-036 (2001).

No. 55 Ferrière R, Le Galliard J: *Invasion Fitness and Adaptive Dynamics in Spatial Population Models.* IIASA Interim Report IR-01-043 (2001). Clobert J, Dhondt A, Danchin E, Nichols J (eds): Dispersal, Oxford University Press, pp. 57-79 (2001).

No. 56 de Mazancourt C, Loreau M, Dieckmann U: *Can the Evolution of Plant Defense Lead to Plant-Herbivore Mutualism.* IIASA Interim Report IR-01-053 (2001). The American Naturalist 158: 109-123 (2001).

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No. 58 Brandt H: *Correlation Analysis of Fitness Landscapes.* IIASA Interim Report IR-01-058 (2001).

No. 59 Dieckmann U: *Adaptive Dynamics of Pathogen-Host Interacations.* IIASA Interim Report IR-02-007 (2002). Dieckmann U, Metz JAJ, Sabelis MW, Sigmund K (eds): Adaptive Dynamics of Infectious Diseases: In Pursuit of Virulence Management, Cambridge University Press, Cambridge, UK, pp. 39-59 (2002).

No. 60 Nowak MA, Sigmund K: *Super- and Coinfection: The Two Extremes.* IIASA Interim Report IR-02-008 (2002). Dieckmann U, Metz JAJ, Sabelis MW, Sigmund K (eds): Adaptive Dynamics of Infectious Diseases: In Pursuit of Virulence Management, Cambridge University Press, Cambridge, UK, pp. 124-137 (2002).

No. 61 Sabelis MW, Metz JAJ: *Perspectives for Virulence Management: Relating Theory to Experiment.* IIASA Interim Report IR-02-009 (2002). Dieckmann U, Metz JAJ, Sabelis MW, Sigmund K (eds): Adaptive Dynamics of Infectious Diseases: In Pursuit of Virulence Management, Cambridge University Press, Cambridge, UK, pp. 379-398 (2002).

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No. 63 Bürger R: *Additive Genetic Variation Under Intraspecific Competition and Stabilizing Selection: A Two-Locus Study.* IIASA Interim Report IR-02-013 (2002). Theoretical Population Biology 61:197-213 (2002).

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No. 65 Dercole F, Ferrière R, Rinaldi S: *Ecological Bistability and Evolutionary Reversals under Asymmetrical Competition.* IIASA Interim Report IR-02-053 (2002). Evolution 56:1081-1090 (2002).

No. 66 Dercole F, Rinaldi S: *Evolution of Cannibalistic Traits: Scenarios Derived from Adaptive Dynamics.* IIASA Interim Report IR-02-054 (2002). Theoretical Population Biology 62:365-374 (2002).

No. 67 Bürger R, Gimelfarb A: *Fluctuating Environments and the Role of Mutation in Maintaining Quantitative Genetic Variation.* IIASA Interim Report IR-02-058 (2002). Genetical Research 80:31-46 (2002).

No. 68 Bürger R: *On a Genetic Model of Intraspecific Competition and Stabilizing Selection.* IIASA Interim Report IR-02-062 (2002). Amer. Natur. 160:661-682 (2002).

No. 69 Doebeli M, Dieckmann U: *Speciation Along Environmental Gradients.* IIASA Interim Report IR-02-079 (2002). Nature 421:259-264 (2003).

No. 70 Dercole F, Irisson J, Rinaldi S: *Bifurcation Analysis of a Prey-Predator Coevolution Model.* IIASA Interim Report IR-02-078 (2002). SIAM Journal on Applied Mathematics 63:1378-1391 (2003).

No. 71 Le Galliard J, Ferrière R, Dieckmann U: *The Adaptive Dynamics of Altruism in Spatially Heterogeneous Populations.* IIASA Interim Report IR-03-006 (2003). Evolution 57:1-17 (2003).

No. 72 Taborsky B, Dieckmann U, Heino M: *Unexpected Discontinuities in Life-History Evolution under Size-Dependent Mortality.* IIASA Interim Report IR-03-004 (2003). Proceedings of the Royal Society of London Series B 270:713-721 (2003).

No. 73 Gardmark A, Dieckmann U, Lundberg P: *Life-History Evolution in Harvested Populations: The Role of Natural Predation.* IIASA Interim Report IR-03-008 (2003). Evolutionary Ecology Research 5:239-257 (2003).

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No. 75 Dercole F: *Remarks on Branching-Extinction Evolutionary Cycles.* IIASA Interim Report IR-03-075 (2003). Journal of Mathematical Biology 47: 569-580 (2003).

No. 76 Hofbauer J, Sigmund K: *Evolutionary Game Dynamics.* IIASA Interim Report IR-03-078 (2003). Bulletin of the American Mathematical Society 40: 479-519 (2003).

No. 77 Ernande B, Dieckmann U, Heino M: *Adaptive Changes in Harvested Populations: Plasticity and Evolution of Age and Size at Maturation.* IIASA Interim Report IR-03-058 (2003). Proceedings of the Royal Society of London Series B-Biological Sciences, 271: 415-423 (2004).

No. 78 Hanski I, Heino M: *Metapopulation-Level Adaptation of Insect Host Plant Preference and Extinction-Colonization Dynamics in Heterogeneous Landscapes.* IIASA Interim Report IR-03-028 (2003). Theoretical Population Biology 63:309-338 (2003).

No. 79 van Doorn G, Dieckmann U, Weissing FJ: *Sympatric Speciation by Sexual Selection: A Critical Re-Evaluation.* IIASA Interim Report IR-04-003 (2004). American Naturalist 163: 709-725 (2004).

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ARTICLE

Size and the Not-So-Single Sex: disentangling the effects of size and budget on sex allocation in hermaphrodites

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Abstract

Sex allocation theory explains how size-related variations in male and female fitness may favour the evolution of size-dependent sex allocation in hermaphrodites. Although empirical studies show that sex allocation changes gradually with size in many species, theoretical studies tend to predict an abrupt sex reversal from one sex to the other, i.e., single-sexed sequential hermaphrodites. We show that this discrepancy between data and theory collapses if one takes into account that size affects male and female fitness through distinct routes. Using the classification of budget (larger individuals spend a greater budget on reproduction) and direct (e.g. larger plants are taller and may disperse pollen more efficiently) effects of size suggested by Klinkhamer et al. (1997), we propose a simple general framework incorporating appropriately these two categories of size effects in male and female fitness expressions. Analytical and numerical results show that a gradual sex change is evolutionarily stable (ESS) for a large set of parameter values. Sex reversal is selected only in the absence of budget effects of size. We provide further predictions on size-dependent sex allocation and assess the relative importance of budget and direct effect for creating different patterns.

1 Introduction

Sex allocation theory (Ghiselin 1969, Warner 1975, Charnov 1982) provides evolutionary arguments for explaining patterns of relative investment in male versus female function in hermaphrodites. Classically, a clear distinction has been made between two types of hermaphroditism: simultaneous hermaphroditism, where individuals produce both male and female gametes; sequential hermaphroditism, where individuals are one sex at birth then switch to the other sex later in life. Models for simultaneous hermaphrodites typically predict the constant optimal sex allocation (relative investment in male versus female function), independent of individual or environmental conditions (Charnov 1982, Charnov 1996, Pen and Weissing 1999, Greeff and Michiels 1999), whereas models for sequential hermaphrodites focus on the optimal time – or, more generally, size – at which individuals should reverse sex (Ghiselin 1969, Warner 1975, Charnov 1982, 1993, Iwasa 1991).

Recent years have shown that such a sharp distinction is not realistic (DeWitt 1996, Petersen and Fisher 1996, Klinkhamer et al. 1997, St Mary 1997, Schärer et al. 2001, Angeloni et al. 2002). Many species show intermediate patterns, where individuals are simultaneous hermaphrodites but change their sex allocation gradually during their growth. In animals, examples include fishes (St Mary 1994, Petersen and Fisher 1996), snails (DeWitt 1996), worms (Vreys and Michiels 1998, Trouvé et al. 1999, Schärer et al. 2001), and sea slugs (Angeloni and Bradbury 1999). In plants a gradual shift in sex allocation with increasing size is the rule rather than the exception, and sequential hermaphroditism is rare (reviews in Freeman et al. 1980, Lloyd and Bawa 1984, Klinkhamer et al. 1997). In both plants and animals, the exact shape of the change depends on the species considered.

Therefore, the challenge now is to bring theory and experimental data together. Traditional theory for sequential hermaphrodites relies on the size-advantage argument, which assumes dissimilarities in size-dependent fitness gains through male and female function, that give an advantage of being one sex when small and the other when large (Ghiselin 1969, Warner 1975, Charnov 1982, 1993, Iwasa 1991). An abrupt sex reversal at a calculated threshold size is predicted, even when some dynamics is incorporated in the framework (Iwasa 1991). On the other hand, a few recent models have managed to predict a gradual sex change (Petersen and Fischer 1996, St Mary 1997, Angeloni et al. 2002). However, it is not clear what factors favour a gradual change as opposed to sex reversal in these models. Many specific components are included, in particular in the two species-specific models (Petersen and Fischer 1996, St Mary 1997), that render the interpretation of the results in a general context difficult. Compared to traditional models, they for instance include mating preferences and mating size recognition (Petersen and Fischer 1996, Angeloni et al. 2002), density dependence (St Mary 1997), sperm competition (Petersen and Fischer 1996, Angeloni et al. 2002), variation of the amount of resources available (Petersen and Fischer 1996, St Mary 1997, Angeloni et al. 2002), or costs to sex change (St Mary 1997). To what extent these different factors matter for selecting for gradual change is not assessed. Therefore, the question about why sex allocation theory fails to predict continuous sex reversal, and more generally the diversity of size-dependent sex allocation patterns, remains unanswered.

At the core of the problem is the ambiguous way that various effects of size are incorporated in models. From the very beginning of sex allocation theory (Ghiselin 1969, Warner 1975, Charnov 1982), many mechanisms have been described that explain how large individuals may get some advantage for reproduction over small individuals. These various effects can be classified in two main categories. First, size itself can be an advantage for reproduction, because of mating preferences or within-sex dominance effects in animals, because of a facilitation of dispersal, for instance, in plants. Following Klinkhamer et al. (1997), we will denote this class of effects as the *direct effect* of size. Second, larger individuals will generally have more resources and produce more gametes and offspring. Compared to smaller plants, this may lead to e.g. increased local mate or local resource competition for a given sex allocation pattern. This as a whole we will denote as the indirect effect of size or, rather, the *budget effect* (Klinkhamer et al. 1997). The key point is that the effects of size depend both on the size itself and on the budget invested, which by itself is a function of size and sex allocation. For this reason, budget effects of size are fundamentally different from direct effects in their effect on the evolution of sex allocation. Yet, traditional models of sex allocation never account for this fundamental difference, which may well explain why they fail to predict gradual sex change.

We provide in this paper a simple general framework that incorporates both direct and budget effects of size on male and female fitness in hermaphrodites. We include basic density and frequency dependence effects and we determine the size-dependent sex allocation patterns at the ESS. We explain the simple but crucial points that allow relating common size-advantage models to our unifying model. Using the classical power law functions for describing fitness gain curves (e.g. Charnov 1982, Lloyd and Bawa 1984, Klinkhamer et al. 1997, Muñoz and Warner 2003), we assess the relative importance of direct versus budget effect for the evolution of various sex allocation patterns. We will show that, in the absence of other physiological constraints, there are indeed few reasons why hermaphrodites should live a dramatic sex reversal rather than a gradual change of sex allocation. In most cases, evolution does not favour single-sexed sequential hermaphrodites.

2 Disentangling the effects of size on male and female fitness

2.1 Budget and direct effects of size influence differently the expression of fitness

We consider a hermaphrodite, either a plant or an animal, of size s. Total fitness of the individual depends on its fitness via the male function (m) and via the female function (f).

Fitness via the male function depends on the quantity of male gametes produced (c_m) - also denoted hereafter as 'the male clutch size' - and the fitness return per male gamete (F_m):

$$m = c_m \times F_m . \quad (1)$$

Similarly, fitness via the female function depends on the number of female gametes produced (c_f) - the female clutch size - and the fitness return per female gamete (F_f):

$$f = c_f \times F_f . \quad (2)$$

Size may affect both the number of gametes produced and their fitness returns (fig.1). An increase in size is usually correlated with an increase in resources available for reproduction R, therefore larger individuals will produce more gametes. For instance, large trees will bear more flowers and seeds, gonads will be heavier in large animals. Sex allocation p determines how much of the resources R are allocated to male versus female reproduction and depends also on size. The resources invested in male function (Rp) are divided up among c_m male gametes, each costing E_m resources, while the amount invested in the female function ($R(1\text{-}p)$) are used for producing c_f female gametes, each costing E_f resources. Therefore,

$$c_m(s) = \frac{R(s)\ p(s)}{E_m} \quad (3) \qquad \text{and} \qquad c_f(s) = \frac{R(s)\ (1-\ p(s))}{E_f}, \qquad (4)$$

where the notation expresses that c_m, c_f, R and p depend on size s.

The effect of size on the fitness returns per gamete is twofold (fig.1):

- The direct effect summarises all effects of size that correspond to a direct link between size itself and fitness returns, independently of other factors. Through, for example, dominance effects or mating preferences in animals, or facilitated propagation of pollen and seeds in plants, larger individuals may have a higher probability of reproducing than small ones. In this case, everything else being equal, male and female fitness returns per gamete can be written as simple increasing (accelerating, linear or decelerating) functions of size s.

- The budget effect corresponds to all indirect effects of size on fitness returns via the production of gametes. The increase in the quantity of gametes in large individuals will often enhance competition effects between gametes (e.g. sperm competition or geinotogamy), leading to a reduction of fitness return per gamete as clutch sizes increase. Male and female fitness gain returns tend to be either constant (no budget effect) or to decrease with clutch size (because of gamete competition), although theoretically they could also be increasing (because of Allee effects).

The incorporation of the two categories of effects leads to the expressions of male and female fitness gain curves as:

$$m(s, c_m(s)) = c_m(s) \times F_m\big(s, c_m(s)\big) \quad (5) \qquad \text{and} \qquad f(s, c_f(s)) = c_f(s) \times F_f\big(s, c_f(s)\big) \quad ,(6)$$

where in the expressions for the fitness returns F_m and F_f, the first argument represents the direct effect of size and the second argument the budget effect. Combining equations (5) and (6) with (3) and (4) leads to:

$$m(s, c_m(s)) = m(s, R(s), p(s)) = \frac{p(s)R(s)}{E_m} \times F_m\left(s, \frac{p(s)R(s)}{E_m}\right) \qquad (7)$$

and

$$f(s, c_f(s)) = f(s, R(s), p(s)) = \frac{(1-p(s))\,R(s)}{E_f} \times F_f\left(s, \frac{(1-p(s))\,R(s)}{E_f}\right), \qquad (8)$$

Resources $R(s)$ are generally assumed as a simple function of size s, while p(s) is an unknown variable of s. In this case, male and female fitness can be rewritten as:

$$m\big(s, p(s)\big) \quad (9) \qquad \text{and} \qquad f\big(s, p(s)\big). \quad (10)$$

2.2 Evolutionarily stable sex allocation rules

At the level of the individual, total fitness is relative to male and female fitness of the other individuals present in the population. For a mutant with sex allocation p and size s appearing in a population with sex allocation pattern p^* (p^* is not a fixed value but the function that assigns sex allocation $p^*(s)$ at each value of size s), total fitness can be written in the usual form (Shaw and Mohler 1953, Charnov 1982, Pen and Weissing 2002):

$$W(s,p,p^*) \propto \frac{m(s,p)}{\overline{m}(p^*)} + \frac{f(s,p)}{\bar{f}(p^*)} \qquad (11)$$

where $\overline{m}(p^*)$ and $\bar{f}(p^*)$ are respectively the mean fitness via the male and via the female function in the resident population:

$$\overline{m}(p^*) = \int_{\Omega} m(s,p^*)\,\omega(s)\,ds \quad \text{and} \quad \bar{f}(p^*) = \int_{\Omega} f(s,p^*)\,\omega(s)\,ds \qquad (12)$$

where ω is the size distribution in the population and Ω the set of all sizes represented in the population.

To determine the evolution of size-dependent sex allocation, we determine the optimal sex allocation at each size s. The evolutionarily stable strategy $\hat{p}$, when assigning at each value of size s the sex allocation $\hat{p}(s)$, must satisfy:

$$\left.\frac{\partial W(s,p,p^*)}{\partial p}\right|_{p=p^*=\hat{p}} = 0 \quad \text{and} \quad \left.\frac{\partial^2 W(s,p,p^*)}{\partial p_2}\right|_{p=p^*=\hat{p}} < 0 \qquad (13)$$

2.3 A specific model

Analytical approaches are rapidly limited and we have to take recourse to numerics for the main part of the study. With this goal in mind, and following other authors (e.g. Charnov 1982, Lloyd and Bawa 1984, Klinkhamer et al. 1997, Muñoz and Warner. 2003), we will make the simplifying assumptions that male and female fitness returns are power functions of individual size and clutch size (fig.2):

$$F_m(s,c_m(s)) = \alpha\, s^a\, (c_m(s))^u \quad (14) \quad \text{and} \quad F_f(s,c_f(s)) = \beta\, s^b\, (c_f(s))^v, \quad (15)$$

where α, β, a, b, u and v are constants and α, $\beta > 0$, $0 \le a,b \le 1$ and $-1 \le u,v \le 0$. Using equations (1) and (2), we can write male and female fitness as:

$$m(s,c_m(s)) = \alpha\, s^a\, (c_m(s))^{u+1} \quad (16) \quad \text{and} \quad f(s,c_f(s)) = \beta\, s^b\, (c_f(s))^{v+1}. \quad (17)$$

As only relative fitness matters (see equation (11)), the constants α and β do not influence the evolution of sex allocation. Parameter a (resp. b) measures the intensity of the direct effect of size on male (resp. female) fitness, from the absence of direct effect at a=0 (resp. b=0), up to a strong, and linear, direct effect at a=1 (resp. b=1) (fig.2a). Parameter u (resp. v) measures the intensity of competition between male (resp. female) gametes. In the absence of competition, and thus no budget effect (u=0, v=0), fitness returns per gamete are constant, and fitness gain curves increase linearly with clutch size. With extremely strong competition, and thus a very strong budget effect (u=-1, v=-1) fitness returns decrease linearly, and fitness gain curves are constant: they do not vary with clutch size (fig.2b). Since our purpose is to match the fitness curves commonly described in the literature, we will not consider in this study accelerating fitness curves that are believed to lead to dioecy (see also the discussion for S-shaped curves), therefore absolute values of a, b, u and v are kept between 0 and 1. Values of the parameters used for systematic numerical calculations are detailed in the legend to figure 2.

In addition, we assume that the resources allocated to reproduction, $R(s)$, are a power function of s,

$$R(s)=\rho\, s^{\gamma}\ , \quad (18)$$

where ρ and γ are positive constants. For simplicity, we did not vary γ in our simulations and fixed it arbitrarily at 1, but results do not change qualitatively with moderate changes of γ.

We numerically determined the evolutionarily stable sex allocation pattern $\hat{p}$ from (13) on the assumption that the size distribution ω is a gamma one ($\omega(s) = \lambda^2\, s\, e^{-\lambda s}$, fig.2c). This is a skewed distribution whose main advantage is to produce a relatively smooth and continuous distribution of sizes on the positive axis only. We do not expect this choice to affect in a major way the results. Details of the calculations are given in Appendix A.

To verify that results are not overly model-dependent, we also used another specific model, where fitness through male and female functions are linear fractions of individual size and clutch size (see Appendix B). Below we only consider the power law case in some detail as the conclusions for the linear fraction case matched those for the power law one.

3 Results

We found five distinct patterns, corresponding to different combinations of budget and direct effects: (1) sex allocation is independent of size (e.g. fig.3a), (2) strict sex-reversal, with no simultaneous hermaphrodite state (e.g. fig.3d), (3) gradual change from one sex to the other (e.g. fig.3h), (4) small individuals are one sex, large individuals are hermaphrodites (e.g. fig.3i), (5) individuals are always hermaphrodites, but with biased allocation to one sex when small and to the other when large (e.g. fig.3f). The two first extreme cases are rare. The most common pattern is a gradual shift in the relative allocation to male versus female function (cases (3), (4) and (5)). Throughout the text, if not specified, the term "hermaphroditism" refers to the usual sense of the word, i.e. "simultaneous hermaphroditism".

Contrary to what is predicted in previous studies, that consider only one type of effect (e.g. Charnov 1982), we show that the evolution of size-dependent sex allocation depends both on the direct and budget effects of size, but also on the interaction between them. We will therefore present our results as a function of these three key factors: the difference between the male and the female fitness curves for the direct effect (measured by the difference in the exponents a-b in the power law model), this difference for the budget effect (measured by u-v), and the relationship between these differences.

3.1 Sex reversal versus gradual change – the key role of the budget effect

Analytical and numerical results show that the absence or presence of a budget effect for the male and/or the female function completely determines the selection for either abrupt sex reversal or gradual change of sex allocation as size increases.

First, we show that the absence of budget effects leads necessarily to the selection of sex reversal or to constant sex allocation. This result is obtained by using equations (5) and (6) for rewriting the general expression for the fitness of an individual in equation (11) as:

$$W(s,p,p^*) = k_1\, c_m(s) F_m(s, c_m(s)) + k_2 c_f(s) F_f(s, c_f(s)), \qquad (19)$$

where k_1 and k_2 are positive constants. In absence of budget effects, $F_m(s, c_m(s))$ and $F_f(s, c_f(s))$ reduce to $F_m(s)$ and $F_f(s)$. Using additionally equations (3) and (4), we obtain:

$$W(s,p,p^*) = k_1\, c_m(s) F_m(s) + k_2 c_f(s) F_f(s) = k_1 \left(\frac{R(s)\, p}{E_m} \right) F_m(s) + k_2 \left(\frac{R(s)(1-p)}{E_f} \right) F_f(s). \quad (20)$$

Therefore the derivative of the total fitness reads:

$$\frac{\partial W(s,p,p^*)}{\partial p} = R(s)\big(\kappa_1 F_m(s) - \kappa_2 F_f(s)\big), \qquad (21)$$

where κ_1 and κ_2 are positive constants. This derivative does not depend on p, only on s. If it is everywhere zero, as is the case when there is either no direct effect or male and female direct effects are exactly the same, a constant sex allocation will be selected. At those s where it is positive p=1 is selected; if it is negative p=0 is selected. Sex reversal occurs at the value of s where the derivative changes its sign.

Figure 3 illustrates, for the specific model, how this scenario breaks down in the presence of any (even slight) budget effect ($u \neq 0$ or $v \neq 0$): the selected size-dependent sex allocation pattern becomes at once gradual, even if male and female budget effects are similar (u=v, see fig.3).

Thus, the usual prediction of strict sex reversal without any intermediates (e.g. Charnov 1982) is extremely vulnerable to even a slight change in model assumptions. Within the framework of our model family it is valid if, and only if, all size effects on fitness can be classified as direct. A robust prediction of strict sex reversal can only be recovered through the introduction of additional constraints, such as a high physiological or behavioural costs of simultaneous hermaphroditism.

In the field, measurements may exhibit cases that are close to sex reversal. This will happen if there is a relatively sharp change from one sex to the other, such that the very few individuals at the intermediate hermaphroditic state might be missed. Our results indicate that, without additional constraints, this is a relatively unusual pattern, occurring only under restricted conditions. Figure 4 depicts the values of the parameters that favour a sharp change from one sex to the other: such cases occur only if either both male and female budget effects are very small, or if male and female budget effects are extremely different and act in synergy with direct effects (i.e. fitness curves for one sex level off drastically while fitness curves for the other sex are almost linearly increasing).

The previous results show that in general budget effects of size matter more for the shape of sex change than direct effects. This is corroborated by figure 5, where the slope of sex change (estimated by the derivative of the sex allocation slope at the middle value of the population sex allocation range) appears to vary much more with budget than with direct effects; this is confirmed by statistical analyses that show that the slope of sex change depends more on the budget than on the direct effect (linear regression on (u-v): r=0.017, p<0.001, R^2=0.68, n=625; linear regression on (a-b): r=0.008, p<0.001, R^2=0.15, n=625; parameter values used for the numerical calculations are provided in fig.2).

3.2 Maleness versus femaleness

In this part, we first discuss the conditions that create either protogyny (maleness increases with size) or protandry (femaleness increases with size). Second, we consider cases where all individuals of a population will be biased towards one sex, i.e. sex allocation varies gradually but stays either lower than 0.5 or higher. Third, we show that the relative influence of direct and budget effects on sex allocation is not similar for small and large individuals.

Not surprisingly, we found that the slope of sex change decreases (large individuals invest more in female function than small ones) if budget and direct effects act in synergy such that the two male fitness curves level off more than the female ones ($a<b$ and $u<v$), (fig.5a to d). In the opposite case ($a>b$ and $u>v$), this pattern is reversed. Results are not so straightforward when budget and direct effects act oppositely on male and female fitness curves (i.e., $a>b$ and $u<v$ or $a<b$ and $u>v$, fig.5e,f). In this case the exact values of the exponents will determine the direction of sex change. We show numerically that an increase of relative allocation to male function is selected when $u-v>-(a-b)$, while a decrease is selected when $u-v<-(a-b)$. Therefore we cannot conclude that any particular effect is more important for the sign of the slope (contrary to its shape, see above). In the other model considered (Appendix B), the equivalent condition is slightly different and the budget effect seems to matter slightly more than the direct effect.

We found that small and large individuals are both male-biased (sex allocation $p>0.5$ whatever the size) when the budget effect is more important for the male than for the female function ($u>v$) and when in contrast the direct effect is more important for the female than for the male function ($a\leq b$). Conversely, small and large individuals are both female-biased ($p<0.5$) when the budget effect is less important for the male than for the female function ($u<v$) and when in contrast the direct effect is less important for the female than for the male function ($a\geq b$).

Quite unexpectedly, we found different results on the relative importance of the two effects on the sex of small versus large individuals. The sex emphasised by small individuals depends more on the difference in direct effects (linear regression on (a-b), r=-0.771, p<0.001, R^2=0.59, n=625, fig.6a) than on the budget effect (linear regression on (u-v), r=-0.466, p<0.001, R^2=0.21, n=625, fig.6b). For large individuals, it is the reverse (linear regression on (a-b), r=0.291, p<0.001, R^2=0.14, n=625, fig.6c, linear regression on (u-v), r=0.682, p<0.001, R^2=0.75, n=625, fig.6d).

3.3 Circumstances that favour a large proportion of simultaneous hermaphrodites

Some conditions lead to such a gradual change in sex allocation that all individuals, whatever their size, will express both sexes. This simultaneous hermaphroditism is favoured by an opposite influence of direct and budget effects on male versus female fitness ($a>b$ and $u<v$ or $a<b$ and $u>v$). In addition, budget effects need to be considerable (i.e., $u>>0$ and $v>>0$) and the difference between male and female direct effects versus male and female budget effects needs to be of similar amplitude (i.e., $(a-b) \approx -(u-v)$, see figure 7). At the extreme, the slope of sex change is so small that in natural populations changes in sex allocation with size might even not be detected.

We never encountered the case where large individuals would be one sex while small individuals would be hermaphrodite. The reverse is however common. Two preconditions for this seem to be that the differences in the exponents for the budget effect ($|u-v|$) and for the direct effect ($|a-b|$) are not strong and the amplitudes are neither similar nor very different.

4 Discussion

Sex reversal vs gradual change

Our most important result is that prediction of sex reversal at a threshold size, as opposed to gradual change in sex allocation with increasing size, is limited to very specific cases. The classification of the various effects of size on fitness into two categories, the budget and the direct effects, as suggested by Klinkhamer et al. (1997), and made explicit in this paper, proves crucial. We show that evolution favours an abrupt reversal of sex at a threshold size only if there are no budget effects of size. In all other cases, a gradual change in sex allocation with size is predicted.

Why, then, has sequential hermaphroditism so long dominated the literature on sex allocation theory (Ghiselin 1969, Warner 1975, Charnov 1982, 1993, Iwasa 1991, Muñoz and Warner 2003)? Firstly, there is a technical reason. In many traditional models sex reversal is assumed *a priori*; no simultaneously hermaphroditic variants are confronted to sequential types. Secondly, distinct effects of size are not disentangled but rather treated together as if they were all direct effects – this naturally leads to the prediction of sex reversal. Yet, not only direct effects of size are described in this literature, although they prevail (e.g. male dominance, mating choice, inexperience (Warner 1975) and male-male competition for territories (Charnov 1982)). Budget effects – though not treated as such – are mixed with direct effects in the reasoning. For instance, the correlation of clutch size with size is described as a potential factor influencing size-dependent sex allocation (Ghiselin 1969, Charnov 1982).

Why is the distinction between budget and direct effects of size so crucial? The fundamental difference between these effects is the way they affect fitness. While direct effects on individual fitness are additive, because fitness returns per gamete are independent of each other, budget effects introduce a nonlinearity in fitness because of intergamete competition. In the case of additive effects, if at one size it is more interesting to be one sex, each gamete should adopt this sex, therefore individuals will be fully male or female. The introduction of nonlinearity, resulting from a density dependence of the fitness return per gamete, renders balanced strategies valuable, and thus leads to the selection of intermediate patterns of sex allocation.

Our simple general framework allows also to disentangle the crucial factors that lead a few recent studies to predict gradual sex change (Petersen and Fischer 1996, St Mary 1997, Angeloni et al. 2002). In Petersen and Fischer (1996) and Angeloni et al. (2002), a common point is the incorporation of budget effects of size for the male function: sperm competition is introduced and different size classes are assumed to have different resource levels at their disposal for gametes production. These cases are simple since no direct effect is taken into account (although in Petersen and Fischer (1996) assortative mating might be interpreted as such) and no budget effect is considered for the female function. Therefore, in the light of our study, we conclude that independently of other sophistications in the models, a particular type of budget effect of size for the male function is the factor that induces automatically gradual sex change. In St Mary (1997), the interpretation is more tricky because the numerous components of fitness introduced in this species-specific model refer to behavioural states instead of sex allocation patterns. Gradual sex allocation change is predicted only as the result of assuming dynamical costs (see below for a discussion of such costs). An alternative explanation would be that the species studied suffers from budget effects, in which case gradual patterns also result without the assumption of dynamical costs.

Our results affect also the theory of environmental sex determination (Charnov and Bull 1977, Charnov 1982, Charnov and Dawson 1989, Blackmore and Charnov 1989). Traditional models predict that sex may vary along an environmental gradient if resources available for reproduction change with environmental conditions, e.g. with the size of patches (or hosts for parasites) or simply with habitat quality. Predictions classically are that individuals will be one sex below a given threshold and the other sex beyond. Our results for size-dependent sex allocation suggest a less radical picture. Considering the similarity between resources-environment correlation and resources-size correlation, we predict that sex allocation should vary gradually with the environment in most cosexuals. Therefore, the paradigm of patches with homogeneous populations of single-sex individuals drops: most intermediate quality patches should carry simultaneous hermaphrodites.

Sex reversal versus gradual change in plants and animals

Because of their sessile habit, with restricted capacities to disperse as an adult, budget effects are likely to occur in most plant species, e.g. due to increased geitonogamy, pollinator saturation, competition between seeds of the same plant. This may explain why only 0.1% or fewer of all angiosperms show complete sex change (Freeman et al. 1980) while, even in studies on hermaphrodite plants that were not designed for this purpose, 79% showed a significant gradual change in sex allocation (Klinkhamer et al. 1997).

In animals also, low mobility seems to favour simultaneous hermaphroditism, because of the increased competition among siblings (Ghiselin 1969, Charnov 1982, McCartney 1997). In all species where local mate competition (LMC – Hamilton 1967) is important, budget effects may be expected. Sperm competition between related and unrelated individuals has been identified as a probable selective pressure in most of the recent studies that show size-dependent sex allocation in simultaneous hermaphrodites (Angeloni and Bradbury 1999, Petersen and Fischer 1996, DeWitt 1996, Trouvé et al. 1999, Schärer et al. 2001) though other budget effects have been suggested (St Mary 1994, 1997, Trouvé et al. 1999). Our results lead to the prediction that sex reversal will be detected in species where budget effects are absent or direct effects are very high compared to budget effects: in this latter case, the slope of the change can be sufficiently sharp for intermediate hermaphroditic states to be rare. These predictions seem to be supported by experimental data. Strikingly, sequential hermaphroditism is found in animals (e.g. some reef fishes) that form groups consisting of a dominant male or female surrounded by a number of smaller individuals of the smaller sex suggesting that indeed competition for mates plays an extremely important role. However, it must be noted that recent work have shown that such cases can be far more complicated than previously thought (review in Kuwamura and Nakashima 1998, Muñoz and Warner 2003). For instance even in the case of behavioural sex reversal the retention of both male and female tissues may facilitate rapid adjustment of sex allocation, favouring gradual changes with size (St Mary 1994, 1997, Kuwamura and Nakashima 1998). In species where budget effects are potentially important, but where sex reversal seems the law, the traditional sex allocation theory fails to explain selective pressures at play. We probably have to search for other mechanisms, for instance behavioural costs to simultaneous hermaphroditism or strong behavioural control of the sex of dominated individuals in hierarchical groups (see e.g. for reef fishes Fricke and Fricke 1977, Kuwamura and Nakashima 1998).

Protogyny versus protandry in sequential and simultaneous hermaphrodites

Traditional sex allocation theory predicts that, in the case of sequential hermaphroditism, protogyny is favoured if the female fitness gain curve levels off more than the male one, while protandry is selected in the reverse case (Ghiselin 1969, Warner 1975, Charnov 1982, 1993). Our results show that these predictions stay unchanged when considering both direct and budget effects, and extend to gradual sex change, provided that the corresponding fitness curves both level off more for the same sex. Where it is not the case, e.g. via the budget effect the female fitness curve levels off more than for the male function, but it is the reverse via the direct effect, predictions are far less straightforward. Such cases favour smooth sex allocation variations, therefore (simultaneously) hermaphroditic states.

In animals, protandry and protogyny are both encountered (review in Ghiselin 1969, Warner 1975, Charnov 1982). Size effects on male fitness have received more attention than on female fitness. The few precise measures of fitness returns have focused on the male function (McCartney 1997, Yund 1998). In most studies, size effects on female fitness returns are neglected while speculations run on the form of male fitness gain curves. In this context, our results show that the direction of sex change depends on a balance between direct effects (mostly dominance of the larger individual), that select for protogyny, and budget effects (mostly due to sperm competition) that select for protandry. Recent years have seen an increasing interest in sperm competition both in theoretical (Petersen and Fischer 1996, Charnov 1996, Pen and Weissing 1999, Greeff and Michiels 1999, Muñoz and Warner 2003) and empirical (Angeloni and Bradbury 1999, Petersen and Fischer 1996, DeWitt 1996, Trouvé et al. 1996, 1999, McCartney 1997, Yund 1998, Schärer et al. 2001, Schärer and Wedekind 2001) studies. This may explain why most recent studies on size-dependent sex allocation in simultaneous hermaphrodites have predicted and detected protandry in the species studied (Petersen and Fischer 1996, Trouvé et al. 1999, Schärer et al. 2001). However, in species for which territoriality is important, dominance effects might exceed sperm competition and select for protogyny (Charnov 1982). Saturating female fitness curves reinforce the pressure for protogyny (St Mary 1994, 1997), while strong direct effects on female fitness may favour protandry (DeWitt 1996).

In plants, the mode of pollination seems to be an important factor for the direction of size-dependent sex allocation: most wind-pollinated plants show size-independent sex allocation or an increase in maleness with plant size, while most animal-pollinated plants show an increase in femaleness (review in de Jong and Klinkhamer 1994, Klinkhamer et al. 1997, Sakai and Sakai 2003). Klinkhamer et al. (1997) reviewed the different reasons why budget and direct effects of size are expected to be different in wind- and animal-pollinated plants. We investigated the adaptive sex allocation patterns predicted when shaping budget and direct effects corresponding to the two modes of pollination described in Klinkhamer et al. (1997). Pollen export is often less efficient in larger animal-pollinated plants because insects visit more flowers on the same plant. The male budget effect is therefore the most important factor influencing sex allocation. In this case, we find that adaptive sex allocation decreases with size, as generally observed for these species (fig.8a). In wind-pollinated plants, the most important effect is probably an increased efficiency of pollen dispersal with size because large plants are usually taller (a direct effect of size) therefore relative allocation to male function increases with size (fig.8b). However, when size increase results in bigger but not higher plants, such an advantage is absent, which may explain that in wind-pollinated plants there are relatively many exceptions to the general rule (Kinkhamer et al. 1997, Sakai and Sakai 2003).

Fitness curves and population dynamics

Where analytical results were not possible, we had to assume specific fitness curves. For facilitating the comparison with other models, we followed the usual assumption of power law functions (e.g. Charnov 1982, Lloyd and Bawa 1984, Klinkhamer et al. 1997, Schärer et al. 2001, Muñoz and Warner 2003). Results remain however qualitatively unchanged when considering another mathematical expression for male and female fitness (Appendix B), which suggests their overall robustness. We focused on linear or decelerating fitness curves as they are predominant in the literature. Saturating gain curves with gametes increase (budget effect) are best described for male fitness through geitonogamy and pollen saturation in plants (review in Klinkhamer et al. 1997) or sperm competition in animals (Charnov 1982, Petersen and Fischer 1996, Charnov 1996, Pen and Weissing 1999, Greeff and Michiels 1999, Angeloni et al. 2002, Muñoz and Warner 2003). Nonlinear fitness gain curves are more scarcely considered for the female function (Charnov 1982, review in Klinkhamer et al. 1997 and Pen and Weissing 1999). Direct effects of size are also verbally described as increasing (linear; decelerating) functions of size through saturation of the size-advantage for mating. Some authors have suggested that S-shaped fitness curves could also be relevant if some Allee effects are involved (Pen and Weissing 1999, Angeloni 2002). We believe that such cases will not change our main result on the necessity of a budget effect for getting sex reversal, while secondary results will probably be affected (Pen and Weissing 1999). Considering partially or totally accelerating fitness curves is certainly an interesting perspective, in particular when combined with decelerating ones, since such curves are generally believed to favour dioecy (e.g. Thomson and Brunet 1990, Charnov 1996, McCartney 1997).

Our aim in this paper was to present a single framework that integrates the key elements around which the debate on size-dependent sex allocation has so far crystallised. The next step would be to incorporate more realistically population dynamics. Strictly speaking the fitness gain curves for the budget effect can only reflect competition between the gametes of the same individual (for instance, within the pollen of the same flower, or the pollen of different flowers of the same plant). Evidence of diminishing fitness returns with selfing is well documented in plants (review in Klinkhamer et al. 1997). In animals such studies are less common (Trouvé et al. 1996, Johnston et al. 1998); much more attention has been paid to competition between related individuals (Local Mate Competition, Hamilton 1967) or even between unrelated individuals (e.g. Charnov 1996, Petersen and Fischer 1996, Angeloni et al. 2002). In this case the success of sex allocation strategies will depend on the population structure. For instance, several studies have shown variation of sex allocation with mating group size (Raimondi and Martin 1991, West et al. 1999, Schärer and Wedekind 2001). In populations with fluctuating densities, we cannot assume a fixed size distribution as in most models, including ours. Moreover, sex allocation strategies are likely to influence population dynamics via feedback effects. In these cases fitness curves cannot be considered as absolute functions independent of size and kin relationships: these two components need to be introduced as variables in male and female fitness functions (see also Pen and Weissing 2001). This will prove useful in particular in studies where mating dynamics is considered (DeWitt 1996, Greeff and Michiels 1999, Trouvé et al. 1999, Hughes et al. 2002, Lüscher and Wedekind 2002, see also Puurtinen and Kaitala 2002). We expect that in most cases this introduction of dynamics will only reinforce the prediction for gradual sex allocation change rather than sex reversal. Incorporating physiological and dynamical costs for sex reversal will also favour gradual change (St Mary 1997, Kuwamura and Nakashima 1998). Sex reversal on the other hand may be favoured when there are behavioural costs for hermaphrodites in not clearly behaving as a single-sexed individual, e.g. for parental care or mating selection. Coevolution of size-dependent sex allocation with sexual selection is an important issue that certainly requires more attention in the future.

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Appendix A – Determining the optimal sex allocation (online enhancement)

Optimal sex allocation $\hat{p}(s)$ is the solution of equations (13). For solving these relatively complex equations, we proceed in two steps.

First, we set $\tilde{m} = \overline{m}(p^*)$ and $\tilde{f} = \bar{f}(p^*)$, and we fix $\tilde{m}$ and $\tilde{f}$ as constant. The expression of the fitness function in equation (11) can then be written as:

$$W(s,p,p^*) \propto \left(\frac{m(s,p)}{\tilde{m}} + \frac{f(s,p)}{\tilde{f}} \right). \quad \text{(A1)}$$

If we substitute (A1) into (13) we can calculate the optimal sex allocation as a function of $\tilde{m}$ and $\tilde{f}$, that we denote as $\tilde{p}(s,\tilde{m},\tilde{f})$.

Next we relax the assumption that $\tilde{m}$ and $\tilde{f}$ are constant. At the maximum, their values $\hat{m}$ and $\hat{f}$ are solutions of the system $\begin{cases} \hat{m} = \overline{m}\left(\tilde{p}(s,\hat{m},\hat{f})\right) \\ \hat{f} = \bar{f}\left(\tilde{p}(s,\hat{m},\hat{f})\right) \end{cases}$. (A2)

We use the Newton-Raphson iteration to solve this system. Finally, we find the optimal sex allocation as a function of size:

$$\hat{p}(s) = \tilde{p}(s,\hat{m},\hat{f}). \quad \text{(A3)}$$

Appendix B – Similar results with another specific model (online enhancement)

For testing the consistency of the results with the power law model, we used another specific model, where fitness through male and female functions are linear fractions of individual size and clutch size:

$$F_m(s,c_m) = \chi \frac{s}{1+d\,s}\,\frac{1}{1+e\,c_m} \quad \text{and} \quad F_f(s,c_f) = \eta \frac{s}{1+h\,s}\,\frac{1}{1+k\,c_f}\ , \quad \text{(B1)}$$

where κ, η, d, e, h and k are constants and κ, $\eta > 0$, $0 \le d, e, h, k \le 1$.

If we substitute expressions (1) and (2) in equations (B1), we obtain:

$$m(s, p) = \chi \frac{s}{1+d\ s} \frac{c_m}{1+e\ c_m} \qquad \text{and} \qquad f(s,p) = \eta \frac{s}{1+h\,s} \frac{c_f}{1+k\ c_f}\ . \qquad \text{(B2)}$$

In this case, we assumed that resources allocated to reproduction, *R,* are linearly dependent on size *s*.

Numerical calculations similar to the ones used for the power law models (see Appendix A) lead to similar results. In particular the conditions for obtaining sex reversal are equivalent. With respect to more detailed predictions, the results are very similar, with only slight differences in the exact shapes of sex allocation patterns due to the differences in the exact shapes of the fitness curves for the two models.

Literature cited

Angeloni, L., and J. W. Bradbury 1999. Body size influences mating strategies in a simultaneously hermaphroditic sea slug, *Aplysia vaccaria*. Ethology, Ecology and Evolution 11:187-195.

Angeloni, L., J. W. Bradbury, and E. L. Charnov 2002. Body size and sex allocation in simultaneously hermaphroditic animals. Behavioral Ecology 15:419-426.

Blackmore, M. S., and E. L. Charnov 1989. Adaptive variation in environmental sex determination in a nematode. American Naturalist 134:817-823.

Charnov, E. L. 1982. The theory of sex allocation. Princeton University Press, Princeton, NJ.

Charnov, E. L. 1993. Life history invariants. Oxford University Press, Oxford.

Charnov, E. L. 1996. Sperm competition and sex allocation in simultaneous hermaphrodites. Evolutionary Ecology 10:457-462.

Charnov, E. L., and J. J. Bull. 1977. When is sex environmentally determined? Nature 266:828-830.

Charnov, E. L., and T. E. Dawson 1989. Environmental sex determination with overlapping generations. The American Naturalist 134:806-816.

DeWitt, T. J. 1996. Gender contests in a simultaneous hermaphroditic snail: a size-advantage model for behaviour. Animal Behaviour 51:345-351.

de Jong, T. J., and P. G. L. Klinkhamer 1994. Plant size and reproductive success through female and male function. Journal of Ecology 82:399-402.

Freeman, D. C., K. T. Harper, and E. L. Charnov 1980. Sex change in plants: old and new observations and new hypothesis. Oecologia 47:212-232.

Fricke, H., and S. Fricke. 1977. Monogamy and sex change by aggressive dominance in coral reef fish. Nature 266: 830-832.

Ghiselin, M. T. 1969. The evolution of hermaphroditism among animals. Quarterly Review of Biology 44:189-208.

Greeff, J. M., and N. K. Michiels. 1999. Sperm digestion and reciprocal sperm transfer can drive hermaphrodite sex allocation to equality. American Naturalist 153:421-430.

Hamilton, W. D. 1967. Extraordinary sex ratios. Science 156:477-488.

Hughes, R. N., P. H. Manriquez and J. D. D. Bishop 2002. Female investment is retarded pending reception of allosperm in a hermaphroditic colonial invertebrate. Proceedings of the National Academy of Science 99:14884-14886.

Iwasa, Y. 1991. Sex change evolution and cost of reproduction. Behavioral Ecology 2:56-68.

Johnston, M. O., B. Das, and W. R. Hoeh 1998. Negative correlation between male allocation and rate of self-fertilization in a hermaphroditic animal. Proceedings of the National Academy of Science 95:617-620.

Klinkhamer, P. G. L., T. J. de Jong, and J. A. J. Metz 1997. Sex and size in cosexual plants. Trends in Ecology & Evolution 12:260-265.

Kuwamura, T., and Y. Nakashima 1998. New aspects of sex change among reef fishes: recent studies in Japan. Environmental Biology of Fishes 52:125-135.

Lloyd, D. G., and K. S. Bawa 1984. Modification of gender in seed plants in varying conditions. Evolutionary Biology 17:255-338.

Lüscher, A., and C. Wedekind. 2002. Size-dependent discrimination of mating partners in the simultaneous hermaphroditic cestode *Schistocephalus solidus*. Behavioral Ecology 13:254-259.

McCartney, M. A. 1997. Sex allocation and male fitness gain in a colonial, hermaphroditic marine invertebrate. Evolution 51:127-140.

Muñoz, R. C., and R. R. Warner 2003. A new version of the size-advantage hypothesis for sex change: incorporating sperm competition and size-fecundity skew. American Naturalist 161:749-761.

Pen, I., and F. J. Weissing 1999. Sperm competition and sex allocation in simultaneous hermaphrodites: A new look at Charnov's invariance principle. Evolutionary Ecology Research 1:517-525.

Pen, I., and F. J. Weissing 2002. Optimal sex allocation: steps towards a mechanistic theory, Pages 26-45 *in* Hardy, I., ed. Sex Ratios - Concepts and Research Methods. Cambridge University Press, Cambridge.

Petersen, C. W., and E. A. Fischer 1996. Intraspecific variation in sex allocation in a simultaneous hermaphrodite: the effect of individual size. Evolution 50:636-645.

Puurtinen, M., and V. Kaitala 2002. Mate-search efficiency can determine the evolution of separate sexes and the stability of hermaphroditism in animals. American Naturalist 160:645-660.

Raimondi, P. T., and J. E. Martin 1991. Evidence that mating group size affects allocation of reproductives resources in a simultaneous hermaphrodite. American Naturalist 138:1206-1217.

Sakai, A., and S. Sakai 2003. Size-dependent sex allocation in wind-pollinated cosexual plants: fecundity vs stature effects. Journal of Theoretical Biology 222:283-295.

Shaw, R. F., and J. D. Mohler 1953. The selective advantage of the sex ratio. American Naturalist 87:337-342.

Schärer, L., L. M. Karlsson, M. Christen, and C. Wedekind 2001. Size-dependent sex allocation in a simultaneous hermaphrodite parasite. Journal of Evolutionary Biology 14:55-67.

Schärer, L., and C. Wedekind 2001. Social situation, sperm competition and sex allocation in a simultaneous hermaphrodite parasite, the cestode *Schistocephalus solidus*. Journal of Evolutionary Biology 14:942-953.

St Mary, C. M. 1994. Sex allocation in a simultaneous hermaphrodite, the blue-banded goby (*Lythrypnus dalli*): the effects of body size and behavioral gender and the consequences for reproduction. Behavioral Ecology 5:304-313.

St Mary, C. M. 1997. Sequential patterns of sex allocation in simultaneous hermaphrodites: do we need models that specifically incorporate this complexity? American Naturalist 150:73-97.

Thomson, J. D., and J. Brunet 1990. Hypotheses for the evolution of dioecy in seed plants. Trends in Ecology & Evolution 5:11-16.

Trouvé, S., F. Renaud, P. Durand, and J. Jourdane 1996. Selfing and outcrossing in a parasitic hermaphrodite helminth (Trematoda, Echinostomatidae). Heredity 77:1-8.

Trouvé, S., J. Jourdane, F. Renaud, P. Durand, and S. Morand 1999. Adaptive sex allocation in a simultaneous hermaphrodite. Evolution 53:1599-1604.

Vreys, C., and N. K. Michiels 1998. Sperm trading by volume in a hermaphroditic flatworm with mutual penis intromission. Animal Behaviour 56:777-785.

Warner, R. R. 1975. The adaptive significance of sequential hermaphroditism in animals. American Naturalist 109:61-82.

West, S. A., K. E. Flanagan, and H. C. J. Godfray 1999. Sex allocation and clutch size in parasitoid wasps that produce single-sex broods. Animal Behaviour 57:265-275.

Yund, P. O. 1998. The effect of sperm competition on male gain curves in a colonial marine invertebrate. Ecology 79:328-339.

Figure legends

Figure 1: The effects of size and sex allocation on fitness.

Individual size *s* can influence male and female fitness directly or indirectly, because it correlates with an increase of resources. Part of the resources (*Q*) will affect both male and female fitness and are not partitioned. (The effect of indivisible resources *Q* and direct size effects are usually confounded. On a theoretical level this does no harm if *Q* is a simple function of size. However, in the translation step to concrete cases the distinction can be most helpful.) Part of the resources (*R*) represent the budget available for reproduction and are partitioned into male or female gamete production. A fraction *p* of these resources (sex allocation) are used to produce c_m male gametes, with an amount of energy E_m invested in each gamete. A fraction (1-*p*) is used for production of c_f female gametes, with an amount of energy E_f invested in each gamete. An increase in clutch size will, however, increase the level of local competition between gametes, and thus affect the fitness return per gamete. The signs + and - indicate how an increase of size is expected to affect the different components.

Figure 2: Fitness curves and size distribution: the specific model

(a) Male fitness (gamete production) as a function of size (direct effect). No budget effect is considered. When there is no direct effect for the male function (*a*=0), the curve is constant. At the strongest (*a*=1), the curve is linear. The female fitness curve will be similar, with *a* replaced by *b*. (b) Male fitness gain curve as a function of clutch size (budget effect). No direct effect is considered. When there is no budget effect for the male function (*u*=0), the fitness return per gamete is constant, thus fitness for the individual increases linearly with clutch size. At the strongest (*u*=-1), the linear return in number of gametes is exactly balanced by the linear loss in fitness per gametes, thus at the level of the individual, fitness is constant. (c) We assume for numerical calculation that the size distribution within the population is a gamma one: $\omega(s) = \lambda^2\ s\ e^{-\lambda s}$ with λ=0.1. We calculated ESSes for the parameters *a* and *b* varying from 0 to 1 and *u* and *v* varying from –1 to 0. Because numerical calculations at the extreme values were very time-consuming because of convergence problems, systematic data for statistical analyses were obtained with a restricted range of the parameters: *a* and *b* varied from 0.1 to 0.9 with step 0.2; *u* and *v* ranged from –0.9 to –0.1 with step 0.2. Thus *n*=625 sex allocation patterns were obtained.

Figure 3: Strict sex reversal only occurs in the absence of a budget effect.

As soon as there is a slight budget effect, there is no true sex reversal: a gradual sex change results. For the clarity of the illustration, this figure shows a case where male and female budget effects are equal (considering a difference in budget effects would only render the figure a bit less illustrative; same qualitative results would be obtained except for the two right figures on the top line). Columns from left to right correspond to no budget effect (*u*=*v*=0), a slight budget effect (*u*=*v*=-0.05), a median budget effect (*u*=*v*=-0.5). Lines from top to bottom correspond to no difference in the direct effects for male and female fitness (*a*=*b*=0.3), a slight difference in direct effects (*a*=0.1, *b*=0.3), a strong difference in direct effects (*a*=0.1, *b*=0.9). When there is no difference between male and female fitness for the two effects (top line), the optimal sex allocation is size-independent. When there is no budget effect (first column) and but some difference between male and female direct fitness effects (two last figures of this column), sex reversal is selected, independent of the amplitude of the difference. As soon as there is some budget effect (two last columns), however slight, together with some difference in direct effects (two bottom lines), a gradual sex change is selected.

Figure 4: Conditions for an apparent sex reversal (small individuals are one sex, large individuals are the other sex, with a relatively abrupt shift)

From our entire set of numerical calculations (details in legend to figure 2), we extracted the values that lead to sex allocation patterns that resemble sex reversal (sex allocations for small and large individuals are either smaller than 0.05 or larger than 0.95; the strength of the shift, calculated at the middle of the slope, is higher than a certain threshold value – only slightly sharper than the slope in fig.3e). In the figure are plotted such values in terms of the differences in the exponents for respectively direct and budget effects. The four points for which the difference (u-v) is zero correspond to u=v=-0.1 (slight budget effect) and to a strong difference in the direct effects for male and female functions. The other points show that a sharp sex change occurs also when the difference between male and female fitness via the budget effect is strong, but only if the difference in the direct effects for male and female fitness is of the same sign.

Figure 5: The relative effects of budget and direct effects of size on evolutionarily stable sex allocation.

In (a) to (d), the difference between male and female exponents is negative for both budget and direct effects, therefore the two effects act in synergy. In this case sex allocation patterns show a decrease in maleness. The shape of the slope is more affected by the budget than by the direct effect. In (e) and (f) budget and direct effects are opposite: in (e) the difference between male and female exponents is strong and negative for the budget effect, slight and positive for the direct effect; in (f) the difference between male and female exponents is slight and negative for the budget effect, strong and positive for the direct effect. The effect with the strongest difference decides for the direction of sex change. Parameter values: (a) a=0.1, b=0.9, u=-0.9, v=-0.7. (b) a=0.1, b=0.9, u=-0.9, v=-0.1. (c) a=0.1, b=0.3, u=-0.9, v=-0.1. (d)

a=0.1, b=0.3, u=-0.9, v=-0.1. (e) a=0.3, b=0.1, u=-0.9, v=-0.1. (f) a=0.9, b=0.1, u=-0.9, v=-0.7.

Figure 6 (online enhancement): Influence of budget and direct effects on the sex allocation of small and large individuals

The optimal sex allocation points are plotted for small (top line) or large (bottom line) individuals, as a function of the value of the difference between male and female fitness for the direct effect (left column) or for the budget effect (right column). In each plot, the solid line corresponds to the linear regression. The figures depicts that direct effects influence more the sex allocation of small individuals than the budget effect. In contrast, budget effects affect the sex allocation of large individuals more than the direct effect. Values are extracted from our entire set of systematic numerical calculations (details in legend to figure 2). 'Small' corresponds to a size of 0.05, 'large' to a size of 60.

Figure 7: Conditions for which all individuals in the population are simultaneous hermaphrodites

From our entire set of numerical calculations (details in legend to figure 2), we extracted the values that lead to sex allocation patterns where all individuals of the population, whatever their size, invest in both sexes (sex allocation stays between 0.2 and 0.8). In the figure those values are plotted against the differences in the exponents for respectively direct and budget effects. The figure shows that permanent hermaphroditism obtains when budget and direct effects are opposite and fairly similar in amplitude.

Figure 8 (online enhancement): Sex allocation patterns in animal- and wind-pollinated plants

The figure shows the effect of the mode of pollination on the selected size-dependent sex allocation. We used model parameters that fit the generic fitness curves described in Klinkhamer et al. (1997). (a) For animal-pollinated plants, the saturation of male fitness curve with large clutch size is generally the most important factor. This leads to an increase in femaleness with plant size. Parameters values a=0.3, b=0.4, u=-0.9, v=-0.4. (b) For wind-pollinated plants, the quasi-linear increase of male fitness with size is generally the most important factor. This leads to an increase in maleness with plant size. Parameters values a=0.7, b=0.4, u=-0.2, v=-0.4.

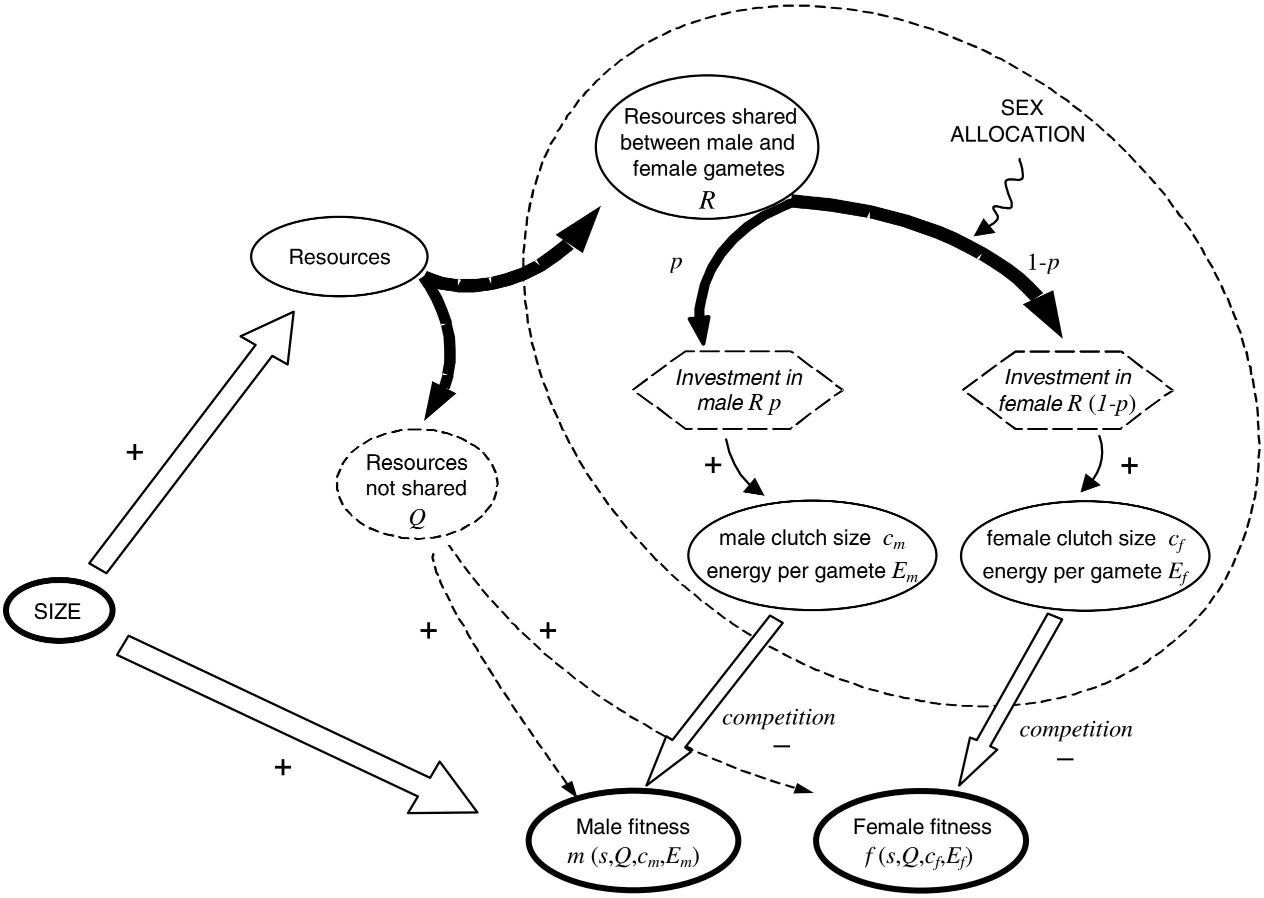
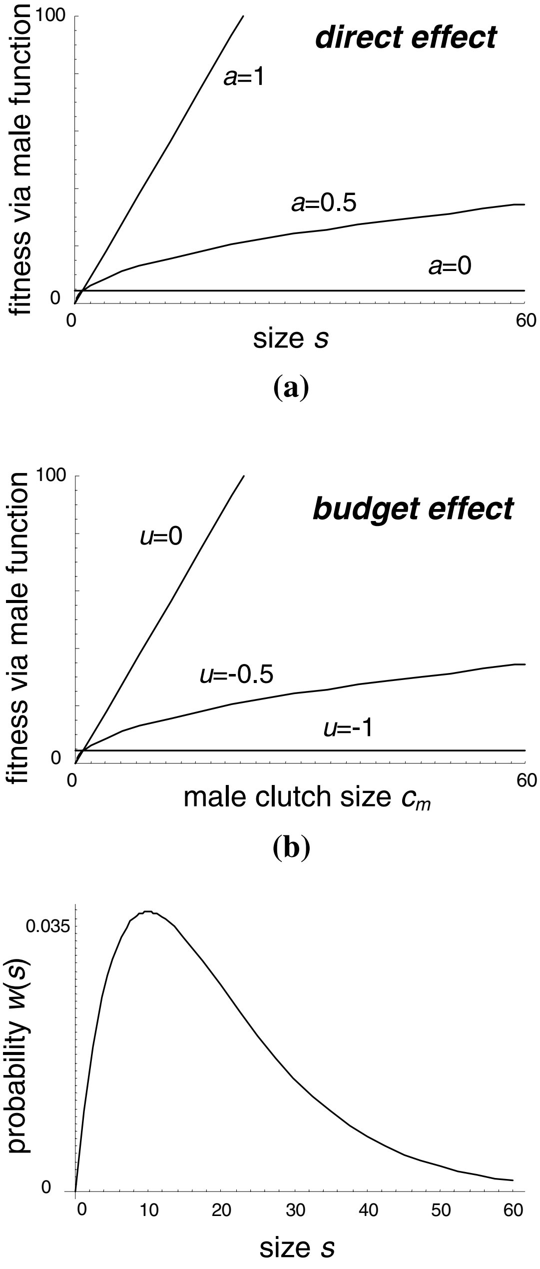

Resources shared between male and female gametes
R
SEX ALLOCATION
Resources
p
1-p
Investment in male R p
Investment in female R (1-p)
+
+
+
Resources not shared
Q
male clutch size c_m
energy per gamete E_m
female clutch size c_f
energy per gamete E_f
SIZE
+
+
competition
–
competition
–
+
Male fitness
$m(s,Q,c_m,E_m)$
Female fitness
$f(s,Q,c_f,E_f)$

Figure 1


fitness via male function
100
0
direct effect
a=1
a=0.5
a=0
0
60
size s
fitness via male function
100
0
budget effect
u=0
u=-0.5
u=-1
0
60
male clutch size c_m
probability $w(s)$
0.035
0
0
10
20
30
40
50
60
size s

(a)

(b)

(c)

Figure 2

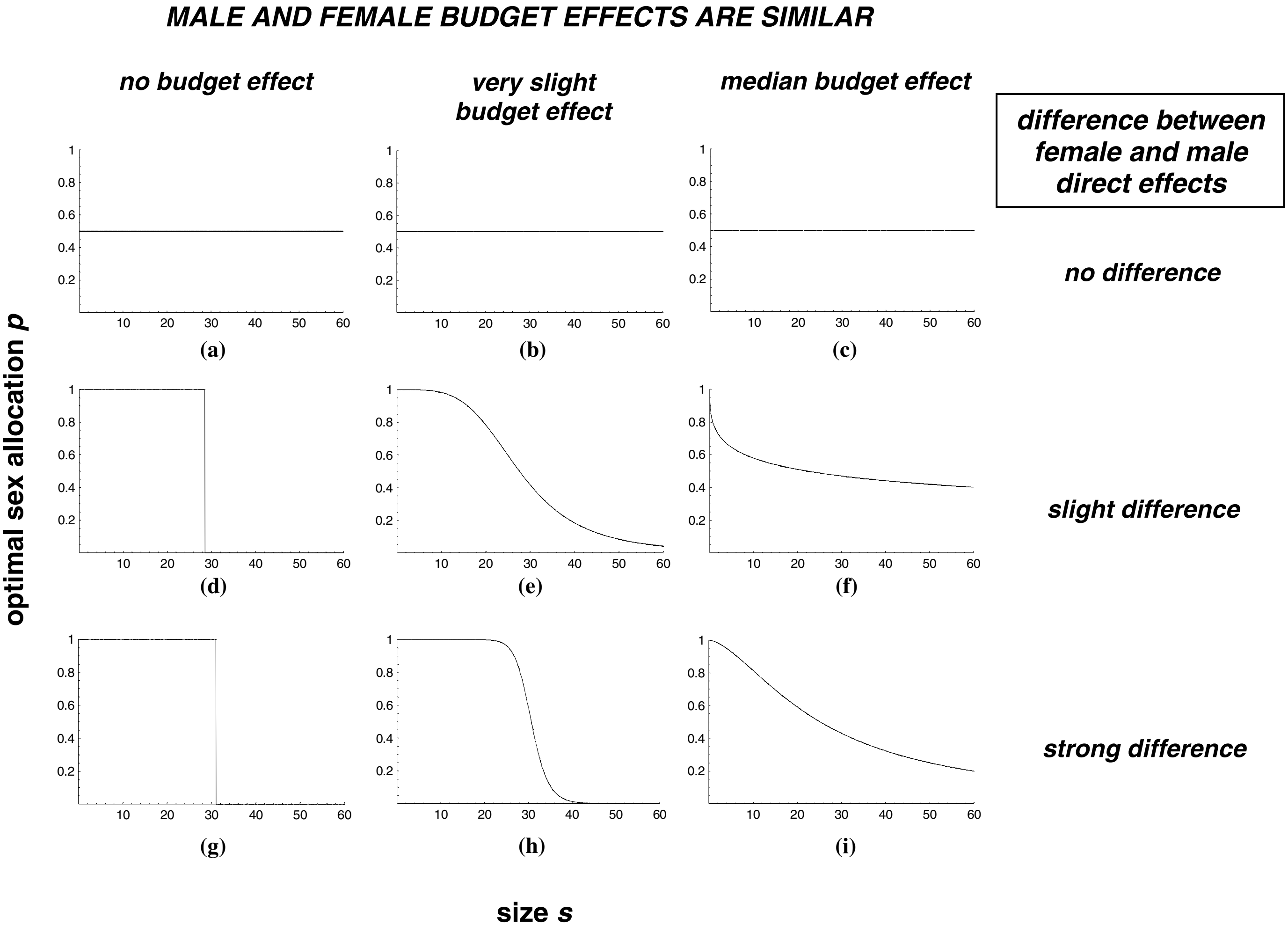

MALE AND FEMALE BUDGET EFFECTS ARE SIMILAR
no budget effect
very slight budget effect
median budget effect
difference between female and male direct effects
no difference
slight difference
strong difference
optimal sex allocation p
size s
1
0.8
0.6
0.4
0.2
10
20
30
40
50
60
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)

Figure 3

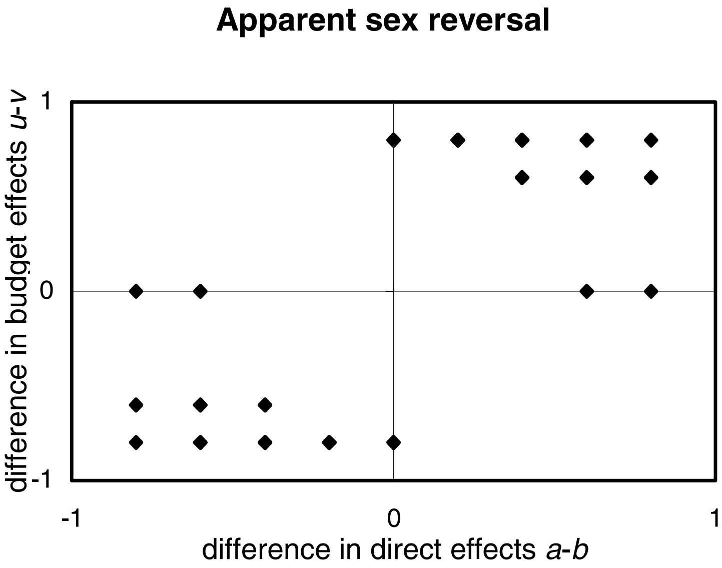

Apparent sex reversal
difference in budget effects *u-v*
1
0
-1
-1
0
1
difference in direct effects *a-b*

Figure 4

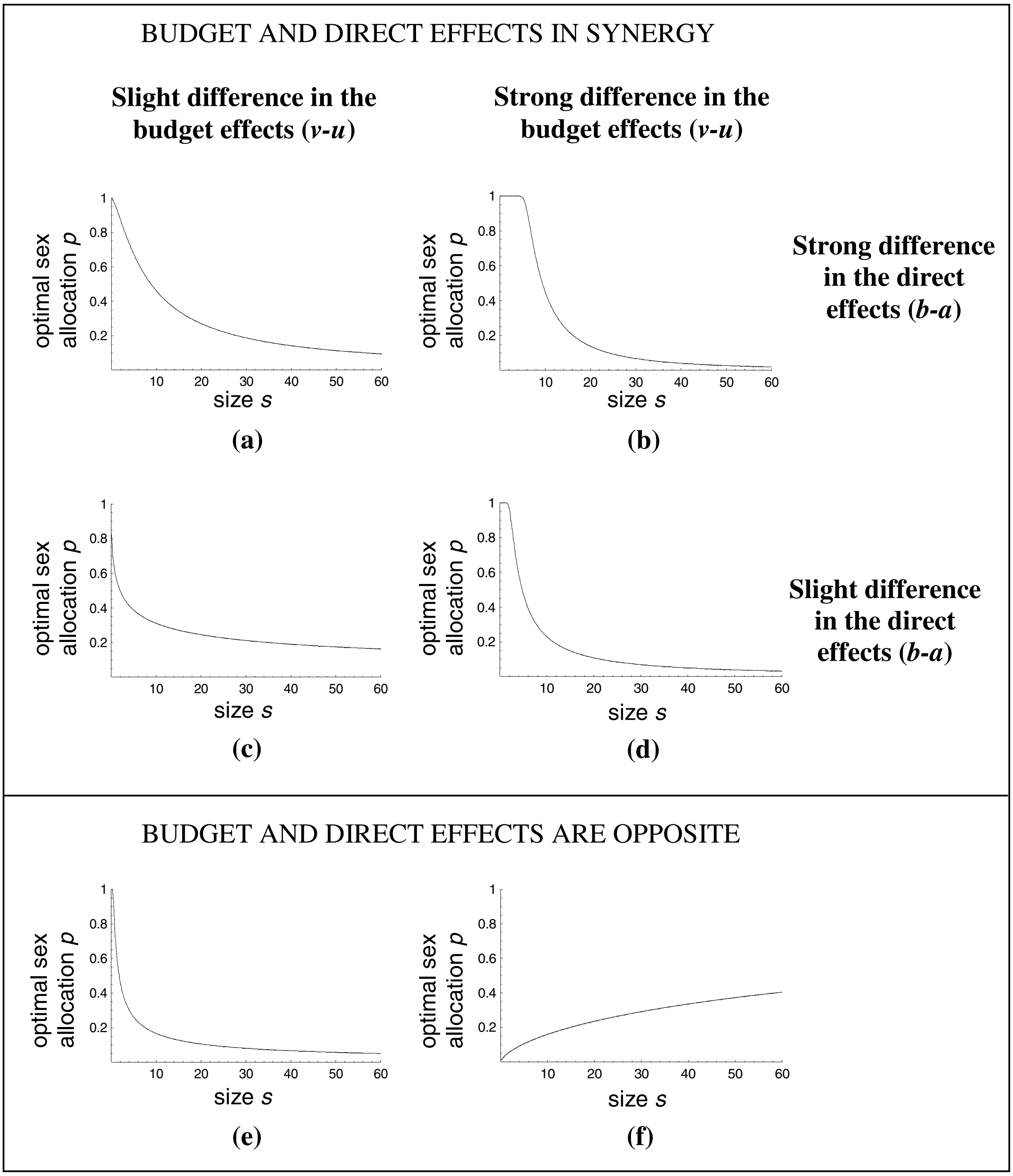

BUDGET AND DIRECT EFFECTS IN SYNERGY
Slight difference in the budget effects (v-u)
Strong difference in the budget effects (v-u)
Strong difference in the direct effects (b-a)
Slight difference in the direct effects (b-a)
optimal sex allocation p
size s
1
0.8
0.6
0.4
0.2
10
20
30
40
50
60
(a)
(b)
(c)
(d)
BUDGET AND DIRECT EFFECTS ARE OPPOSITE
(e)
(f)

Figure 5

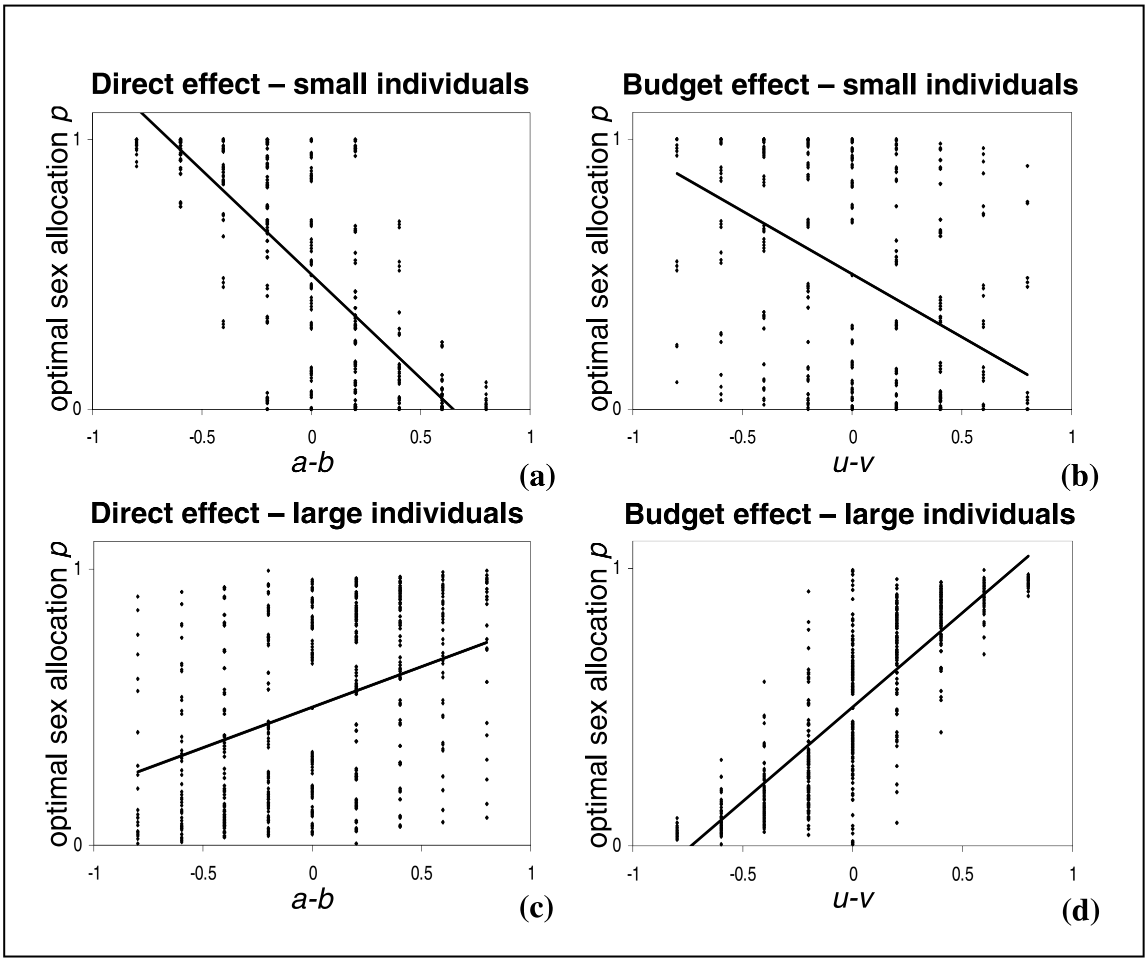

Direct effect – small individuals
Budget effect – small individuals
Direct effect – large individuals
Budget effect – large individuals
optimal sex allocation p
1
0
-1
-0.5
0
0.5
1
a-b
u-v
(a)
(b)
(c)
(d)

Figure 6

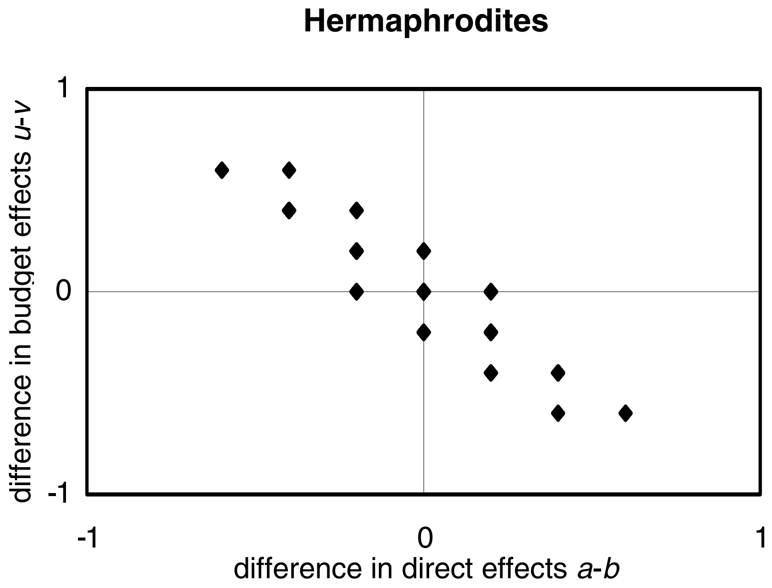

Hermaphrodites
1
0
-1
-1
0
1
difference in budget effects u-v
difference in direct effects a-b

Figure 7

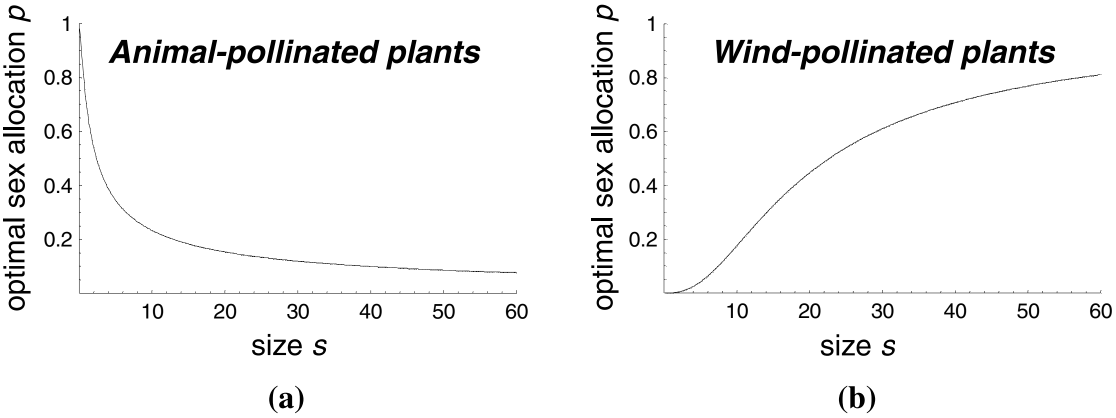

Animal-pollinated plants
optimal sex allocation p
1
0.8
0.6
0.4
0.2
10
20
30
40
50
60
size s
(a)
Wind-pollinated plants
optimal sex allocation p
1
0.8
0.6
0.4
0.2
10
20
30
40
50
60
size s
(b)

Figure 8