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Dioecy as a specialization promoting sperm delivery

Priya Iyer and Joan Roughgarden

Department of Biological Sciences, Stanford University, Stanford, California, USA

ABSTRACT

Question: Is dioecy primitive to metazoans? When should hermaphrodism or dioecy be selected?

Data description: Classification of animal phyla as hermaphroditic/dioecious, broadcast spawning/localized fertilizing.

Analysis method: Ancestral trait reconstruction using the maximum parsimony method.

Hypothesis: Specialization to dioecy is selected when males are more effective than hermaphrodites in concentrating sperm.

Mathematical method: Population genetic model to derive ESS conditions for hermaphrodism and dioecy.

Assumptions: Trade-off between resources available for gamete production and sperm concentrating capability.

Conclusions: Dioecy evolves from hermaphrodism when increasing sperm concentration is adaptive, even though total resources available for sperm and egg production decrease.

Keywords: broadcast spawning, dioecy, evolution of sexes, fertilization behaviour, hermaphrodism, internal fertilization.

INTRODUCTION

Sexual reproduction often involves fusions between two kinds of gametes – small sperm and big eggs. Each individual of an anisogamous species may produce both eggs and sperm (hermaphrodite), only eggs (female) or only sperm (male). Almost all metazoan species are either hermaphroditic or dioecious (all individuals are either male or female). Hermaphrodism is widespread among animals, occurring in 70% of the phyla, and a third of the non-insect species (Jarne and Auld, 2006).

Tomlinson (1966) and Ghiselin (1969) suggested that hermaphrodites may benefit from being able to mate with all individuals encountered, and Heath (1977) proposed that hermaphrodites may suffer from paying the fixed costs of both male and female functions. More formal models examine the evolutionary stability of different sex allocation strategies (Charnov, 1979; Charnov *et al.*, 1976) and consider the effects of inbreeding and selfing (Charlesworth and Charlesworth, 1978) and mobility and mate access (Puurtinen and Kaitala, 2002) on selection on

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* Correspondence: P. Iyer, Department of Biological Sciences, Stanford University, Herrin 424 Serra Mall, Stanford, CA 94305, USA. e-mail: priyai@stanford.edu

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the different sexual systems. However, explaining the distribution of hermaphrodism and dioecy among taxa largely remains an open question.

The contribution of this paper to our understanding of the evolution of hermaphrodism and dioecy is two-fold. First, we map the distribution of the two sexual systems on the animal phylogenetic tree to present evidence that hermaphrodism is ancestral to metazoans. This is contrary to Ghiselin's claim that hermaphrodism is generally derived (Ghiselin, 1969, 2006). The phylogenetic analysis also suggests that the ancestral taxa broadcast their sperm into water, and fertilization behaviours such as internal fertilization and spermatophore dispersal are derived. We hypothesize that these two broad trends from hermaphrodism to dioecy, and from broadcast spawning to sperm localization to the vicinity of the eggs, are coupled. The joint trend suggests that the specialization to males and females may aid in more effective delivery of sperm to eggs. We then model this hypothesis to derive conditions for the stability of hermaphrodism and dioecy.

Increased sperm density at the eggs leads to greater fitness from sperm production, both from a higher probability of egg fertilization, and subsequently from greater sperm competitiveness. Sperm limitation is prevalent in broadcast spawning species (Levitan and Petersen, 1995), and may be instrumental in selecting for anisogamy in the first place (Iyer and Roughgarden, 2008), as well as for behaviours such as spawning synchrony or aggregations (Levitan and Petersen, 1995). A mutant may concentrate its sperm by behavioural changes, such as movement to the site of egg production to release sperm, or by morphological adaptations, such as internal fertilization and sperm packaging. The costs and benefits of effecting the increased sperm density depend on the actual strategies adopted, environmental factors such as the total resources available for reproduction, demographic factors such as the population density, and physiological factors such as the cost of mobility. If the net benefit is greater than the cost, the strategy to increase sperm density is selected.

When the increase in sperm concentration is adaptive, but results in decreasing the resources available for both sperm and egg production, specialization to males and females becomes advantageous. We formalize this idea using a population genetic model to show that an initially hermaphroditic population can be invaded by males that are more effective at concentrating sperm. This decreases the fitness the hermaphrodites gain from the male function, allowing females to invade the population and leading eventually to the establishment of dioecy.

PHYLOGENETIC TRENDS

Data used for the phylogenetic analysis were obtained from the books *Classification and Synopsis of Living Organisms* (Parker, 1982), *Reproductive Biology of Invertebrates*, Vol. 5 (Adiyodi and Adiyodi, 1983), *Reproduction of Marine Invertebrates*, Vols. 1–9 (Giese and Pearse, 1974–1991), *Invertebrates* (Brusca and Brusca, 2002), *Sponges* (Bergquist, 1978), and from the websites Tree of Life Web Project (Maddison and Schulz, 2007) and The Animal Diversity Web (Myers *et al.*, 2006). We collected data about the sexual systems (sequential/simultaneous hermaphrodism or dioecy) and fertilization modes in all animal phyla. The fertilization modes were broadly categorized as being one of the following:

1. *Broadcast* or *spermcast* (Bishop and Pemberton, 2006) *spawning*, where the sperm released can be approximated as being uniformly distributed over eggs produced by many individuals/

the entire population. The eggs may also be released, or may be fertilized inside the parent.

2. *Localized fertilization*, including internal fertilization, pseudo-copulation, hypodermic impregnation, and most cases of spermatophore release, wherein the sperm are concentrated at the sites where the eggs are available, and are scarce elsewhere.

The data collected include information up to the level of families, and were used to assign two states for each phylum for which sexual reproduction is the dominant mode of reproduction: (1) hermaphrodism, dioecy or both and (2) broadcast spawning, localized fertilizations or both.

As a sequentially hermaphroditic population consists at any instant in time of individuals that are male or female, we classify sequential hermaphrodites as dioecious. If the majority of classes/families in the phylum were in one state, that was the state assigned to the phylum. When a large amount of diversity was encountered within a phylum, we attempted to reconstruct the ancestral trait of the phylum from the data available [e.g. for Mollusca, Annelida, and Chordata, see Figs. 1–3; phylogenies from Passamaneck *et al.* (2004), McHugh (1997), and Halanych (2004)]. Taxa for which the ancestral trait could not be clearly reconstructed, especially due to the unavailability of a clear phylogeny (e.g. Sponges), were classified as being polymorphic.

Once the states were assigned to the phyla (Table 1), the software *Mesquite* (Maddison and Maddison, 2007) was used to perform ancestral trait reconstructions for these traits using a maximum parsimony algorithm. The phylogenetic trees used are those proposed by Halanych (2004) and Cracraft and Donoghue (2004). As the branch length information is not clearly available, and the rates of evolution of these traits are not expected to be similar

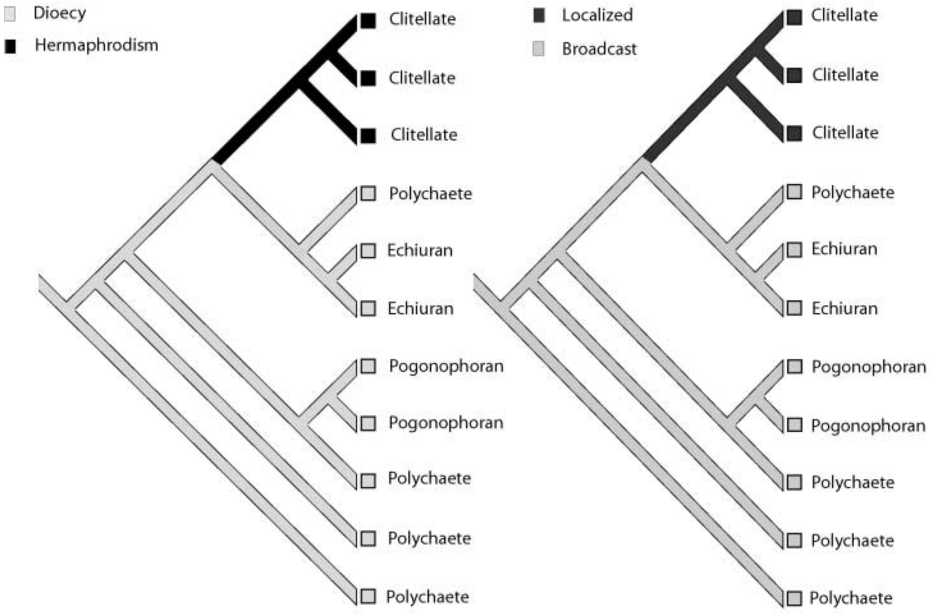

Fig. 1. Ancestral trait reconstruction of annelids. Phylogenetic tree from Passamaneck *et al.* (2004).

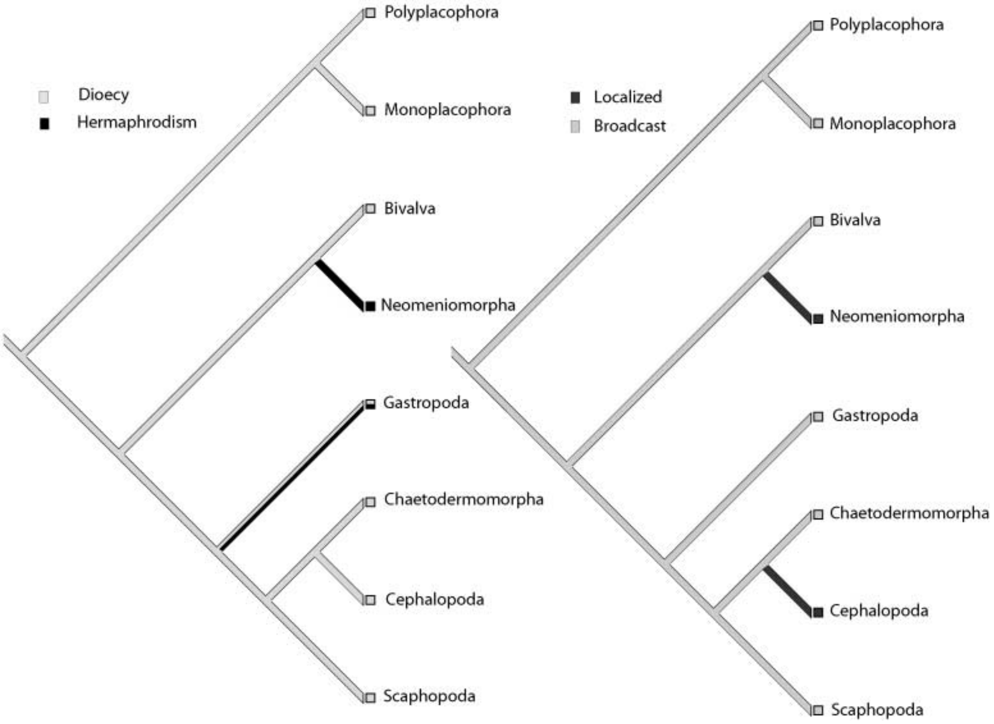

Fig. 2. Ancestral trait reconstruction of molluscs. Phylogenetic tree from McHugh (1997).

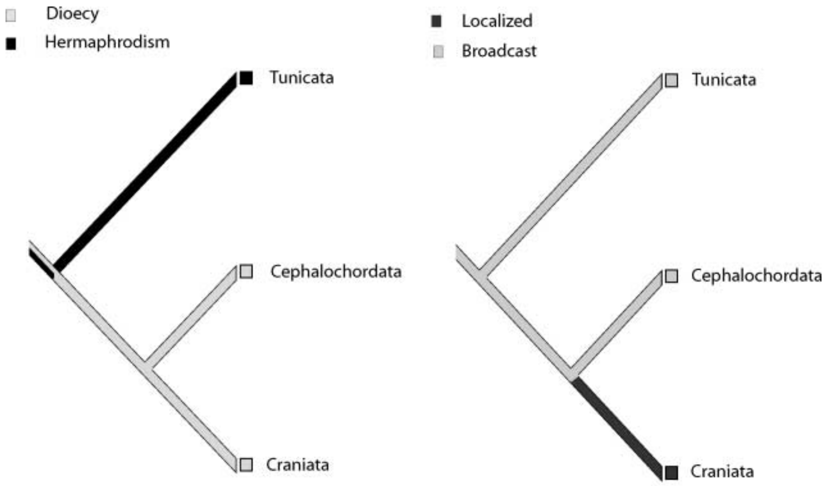

Fig. 3. Ancestral trait reconstruction of chordates. Phylogenetic tree from Halanych (2004).

across the taxa considered, the maximum parsimony method for trait reconstruction is preferred to the maximum likelihood method.

Phylogenetic trees with the ancestral traits reconstructed are shown in Figs. 4–7. This analysis suggests that hermaphrodism and free spawning of sperm may be primitive among

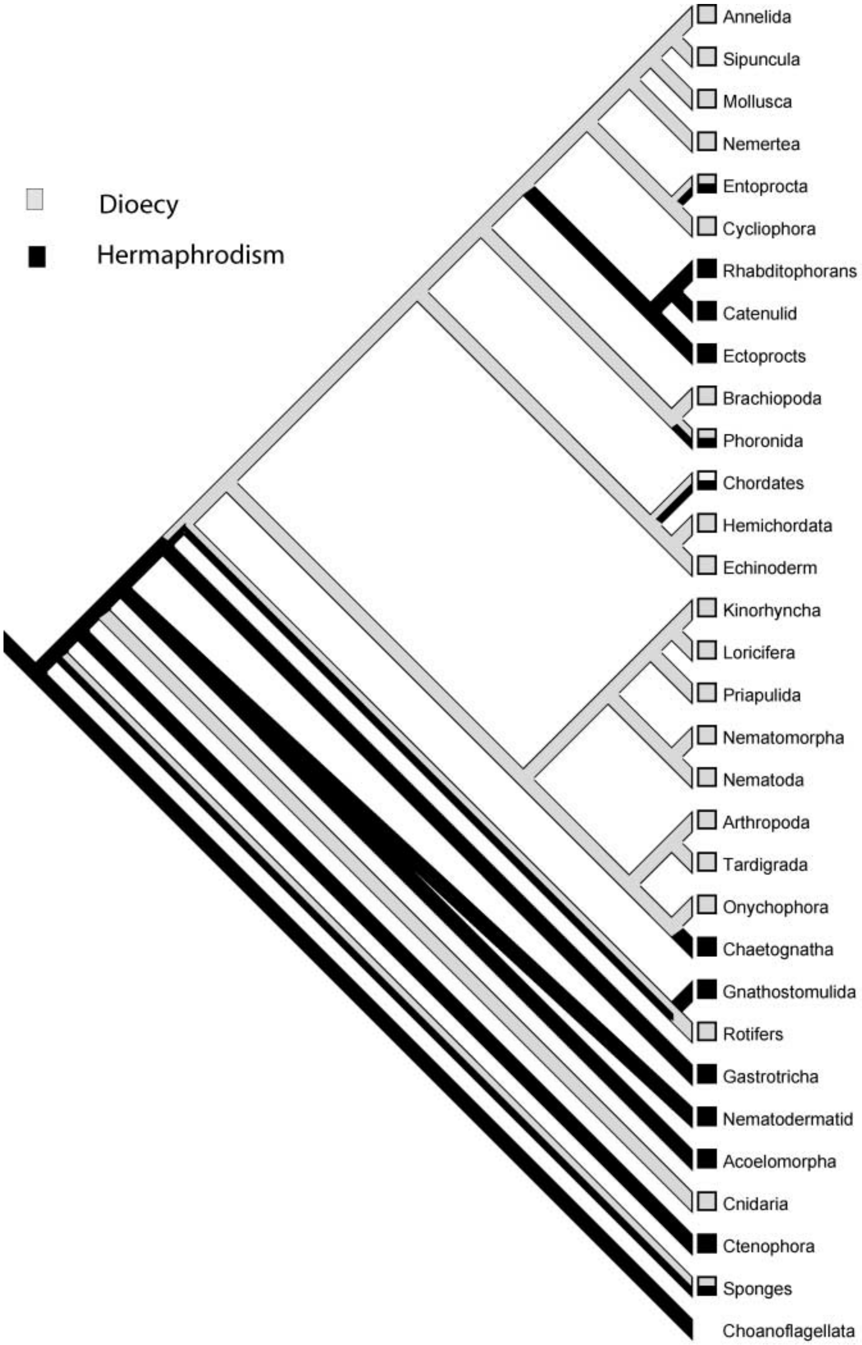

Fig. 4. Ancestral trait (H/D) reconstruction of metazoans. Phylogenetic tree from Cracraft and Donoghue (2004).

Table 1. Data used for phylogenetic analysis

Taxa	Hermaphroditic/dioecious	H/D	Fertilization mode	L/B
Kinorhyncha	Dioecious	D	Likely to be internal	L
Loricifera	Dioecious	D	Likely to be internal	L
Priapulida	Dioecious	D	Free spawn	B
Nemata	Dioecious	D	Internal fertilization	L
Nematomorpha	Dioecious	D	Internal fertilization	L
Arthropoda	Dioecy ancestral	D	Internal fertilization	L
Pancrustaceans	Hermaphroditic and dioecious	H/D	Internal/localized fertilization	L
Myriapoda	Dioecious	D	Internal fertilization/spermatophore transfer	L
Chelicerata	Dioecious	D	Internal fertilization	L
Tardigrada	Dioecious	D	Internal fertilization	L
Onychophora	Dioecious	D	Spermatophore deposition	L
Annelida	Dioecy ancestral	D	Broadcast ancestral	B
Sipuncula	Mostly dioecious	D	Free spawning	B
Mollusca	Dioecy ancestral	D	Broadcast ancestral	B
Phoronida	Hermaphroditic/dioecious	H/D	Broadcast spermatophores into water	B
Brachiopoda	Mostly dioecious	D	Free spawning	B
Nemertea	Mostly dioecious	D	Internal fertilization	L
Gastrotricha	Hermaphroditic	H	Internal fertilization	L
Cycliophora	Dioecious	D	Likely to be internal	L
Entoprocta	Zooids hermaphroditic or dioecious	H/D	Broadcast sperm	B

Gnathostomulids	Hermaphroditic	H	Localized fertilization	L
Syndermata	Hermaphroditic	H	Localized fertilization	L
Dicyemida	Hermaphroditic	H	Internal fertilization	L
Myzostomida	Simultaneous/sequential hermaphroditic/dioecious	H/D	Internal fertilization	L
Platyhelminthes	Hermaphroditic	H	Sperm injection	L
Rhabditophora	Hermaphroditic	H	Sperm injection	L
Catenulid	Hermaphroditic	H	Sperm injection	L
Ectoprocta (Bryozoa)	Most zooids hermaphroditic	H	Broadcast sperm	B
Chaetognatha	Hermaphroditic	H	Spermatophore deposition	L
Xenoturbella	Dioecious	D	Localized fertilization	L
Chordata	Ancestrally hermaphroditic/dioecious	H/D	Broadcast ancestral	B
Tunicata	Mostly hermaphroditic	H	External fertilization	B
Cephalochordata	Mostly dioecious	D	External fertilization	B
Craniata	Mostly dioecious	D	Mostly internal fertilization	L
Hemichordata	Dioecious	D	Free spawn sperm	B
Echinodermata	Almost all dioecious	D	External fertilization	B
Orthonectida	Dioecious	D	Insemination	L
Nematodermatida	Hermaphroditic	H	Localized fertilization	L
Acoela	Hermaphroditic	H	Sperm injection	L
Cnidaria	Mostly dioecious	D	Sperm and often eggs spawned	B
Ctenophora	Mostly hermaphroditic	H	Spawn gametes	B
Sponges	Hermaphroditic (sequential and simultaneous) and dioecious	H/D	Spawn sperm	B
Choanoflagellata	Asexual	—	—	—

Abbreviations: D = dioecious, H = hermaphroditic, B = broadcast spawning, L = localized fertilization.

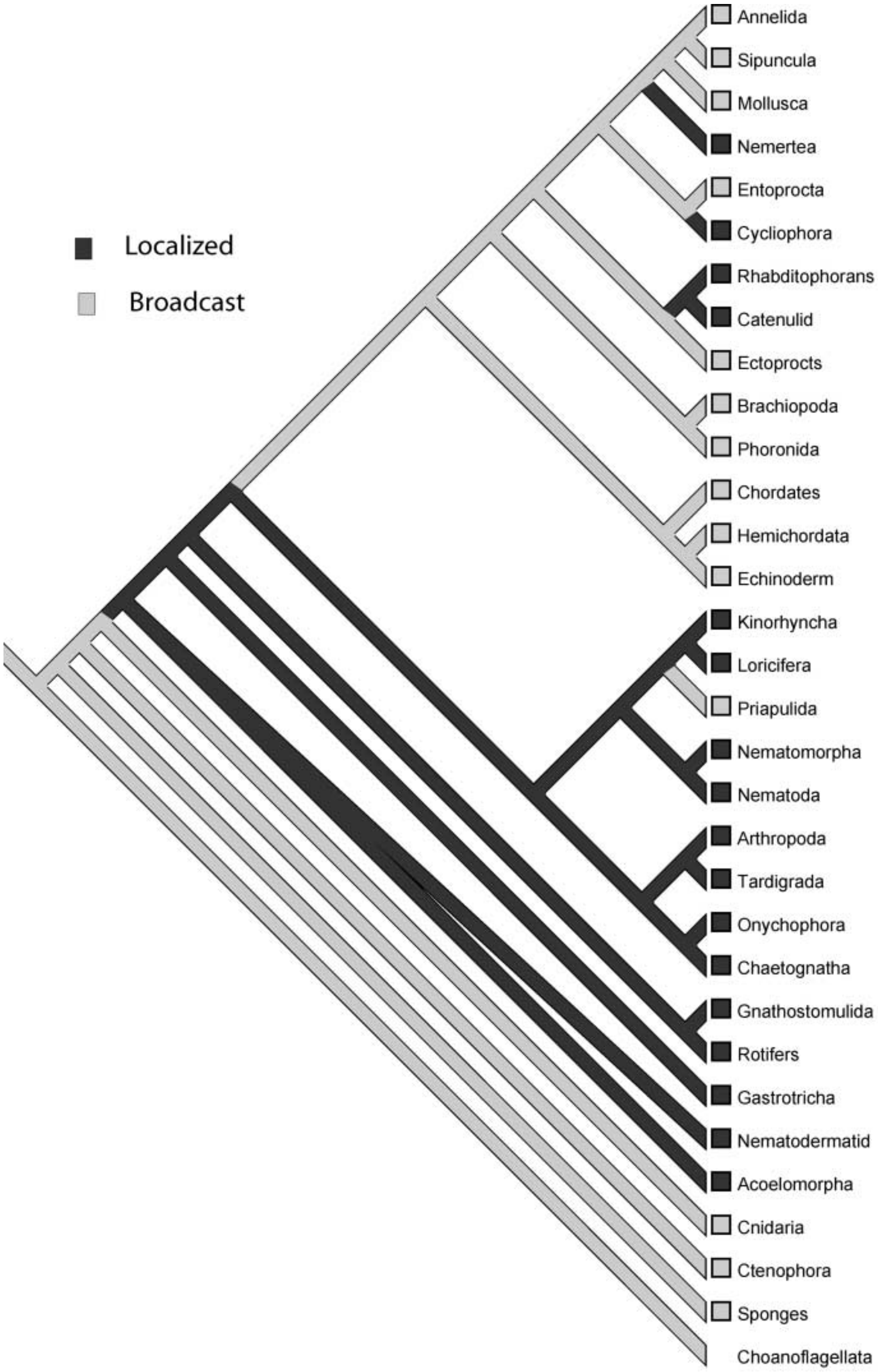

Fig. 5. Ancestral trait (B/L) reconstruction of metazoans. Phylogenetic tree from Cracraft and Donoghue (2004).

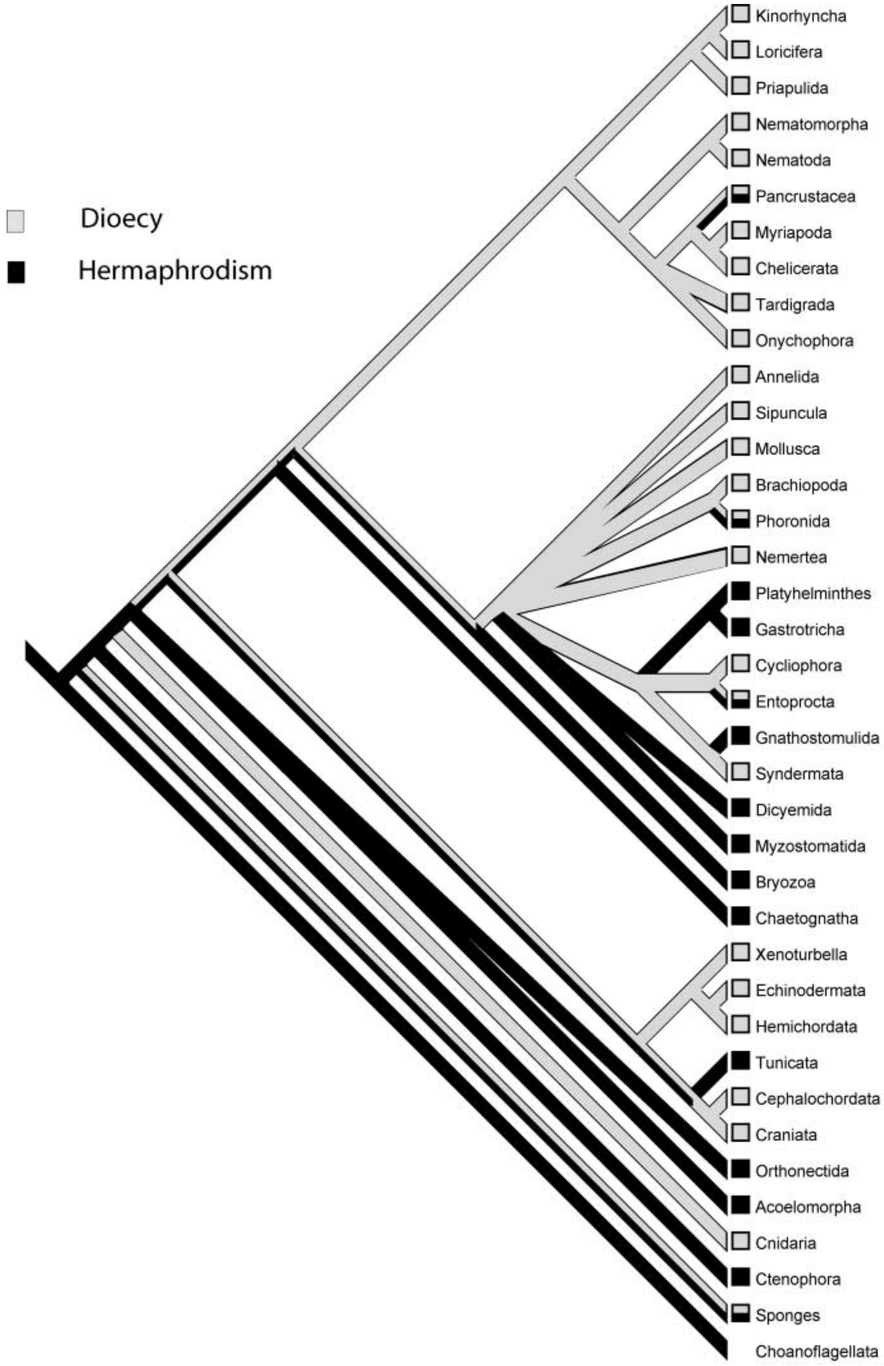

Fig. 6. Ancestral trait (H/D) reconstruction of metazoans. Phylogenetic tree from Halanych (2004).

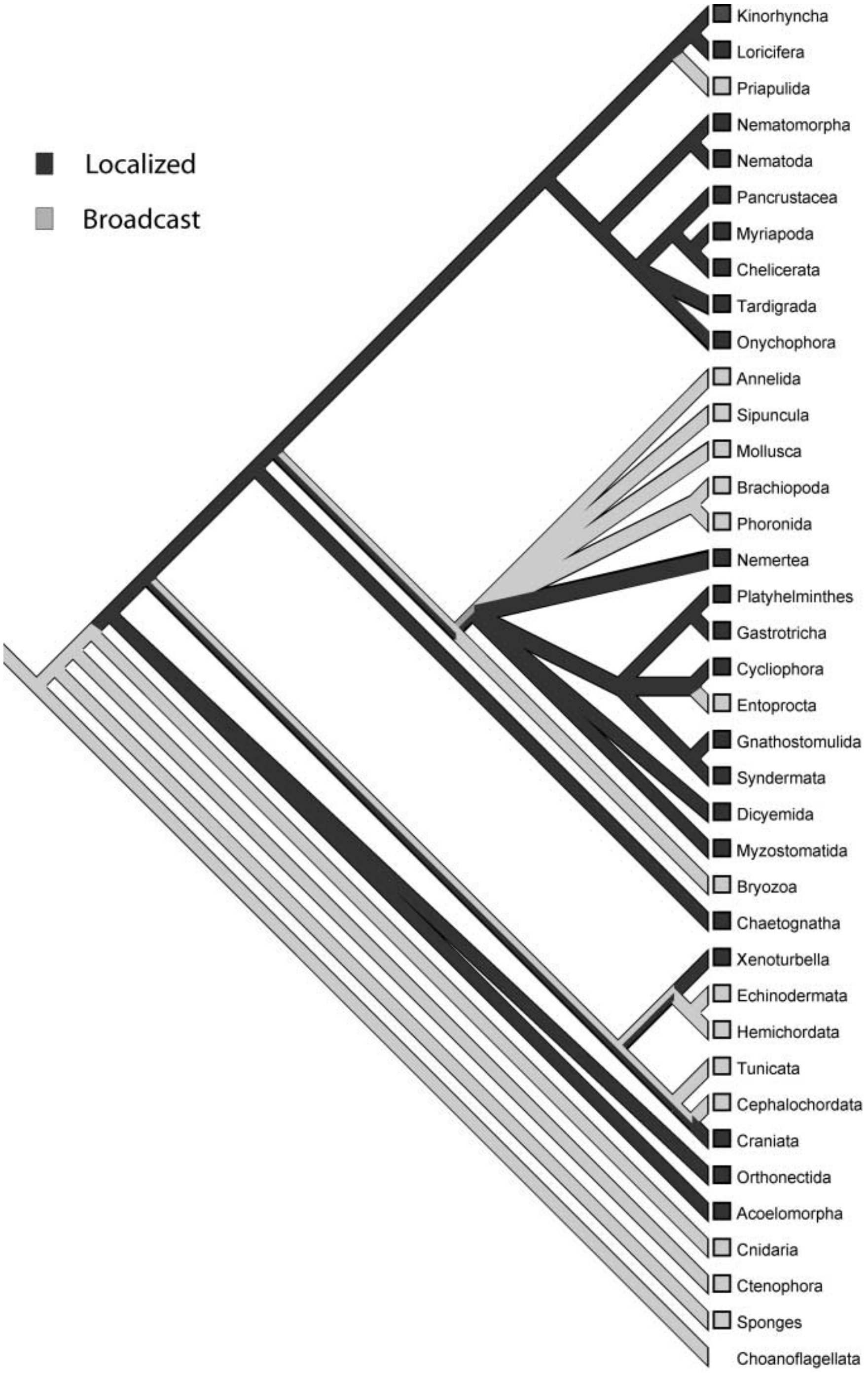

Fig. 7. Ancestral trait (B/L) reconstruction of metazoans. Phylogenetic tree from Halanych (2004).

metazoans, and both dioecy and localized fertilization derived. Transitions occur in both directions between hermaphrodism and dioecy, and between broadcast spawning and localized fertilizations. We do not find the branches on which transitions occur on the hermaphrodism–dioecy tree to be correlated with the branches on which transitions occur on the broadcast–localized fertilization tree.

The ancestral states reconstructed using the maximum parsimony method are those that would ensure the minimum number of evolutionary changes in the entire phylogenetic tree. This assumption need not result in an accurate reconstruction, especially when estimating states in the distant past. The states inferred are also sensitive to the taxa sampled and the phylogenetic relationships assumed (Cunningham *et al.*, 1998; Martins, 2000). Hence the results obtained by this analysis are not conclusive about actual ancestral states. However, we currently lack more accurate ways of estimating them.

Despite its limitations, the analysis suggests that hermaphrodism being ancestral to metazoans and dioecy being derived is a strong possibility. That hermaphrodism in large groups such as molluscs, annelids, and arthropods is derived (Figs. 1, 2) is perhaps responsible for the strongly advocated view to the contrary (Ghiselin, 1969, 2006). Phylogenetic analysis using ancestral trait reconstruction methods provides a tool to infer the multiple transitions that have occurred between hermaphrodism and dieocy in the evolution of animals.

MODEL

We now construct a model to derive the conditions under which hermaphrodism or dioecy may be selected. We show that specialization to males and females is adaptive when investment in sperm concentration is selected, but decreases the resources available for both sperm and egg production.

To formulate the concept of sperm concentration, we introduce a parameter V corresponding to the volume to which sperm produced by a single individual disperses around the eggs in the population. In the case of broadcast spawning, V corresponds to one large, contiguous volume, while it is a sum of smaller volumes for a localized fertilizing population (Fig. 8). Hence the smaller the value of V, the higher the sperm density resulting

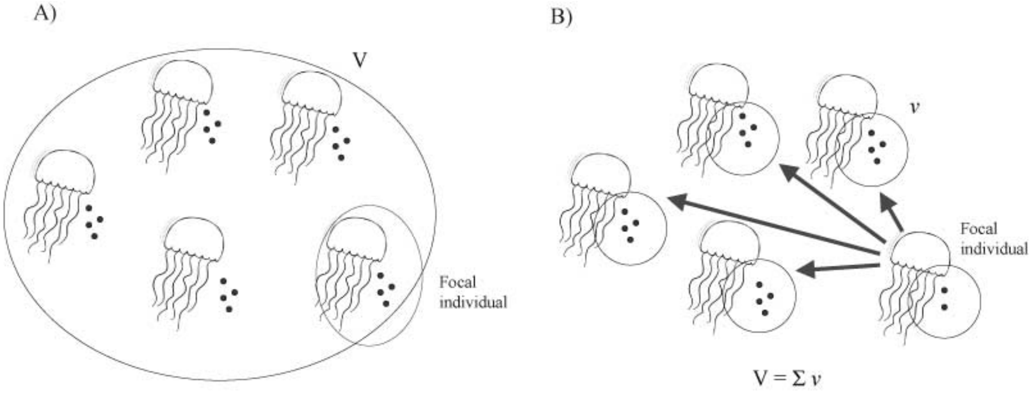

Fig. 8. Illustration of the volume V to which sperm disperses in (A) a broadcast spawning population and (B) a localized fertilizing population in which the sperm is concentrated to volume v around the eggs produced by each individual. In this case, V is the sum of the smaller volumes v.

from the dispersal of the same quantity of sperm, and the higher the fertilization probability of the eggs. We also assume that sperm restriction to smaller volumes is costly, and results in a decrease in the total amount of resources available for gamete production.

Consider a population of sexually reproducing individuals, each of whom may be hermaphroditic or male or female. Suppose each individual has access to a total of Q resources for gamete production; the value of Q depends on the choice of V as mentioned above, hence $Q = Q(V)$. Since we are interested in modelling a trade-off between sperm effectiveness and the cost of gamete production, we assume that $Q(V)$ decreases as V decreases (and hence the sperm density increases), i.e. $Q(V)$ is a monotonically increasing function of V.

Each individual allocates a fraction u of $Q(V)$ to egg production. Hence $u = 1$ for females and $u = 0$ for males. If the cost of making a single egg is c_e, the number of eggs produced is $\frac{uQ(V)}{c_e}$. The remaining resources are allocated to sperm production, and the number of sperm produced is $\frac{(1-u)\,Q(V)}{c_s}$, when the cost of making a single sperm is c_s. The sperm density resulting from this sperm is then $\frac{(1-u)\,Q(V)}{Vc_s}$. We assume that the sperm density from the focal individual is the same for all eggs in the population.

Finally, the constraints: $V_{\text{min}} > 0$ is the minimum volume that individuals can restrict their sperm to [let's say that $Q(V_{\text{min}}) = 0$], and Q_{max} is the maximum resource amount that can be invested in gamete production. We call V_{max} the volume corresponding to Q_{max}.

Consider first a hermaphroditic population that localizes its sperm to a volume V, and hence has $Q(V)$ resources available for gamete production. These resources are allocated as $uQ(V)$ into egg production to make $E = \frac{uQ(V)}{c_e}$ eggs, and $(1-u)Q(V)$ into sperm production to create a sperm density of $s = \frac{(1-u)\,Q(V)}{Vc_s}$ at each egg fertilized. This population will be evolutionarily stable if it cannot be invaded by mutants that have different values of u or V. To derive the conditions for evolutionary stability, let us consider a population genetic model with the genotype at a single locus coding for both the sex allocation strategy u and the sperm localization volume V.

Population genetic model

Consider a population with two alleles, 1 and 2, at the locus coding for u and V. Suppose genotype 11 is present in the population with frequency x_{11} and codes for sex allocation strategy u_{11} and volume V_{11} (and hence makes E_{11} eggs and s_{11} sperm), genotype 12 with frequency x_{12} codes for u_{12} and V_{12}, and genotype 22 with frequency x_{22} codes for u_{22} and V_{22}.

Then, the abundance of eggs with allele 1 in the population is proportional to $x_{11}E_{11} + \frac{x_{12}E_{12}}{2}$, as they are made by individuals with genotypes 11 and 12. Similarly, the probability that these eggs are fertilized by sperm carrying allele 1 is proportional to the sperm density, $x_{11}s_{11} + \frac{x_{12}s_{12}}{2}$. Hence the genotype frequency of genotype 11 in the subsequent generation is the product $\left(x_{11}E_{11}+\frac{x_{12}E_{12}}{2}\right)\left(x_{11}s_{11}+\frac{x_{12}s_{12}}{2}\right)$ normalized by the abundance of all zygotes produced in the population $(x_{11}E_{11}+x_{12}E_{12}+x_{22}E_{22})(x_{11}s_{11}+x_{12}s_{12}+x_{22}s_{22})$. Similarly, we can calculate the frequencies of genotypes 12 and 22 after one generation:

$$x_{11}'=\frac{\left(x_{11}E_{11}+\frac{x_{12}E_{12}}{2}\right)\left(x_{11}s_{11}+\frac{x_{12}s_{12}}{2}\right)}{(x_{11}E_{11}+x_{12}E_{12}+x_{22}E_{22})\,(x_{11}s_{11}+x_{12}s_{12}+x_{22}s_{22})}$$

$$x_{12}'=\frac{\left(x_{11}E_{11}+\frac{x_{12}E_{12}}{2}\right)\left(x_{22}s_{22}+\frac{x_{12}s_{12}}{2}\right)+\left(x_{22}E_{22}+\frac{x_{12}E_{12}}{2}\right)\left(x_{11}s_{11}+\frac{x_{12}s_{12}}{2}\right)}{(x_{11}E_{11}+x_{12}E_{12}+x_{22}E_{22})\,(x_{11}s_{11}+x_{12}s_{12}+x_{22}s_{22})}$$

$$x_{22}'=\frac{\left(x_{22}E_{22}+\frac{x_{12}E_{12}}{2}\right)\left(x_{22}s_{22}+\frac{x_{12}s_{12}}{2}\right)}{(x_{11}E_{11}+x_{12}E_{12}+x_{22}E_{22})\,(x_{11}s_{11}+x_{12}s_{12}+x_{22}s_{22})}$$

To determine if genotype 11 is stable to invasion by allele 2, let us consider the case that $x_{11}=1-\varepsilon$, $x_{12}=\varepsilon$, and $x_{22}=0$. Allele 2 increases in frequency when rare if genotype 11 decreases in frequency, $x_{11}'<1-\varepsilon$. If we assume ε to be small enough that $\varepsilon^2\approx 0$, this condition reduces to:

$$2\,E_{11}\,s_{11}<E_{11}s_{12}+E_{12}\,s_{11}$$

or

$$2\,\frac{u_{11}(1-u_{11})\,Q(V_{11})^2}{V_{11}}<u_{11}\,Q(V_{11})\,\frac{(1-u_{12})\,Q(V_{12})}{V_{12}}+u_{12}\,Q(V_{12})\,\frac{(1-u_{11})\,Q(V_{11})}{V_{11}}$$

The opposite inequality needs to be satisfied for a population with allele 1 fixed to be stable to invasion by allele 2.

Evolutionarily stable hermaphroditic populations

We use the stability condition above to derive the conditions for a population of hermaphrodites with strategy u and V to be evolutionarily stable. First, while a population with $u_{11}\neq 1/2$ can be invaded by a mutant with $u_{12}=1/2$ (with V unchanged), the allocation $u_{11}=1/2$ is stable to invasion by mutants with the same V but different sex allocations. Hence a requirement for a hermaphroditic population to be evolutionarily stable is that $u=1/2$, i.e. that it split the resources $Q(V)$ equally between egg and sperm production.

Hence to analyse the evolutionary stability of the sperm localization strategy V, we next consider a hermaphroditic population with 1 : 1 sex allocation. If $V<V_{\max}$ [and hence $Q(V)<Q_{\max}$], a mutant hermaphrodite with strategy $u=1/2$ and $V=V_{\max}$ can often invade. Moreover, because a female does not pay the cost of sperm localization and has $Q_{\max}$ resources available for egg production, female mutants can always invade this population.

Hence for a hermaphroditic population to be stable to mutants that are either hermaphrodites or females, $V = V_{\mathbf{max}}$ and $u = 1/2$.

Finally, we consider the stability of a hermaphroditic population with 1 : 1 sex allocation and $V = V_{\mathbf{max}}$ to invasions by males. This population is stable to invasion by males that also adopt the sperm localization volume $V_{\mathbf{max}}$, but not necessarily to males that localize their sperm to smaller volumes. Whether or not the hermaphroditic population is also stable to these mutants depends on the form of $Q(V)$ at $V = V_{\mathbf{max}}$.

Invasion by males with greater sperm effectiveness

Consider a mutant that is male and localizes its sperm to a volume V' smaller than V. This individual can only use $Q(V')$ resources for gamete production, and hence produces a sperm density of $\frac{Q(V')}{c_s\, V'}$. Using the condition for increase when rare, the mutant strategy (coded by allele 2) has a higher fitness than the resident hermaphroditic strategy (coded by allele 1) if

$$2\,\frac{u_{11}(1-u_{11})\,Q(V_{11})^2}{V_{11}} < u_{11}\,Q(V_{11})\,\frac{(1-u_{12})\,Q(V_{12})}{V_{12}} + u_{12}\,Q(V_{12})\,\frac{(1-u_{11})\,Q(V_{11})}{V_{11}}$$

Since $u_{11} = 1/2$, $u_{12} = 0$, $V_{11} = V$, and $V_{12} = V'$, this condition becomes

$$\frac{Q(V)^2}{2V} < \frac{Q(V)\,Q(V')}{2V'}$$

or

$$\frac{Q(V')}{V'} > \frac{Q(V)}{V}$$

For V' close to and smaller than V, say $V' = V(1-\varepsilon)$, we have by Taylor expansion of $Q(V(1-\varepsilon))$ around V, and the geometric series expansion of $\frac{1}{1-\varepsilon}$,

$$\frac{Q(V(1-\varepsilon))}{V(1-\varepsilon)} = \frac{Q(V) - V\varepsilon\,\dfrac{\mathrm{d}Q(V)}{\mathrm{d}V} + \dfrac{(V\varepsilon)^2}{2}\,\dfrac{\mathrm{d}^2Q(V)}{\mathrm{d}V^2} - \ldots}{V}\,(1+\varepsilon+\varepsilon^2+\ldots)$$

For ε small, so ε^2 is nearly 0, this is equivalent to

$$\frac{Q(V) - V\varepsilon\,\dfrac{\mathrm{d}Q(V)}{\mathrm{d}V} + \varepsilon Q(V)}{V} > \frac{Q(V)}{V}$$

$\frac{Q(V)}{V}$ cancels from both sides of the inequality, giving us

$$-\,\varepsilon\,\frac{\mathrm{d}Q(V)}{\mathrm{d}V} + \varepsilon\,\frac{Q(V)}{V} > 0$$

Since $\varepsilon > 0$,

$$\frac{Q(V)}{V} > \frac{\mathrm{d}Q(V)}{\mathrm{d}V}$$

This is the condition for a male that increases its sperm concentration by an infinitesimal amount to invade a population of hermaphrodites.

Graphically, the condition above requires that the slope of the line joining the origin to the point (V, $Q(V)$) be greater than the slope of the curve $Q(V)$ at V.

The intuition behind this condition is as follows: for a small decrease in volume of δV, with no change in the resources available for gamete production $Q(V)$, the increase in sperm density is

$$\frac{Q(V)}{V-\delta V} - \frac{Q(V)}{V}$$

$$= \frac{Q(V)\,\delta V}{V(V-\delta V)}$$

$$= \frac{Q(V)\,\delta V}{V^2\left(1-\frac{\delta V}{V}\right)}$$

$$= \frac{Q(V)\,\delta V}{V^2}\left(1+\frac{\delta V}{V}+\frac{\delta V^2}{V^2}+\ldots\right)$$, again from the geometric series expansion.

$$\approx \frac{\delta V}{V}\frac{Q(V)}{V}$$, by approximating δV^2 to 0.

Hence the increase in sperm density from the infinitesimal decrease in volume is proportional to the standing sperm density $Q(V)/V$. This corresponds to the benefit of the volume reduction.

The relationship between the standing sperm density and the benefit from sperm concentration can be understood as follows: We know that a male that does not invest in sperm concentration (i.e. does not decrease V) has the same fitness as the resident hermaphrodite. Relative to this male, a mutant male that further decreases the volume to which its sperm disperse to $V - \delta V$ gains the resources dispersed over the volume δV to be invested into the smaller volume $V - \delta V$. The resources spent on the volume δV is equal to the product of the sperm density $Q(V)/V$ and the volume δV. Hence the gain in resources from the volume reduction is

$$\frac{Q(V)}{V}\,\delta V.$$

This volume reduction is also costly, and contributes to a decrease in sperm density due to the decrease in the resources available for sperm production. This decrease is equal to

$$\frac{Q(V)-Q(V-\delta V)}{V}$$

$$= \frac{Q(V)-Q(V-\delta V)}{\delta V}\,\frac{\delta V}{V}$$

As $\lim_{\delta V \to 0} \frac{Q(V) - Q(V - \delta V)}{\delta V} = \frac{\mathrm{d}Q(V)}{\mathrm{d}V}$, the decrease in sperm density is approximately the same as $\frac{\delta V}{V} \frac{\mathrm{d}Q(V)}{\mathrm{d}V}$. This corresponds to the cost of the volume restriction – investing in decreasing the volume by δV decreases the resources available for gamete production by approximately $\frac{\mathrm{d}Q(V)}{\mathrm{d}V} \delta V$.

Hence a reduction in sperm volume leads to an overall increase in fitness if the benefit of increased sperm concentration due to decreased volume is more than the cost due to the reduced resources. And hence the condition $\frac{\delta V}{V} \frac{Q(V)}{V} > \frac{\delta V}{V} \frac{\mathrm{d}Q(V)}{\mathrm{d}V}$ or $\frac{Q(V)}{V} > \frac{\mathrm{d}Q(V)}{\mathrm{d}V}$. Hence the greater the initial sperm density $Q(V)/V$, and the smaller the rate of change of $Q(V)$ with V, the more likely the invasion by males.

The condition for invasion by hermaphrodites (instead of males) that localize their sperm and also invest equally in egg and sperm production can similarly be derived as $\frac{Q(V)}{V} > 2 \frac{\mathrm{d}Q(V)}{\mathrm{d}V}$. The left-hand side is the benefit from greater sperm localization. The cost on the right-hand side is the cost of reduction in both egg and sperm production, and hence is twice the cost that a mutant male has to pay. Thus for the same increase in sperm density, it is easier for mutant males than mutant hermaphrodites to invade.

Stability conditions for hermaphrodism and dioecy

Now we examine the conditions under which $Q(V)/V > \mathrm{d}Q(V)/\mathrm{d}V$ holds, hence allowing males to invade a hermaphroditic population. Suppose $Q(V)$ is an accelerating function of V (Fig. 8). Then, for all values of V (including $V = V_{\max}$), $Q(V)/V < \mathrm{d}Q(V)/\mathrm{d}V$; the cost of any decrease in $Q(V)$ is always too large to counter the benefit from a smaller V, and hence males cannot invade a hermaphroditic population with $V = V_{\max}$. Thus if $Q(V)$ is an accelerating function of V, a hermaphroditic population that divides $Q_{\max}$ equally into egg and sperm production is evolutionarily stable to all invasions (by females, hermaphrodites with other sex allocation/sperm localization strategies, and males with other sperm localization strategies). In this case, dioecy with no investment by males in sperm localization ($V = V_{\max}$) is also evolutionarily stable.

Next, suppose the form of $Q(V)$ is saturating with V. Then the value of $\mathrm{d}Q(V)/\mathrm{d}V - Q(V)/V$ can be positive or negative, depending on the value of V. It is positive for small V and negative for large V. Let us call $\hat{V}$ the value of V for which $\left.\frac{\mathrm{d}Q(V)}{\mathrm{d}V}\right|_{V=\hat{V}} = \frac{Q(\hat{V})}{\hat{V}}$. Again, $\mathrm{d}Q(V)/\mathrm{d}V$ is a measure of the cost of sperm concentration, and $Q(V)/V$ is a measure of its benefit. For $V < \hat{V}$, the cost of sperm concentration is greater than its benefit $[\mathrm{d}Q(V)/\mathrm{d}V > Q(V)/V]$, and the other way around for $V > \hat{V}$.

Therefore, if the value of $V_{\max}$ that corresponds to $Q_{\max}$ is less than $\hat{V}$, the stable strategy is not to localize the sperm. Hence if $Q(V)$ is a saturating function of V and $V_{\max} < \hat{V}$, a hermaphroditic population with 1 : 1 sex allocation and $V = V_{\max}$ (and hence no investment in sperm localization) is evolutionarily stable. Again under these conditions, a dioecious population with no investment by males in sperm localization ($V = V_{\max}$) is also evolutionarily stable.

If instead $V_{\max} > \hat{V}$ (and $Q(V)$ is still a saturating function of V), $\left.\frac{\mathrm{d}Q(V)}{\mathrm{d}V}\right|_{V=V_{\max}} < \frac{Q(V_{\max})}{V_{\max}}$, and hence male mutants with sperm localization strategy V' such that $\hat{V} \leq V' < V_{\max}$ increase when rare in the population of hermaphrodites with no sperm localization ($V = V_{\max}$). Subsequently, these dynamics always converge to a stable polymorphism between males and hermaphrodites. This is because the mapping of genotype frequencies from one generation to the next in our model can be transformed to another mapping whose dynamics always converges to a fixed point (Selgrade and Ziehe, 1987).

The genotype frequencies at the polymorphic equilibrium depend on the value of V'. To see this, we simulated the dynamics of genotype frequency change with different values of V' in initially hermaphroditic populations with $u = 1/2$ and $V = V_{\max}$. Suppose that $Q(V) = (V - 0.1)/V$ is the equation describing the saturating form of $Q(V)$, and hence $\hat{V} = 0.2$.

We assume that the heterozygote genotype has the male phenotype half of the time and the hermaphroditic phenotype otherwise. We plot the equilibrium frequencies of the three genotypes as functions of V' in Fig. 9. All such equilibria are then invadable by mutant females, leading to the elimination of the hermaphroditic genotypes and the evolution of dioecy. Dioecy with males localizing their sperm to volume $\hat{V}$ is evolutionarily stable to invasions by all mutants with other sex allocation or sperm localization strategies.

Hence if the amount of resources invested in gamete production $Q(V)$ is reduced by investment in sperm localization, a population of hermaphrodites is stable to invasion by females only when they do not invest in sperm localization. To be stable to invasion by hermaphroditic mutants, the optimal sex allocation is 1 : 1. If $Q(V)$ is an accelerating function of V, or if $Q(V)$ is a saturating function of V but $Q_{\max}$ is small, sperm localization does not confer a higher fitness, and hence males cannot invade this population. On the other hand, when $Q(V)$ is a saturating function of V and $Q_{\max}$ is large, specialization to males that localize their sperm and females that do not invest in sperm localization evolves, and dioecy is the only evolutionarily stable strategy (Fig. 10).

Finally, let us consider the case of a hermaphroditic population in which investment in sperm localization does not affect egg production. Suppose $uQ_{\max}$ is the resource available for egg production, and $(1 - u)\, Q(V)$ that for sperm production, in an individual adopting the sperm restriction strategy V and sex allocation strategy u. The evolutionarily stable sex allocation is still $u = 1/2$, and this population is always neutrally stable to invasions by females.

This hermaphroditic population can be invaded by males or hermaphrodites with a higher sperm density if $Q(V)/V > \mathrm{d}Q(V)/\mathrm{d}V$, and by mutants with a lower sperm density if $Q(V)/V < \mathrm{d}Q(V)/\mathrm{d}V$. Hence if $Q(V)$ is accelerating in V, or a saturating function and $V_{\max} < \hat{V}$, hermaphrodites or males adopting the strategy $V_{\max}$ are evolutionarily stable. If instead $V_{\max} > \hat{V}$ and $Q(V)$ is a saturating function, both dioecy and hermaphrodism with sperm localized to $\hat{V}$ are evolutionarily stable strategies. Hence if the investment in sperm localization is not costly for egg production, there is always a hermaphroditic strategy that is evolutionarily stable.

Transitions between hermaphrodism and dioecy can occur as follows:

1. If in an initially hermaphroditic population with a saturating form of $Q(V)$ and $V_{\max} < \hat{V}$, an increase in the resource $Q_{\max}$ available for gamete production causes $V_{\max}$ to now become larger than $\hat{V}$, then dioecy becomes the only evolutionarily stable state.

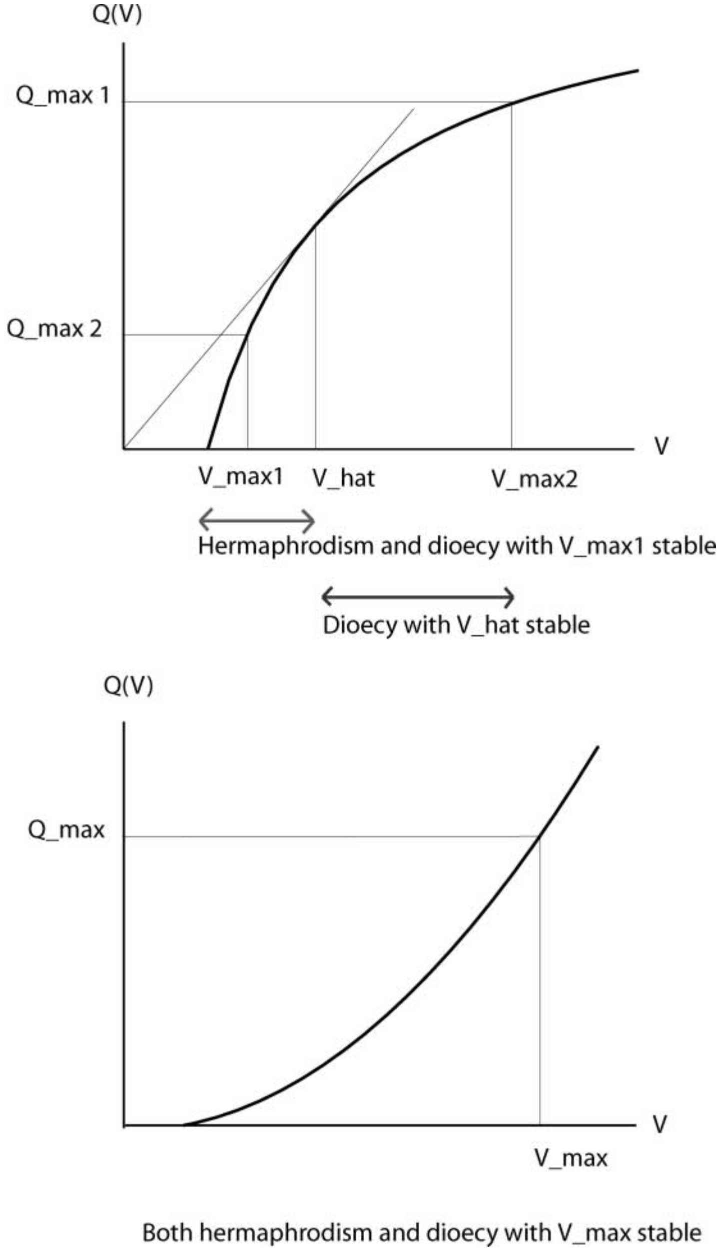

Fig. 9. Regions of stability of hermaphrodism and dioecy for saturating and accelerating forms of $Q(V)$.

2. If in an initially hermaphroditic population with an accelerating form of $Q(V)$, circumstances change so $Q(V)$ becomes a saturating function, and $Q_{\max}$ is large enough that $V_{\max} > \hat{V}$, then again dioecy is the only evolutionarily stable strategy in the new circumstances.

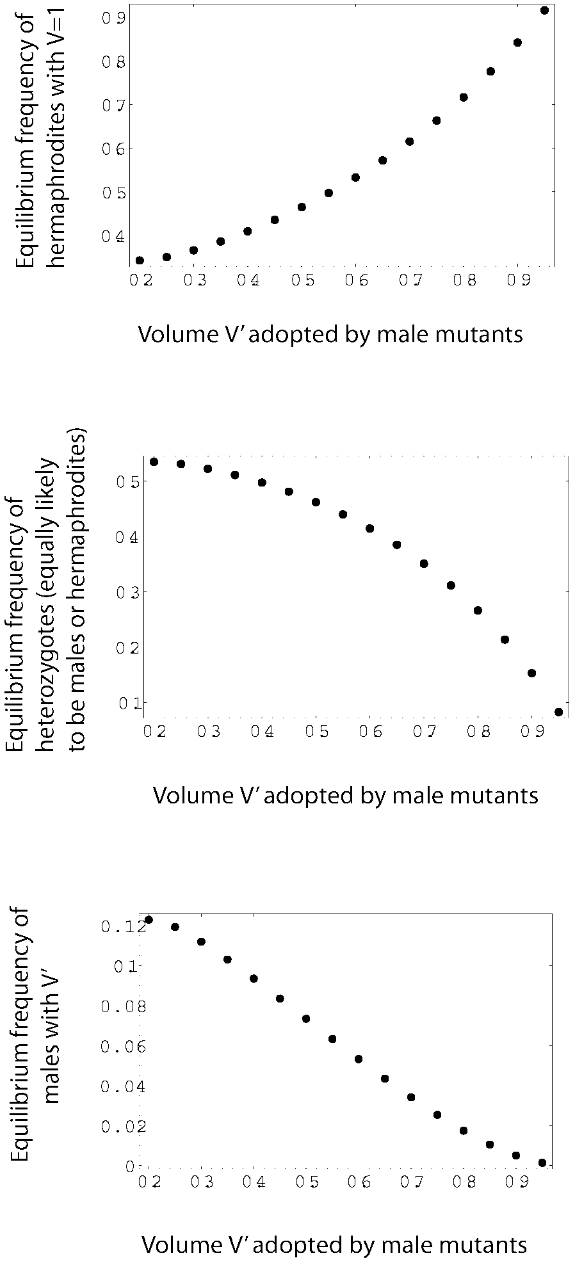

Fig. 10. Genotype frequencies of hermaphrodites, heterozygotes, and males at the polymorphic equilibrium, plotted against the sperm localization volume V' of males. $V = 1$ for resident hermaphrodites, $Q(V) = (V - 0.1)/V$, and $\hat{V} = 0.2$.

Both transitions 1 and 2 involve changes in the sperm localization strategy from $V_{\max}$ to $\hat{V}$. Hence we hypothesize that these are the transitions underlying the observed trends from hermaphrodism and broadcast spawning to dioecy and localized fertilization.

3. An initially dioecious population with sperm localization volume $V_{\max}$ can make the transition to hermaphrodism and $\hat{V}$ following changes in $Q_{\max}$ and the shape of $Q(V)$ similar to those in transitions 1 and 2. If the resources allocated to egg production are separate from those allocated to sperm production and localization, hermaphrodism with sperm localization strategy $\hat{V}$ is evolutionarily stable.
4. In regions where both hermaphrodism and dioecy are stable (saturating $Q(V)$ and small $V_{\max}$, or accelerating $Q(V)$), drift can cause shifts between the two equilibria. Since both equilibria have $V = V_{\max}$, such transitions would not involve changes in the fertilization strategy.

We hypothesize that some of the back-transitions observed from dioecy to hermaphrodism may be explained by transitions 3 and 4.

EMPIRICAL SUPPORT FOR THE MODEL

We conclude from our model that transitions between hermaphrodism and dioecy, and between broadcast spawning and localized fertilizations, result from changes in both the form of $Q(V)$ and the total resources available for gamete production, $Q_{\max}$. The shape of $Q(V)$ reflects the cost of concentrating sperm. The same reduction in the sperm volume reduces the amount of resources available for gamete production much more when $Q(V)$ is accelerating than when $Q(V)$ is saturating.

From the phylogenetic analysis, we conclude that hermaphrodism and broadcast spawning are ancestral and dioecy and localized fertilizations derived. Sperm and egg producing individuals need to come into contact with each other to make the transition from broadcast spawning to localized fertilizations. This change could result either as an adaptation from sessility to mobility, or from behavioural changes in already mobile individuals. Hence such a transition may be less costly when:

1. The cost of mobility is low and/or the population density is high, hence the cost of contacting a similar number of mates by moving to them, as would be possible by releasing sperm into water, is small.
2. Resources available for reproduction are high, hence the surplus of resources left for gamete production after investment in the mechanism to increase sperm concentration is sufficient to create high sperm densities.

Hence the ancestral metazoans may have been broadcast spawning as a result of the small amount of resources available for gamete production in these species (small $Q_{\max}$), or due to low population densities or a high cost of mobility (leading to accelerating $Q(V)$). We propose that increases in resource availability (leading to large $Q_{\max}$), population density, and mobility may have led to an overall decrease in the cost of sperm delivery in metazoans (and hence $Q(V)$ saturating). These changes would select for the evolution of localized fertilizations and the specialization to dioecy. Thus increases in mobility, population density, and resource availability may contribute indirectly to the evolution of dioecy.

Back-transitions from localized fertilization to broadcast spawning may occur due to changes in life-history traits to favour a more sessile or lower density habit. This could increase the cost of sperm localization by changing the shape of the $Q(V)$ curve, or the amount of resources available.

The prevalence of both hermaphroditic and dioecious species among the broadcast spawning taxa could be in support of the model in two ways. The first is if they correspond to the two possible evolutionarily stable strategies when investment in sperm localization is minimal. Alternatively, 'broadcast spawning' as used in our study may actually be an umbrella term for a diversity of fertilization behaviours. It is then possible that male broadcast spawners invest in strategies to ensure higher sperm effectiveness in fertilization compared with related hermaphroditic species.

In taxa such as molluscs and annelids, hermaphroditic species with localized fertilizations have evolved from ancestors that were likely to have been dioecious and broadcast spawning. In these species, dioecy being ancestral may have led to the separation of investments in the male and female functions. We speculate that when ecological conditions change so that investment in increasing sperm density becomes adaptive, the resources invested in such adaptations may continue to remain separate from the ones invested in egg production. Investment in sperm effectiveness being costless for egg production makes hermaphrodism with sperm localization a stable strategy.

Agent pollination in plants may be the counterpart of sperm delivery and wind pollination that of broadcast spawning. In contrast to investment in sperm delivery in animals, investment in agent pollination simultaneously benefits both sperm donation and sperm receipt. This may select for many angiosperm species (which are often agent pollinated) to be hermaphroditic. Agent pollinated species in which investment in sperm donation is detrimental to the female function [such as beetle-hosting in cycads, with the consequence of having the male cones destroyed (Hall *et al.*, 2004)] should be selected to be dioecious. Gymnosperms are mostly wind pollinated, and our model would predict both hermaphrodism and dioecy to be evolutionarily stable strategies in these species. This may explain how nearly a third of the gymnosperm species are dioecious (Raven *et al.*, 1999).

Support for our model among animals could be tested using the following predictions:

1. Transitions from hermaphrodism to dioecy involve adaptations to increase sperm effectiveness in ensuring fertilizations. The costs of such adaptations may be low compared with the benefits as a result of differences in mobility, population density or resources available for reproduction between these species.
2. Transitions from dioecy and broadcast spawning to hermaphrodism and localized fertilizations are expected to occur when conditions favour adaptations to increase sperm effectiveness, and the investment in such adaptations is not costly to egg production. Hence, among the secondarily derived hermaphroditic species that do invest in sperm localization strategies, changes in investment in the adaptations to increase sperm effectiveness are not expected to change egg production.

DISCUSSION

We map hermaphrodism, dioecy, and the fertilization modes on the metazoan phylogenetic tree to suggest that the ancestral metazoans were hermaphroditic and broadcast spawning. Hence both dioecy and localized fertilization behaviours such as internal fertilization and spermatophore transfer are derived, and need to be understood as adaptations. Despite the problems involved in using maximum parsimony to reconstruct ancestral traits accurately (Cunningham *et al.*, 1998; Martins, 2000), this study provides reason to question the dominant view that hermaphrodism is generally derived among animals (Ghiselin, 1969, 2006). The inference that over time animals have evolved separate sexes as well as become more specialized in their fertilization behaviour suggests that the selection for the two traits may be coupled. Hence the construction of a model to explore the hypothesis that specialization to males and females evolves in response to selection for more concentrated sperm around eggs. Our formulation of the sperm concentration strategy (using the parameter V) is biologically general, and can be applied to a number of different fertilization behaviours. From evolutionary stability analyses, we predict that dioecy evolves from hermaphrodism when mechanisms to localize sperm are adaptive, but decrease the resources available for both sperm and egg production.

Ghiselin's view that hermaphrodism is derived arises from focusing on speciose taxa such as molluscs and echinoderms in which hermaphrodism is secondarily derived from dioecy. Our model predicts both hermaphrodism and dioecy to be evolutionarily stable when investment in sperm localization is not adaptive, in which case transitions could occur from dioecy to hermaphrodism. Alternatively, changes in population density, mobility or resource availability in an initially dioecious population may make sperm localization adaptive. Then, if the investment does not decrease resources available for egg production, hermaphrodism with the new fertilization behaviour can evolve from dioecy. Previous models by Tomlinson (1966), Ghiselin (1969), and Heath (1977) suggest that when encounters between mates are rare enough, a hermaphrodite benefits from having the potential to mate with every individual encountered. This hypothesis may explain some of the transitions from dioecy to hermaphrodism, and is consistent with our model as we assume that access to mates is not limiting.

Many models for the evolution of hermaphrodism and dioecy, especially for plants, consider the advantages of selfing and the disadvantages of inbreeding depression as the important selective forces. However, simultaneous hermaphrodites often do not self, and selfing rates among hermaphrodites vary greatly among animals (Jarne and Auld, 2006). Many plant species are self-incompatible, and dioecy may evolve mainly in self-compatible populations (Charlesworth, 2001). Hence the factors that play a role in the evolution of hermaphrodism and dioecy are not restricted to the effects of selfing. To study the other factors involved, we have ignored any advantages or disadvantages to selfing in our model, or equivalently assumed that hermaphrodites always cross-fertilize.

An influential class of models for the evolution of hermaphrodism and dioecy are the sex allocation models. They can be used to examine the stability of the two sexual strategies based on trade-offs between gains from sperm and egg production (Charnov *et al.*, 1976). Charnov (1979) suggests different functional forms for male or female fitness with allocations into them, leading to differently shaped trade-off functions. The variation in functional forms is speculated to arise from variation in species traits such as mobility or density, but the mechanistic connections are not made explicit. One rationale for the differently shaped functions is the local male competition hypothesis (Charnov, 1982), according to which a saturating male fitness response to allocation results at low population sizes. In the Appendix, we show how this model incorrectly analyses the evolutionary stability of sex allocation strategies – it turns out that irrespective of the mating group size, the ESS sex allocation is always 1 : 1 in the presence of any amount of sperm competition.

In our model as well, a hermaphroditic population with 1 : 1 sex allocation cannot be invaded by mutants that only change their sex allocation strategy. Hence instead of considering a trade-off between sex allocation and fitness, we focus on selection on the mechanism to increase sperm concentration, and when that might lead to the evolution of dioecy. Factors such as mobility and population density then influence selection for hermaphrodism or dioecy by influencing the costs and benefits of such mechanisms. Hence our model can be viewed as one that provides a mechanistic explanation based on fertilization probability for the shape of the trade-off curves in Charnov and colleagues' (1976) model. Although Charnov *et al.* provide other reasons why the trade-off curves may be shaped differently in different biological circumstances, selection to increase sperm concentration is expected to be a pervasive force shaping these curves in all anisogamous taxa. Hence we predict our hypothesis to be one that contributes in general to the evolution of sexual systems.

To develop the intuition of males as the mobile sex, Puurtinen and Kaitala (2002) consider a simulation model for the evolution of hermaphrodism and dieocy. The parameters of their model are population density, cost of mate search, cost of mating as a male, and velocities while searching and not searching. Individuals acquire the resources to be spent on reproduction when not searching for mates. Each individual adopts a strategy for the time allocated to mate search and the fraction of mating encounters in which the male role is adopted, resulting in a trade-off between number of mates accessed and resources available for gamete production. The authors report that hermaphrodism is stable under a wide range of conditions, but dioecy (specialization to searching males and non-searching females) is selected only under a narrow range of parameters corresponding to moderate population density and high search velocity. While the model demonstrates the evolution of dioecy, the link between the ecological conditions of mobility and population density and the coincidence of disruptive selection on mate search and sex allocation is not evident from this model.

The Puurtinen–Kaitala model differs from ours in considering a fixed cost of mating as a male. This implies that the fitness from the male function depends only on the number of egg producers mated with, and the number of competitors for each mate. Hence the only way for a mutant to increase its fitness from sperm production in this model is to increase its number of mates. In contrast, we allow the mutant to increase the effectiveness of its sperm at fertilizing eggs, while keeping the number of mates constant. The condition for dioecy to be selected over hermaphrodism then reduces to the condition that the mutant be more successful in this task compared with the resident hermaphrodite. The ease with which dioecy evolves in such a model, compared with the formulation by Puurtinen and Kaitala, suggests that effectiveness in ensuring fertilizations rather than effectiveness in mate access may be key to selecting for specialization to males. Strategies to increase fertilizations then include, but are not restricted to, strategies to access mates.

In conclusion, this paper contributes to the theoretical literature of evolution of dioecy by focusing on what it is that males may be able to do that gives them an advantage over their hermaphroditic peers. This idea finds support in the overall trend from hermaphrodism and broadcast spawning of sperm to dioecy and localized fertilizations in animals.

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APPENDIX

We show that the local male competition (LMC) hypothesis that the ESS sex allocation depends on the number of male competitors in the mating group is mistaken. Instead, in any group with sperm competition between individuals, the ESS sex allocation for hermaphrodites is 50 : 50, as is the ESS sex ratio for dioecious species.

Charnov (1982) considers a group of k hermaphrodites, each allocating a fraction r of its resources to sperm production, the remaining $1 - r$ being allocated to egg production. All eggs are assumed to be fertilized, hence the fitness from the female function is proportional to the investment in egg production. The fitness from sperm production is proportional to the fraction of the sperm pool contributed by the focal individual. If a mutant then allocates a fraction $\hat{r}$ to sperm production, its fitness is proportional to:

$$w_{\text{mut}} = 1 - \hat{r} + k\,(1 - r)\,\frac{\hat{r}}{\hat{r} + (k-1)\,r}$$

The first term $1 - \hat{r}$ is proportional to the number of eggs produced by the mutant. Its sperm comprise a fraction $\frac{\hat{r}}{\hat{r} + (k-1)\,r}$ of the sperm density available at each of the k mates, each producing $1 - r$ eggs. Hence the second term is the fitness gained from sperm production.

Charnov then sets $\left.\frac{\mathrm{d}w_{\text{mut}}}{\mathrm{d}\hat{r}}\right|_{\hat{r}=r} = 0$ to get $\hat{r} = \frac{(k-1)}{2k-1}$, and assumes that this $\hat{r}$ is the ESS sex allocation. For a finite k, $\hat{r}$ is less than 1/2, and the rationale provided for this is that the fitness accrued by a mutant from its female function $(1 - \hat{r})$ is linear in $\hat{r}$, while that gained from its male function is $\frac{\hat{r}}{\hat{r} + (k-1)\,r}$, which is saturating in $\hat{r}$.

$\hat{r}$ would indeed be the ESS sex allocation if in a population with all individuals adopting the strategy $\hat{r}$, a mutant with a different strategy r' has a lower fitness compared with the residents. We check if this is the case by calculating the mutant and resident fitnesses in a mating group of size k [and hence with a total of $(k-1)(1-\hat{r}) + (1-r')$ eggs]:

$$w_{\text{mut}} = 1 - r' + \Big((k-1)(1-\hat{r}) + (1-r')\Big)\frac{r'}{(k-1)\,\hat{r} + r'}$$

$$w_{\text{res}} = 1 - \hat{r} + \Big((k-1)(1-\hat{r}) + (1-r')\Big)\frac{\hat{r}}{(k-1)\,\hat{r} + r'}$$

We find that for a population with $\hat{r} = \frac{k-1}{2k-1}$ fixed, there are indeed values of r' such that $w_{\text{mut}} > w_{\text{res}}$, and in particular, this is always true for $r' = 0.5$. On the other hand, $\hat{r} = 0.5$ is not invadable by any other strategy. We plot the invasability conditions for different values of $\hat{r}$ and r' for a mating group of size 4 in Fig. A1. If $w_{\text{mut}} > w_{\text{res}}$, r' can invade $\hat{r}$, and the point

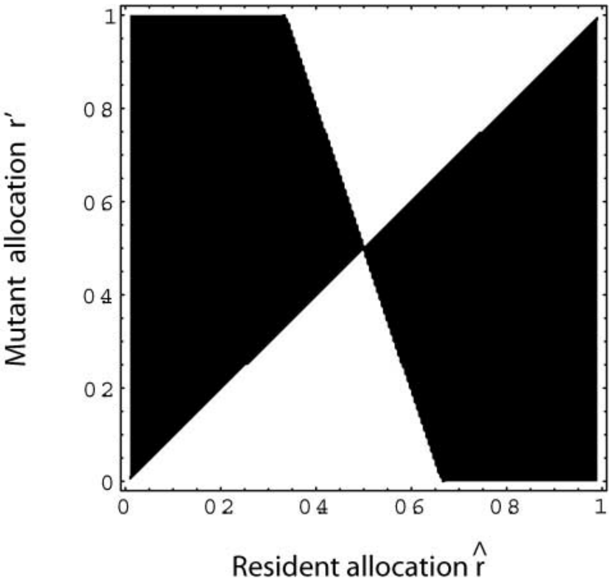

Fig. A1. Invasability plot for sex allocation strategies for a hermaphroditic mating group of size 4. The point ($\hat{r}$, r') is shown in black if a mutant with allocation r' can increase when rare in a group of individuals with allocation $\hat{r}$, and white otherwise.

($\hat{r}$, r') is shown in black. If instead r' cannot invade $\hat{r}$, the point ($\hat{r}$, r') is shown in white. Hence we see that $\hat{r} = 0.5$ is the only sex allocation that is evolutionarily stable.

Thus although the relative fitness of a mutant from sperm production as a function of the allocation in sperm may be a saturating function, the ESS sex allocation remains 1 : 1 for a population of hermaphrodites. This hermaphroditic population is stable to the invasion of males or females, but so is a dioecious population with a 1 : 1 sex ratio stable to invasion by hermaphrodites. Hence the mating group size by itself need not have an effect on which of hermaphrodism and dioecy is evolutionarily stable.