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Sperm competition and sex allocation in simultaneous hermaphrodites

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Summary

Sex allocation theory is developed for hermaphrodites having frequent copulations and long-term sperm storage. Provided the sperm displacement mechanisms are similar to those known in insects, the ESS allocation to sperm versus eggs satisfies a rather simple rule. There are no data to test this rule, as yet.

Keywords: sperm competition; sex allocation; hermaphrodites

Quantitative evolutionary theory based upon maximization of Darwinian fitness has been successfully used for many specific questions within the area of sex allocation (Charnov, 1982, 1993), including dioecious sex ratios (Hamilton, 1967; Trivers and Hare, 1976; Charnov *et al.*, 1981; Werren, 1987; Wrensch and Ebbert, 1993; Godfray, 1994), age-at-sex-change (Ghiselin, 1969; Charnov *et al.*, 1978; Charnov, 1979b; Warner, 1988; Charnov and Bull, 1989) and male/ female function in (simultaneous) hermaphrodites (Charnov *et al.*, 1976; Fischer, 1981; Leonard, 1990; Petersen, 1990a,b). While such theories have yielded capital results for hermaphroditic sea bass (Fischer, 1980, 1981, 1984; Fischer and Petersen, 1987; Petersen, 1987, 1990a,b; Leonard, 1993) and polychaetes (Sella, 1988, 1990, 1991) with external fertilization, a great many more invertebrates are hermaphrodites. The vast majority of these have some form of copulation, sperm storage and internal fertilization; this majority has been ignored by sex allocation theories (but see Leonard, 1990). This paper unites recent work on mechanisms of sperm displacement in insects with male/female fitness options to produce the first quantitative theory for sex allocation in hermaphroditic invertebrates with sperm storage. The equilibrium sex allocation here maximizes a product of female fitness × male fitness, the latter being solely a function of the proportion of sperm displaced per mating. The new theory predicts that allocation will favour female function and makes the novel prediction that the extent of female bias is controlled by a simple dimensionless comparison between two mates: female allocation increases with the ratio (donor individual's potential sperm production/recipient individual's sperm stores). The allocation is surprisingly independent of the exact form of sperm displacement.

Evolution of sex allocation controlled by nuclear autosomal genes is a form of frequency-dependent natural selection, since half of the genes passed to zygotes come from sperm and half come from eggs (Fisher, 1958). For example, if hermaphrodites are giving lots of resource to eggs, greater than average reproductive gains accrue to genotypes who give more to sperm (male function). The equilibrium (or ESS) balances reproductive opportunities for each of the two gender functions (Charnov *et al.*, 1976); the ESS becomes a quantitative, testable, often non-intuitive, hypothesis for the action of natural selection.

This paper considers a hermaphrodite with long-term sperm stores. An individual has a sperm storage vessel and draws sperm from it to fertilize eggs. A copulation gives it more (new) sperm. The new sperm mixes with and displaces existing stores according to some displacement rule. The number of sperm received in a copulation may well exceed the size of the stores, so the displacement rule tells us what proportion of the stores get displaced after each copulation.

Consider a hermaphroditic snail over an interval of time yielding one mating. All individuals are alike and each has R resources to make eggs or the sperm to give to the single mate. Suppose a typical individual gives $(1 - r)R$ to eggs and $r \cdot R$ to sperm. A rare mutant individual who alters r to $\hat{r}$ will produce $R(1 - \hat{r})$ as many eggs and $R \cdot \hat{r}$ as many sperm. How many eggs will the mutant fertilize due to this allocation ($\hat{r}$) decision? Suppose giving $R \cdot \hat{r}$ in sperm to a partner causes the displacement of a $\phi(R \cdot \hat{r})$ proportion of the sperm from the partner's sperm stores. Then the next time the partner lays eggs the mutant will fertilize a $\phi(R \cdot \hat{r})$ proportion of them. Sometime later the partner mates again, almost surely with a non-mutant, and this mating displaces $\phi(R \cdot r)$ of the sperm stores or $1 - \phi(R \cdot r)$ is not displaced. If sperm is thoroughly mixed, the mutant's copulation will now fertilize a $\phi(R \cdot \hat{r}) [1 - \phi(R \cdot r)]$ proportion of the partner's eggs. The next mating by the partner will again not-displace $1 - \phi(R \cdot r)$ of the sperm stores so that now the mutant will fertilize a $\phi(R \cdot \hat{r}) [1 - \phi(R \cdot r)]^2$ proportion of the partner's eggs, and so on for subsequent matings by the partner. The rare mutant will surely be mated to a typical individual who will be producing $R(1 - r)$ eggs between each mating. Thus, the total eggs fertilized by the mutant's decision to give away $R \cdot \hat{r}$ in sperm to the partner is

$$R(1-r) \cdot \phi(R \cdot \hat{r})[1 + [1 - \phi(r \cdot R)] + [1 - \phi(r \cdot R)]^2 + \ldots]$$

or, summing the geometric series

$$= \frac{R(1-r) \cdot \phi(R \cdot \hat{r})}{\phi(R \cdot r)} \tag{1}$$

The total fitness (W) for the mutant over this interval is the eggs produced plus the eggs fertilized, or

$$W = R(1-\hat{r}) + \frac{R(1-r) \cdot \phi(R \cdot \hat{r})}{\phi(R \cdot r)} \tag{2}$$

Equation 2 assumes matings to be frequent, so that we can sum the entire geometric series (Equation 1) and ignore mortality, assume population size constant and assume that virgin individuals can be ignored (discussed further below). The ESS is r^* such that the mutant cannot increase W by setting $\hat{r} \neq r^*$ and may be found by setting $\partial W / \partial \hat{r} = 0$ when $\hat{r} = r$ and solving for r. $\partial W / \partial \hat{r} = 0$ yields

$$0 = -R + \frac{\partial \phi}{\partial \hat{r}} \left[\frac{R(1 - r)}{\phi(R \cdot r)} \right]$$

Putting $\hat{r} = r$ gives

$$0 = \frac{-1}{1 - r} + \frac{\partial \phi / \partial r}{\phi(R \cdot r)}$$

This condition solves for the r value which maximizes the product of $(1 - r) \cdot \phi(r)$ (Equation 3), a result easily seen if one puts $\partial[(1 - r) \cdot \phi(r)] / \partial r = 0$. Of course, a boundary optimum ($\phi = 1$) will usually have $\partial[(1 - r) \cdot \phi(r)] / \partial r > 0$ at r^*. For hermaphroditism itself to be stable (when natural selection does not favour pure males or females), $\phi(r)$ must be linear or show diminishing returns, a condition that is met for the mechanisms discussed below.

While apparently little is known about the mechanisms of sperm transfer and displacement in hermaphrodites, work on insects (Parker, 1970; Parker *et al.*, 1990; Parker and Simmons, 1991,

1994) suggests a number of possibilities for the φ function. Three of these, representing extreme cases, are considered here. The mechanisms or variations/combinations of them are documented for several insect groups. Suppose the sperm storage vessel contains μ sperm. Case 1 is one-to-one (perfect) displacement, so that $\phi = r \cdot c \cdot R/\mu$, until $\phi = 1$, where c converts resource $(r \cdot R)$ into sperm number. This linear case is also true if old sperm are mechanically removed from storage by a donor prior to the vessel being filled with donor sperm. Case 2 is where the sperm are dumped from the storage vessel into another vessel and mixed with the incoming $r \cdot c \cdot R$ sperm, a fair sample of which is then stored. This makes

$$\phi = \frac{r \cdot R \cdot c}{r \cdot R \cdot c + \mu} = \frac{r \cdot R \cdot c/\mu}{r \cdot R \cdot c/\mu + 1}$$

The third case, known from dung flies (Parker and Simmons, 1994), is where sperm flows smoothly into the stores with constant mixing and flushing of new and old sperm; this yields an exponential φ function, or $\phi = 1 - \exp(-r \cdot c \cdot R/\mu)$. While the three displacement mechanisms differ in details of functional form, each yields $\phi(r)$ to be solely a function of a single dimensionless comparison $(c \cdot R/\mu)$ between the two mates. This number (now called δ) is the ratio of the potential sperm production by a donor $(c \cdot R)$ divided by the total sperm stored by a recipient, μ. While a few other displacement mechanisms are documented in insects (Parker, 1970; Parker *et al.*, 1990; Parker and Simmons, 1991, 1994), the present discussion will focus on these as comprising a plausible range for hermaphroditic invertebrates.

Forming the product $(1 - r) \cdot \phi(r, \delta)$ and setting $\partial(\text{product})/\partial r = 0$ finds the optimal r^* for each mechanism, as shown in Fig. 1. r^* is $\leq 1/2$ and decreases with δ. Perfect displacement (curve C in Fig. 1) has $\phi = 1$ with $r = 1/\delta$ for $\delta > 2$. Smaller δ yields $r = 1/2$ for this case. The two mixing mechanisms with non-perfect displacements are virtually indistinguishable, while perfect displacement crosses the others at $\delta \approx 3$; note that with $\delta > 3$ the two mixing mechanisms have the recipients obtaining more sperm per mating than their stored number, a result of the
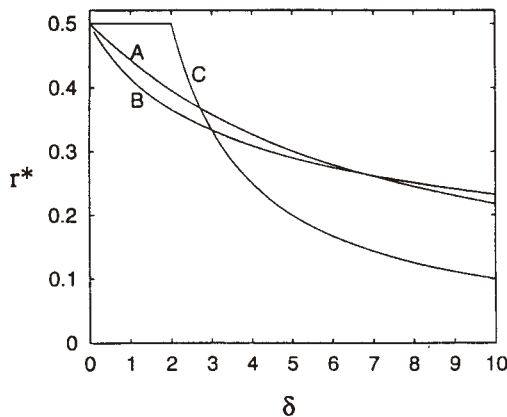

Figure 1. Evolutionary equilibrial (ESS) allocation to sperm (male function) (r^*) is a function of a dimensionless ratio comparison between two mates. δ is the ratio of a donor individual's potential sperm production $(R \cdot c)$ divided by the recipient individual's sperm stores (μ). The three cases (A–C) refer to the three sperm displacement mechanisms developed in the text (case 1 is C, case 2 is B and case 3 is A). Notice that r^* is similarly related to δ for the three mechanisms. The derivation of the ESS rules is in the text.

negatively accelerated nature of the sperm displacement (ϕ) functions (excess and displaced sperm may be used for nutrition; e.g. Charnov, 1979a). The predictions of Fig. 1 are similar enough for all three to claim r^* as approximately independent of the mechanism of sperm displacement, at least for these three rather different mechanisms; r^* mostly depends upon the between-mate comparison captured by the ratio δ. Of course, the three mechanisms can be distinguished by the proportion of sperm displacement, the ϕ values themselves which are rather different at each δ value. These general results clearly focus attention on δ as a key parameter for evolution of reproduction in simultaneous hermaphrodites with long-term sperm storage; the results are quite novel in that here an individual's total resource level (R) clearly affects an ESS rule for sex allocation, whereas elsewhere it almost never does (Charnov, 1982).

Previous sex allocation theories for simultaneous hermaphroditic animals have focused upon the effects of mating group structure in fish and polychaetes (work of Fischer, Petersen and Sella, cited earlier) with external fertilization and/or barnacles (Raimondi and Martin, 1991) without sperm storage. The results obtained here apply to a much larger number of species since most hermaphroditic invertebrates have internal sperm competition through displacement of sperm stores. While there are no measurements of sperm displacement or sex allocation for hermaphroditic invertebrates, these theoretical results now make such measurements especially worthwhile. The new theory may be developed further in several directions, a few of which are worth noting here.

Firstly, substantial mortality rates decrease r^* from the values in Fig. 1, since mortality will now enter the sum leading to Equation 1; this yields a product rule similar to Equation 3, but devaluing even more gain through sperm. Likewise, if the number of mates is small, the infinite sum (Equation 1) must be replaced with a truncated sum. Secondly, individuals need not all be the same size (same R) and sex allocation could be size or condition dependent (Charnov and Bull, 1977, 1989). Two size classes yield four different r^* values, one for each direction of sperm donation, dependent upon four values of δ and other dimensionless parameters which set the mating opportunities for members of each size class. Thirdly, individuals as sperm recipients might discriminate for or against sperm from some donors, while individuals as donors might manifest characters to enhance use of their sperm (Charnov, 1979a). An elaborate pre-copulatory display might well be involved in mutual assessment of reproductive opportunities with a potential partner (e.g. Leonard 1990, 1991, 1992; Leonard and Lukowiak, 1991) (e.g. virgins should be treated differently as they have no sperm stores). Fourthly, Baur (1994) has found great variability in the proportion of sperm displacement per mating pair in a land snail, strongly suggesting that the ϕ function be more realistically modelled as a probability distribution. Doing this results in $\phi(r)$ in Equation 3 being replaced by the 'average of $\phi(r)$'. Interestingly, this may not significantly alter the results in Fig. 1. For example, if the recipient digests completely the results of some matings ($\phi = 0$ for q proportion of the matings), the average ϕ will be $q \cdot 0 + (1 - q) \cdot \phi(r)$, and the ESS r maximizes $(1 - r)(1 - q) \cdot \phi(r)$, which is $\propto (1 - r) \cdot \phi(r)$, the same as before. Finally, the flowers of many hermaphroditic plants put self-pollen on, and take pollen off, the bodies of insects. This results in sperm (pollen) displacement similar to the ϕ process developed here (Morris *et al.*, 1995; often referred to as 'pollen carry-over'). Perhaps the sex allocation rules (Charnov, 1979a; Charlesworth and Charlesworth, 1987; Charlesworth and Morgan, 1991; Brunet 1992) will likewise be similarly based on ϕ (Equation 3 here)?

It is surprising that r^* depends upon δ in a manner approximately invariant with respect to the sperm displacement mechanism (Fig. 1); such a trade-off invariance is, as yet, known for only a few other problems in the evolution of sex allocation and life histories (Charnov, 1993; Charnov and Downhower 1995).

Acknowledgements

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