

Sperm competition and sex allocation in simultaneous hermaphrodites: A new look at Charnov's invariance principle

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ABSTRACT

Recently, Charnov (1996) investigated the consequences of sperm competition for optimal sex allocation in simultaneous hermaphrodites. Charnov argued that the optimal sex allocation strategy can be derived on the basis of the 'sperm displacement rule'; that is, the function describing the relationship between sperm production and sperm displacement. Based on three specific examples of such sperm displacement rules, Charnov claimed that the details of the relationship between ejaculate volume and sperm displacement have only a minor effect on the optimal sex allocation strategy. We demonstrate that this 'invariance principle' is less general than suggested. The optimal sex allocation strategy as a function of the dimensionless quantity δ (ratio of maximum sperm volume to sperm storage volume) can have a wide variety of shapes. This is because Charnov's results depend crucially on two assumptions of questionable generality: diminishing displacement with investment in sperm and linear fitness returns with investment in eggs. We argue that deeper insights into optimal sex allocation are obtained if the allocation decision is partitioned into multiple components. Using this approach, we find a novel invariance principle: if egg survival only depends on the investment per egg (and not on clutch size), then the shape of this relationship has no effect whatsoever on optimal allocation to eggs versus sperm.

Keywords: allocation components, evolutionary stability, fitness, hermaphrodites, sex allocation, sperm displacement.

INTRODUCTION

In a recent paper, Charnov (1996) analysed the consequences of sperm competition for optimal sex allocation in simultaneous hermaphrodites that have frequent copulations and long-term sperm storage. We think that Charnov's paper is an important contribution, but its main conclusion is less general than suggested. Before we explain why, we present a brief account of Charnov's model and the main results. Consider a wild-type population of hermaphrodites where all individuals have R units of resource available per mating. All invest a fraction r^* of resources into sperm, the rest $(1 - r^*)$ into eggs. During mating, the

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ejaculate displaces a proportion $\phi(r^*\delta)$ of the sperm already present in the partner's sperm stores. The dimensionless quantity $\delta = sR/\mu$ represents the ratio of maximum ejaculate volume to sperm storage volume, where s is a resource-to-sperm volume conversion factor and μ is total sperm storage volume. The question is: What is the optimal or ESS fraction r^* of resources allocated to sperm? Suppose a rare mutant allocates r instead of the wild-type fraction r^* to sperm. The mutant's fate is determined by a fitness function of the familiar form (Charnov, 1982):

$$w(r, r^*) = \frac{f(r)}{f(r^*)} + \frac{m(r)}{m(r^*)} \quad (1)$$

where f is fitness through female function and m is fitness through male function. If $w(r, r^*) > w(r^*, r^*) = 2$ the mutant will spread and if the inequality is reversed the mutant will go extinct. Hence, an ESS is found by maximizing $w(r, r^*)$ with respect to r . An ESS can therefore be calculated by solving:

$$\left. \frac{\partial w}{\partial r} \right|_{r=r^*} = \frac{f'(r^*)}{f(r^*)} + \frac{m'(r^*)}{m(r^*)} = 0 \quad (2)$$

where the prime denotes differentiation.

Charnov assumed that female fitness is proportional to the number of eggs produced, and male fitness is proportional to the proportion of sperm displaced per mating. In short,

$$f(r) = (1 - r)R \quad \text{and} \quad m(r) = \phi(r\delta) \quad (3)$$

Equation (2) then yields the ESS condition:

$$r^* = 1 - \frac{\phi(r^*\delta)}{\delta\phi'(r^*\delta)} \quad (4)$$

An ESS r^* is thus completely determined by the shape of ϕ and the value of δ . What is a biologically reasonable choice of ϕ ? Obviously, if no sperm is transferred, then there is no displacement; that is, $\phi(0) = 0$. Furthermore, ϕ is expected to be an increasing function of the ejaculate volume $r\delta$ that approaches unity as $r\delta$ goes to infinity. If we adhere to a strict physical interpretation of displacement of ϕ , then we would also want $\phi(r\delta) \leq r\delta$ (implying $\phi'(0) \leq 1$); that is, the amount of sperm displaced does not exceed the amount injected. Anything else? For biological reasons not quite clear to us (see below), Charnov claims that ϕ must show diminishing returns, since otherwise simultaneous hermaphroditism itself could not be stable. Formally, this implies the additional condition $\phi'' \leq 0$. Since no data are available about mechanisms of sperm competition in hermaphrodites, Charnov based his choice of ϕ on what is known about sperm transfer and displacement in insects (Parker, 1970; Parker *et al.*, 1990; Parker and Simmons, 1991, 1994). This led him to consider the following three scenarios:

$$\phi(r\delta) = r\delta \quad (5a)$$

$$\phi(r\delta) = \frac{r\delta}{1 + r\delta} \quad (5b)$$

$$\phi(r\delta) = 1 - \exp(-r\delta) \quad (5c)$$

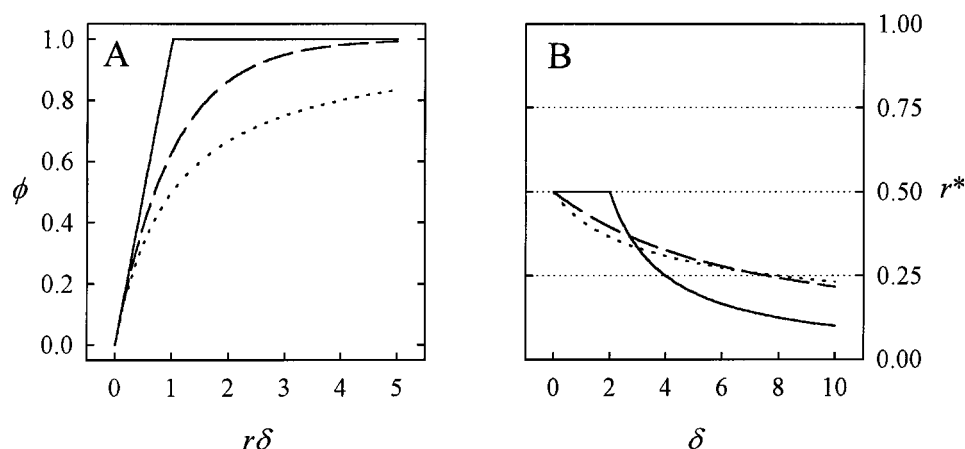


Fig. 1. Examples used by Charnov (1996) of (A) sperm displacement rules and (B) the corresponding optimal sex allocation rules. Solid lines: $\phi(x) = x$; dashed lines: $\phi(x) = 1 - \exp(-x)$; dotted lines: $\phi(x) = x/(1+x)$.

These functions and their corresponding optimal allocation rules $r^*(\delta)$ as functions of δ are shown in Fig. 1. The optimal allocation rules share the following features: r^* tends to $\frac{1}{2}$ as $\delta \rightarrow 0$ and r^* decreases in a convex fashion with δ . As a consequence, allocation is never male-biased. Because of these shared characteristics, Charnov concludes that 'it is surprising that r^* depends upon δ in a manner approximately invariant with respect to the sperm displacement mechanism; such a trade-off invariance is, as yet, known for only a few other problems'.

We certainly consider it a worthwhile enterprise to search for biological principles that are independent of the details of the underlying trade-off structure, if only because the shapes of trade-off are so notoriously hard to measure. However, we show that Charnov's main conclusion does not reflect a general principle but rather reflects specific properties of the chosen sperm displacement functions and a couple of assumptions that appear too restrictive. We extend Charnov's analysis by investigating the consequences of relaxing two important assumptions. In particular, the assumption that sperm displacement must show diminishing returns is too restrictive and it has a major qualitative impact on the results. Furthermore, the assumption of linear returns on investment in eggs is not always justified and, again, it may have important consequences for the model predictions.

EFFECT OF THE SPERM DISPLACEMENT RULE ON OPTIMAL SEX ALLOCATION

In this section, we assess how the shape of the sperm displacement rule affects the optimal sex allocation decision. We start with a formal proof of Charnov's assertion that optimal allocation cannot be sperm-biased when sperm is displaced with diminishing returns.

Result 1. *If the sperm displacement rule $\phi(r\delta)$ shows diminishing returns for all $r\delta \geq 0$, that is if $\phi'' \leq 0$, then the optimal sex allocation is never sperm-biased, that is $r^*(\delta) \leq \frac{1}{2}$ for all $\delta \geq 0$.*

Proof. Implicitly differentiating (4) with respect to δ , we obtain:

$$\frac{\partial r^*}{\partial \delta} = \frac{1 - 2r^*}{\delta(1 - r^*)^2} + \frac{r^*}{1 - r^*} \frac{\phi''(r^*\delta)}{\phi'(r^*\delta)} \quad (6)$$

Since $\phi'' \leq 0$, $\partial r^*/\partial \delta \leq 0$ near $r^* = \frac{1}{2}$, which implies that $r^*(\delta)$ cannot cross the line $r^* = \frac{1}{2}$ from below. In the Appendix we show that $r^*(0) \leq \frac{1}{2}$; it follows by continuity of $r^*(\delta)$ that the optimal allocation to male function cannot exceed $\frac{1}{2}$. ■

But how reasonable is it to impose upon the sperm displacement rule ϕ the restriction that it be linear or concave everywhere? According to Charnov, this must necessarily be so, otherwise selection would favour pure males and females (or sequential hermaphrodites). We agree that if ϕ were convex everywhere – that is, an accelerating function of $r\delta$ – then there would indeed be selection against simultaneous hermaphrodites. This follows immediately from the Jensen inequality:

$$E(\phi(x)) \geq \phi(E(x)) \quad (7)$$

which holds for all convex functions ϕ (e.g. Hofbauer and Sigmund, 1988). However, this need not be true for sperm displacement rules $\phi(r\delta)$ that are convex only for sufficiently small values of $r\delta$. S-shaped curves would then be admissible. Indeed, it is not hard to imagine biological scenarios where sperm displacement would follow such a rule. It is conceivable that sperm is ‘cooperative’, in the sense that significant displacement is only possible when plenty of sperm is produced. For example, it may be that sperm in sufficient amounts forms clots large enough so as to block the passage of future sperm. Or, conversely, only by injecting large amounts of sperm such blockages by sperm of predecessors may be overcome. Another possible reason why ϕ might be S-shaped is that sperm may differ in quality (e.g. longer tails or more mitochondria), quality being an increasing function of investment. Peter Taylor pointed out to us that an effectively S-shaped curve is also obtained if a certain minimum investment in male function is needed to get any sperm at all and, once this is taken care of, the subsequent displacement function is concave.

Let us therefore work out the consequences for optimal sex allocation if we allow S-shaped sperm displacement rules; that is, we allow $\phi''(r\delta) > 0$ for sufficiently small values of $r\delta$. An immediate consequence is that it is now possible that $\phi'(0) = 0$. As we show in the Appendix, $r^*(0)$ can attain any value between $\frac{1}{2}$ and 1. It is also possible that $r^*(\delta)$ is a non-monotonic function of δ . Consider any function ϕ with $\phi'(0) > 0$ and $\phi''(0) > 0$. By the proposition in the Appendix, $r^*(0) = \frac{1}{2}$ and by equation (6) $\partial r^*/\partial \delta|_{\delta=0} > 0$; that is, optimal sex allocation becomes more male-biased. Since ϕ converges towards the asymptotic value 1, ϕ'' must eventually become negative. Equation (6) shows that $\partial r^*/\partial \delta < 0$ for $\phi'' < 0$, at least as long as r^* remains male-biased. Hence, $\partial r^*/\partial \delta$ changes sign. In summary, we have shown:

Result 2. *If the sperm displacement rule $\phi(r\delta)$ is convex for sufficiently small $r\delta \geq 0$, then we have:*

- (a) *Optimal sex allocation may be male-biased. In fact, r^* may attain any value between $\frac{1}{2}$ and 1.*
- (b) *Optimal sex allocation may be a non-monotonic function of δ .*

Some illustrative examples of S-shaped sperm displacement rules and the corresponding optimal sex allocation rules are shown in Fig. 2.

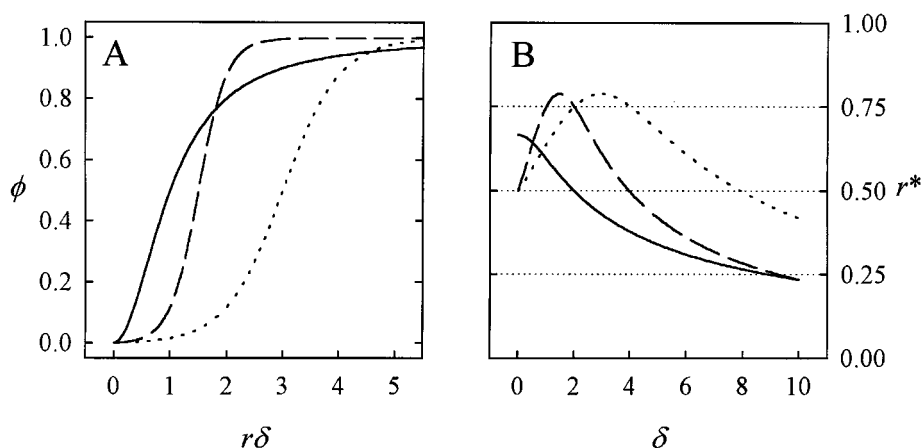


Fig. 2. Examples of (A) S-shaped sperm displacement rules and (B) the corresponding optimal sex allocation rules. Solid lines: $\phi(x) = x^2/(1 + x^2)$; dashed lines: $\phi(x) = [1 + \exp(-4x + 6)]^{-1} - [1 + \exp(6)]^{-1}$; dotted lines: $\phi(x) = [1 + \exp(-2x + 6)]^{-1} - [1 + \exp(6)]^{-1}$.

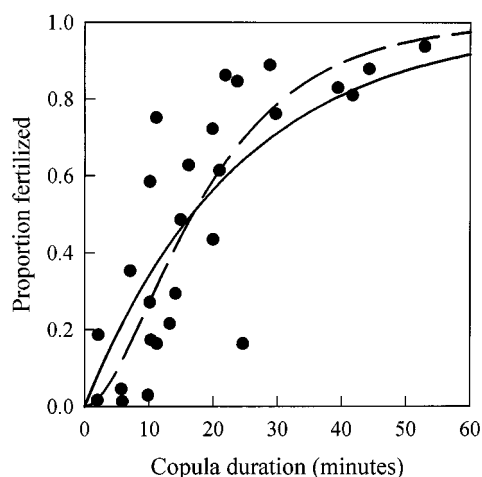


Fig. 3. Proportion of dungfly eggs fertilized versus copula duration. Redrawn from Parker and Simmons (1994, fig. 1b). Solid line: fitted curve used by Parker and Simmons, $y = 1 - \exp(-0.0416x)$ ($R^2 = 0.63$); dashed line: fitted curve $y = [1 - \exp(-0.0731x)]^2$ ($R^2 = 0.64$).

How solid is the evidence really that sperm displacement obeys a law of diminishing returns? One of the papers cited by Charnov concerns the work of Parker and Simmons (1994) on sperm displacement in dungflies. Parker and Simmons conclude on theoretical grounds that sperm displacement should follow a rule of the form $1 - \exp(-ax)$. A curve of this type is then fitted to the data. We have reproduced part of their figure 1b here in Fig. 3, where the proportion of eggs fertilized by a male is plotted against copula duration. Let us look at the data and refrain from the obvious critique that copula duration is not

necessarily an adequate measure of sperm production. Although a curve with diminishing returns explains a significant proportion of the variation, the data are also consistent with an S-shaped curve of the form $[1 - \exp(-ax)]^2$. For sufficiently small δ , such a curve leads to sperm-biased allocation, but not to a non-monotonic $r^*(\delta)$. We conclude that in insects the available evidence does not rule out the possibility that sperm displacement obeys an S-shaped rule. But, of course, what we really need is this kind of data for hermaphrodites.

NON-LINEAR RETURNS ON INVESTMENT IN EGGS

In Charnov's model, egg production was used as a measure of fitness through female function. In other words, $f(r)$ was taken to be a linear function of $1 - r$, the proportion of resources invested in female function. This is certainly the right place to start, but the assumption may be rather unrealistic. For example, it will almost invariably be the case that the marginal increase of egg survival with investment levels off with sufficiently high investment. Alternatively, given a fixed level of investment per egg, egg survival might decrease with the number of eggs, because, say, the local oxygen concentration tends to drop as the number of eggs increases. What are the consequences of such non-linearities for optimal sex allocation? Sometimes considerable and sometimes none at all, depending on the specific mechanistic nature of the trade-off between number and quality of eggs, as we shall see.

As before, suppose every individual has R units of resource and allocates a fraction $1 - r$ to eggs. But let us now be more specific and further suppose that the $(1 - r)R$ units of resource are used to produce a clutch of c eggs. Assuming each egg receives the same investment, this implies that each egg receives $I = (1 - r)R/c$ units of resource. In general, egg survival $s_0 = s_0(I, c)$ will be a function of investment $I = I(r)$ and clutch size c . Taking recruitment (clutch size $\times$ egg survival) as a measure of female fitness, we now have:

$$f(r) = cs_0(I(r), c) \quad (8)$$

Hence:

$$f'(r^*) = -R \frac{\partial s_0}{\partial I} \Big|_{I=I^*} \quad (9)$$

where $I^* = I(r^*)$. If egg survival is proportional to investment – that is, $s_0(I(r), c) = a(c)I(r)$ – we get

$$\frac{f'(r^*)}{f(r^*)} = \frac{-1}{1 - r^*} \quad (10)$$

as in Charnov's model. Hence, in this special case, the previous results still apply. In general, however, optimal sex allocation will reflect specific properties of the egg survival function s_0 . Basically, anything is possible, and very specific information on s_0 is required to derive the properties of r^* .

OPTIMIZATION OF CLUTCH SIZE AND SEX ALLOCATION

Fortunately, there is a partial way out of the situation sketched above if we are willing to make two extra assumptions. First, we have to assume that egg survival depends only on the

amount of resources invested per egg. That is, the *number* of eggs in the clutch has no effect *per se* on egg survival. In other words, $s_0(I, c) = s_0(I)$. Second, we assume that not only sex allocation r but also clutch size c is under genetic control and optimized in the course of evolution. The latter assumption has, as a consequence, that female fitness is now viewed as a function of two parameters:

$$f(r, c) = cs_0(I), \quad \text{where } I(r, c) = \frac{(1-r)R}{c} \quad (11)$$

By maximizing f with respect to c , we obtain the condition:

$$\left. \frac{\partial f}{\partial c} \right|_{(r, c) = (r^*, c^*)} = s_0(I^*) - \frac{(1-r^*)R}{c^*} s_0'(I^*) = 0 \quad (12)$$

As a consequence (see equation 9):

$$\left. \frac{\partial f}{\partial r} \right|_* = -R s_0'(I^*) = -\frac{c^* s_0(I^*)}{1-r^*} = -\frac{f(r^*, c^*)}{1-r^*} \quad (13)$$

which yields:

$$\frac{f'(r^*, c^*)}{f(r^*, c^*)} = \frac{-1}{1-r^*} \quad (14)$$

as in Charnov's model. In other words, we recover the original ESS condition (4). All previous results still apply and are truly invariant with respect to the details of the egg survival function s_0 , so long as s_0 only depends on the per-egg investment I . Hence, we have shown:

Result 3. *If the survival $s_0(I)$ of an egg only depends on the amount of resources invested in it (and not on clutch size), then the optimal allocation to eggs versus sperm is independent of the shape of $s_0(I)$, provided that clutch size is optimized at equilibrium.*

The message to extract from this is two-fold. First, by maximizing fitness with respect to an additional variable, we make the model more complicated at first sight. But what we actually see is that the result is much simpler. The same principle applies to a much wider range of resource allocation models (I. Pen and F.J. Weissing, in prep.). Second, we have added more biology to the model by partitioning the allocation process into multiple allocation components. This yields a better intuition of when it is biologically reasonable to assume that returns on investment are linear. The linearity assumption leads to the right conclusions (but for the wrong reasons) whenever the survival of an individual offspring does not depend on the number of offspring produced by the parent at the same time.

By a similar argument – that is, by partitioning sperm production into the number of spermatozoa and the investment per individual spermatozoon – it can be demonstrated that the shape of the sperm displacement rule ϕ has no effect on optimal allocation to sperm versus eggs, provided the number of spermatozoa *per se* does not affect the

displacement probability. However, while the latter proviso may often be reasonable for eggs, it seems very unlikely that the sperm count has no effect on the probability of outcompeting the predecessor's sperm.

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APPENDIX

Here, we calculate optimal allocation to eggs versus sperm when the ejaculate volume is small compared with the sperm storage volume. The starting point is the ESS condition (4), so these results need not hold true if the returns on investment in eggs are non-linear (but see Result 3).

Proposition. *If δ is small – that is, if the maximum ejaculate volume is much smaller than the storage capacity – the optimal sex allocation is determined by $\phi'(0)$, the first derivative of the sperm displacement rule ϕ at zero:*

- (a) *If $0 < \phi'(0) < \infty$, the optimal sex allocation tends to equal allocation as δ goes to zero; that is, $r^*(\delta) \rightarrow \frac{1}{2}$ as $\delta \rightarrow 0$.*
- (b) *If $\phi'(0) = 0$, the optimal sex allocation becomes male-biased as δ tends to zero. In fact, $r^*(0)$ can have any value between $\frac{1}{2}$ and 1.*

Proof. (a) Expanding numerator and denominator of the quotient in the right-hand side of (4) around $\delta = 0$, and cancelling higher-order terms, we get:

$$r^* = 1 - \frac{r^* \phi'(r^* \delta)}{\phi'(r^* \delta) + r^* \delta \phi''(r^* \delta)} \rightarrow 1 - r^* \quad \text{as} \quad \delta \rightarrow 0 \quad (15)$$

Solving for r^* yields $r^*(0) = \frac{1}{2}$.

(b) Take any sperm displacement function ψ with $0 < \psi'(0) < \infty$. Then for any $a > 0$, the function $\phi(x) = \psi(x^a)$ is also a candidate for a sperm displacement function: $\phi(0) = 0$, $\lim_{x \rightarrow \infty} \phi(x) = 1$ and $\phi' \geq 0$. However, since $\phi'(x) = ax^{a-1}\psi'(x^a)$, $\phi'(0) = 0$ if $a > 1$. Taking ϕ as the sperm displacement function, we obtain an expression analogous to (15):

$$r^* = 1 - \frac{r^* \psi'(r^* \delta)}{a \psi'(r^* \delta) + \delta a (r^* \delta)^{a-1} \psi''(r^* \delta)} \rightarrow 1 - \frac{r^*}{a} \quad \text{as} \quad \delta \rightarrow 0 \quad (16)$$

This implies $r^*(0) = a/(1+a)$. For $a > 1$, $r^*(0) > \frac{1}{2}$. It can be shown that any smooth function ϕ whose first derivative has a finite zero ($\phi'(0) = 0$) in zero can be represented in the manner indicated above. ■