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Body size and sex allocation in simultaneously hermaphroditic animals

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Sex allocation theory predicts that hermaphrodites optimally divide resources between male and female function, and this strategy may vary with a wide range of individual and population traits. We present a model of reproductive strategies for simultaneously hermaphroditic animals that incorporates multiple sex allocation tactics depending on the traits of an individual, its current mate, and the population at large. We examined the effect of resource variation on sex allocation in a sperm-storing population with two body-size classes. We found that an individual's sex allocation depends on its own size relative to its mate; when stored sperm is displaced exponentially, small animals (with fewer resources) invest a greater proportion of resources in male function than do large animals, and animals of either size invest more in male function when mating with a large mate than with a small mate. Optimal sex allocation depends on the size distribution in the population, the disparity of resources between size classes, the cost of filling a sperm storage organ, and the shape of the sperm displacement function. A function with S-shaped returns to sperm transfer results in a contrary finding: large animals invest more resources in male function than small animals when the cost of filling a sperm storage organ is high. Under many conditions, pronounced sex allocation differences between individuals result in similar proportions of sperm displaced and paternity gained. Thus, variation in individual traits within a population leads to multiple sex-allocation strategies that can produce equal outcomes in the game of sperm competition. *Key words:* body size, mating strategies, resources, sex allocation, simultaneous hermaphrodites, sperm competition. *[Behav Ecol 13:419–426 (2002)]*

Optimal partitioning of limited resources among life-history components is a fundamental determinant of lifetime reproductive success and may require an assessment of internal and environmental conditions (Charlesworth, 1980; Maynard Smith, 1982; Stearns, 1976). For simultaneous hermaphrodites, the division of reproductive resources into male and female function is an important strategy for optimizing fitness (Charnov, 1982). To partition resources efficiently, simultaneous hermaphrodites should adjust the number of sperm transferred and eggs produced depending on relative traits of the sperm donor and sperm recipient. A few empirical studies have shown that hermaphrodites do flexibly adjust mating strategies depending on relative behaviors or traits of the current mate (DeWitt, 1996; Peters and Michiels, 1996; Tomiyama, 1996; Vreys and Michiels, 1998; Yusa, 1996). Recent models of sex allocation have begun to elucidate the theoretical basis for hermaphroditic mating strategies (e.g., Charnov, 1996; Greeff and Michiels, 1999; Pen and Weissing, 1999; Petersen and Fischer, 1996). The present study builds on previous models and is the first to examine how individual variation in a trait, reproductive resource, affects sex allocation in sperm-storing hermaphrodites.

Simultaneous hermaphroditism is widespread throughout the animal kingdom and is the primary mode of reproduction among several invertebrate groups including flatworms, arrow worms, sea slugs, land snails, barnacles, earthworms, and leeches (Ghiselin, 1969; Michiels, 1998). Many simultaneous hermaphrodites have internal fertilization and long-term sperm storage in an organ that can hold a limited amount of sperm (Baur, 1998; Michiels, 1998). Therefore, they can evolve sperm competition strategies similar to those studied in dioecious species (Baur, 1998; Charnov, 1996; Michiels, 1998). Assuming a trade-off between resources (or energy) invested in sperm and eggs, any amount of resource devoted to sperm competition reduces that available for female function. Hence, there should be an optimal strategy for reproductive investment that is a product of the combined forces of sex allocation and sperm competition (Charnov, 1996). An individual's optimal strategy is likely to depend on the total amount of reproductive resources available to it and how that compares to the resources of potential mates.

In an earlier model, Charnov (1996) provided the first predictions of sex allocation for sperm-storing simultaneous hermaphrodites that mate multiply. When there are diminishing returns to sperm transfer in species with limited sperm-holding capacity, less than half of the reproductive resources for one mating event should be invested in male function. An increase in the reproductive resources available to individuals, an increase in the efficiency of converting resources into sperm, or a decrease in the size of the sperm storage organ all result in greater potential to displace sperm, which in turn leads to selection for reduced investment in male function in a population. Therefore, the sex allocation strategy in a given population is highly dependent on the average amount of resource available for reproduction relative to the average sperm-holding capacity (Charnov, 1996).

Individual variation in traits and circumstances may lead to the adoption of diverse strategies within populations rather than a single common strategy. Actual mating strategies do vary between individuals within populations (e.g., Angeloni and Bradbury, 1999; DeWitt, 1996; Otsuka et al., 1980; Petersen, 1995; Petersen and Fischer, 1996; Schärer et al., 2001; St.

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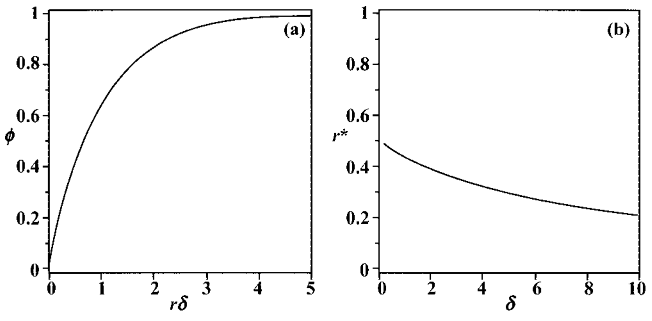

Figure 1
(a) Exponential sperm displacement used by Charnov (1996) and in this model, with diminishing fitness returns to sperm transfer [$\phi(x) = 1 - \exp(-x)$], and (b) the resulting optimal sex allocation strategy for a population without body size variation.

Mary, 1994; Tomiyama, 1996; van Duivenboden and ter Maat, 1985; Yusa, 1996), and this variation is not currently explained by models that predict a single population strategy. In this study we considered the importance of resource variation within a population and its effect on individual sex allocation. In natural populations individual resources can vary with body size. Many of the invertebrate hermaphrodites listed above exhibit indeterminate growth and/or asynchronous breeding or settlement. This creates natural populations of sexually mature individuals with considerable heterogeneity in body size (e.g., Angeloni et al., 1999; Audesirk, 1979; Carefoot, 1987; Crozier, 1918; Trowbridge, 1993; Vreys and Michiels, 1997). Body size affects sex allocation of sequential hermaphrodites through the timing of sex change (Ghiselin, 1969; Warner, 1975), and there is growing evidence that body size affects reproductive strategies of simultaneous hermaphrodites (e.g., Angeloni and Bradbury, 1999; Charnov, 1987; Crozier, 1918; DeWitt, 1996; Otsuka et al., 1980; Peters and Michiels, 1996; Petersen, 1995; Petersen and Fischer, 1996; Schärer et al., 2001; St. Mary, 1994; Tomiyama, 1996; Vreys and Michiels, 1997; Yusa, 1996). Body size can reflect an individual's total resource level, which is likely to affect two key determinants of sex allocation: the energy available for gamete production and the energy put into the construction of the sperm storage organ, and thus the number of sperm it can hold. Because both of these factors are likely to vary within populations and increase with body size, there is a clear need to demonstrate the effects of size variation on sex allocation strategies in sperm-storing simultaneous hermaphrodites. We offer a model of a population of individuals with two resource levels which, for simplicity, we will refer to as size classes (small and large) as a first step toward understanding the effect of within-population variation on sex allocation.

Adding body size to Charnov's model

Charnov's (1996) model describes a population where R units of resource are available to each individual for reproduction per mating event, and r is the proportion of R allocated to sperm production, leaving $(1 - r)$ for egg production. The constant c converts resource into sperm number so that the resources allocated to male function, rR, are used to produce and transfer rRc sperm to a mate. As sperm flows into the sperm stores, a constant mixing and flushing of new and old sperm results in exponential sperm displacement (Parker and Simmons, 1994). Upon completion of sperm transfer, the donor's sperm now make up a proportion, $\phi = 1 - \exp(-r\delta)$, of the total number of sperm (μ) that can be stored (Figure 1a); $\delta = Rc/\mu$ and is the amount of sperm that can be produced (if all resource were invested in sperm) relative to the amount of sperm that can be stored.

For simplicity we retain many of the assumptions of Charnov's (1996) model: animals mate frequently at regular intervals with reciprocal insemination and follow each mating event with the production of eggs. A sperm donor fertilizes a proportion of those eggs based on the proportion of its own sperm within the storage organ; thus, we assume that there is no sperm layering or selective sperm use. The resources expended in one mating event in no way affect the amount of resource available for the next mating event. There is no mortality and there are no virgins. The assumption that we have not retained is that all animals are identical. Other studies have extended Charnov's (1996) model to explore the effects of different assumptions (see Discussion; Greeff and Michiels, 1999; Pen and Weissing, 1999).

In Charnov's (1996) model a rare mutant allocating $\hat{r}$ of its resources to sperm, in a population of individuals that allocate r to sperm, gains fitness through female function proportional to $(1 - \hat{r})R$. The mutant gains fitness through male function from the mate's first egg clutch and reduced paternity in subsequent clutches as other nonmutants displace the mutant's sperm. This male fitness is proportional to an infinite series, $(1 - r)(R)[\phi(\hat{r}R)]\{1 + [1 - \phi(rR)] + [1 - \phi(rR)]^2 + \ldots\}$ which sums to:

$$\frac{(1 - r)\cdot R\cdot \phi(\hat{r}R)}{\phi(rR)}.$$

Because the proportionality constant is the same for male and female function, total fitness gained by the mutant in one mating event is simply the addition of this equation to that for female function, $(1 - \hat{r})R$.

The evolutionarily stable allocation (r^*) was found by analytically solving for the strategy that maximizes fitness, preventing a rare mutant from invading the population with a different strategy (Maynard Smith, 1982); r^* decreased from 0.5 with an increase in the ratio of potential sperm production to the amount of sperm that can be stored ($\delta = cR/\mu$) (Charnov, 1996; Figure 1b).

We extend the model by allowing for two resource levels: R_L for large animals with more resources and R_S for small animals with fewer resources. Large animals occur at frequency P in the population, and small animals occur at frequency $(1 - P)$. We allow an individual to adjust its sex allocation depending on its own resources and those of its mate, so there are four sperm allocation strategies, one for each of the following possible situations: (1) a large animal mating with another large animal (r_{LL}); (2) a large animal mating with a small animal (r_{LS}); (3) a small animal mating with a large animal (r_{SL}); and (4) a small animal mating with another small animal (r_{SS}). There are then four corresponding sperm displacement values that are functions of the sperm allocation of the donor: $\phi(r_{LL})$, $\phi(r_{LS})$, $\phi(r_{SL})$, and $\phi(r_{SS})$. We first use an exponential sperm displacement function so that the proportion of sperm in a small recipient's organ displaced by a large donor is:

$$\phi_{LS} = 1 - \exp(-r_{LS}\cdot \delta_{LS})$$

where

$$\delta_{LS} = \frac{cR_L}{dR_S} = m\frac{R_L}{R_S}.$$

As before, the coefficient c converts resources into number of sperm produced. We have added coefficient d to convert resources into number of sperm stored, effectively allowing for variation in the size of the sperm storage organ. We combine c/d into one variable, m, which represents the conversion

Table 1
Combinations of population traits for which optimal strategies were calculated

R_L/R_S	P range	m range	Sperm stores vary with size?	ϕ function	Strategies vary with mate size?	See fig. no(s).
2	0.1–0.9	0.1–50	Yes	Exponential	Yes	2, 3
1.2	0.1–0.9	0.1–50	Yes	Exponential	Yes	—
5	0.1–0.9	0.1–50	Yes	Exponential	Yes	4
2	0.1–0.9	0.1–50	No	Exponential	Yes	5
2	0.1–0.9	0.1–50	Yes	S-shaped	Yes	7
2	0.1–0.9	0.1–50	Yes	Exponential	No	8

of resources to sperm production relative to sperm storage. For most of this study we have made the resource level of large animals twice the resource level of small animals ($R_L/R_S = 2$). In this case and when $m = 1$, a large animal putting all of its resources into sperm production and none into egg production could hypothetically produce enough sperm to fill a small mate's storage organ two times ($\delta_{LS} = mR_L/R_S = 2$), while a small animal could only produce enough sperm to fill half of a large mate's storage organ ($\delta_{SL} = mR_S/R_L = 0.5$). The variable m is essentially the number of times an individual could fill a sperm storage organ the size of its own if it were investing all of its resources in sperm. Thus, in a population where m is low, it is more costly to fill a sperm storage organ (in terms of resource expenditure) than in a population where m is high.

Fitness through female function of a large mutant that allocates $\hat{r}$ to sperm when mating with a small nonmutant is proportional to:

$$(1 - \hat{r}_{LS})\cdot R_L.$$

Fitness through male function of a large mutant mating with a small nonmutant depends on the number of eggs produced by its mate $[(1 - r_{SL})R_S]$ multiplied by the proportion of sperm the mutant displaces (ϕ_{LS}). We add to this function all of the paternity gained from eggs produced by the nonmutant after subsequent mating events which displace a fraction of the mutant donor's sperm. The paternity gained from those clutches depends on the strategy and size (large or small) of subsequent mates, when P is the probability of mating with a large animal, and $(1 - P)$ is the probability of mating with a small animal. Thus, fitness through male function of a large mutant from a mating event with a small non-mutant is proportional to:

$$\begin{aligned}
&\phi(\hat{r}_{LS})(1 - r_{SL})R_S && \text{\{Fitness from 1st clutch\}}\\
&\quad + P\{\phi(\hat{r}_{LS})(1 - r_{SL})R_S[1 - \phi(r_{LS})]\}\\
&\quad + (1 - P)\{\phi(\hat{r}_{LS})(1 - r_{SS})R_S[1 - \phi(r_{SS})]\} && \text{\{2nd clutch\}}\\
&\qquad + P\{\phi(\hat{r}_{LS})(1 - r_{SL})R_S[1 - \phi(r_{LS})]\}\\
&\qquad \times \{P[1 - \phi(r_{LS})] + (1 - P)[1 - \phi(r_{SS})]\}\\
&\qquad + (1 - P)\{\phi(\hat{r}_{LS})(1 - r_{SS})R_S[1 - \phi(r_{SS})]\}\\
&\qquad \times \{P[1 - \phi(r_{LS})] + (1 - P)[1 - \phi(r_{SS})]\} + \cdots . && \text{\{3rd\}}
\end{aligned}$$

This infinite series sums to

$$\phi(\hat{r}_{LS})R_S \times \left\{(1 - r_{SL}) + \frac{\{P(1 - r_{SL})[1 - \phi(r_{LS})] + (1 - P)(1 - r_{SS})[1 - \phi(r_{SS})]\}}{1 - \{P[1 - \phi(r_{LS})] + (1 - P)[1 - \phi(r_{SS})]\}}\right\}.$$

The mutant's total fitness from one mating event is the addition of this equation to that for female function. Although we only show the equations for a large animal mating with a small animal here, the other three scenarios result in equivalent equations with different subscripts.

Finding optimal sex allocation required solving for the four strategies that simultaneously maximized fitness equations. As the equations were too complex to solve analytically, we used numerical methods. We calculated optimal r^* values for hypothetical populations that varied in the following population parameters: the frequency of large animals ($P = 0.1$, 0.25, 0.5, 0.75, 0.9), the ratio of resources of a large animal to a small animal ($R_L/R_S = 1.2$, 2, 5), and the relative conversion of resources to sperm production over sperm storage ($m = 0.1$–50). Because the trajectories of the r^* values did not change significantly beyond $m = 20$, we only show the data up to that point. See Table 1 for all combinations of parameters explored.

For each set of parameters, we explored the range of possible strategies (from 0 to 1). We began by dividing the potential population and mutant r values into 10 increments and found the four mutant $\hat{r}$ values that provided maximum fitness for each combination of population r values. The set of mutant $\hat{r}$ values that were least deviant from corresponding population r values were then the four optimal sex allocation strategies for that iteration (r_{LL}^*, r_{LS}^*, r_{SL}^*, r_{SS}^*). For each subsequent iteration, the range explored for each r was reduced by half, centered around the r^* from the prior iteration, and divided into 10 increments. The four optimal strategies were calculated again, and this process was repeated until the r^* values were calculated to the nearest 0.005.

Results

The body sizes of an individual and its current mate affect its sex allocation. We found the highest optimal allocation to sperm in small animals mating with large animals (r_{SL}^*) and the lowest allocation to sperm in large animals mating with small animals (r_{LS}^*). Individuals paired with same-size mates invest more evenly in sperm versus eggs (r_{LL}^*, r_{SS}^*). Body size has the greatest effect on sex allocation when m is low; with an increasing m, sex allocation does vary with body size, but all four strategies begin to converge on a relatively low investment in sperm. For example, Figure 2a shows optimal strategies for populations of varying m values and a given size distribution ($R_L/R_S = 2$; $P = 0.5$). When a large and small animal mate with each other and $m \leq 2$, the small animal invests all of its resources in sperm and the large animal invests all of its resources in eggs. The strategies move away from those values as m increases (i.e., it pays for the small animal to also produce eggs and the large animal to inseminate the small animal; Figure 2a). When two small animals mate, the outcome is similar to that of Charnov's (1996) model with only one size class; they invest slightly less than 50% of re-

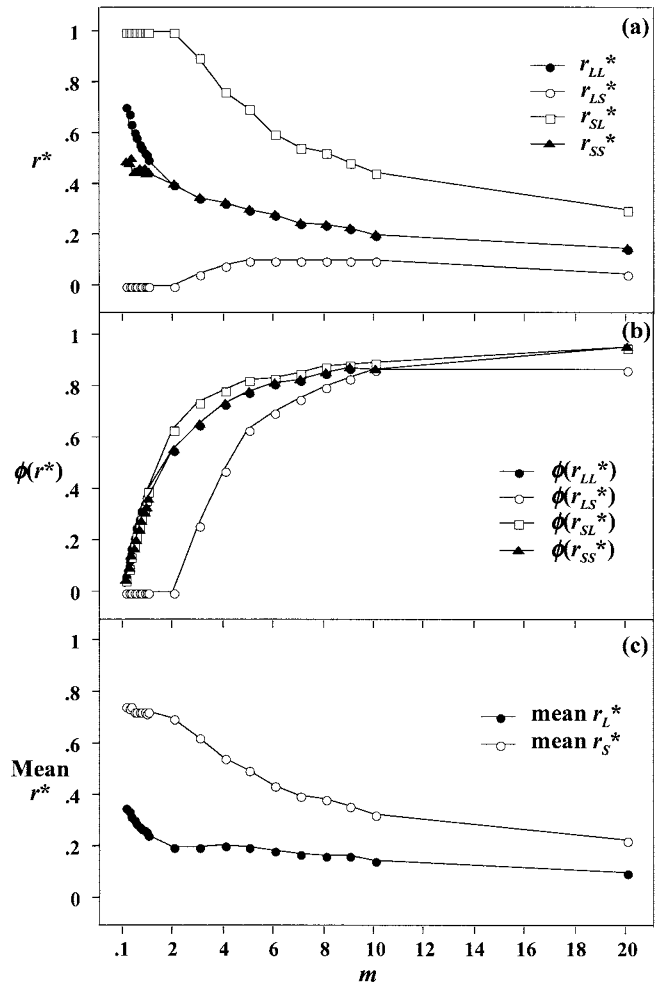

Figure 2
(a) Optimal sex allocation strategies, (b) sperm displaced or paternity achieved in the first egg clutch postmating, and (c) average allocation over an infinite number of matings across a range of sperm production efficiencies (m); [$\phi(x) = 1 - \exp(-x)$; $P = 0.5$; $R_L/R_S = 2$]. Mean r_L^* and r_S^* are respectively calculated as $Pr_{LL}^* + (1 - P)r_{LS}^*$ and $Pr_{SL}^* + (1 - P)r_{SS}^*$.

sources for the mating event in sperm when m is low, with reduced levels of male allocation as m increases (Figure 2a). When two large animals mate, they invest 70% of resources in sperm at a low m, with lower levels of male allocation as m increases. At $m \geq 2$, the strategy of two mating large animals is the same as two mating small animals. When m is high, the cost of filling a sperm storage organ is so low that no animal ever invests more than half of its reproductive resources in male function, and most resources are used for egg production (Figure 2a).

Although body size affects sex allocation strategies, it does not have a pronounced effect on the proportion of sperm displaced or the paternity achieved in the eggs produced by the mate (Figure 2b). Three of the scenarios (small mating with large, large mating with large, small mating with small) result in almost equal displacements that increase with m. A large animal mating with a small one transfers no sperm and thus achieves no fitness through male function when $m \leq 2$ (Figure 2b).

Over an infinite number of matings, large animals invest more energy in female function than in male function (Figure 2c). Small animals can have either male- or female-biased allocations depending on m, but they always invest a greater proportion of resources in sperm than large animals (Figure 2c).

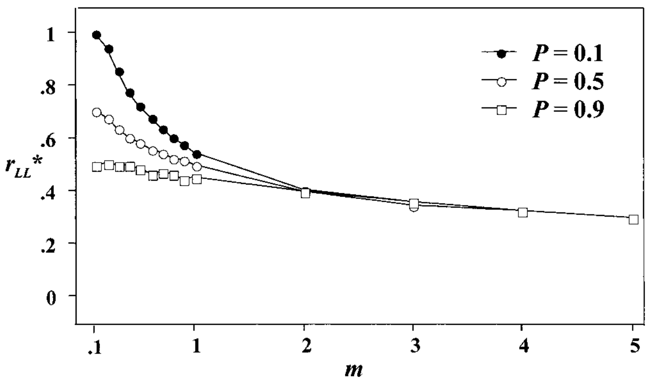

Figure 3
Allocation to sperm by large animals mating with each other when they occur at varying frequencies. Otherwise conditions are as in Figure 2.

Changing the proportion of large and small animals in the population from equality does not have a pronounced effect on strategies; three (r_{LS}^*, r_{SL}^*, r_{SS}^*) remain virtually unchanged. The only effect is on r_{LL}^* in a population with $m < 2$; when mating with each other, large animals invest more in sperm if they are rare than if they are common (Figure 3).

Increasing the disparity in resources ($R_L/R_S = 5$) results in a greater effect of body size on allocation strategies for many potential populations (Figure 4). When a large and small animal mate, the former produces only eggs and the latter produces only sperm over a wider range of potential population m values. A greater disparity in resources results in a slightly higher r_{LL}^* when $m < 6$. There is no effect on r_{SS}^*. Decreasing the resource disparity ($R_L/R_S = 1.2$) affects optimal strategies in the opposite direction: they converge more rapidly with increasing m.

Sperm stores remain constant with body size

Sperm storage organs may not always increase with body size in hermaphroditic populations. To consider a case in which sperm stores remain constant across both body sizes, we modified the model so that an increase in reproductive resources corresponds to an increase in potential sperm production, but

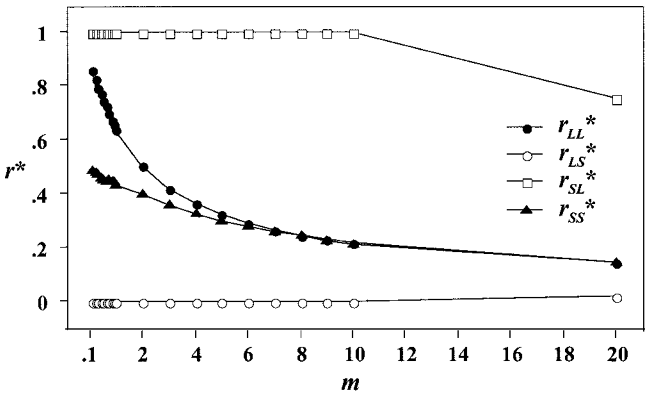

Figure 4
Optimal sex allocation strategies for a population with a greater resource disparity between large and small animals ($R_L/R_S = 5$). Otherwise conditions are as in Figure 2.

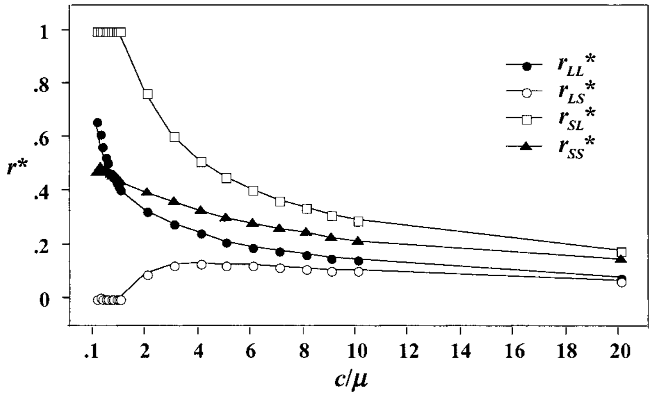

Figure 5
Optimal sex allocation strategies for a population with constant sperm stores (μ) across body sizes. Otherwise conditions are as in Figure 2.

not in sperm storage ability. For example, δ_{LS} (potential sperm production by a large animal divided by sperm stores of a small animal) is now represented by cR_L/μ and is equivalent to δ_{LL}.

Results
Body size still affects sex allocation when all individuals have equal sperm stores, and strategies are similar to those previously described for variable sperm storage. For example, Figure 5 shows strategies for populations of varying c/μ values and a given size distribution ($R_L/R_S = 2$; $P = 0.5$). When compared with Figure 2a, it is clear that the optimal allocations are similar at low m and low c/μ values (when it is more costly to fill a sperm storage organ). The only exception is for r_{LL}*, which is slightly reduced when sperm stores are constant. When c/μ increases, r_{LL}* drops below levels seen before and remains lower than the value for r_{SS}*; both r_{LS}* and r_{SL}* move away from their respective 0 and 1 values more rapidly and at lower c/μ values when sperm stores are constant. The proportion of sperm displaced, and therefore the proportion of paternity gained in the egg clutch produced by the mate, is greater when mating with a large animal (ϕ_{LL} and ϕ_{SL}) than with a small animal (ϕ_{LS} and ϕ_{SS}).

S-shaped sperm displacement

Some hermaphroditic populations may not have exponential sperm displacement, with fitness returns diminishing over the entire range of sperm production. There may be cases where sperm cooperate, or a minimal investment in sperm is needed before any fitness is gained, so that returns to sperm production increase initially (Pen and Weissing, 1999). To investigate this possibility, we modified the model by changing the sperm displacement function to one that is S-shaped, with initially increasing returns to sperm investment (following Pen and Weissing, 1999; Figure 6). When a large animal inseminates a small animal the proportion of sperm displaced now corresponds to

$$\phi_{LS} = [1 + \exp(-4r_{LS}\delta_{LS} + 6)]^{-1} - [1 + \exp(6)]^{-1}.$$

The form and terms (e.g., the use of the number 6) of this equation were chosen because they generate a sigmoid curve within the range of possible sperm displacement values.

Results
An S-shaped sperm displacement function complicates sex allocation strategies. For example, Figure 7a shows strategies for populations of varying m values and a given size distribution ($R_L/R_S = 2$; $P = 0.5$). At a low m, when a large and small animal mate, the roles are reversed from the case of exponential sperm displacement, with the large animal investing all of its reproductive resources in sperm and the small animal investing everything in eggs. If the cost of filling a sperm storage organ is reduced ($m > 2$), the roles revert to those previously described: The large animal invests only in eggs and the small animal invests only in sperm, but moving away from those values at $m > 5$. Two small animals should not inseminate each other unless $m > 1$ (Figure 7a). All four r* values have an intermediate peak with an increasing m before they ultimately decrease, similar to the shape of the allocation curve predicted with only one size class (Figure 6b; Pen and Weissing, 1999). Figure 7b shows the predicted average allocations for large and small animals over an infinite number of mating events.

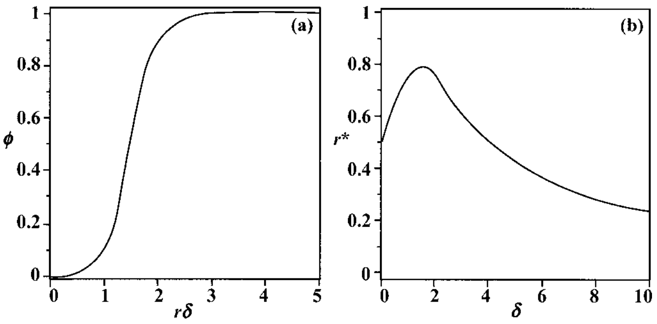

Figure 6
(a) S-shaped sperm displacement with increasing fitness returns to initial sperm transfer {$\phi(x) = [1 + \exp(-4x + 6)]^{-1} - [1 + \exp(6)]^{-1}$} and (b) the resulting optimal sex allocation strategy for a population without body size variation (from Pen and Weissing, 1999).

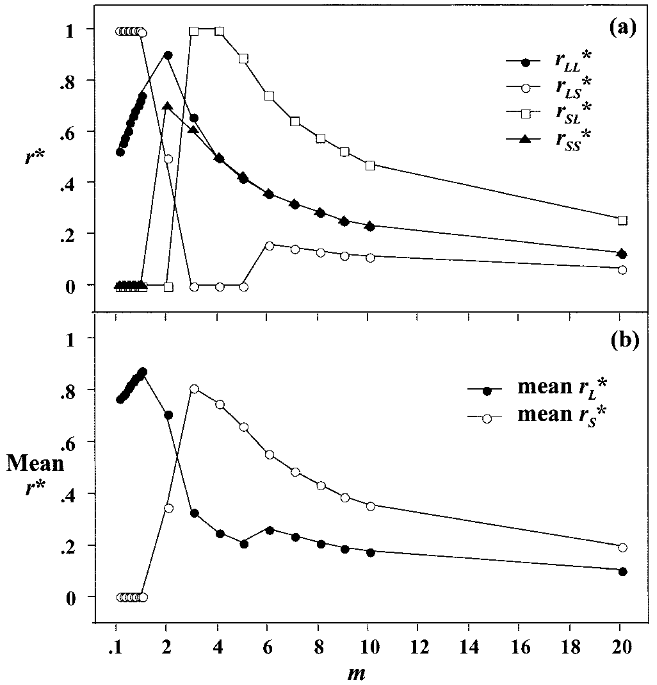

Figure 7
(a) Optimal sex allocation strategies and (b) average allocation over an infinite number of matings for a population with S-shaped sperm displacement ($P = 0.5$; $R_L/R_S = 2$).

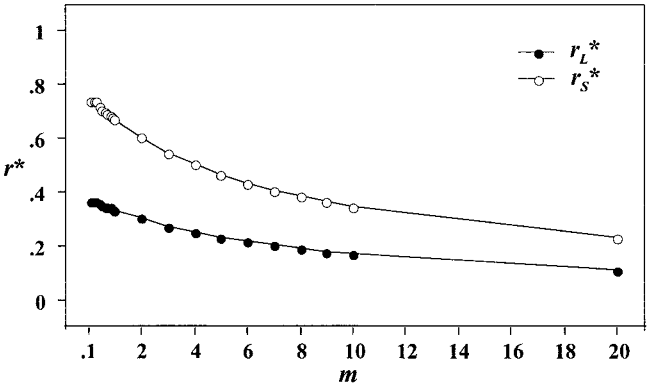

Figure 8

Optimal sex allocation strategies for a population with exponential sperm displacement ($P = 0.5$; $R_L/R_S = 2$) and for animals that lack the ability to flexibly shift sex allocation with mate size ($r_L* = r_{LL}* = r_{LS}*$; $r_S* = r_{SL}* = r_{SS}*$). Note the similarity between these results and those in Figure 2c.

Constant strategies for large and small animals regardless of mate size

Some hermaphrodites may not be capable of flexibly adjusting sex allocation strategies with each mating event. Instead of shifting allocation with the size of the current mate, an individual would continuously allocate resources in the same way dependent only on its body size and population parameters. To predict optimal strategies under these conditions, we modified the model so that only two strategies are possible, one for large animals ($r_L* = r_{LL}* = r_{LS}*$) and one for small animals ($r_S* = r_{SL}* = r_{SS}*$).

Results

In a population of individuals that are unable to adjust sperm and egg investment with the size of the current mate, the optimal strategies are similar to average strategies when allocation is flexible. For example, Figure 8 shows sex allocation for populations with varying m values, exponential sperm displacement, and a given size distribution ($R_L/R_S = 2$; $P = 0.5$). Note the similarities between Figure 8 and Figure 2c. Small animals have either male- or female-biased allocations depending on m. Large animals always invest more in eggs than in sperm and invest a greater proportion of resources in female function than do small animals. The proportion of sperm displaced varies with the size of the sperm recipient, not the size of the sperm donor. A greater proportion of sperm is displaced, and paternity is gained, when inseminating a small animal than a large animal.

DISCUSSION

Our model is the first to show that variation in individual traits can lead to a diversity of mating strategies within populations of sperm-storing simultaneous hermaphrodites. Previous models have predicted a single strategy for an entire population (Charnov, 1996; Greeff and Michiels, 1999; Leonard, 1990; Pen and Weissing, 1999), ignoring differences between individuals. The body size of an individual, the size of its current mate, and the size distribution of the population all influence its sex allocation strategy. Body size has its greatest effect on sex allocation when the resource disparity between size classes is high, when sperm stores vary with body size, and when filling a sperm storage organ is costly (i.e., m is low). The exact relationship between body size and sex allocation depends on the form of sperm displacement.

For species with exponential sperm displacement (where returns to sperm transfer diminish with increasing investment), our model predicts that large animals allocate more energy to female function than do small animals. If an individual can adjust its investment strategy with each mating event, it should increase male allocation when mating with a large animal as compared with its optimal level when mating with a small animal. Strategies are highly dependent on the cost (in terms of resource expenditure) of filling a sperm storage organ in the population. For example, if filling a sperm storage organ is costly, a small animal mating with a large animal should put all of its resources into displacing sperm; this is because the small animal never reaches the point on the sperm displacement curve where returns to investment in sperm are so diminished that it pays to invest in eggs. This strategy of investing nothing in eggs drives the large animal to invest nothing in sperm when mating with a small mate, as it is not worthwhile to inseminate a small mate that will not produce eggs after the mating event. With a reduced cost of filling a sperm storage organ, it eventually becomes profitable for a small animal to divert some energy to egg production when mating with a large animal and for a large animal to invest a minimal amount of resource to inseminate a small mate. In general, as the cost of filling a sperm storage organ is reduced, the optimal investment in sperm is also reduced. If the cost of filling a sperm storage organ is extremely low, sex allocation strategies become less dependent on body size, and all animals converge on low sperm investment because fewer resources are needed to approach 100% paternity.

Support for the prediction that large animals invest more in female function than small animals can be found in the few studies on sex allocation in sperm-storing simultaneous hermaphrodites (Angeloni and Bradbury, 1999; DeWitt, 1996; Otsuka et al., 1980; Yusa, 1996). These studies used the amount of time spent mating in each sexual role as the currency for sex allocation. Although difficult to measure, estimates of egg and sperm production would provide more accurate tests of the prediction that sex allocation varies with body size.

Our model suggests that reciprocal mating (where both members of a mating pair transfer sperm) should occur between animals of similar size, whereas unilateral mating events (where only one individual transfers sperm) are more likely between animals very different in size. However, when the cost of filling a sperm storage organ is reduced, reciprocal mating should be ubiquitous. Reciprocity is widespread in real hermaphroditic populations and has been suggested as a way of resolving conflict between two individuals who prefer to mate in the same sexual role (Fischer, 1988; Leonard, 1991; Michiels, 1998). Distinguishing between reciprocity due to a mutual willingness to transfer sperm (predicted by this model) and reciprocity due to conflict over mating roles has proven difficult empirically (Michiels, 1998). Many hermaphrodites also mate unilaterally (Leonard, 1991; Michiels, 1998), but predictions about the relationship between this trait and body size remain untested. Although our model with exponential sperm displacement predicts unilateral mating events between individuals of different sizes, this is not to be confused with the evolution of separate sexes; these animals also mate reciprocally with same-sized mates and thus are still hermaphrodites.

A population made up almost entirely of large animals or entirely of small animals approximates Charnov's (1996) model with only one size class; the strategy of the common type when mating with each other similarly decreases from 50% allocation with decreasing cost of filling a sperm storage organ. When large animals are rare, they invest greater amounts in sperm when they encounter each other. This can be explained by the high levels of sperm competition they face in the receptacle of a large animal; the competition is greater because the population is dominated by small animals that specialize in sperm production when mating with large animals.

A reduced resource disparity between large and small animals and a constant size of sperm stores both slightly reduce the effect of body size on sex allocation over a wide range of population conditions. However, the overall effect of body size is consistent, suggesting that our findings may be applicable to real populations with mating pairs that vary in size and resource disparity and with different allometric relationships between body size and internal organs. Constant sperm stores result in a reduced investment in sperm between mating large animals because they are less difficult to fill up (more like small animals).

The sperm displacement function can affect sex allocation dramatically. In a population with an S-shaped displacement curve, returns to sperm transfer are initially increasing and then eventually diminishing as the sperm storage organ is filled. This kind of displacement is likely to occur in species that have sperm cooperation or that require an initial minimum investment in sperm or semen before any paternity is gained (Pen and Weissing, 1999). In this case small animals are females, investing only in eggs when it is difficult to transfer enough sperm to take advantage of the steepest segment of the fitness-gain curve. Conversely, large animals (which are capable of producing the amount of sperm needed for optimal returns to sperm transfer) should invest everything in male function when mating with small animals that are only investing in female function. Determining the sperm displacement function of a hermaphrodite is crucial for predicting sex allocation. This function has not been measured in real hermaphrodites, but could be accomplished in controlled experiments to estimate paternity after varying amounts of sperm transfer. At this time it is unclear whether an S-shaped function, an exponential function, or some other function best approximates sperm displacement in real hermaphrodites.

Our model shows that an individual's sex allocation strategy can depend on its own size as well as the size of its mate. Because an individual's own size relative to the population may be constant over a period of time that spans several mating events, sex allocation traits that are less flexible (e.g., structural and gonadal allocation to male vs. female function) should reflect its average optimal allocation [for large animals: $Pr_{LL}^* + (1 - P)r_{LS}^*$; for small animals: $Pr_{SL}^* + (1 - P)r_{SS}^*$]. The sizes of an individual's mates over that same time interval are likely to vary; hence, more flexible sex allocation traits (e.g., sperm and egg production for a particular mating event) should reflect the relative sizes of both the individual and its current mate (r_{LL}^*, r_{LS}^*, r_{SL}^*, r_{SS}^*). In species that are not capable of estimating the body size of a mate or do not have the flexibility to adjust egg and sperm production for each mating event, an individual might instead invest in a constant sex allocation strategy dependent only on its own body size (r_L^*, r_S^*). This strategy is similar to the average allocation over several mating events of an animal that is capable of making adjustments. It remains to be determined whether hermaphroditic animals are capable of making size assessments when mating. Courtship periods that involve tactile, visual, or chemical contact may facilitate this kind of size assessment (e.g., Vreys and Michiels, 1997), and if there is a mechanism available, selection should bring it to fixation.

Although this model predicts that sex allocation varies dramatically with body size, under many conditions this leads to sperm displacement and paternity patterns that are invariant with body size. Individuals that begin with different total resource levels adjust the proportion of those resources invested in sperm, evening out sperm competition abilities. This prediction may prove important to biologists currently working on measuring sperm precedence patterns in hermaphrodites, particularly those who have not found an effect of body size on paternity (Baur, 1994).

A useful extension of this model would allow for individual strategies to change dynamically over time as total resource levels change, either due to growth or resource expenditure in previous mating events. Two other studies have modeled different extensions of Charnov's (1996) model. As confirmed in this study, Pen and Weissing (1999) showed that alternate sperm displacement functions have dramatic effects on sex allocation. They also found that an effect of clutch size on offspring survival results in any number of different outcomes depending on the shape of the egg survival function. A study by Greeff and Michiels (1999) demonstrated that reducing the number of lifetime matings from infinity reduces male allocation, while sperm digestion increases male allocation and can lead to conditional reciprocity with higher levels of sperm donation serving as a nuptial gift. Ideally, a complex model would combine all of these extensions of Charnov's original formulation to predict sex allocation in a population with a continuous body size distribution.

Many studies have shown that sex allocation depends on body size and/or mating group size across a range of animal and plant taxa (Angeloni and Bradbury, 1999; Charnov, 1980, 1982, 1987; DeWitt, 1996; Klinkhamer et al., 1997; Otsuka et al., 1980; Petersen and Fischer, 1996; Raimondi and Martin, 1991; Schärer et al., 2001; Trouvé et al., 1999; Yusa, 1996). Sex allocation shifts toward female function with an increase in body size in organisms very different from the model we describe: barnacles that lack long-term sperm storage (Charnov, 1980, 1987), fish that lack internal fertilization (Petersen and Fischer, 1996), and plants (Klinkhamer et al., 1997). These common trends clearly result from different specific mechanisms not included in this model, yet all are similar in that they can be explained by the shape of fitness gain curves (Charnov, 1982). For example, in animal-pollinated plants, male gain curves may decelerate due to pollinator saturation of pollen or high levels of local mate competition and geitonogamy (pollination from a flower on the same plant), resulting in increased allocation to female function with size and resource level (Klinkhamer et al., 1997). In contrast, increasing fitness returns to male investment in wind-pollinated plants contributes to greater male allocation with size (Klinkhamer et al., 1997). Our findings thus add to a growing understanding of the importance of fitness-gain curves in determining sex allocation of simultaneous hermaphrodites (Charnov, 1982).

Similarities between dioecious species, sequential hermaphrodites, and simultaneous hermaphrodites are proving greater than differences in many ways. Our study emphasizes the importance of fitness-gain curves for simultaneous hermaphrodites, and they play an equally important role in the timing of sex change in sequential hermaphrodites and offspring sex ratio of dioecious animals (Charnov, 1982). Body size affects sex allocation of both simultaneous and sequential hermaphrodites (Ghiselin, 1969; Warner, 1975) and is an important factor in the sexually selected mating strategies of dioecious animals (Andersson, 1994). Although sexual selection research has focused on dioecious species, hermaphrodites face similar selection pressures, and both groups must optimally allocate resources to sperm competition (Charnov, 1996; Galvani and Johnstone, 1998; Michiels, 1998). Future work on hermaphrodites will likely reveal a similar diversity of sexually selected strategies to those of animals with separate sexes, and perhaps insight can be gained by considering the parallels between these groups.

There have been several calls for additional work on hermaphroditic mating systems (Jarne and Charlesworth, 1996; Leonard, 1991; Michiels, 1998), and despite growing research in this field, there are still few empirical studies of sex allocation in sperm-storing hermaphrodites and no measures of the parameters that go into the models. Our model emphasizes the importance of measuring body size and resource distributions within populations, the shape of sperm displacement curves, and the energetic cost of filling sperm-storage organs. Although measuring sperm displacement and its costs present a challenge, these estimates are needed to accurately predict sex allocation strategies within populations.

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