



## Gender contests in a simultaneous hermaphrodite snail: a size-advantage model for behaviour

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**Abstract.** Adaptive gender expression in simultaneous hermaphrodites will reflect the relative costs and benefits of each sexual function. The net gain through either or both functions may vary with body size. Shell length measurements of *Physa gyrina* and *P. heterostropha* in the laboratory and *P. heterostropha* in the field revealed that successful mating generally involved smaller sperm donors and larger recipients. In contrast, attempts by larger snails to donate sperm were contested by smaller snails. These data suggest substantial plasticity in gender expression in accordance with a game-theoretic extension of Ghiselin's (1969, *Q. Rev. Biol.*, **44**, 189–208, 1974; *The Economy of Nature and the Evolution of Sex*) size-advantage model. Specifically, the larger of two interacting snails is more fecund, so the smaller snail has more to gain by donating sperm. This asymmetry creates a contest in which the smaller snail can afford to escalate the contest more and still profit, so long as escalation costs are not greater for the smaller snail. In the present study, the usual form of contest escalation was a visually obvious shell-swinging display, which attracts predators. Thus, the smaller of two contestants can use the risk of predation as a weapon in contest escalations (i.e. a game of chicken), rather than using a purely physical contest that might favour the larger contestant.

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Ghiselin's (1969) size-advantage model explains size-based sex allocation in hermaphrodites. Although the model was primarily derived to explain sex change in sequential hermaphrodites, many theoretical discussions suggested its potential use to explain behavioural strategies in simultaneous hermaphrodites (Ghiselin 1969, 1974; Charnov et al. 1976; Charnov 1979, 1982, 1993). The size-advantage model is based on size asymmetries in potential fitness gains through male and female function. If increased size differentially improves efficiency in one sexual function, then larger individuals should specialize as that sex, either through physiological changes in the allocation to male and female tissues (e.g. sex change) or by behavioural shifts.

The form of facultative sexuality that evolves largely depends on the nature of the environment (i.e. the grain of the environment; sensu Levins

1968). If the relative values for reproducing as male and female change only occasionally or gradually, physiological allocation shifts are expected to evolve to mitigate the payoff fluctuations (Charnov 1979). For hermaphrodites that undergo allocation shifts, the size-advantage model has been successfully used to predict both the size at which sex change occurs (reviewed by Warner 1988), and the intermediate levels of allocation found empirically (e.g. St Mary 1994). However, the value of the sexual functions may change frequently and unpredictably in many hermaphrodite taxa. In these cases, we can expect selection for pure simultaneous hermaphroditism and behavioural gender choice. The term gender is used to indicate the behavioural nature of sexual function in a simultaneous hermaphrodite, because such organisms cannot be labelled as either sex.

The physiological and behavioural aspects of sexuality for hermaphrodites may be correlated and difficult to separate. For example, in the hermaphroditic goby *Lythrypnus dalli*, most individuals allocate to both egg and sperm

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production, but only those individuals with 100% allocation to male reproduce as males (St Mary 1994). In contrast, the physiological and behavioural aspects of sexuality will be uncorrelated in some hermaphrodite taxa. For example, sperm-storing species do not need to behave as female (i.e. receive sperm) continually to physiologically reproduce as such. In these organisms, the utility of the size-advantage model is in calculating the payoffs for donating and receiving sperm.

Despite the potential utility of the size-advantage model for making predictions about mating behaviour, and despite the ubiquity of simultaneous hermaphroditism, apparently no studies have explored how a simultaneous hermaphrodite elects behavioural gender roles apart from allocation issues. Wethington & Dillon (1993) suggested that the freshwater pulmonate snail *Physa* (= *Physella*) is a model organism to study gender decisions because of its physiological and behavioural plasticity in reproduction. The physid capacity to store sperm (Wethington & Dillon 1991) also makes this genus an ideal test case. Furthermore, DeWitt (1954a) remarked that *P. gyrina* copulations often involved relatively small sperm donors and large recipients, indicating that size may influence gender expression. In the present study, I observed mating interactions between physid snails to see whether size influenced gender expression in accordance with Ghiselin's (1969, 1974) size-advantage model.

## METHODS

### Study Organism and Behavioural Definitions

The reproductive physiology of pulmonate snails was reviewed by Geraerts & Joosse (1984). Physid pulmonates may be mildly protandric (Wethington & Dillon 1993), suffer selfing depression (DeWitt 1954b) and can store sperm for at least 60 days (Wethington & Dillon 1991). The ability of physid snails to fertilize eggs does not increase with size, whereas female fecundity does (DeWitt 1991). Physid snails generally copulate unilaterally with only rare occasions of role swapping (e.g. DeWitt 1954a, 1991).

The general mating behaviour of *Physa* was described by DeWitt (1991). Briefly, a sperm donor mounts a potential sperm recipient and attempts insemination. The potential sperm recipient may comply (i.e. successful copulation,

uncontested mating) or may contest the copulation by performing any of several mate-rejection behaviour patterns. The most dramatic and unambiguous mate-rejection behaviour patterns are shell swinging and genital biting, with shell swinging being the most common. Shell swinging is characterized by several vigorous swings of the intended sperm recipient's shell to the left and right about the stationary foot. The arc of the swings often exceeds 180°. Despite the vigour of the shell swinging behaviour, I have never observed the forcible detachment of a would-be sperm donor from the intended recipient's shell. Regardless, the would-be sperm donor generally dismounts following shell swinging, although more than one bout of swinging may be necessary. The other forms of mate rejection described, i.e. genital biting, increasing distance to the gonopore by body positioning and shell jerking, are less frequent and more difficult to score (DeWitt 1991), and I did not include these types of behaviour in the following assays.

### Experimental Procedure

The experimental design was intended to detect size-based patterns inherent in successful and agonistic mating encounters in physid snails. First, I observed seven samples of *P. gyrina* from Massachusetts using a laboratory assay to document the basic mating patterns thoroughly. Second, I observed two samples of *P. heterostropha* from New York using the same laboratory assay to see whether trends were generalizable to another species of physid snail. Third, I observed the behaviour of *P. heterostropha* in the field at another New York site to see whether results from the laboratory reflected the behaviour of snails in the wild.

For *P. gyrina*, I collected seven samples of 300–500 snails each from the litter in a densely populated region of the Fenway drainage in Boston, Massachusetts (site description in DeWitt 1991). Snails were collected between 1200 and 1600 hours, brought to the laboratory, and maintained in a filtered 38-litre aquarium with 20 litres of water (10 litres from the collection site and 10 litres spring water). Population densities in the experimental aquaria were similar to the highest densities observed during collection (approximately one snail per 3 cm<sup>2</sup>). Snails were

kept at 20°C near a natural light source and fed canned vegetables.

Approximately 18 h after collection, I observed interacting snail pairs using focal pair sampling until the interaction could be categorized as a copulation (van Duivenboden & ter Maat 1988). I removed snails involved in successful copulations and measured from the shell apex to the most distal portion of the shell margin using calipers (to the nearest 0.05 mm). For the initial sample, I collected data until I observed 74 copulations. Because the size asymmetry was highly significant, I only conducted observations until I observed 12 copulations in each of the six subsequent replicates with *P. gyrina*. After the first three samples, I defined four types of mate rejection (DeWitt 1991; see also Wethington & Dillon, in press). Thereafter, I also measured the frequency of contested copulatory attempts by shell swinging, the size of snails involved and the size of the remaining snails comprising the samples before returning the snails to the collection site.

To test whether I could generalize results from the Massachusetts population of *P. gyrina* to other physid populations, I conducted two replicates of the laboratory study with *P. heterostropha* from Finch Hollow Creek in Broome County, New York. Methods were the same as those given above, except that I placed the snails in 100% spring water and fed them spirulina flakes (Jennings et al. 1970).

To confirm the size-related mating patterns in the field, I observed *P. heterostropha* in a beaver pond on Binghamton University's Nature Preserve. I focal-sampled snail pairs ( $N=18$  pairs) from the bank or from fallen logs as they interacted in shallow water. Successfully copulating snails and those involved in shell-swinging mate rejection were removed, measured for shell length and released away from the sample site.

### Data Analysis

I analysed the body sizes of sperm donors and recipients by regression to see whether predictable size-ratio occurred over all size classes, and by paired *t*-test to test for asymmetries in body size between sperm donors and recipients. When replicate samples of the paired data occurred, I partitioned the variance using a MANOVA (Wilkinson et al. 1992), which tested for a between-pair effect (i.e. did donor and recipient

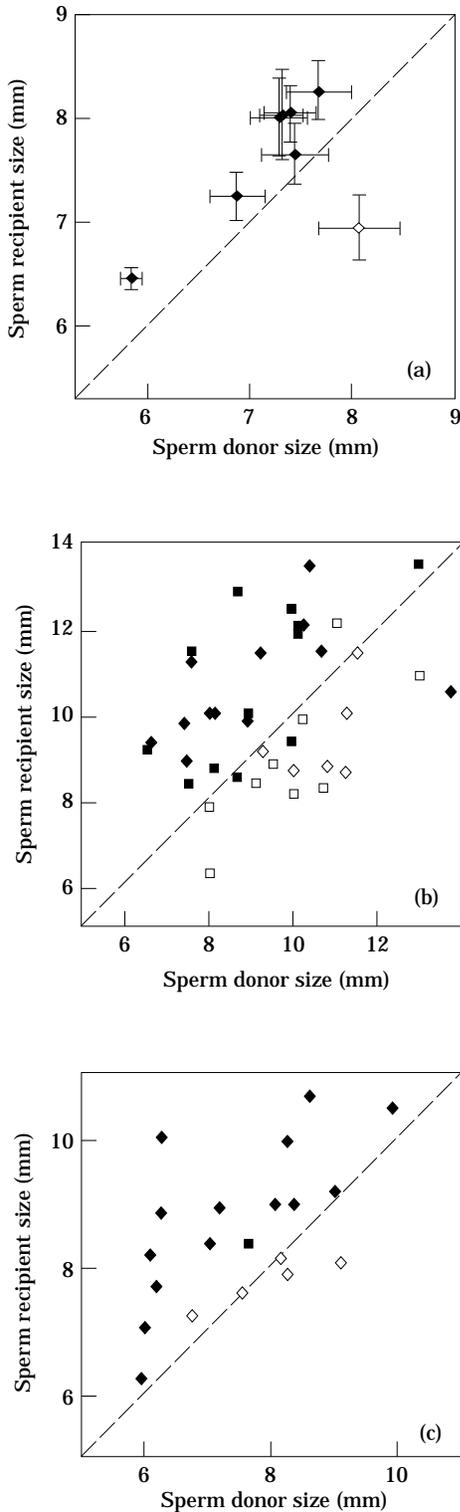
sizes vary by replicate?) and two within-pair effects (i.e. was the size asymmetry within pairs significant, and did that relationship vary by replicate?).

## RESULTS

### Uncontested Copulatory Attempts

Generally, uncontested copulations involved relatively small sperm donors copulating with larger sperm recipients (Fig. 1). Data analysis is summarized in Table I. For all experiments, the size asymmetry within pairs (donors smaller than recipients) was highly significant. The only other significant effect was the replicate main effect for *P. gyrina* in the laboratory study, which occurred because the seven samples of *P. gyrina* were collected in succession as the cohort grew in the field (personal observation for the first three samples; for the four samples that I measured,  $F_{3,1100}=14.21$ ,  $P<0.0001$ ). I performed the two replicates with *P. heterostropha* within 6 days of each other.

The size variation in replicate composition for *P. gyrina* facilitated a test of whether gender was determined by absolute size, or by size relative to other group members. This issue is important because it helps to distinguish between physiological and behavioural causes of the assortative mating. If gender were restricted to fixed size ranges, the size distribution of snails performing as males or females would be fixed, and an interaction would be evident between the size-asymmetry and replicate variables in this model. I interpret the lack of an interaction as evidence that there is no prescribed size range for snails that donate or receive sperm. If physical constraints imposed a prescribed ratio of donor and recipient sizes, we could expect a clear linear relationship between donor and recipient sizes (Crespi 1989). However, the paired data on sperm donor and recipient size showed considerable variation. For example, the  $r^2$  value for the pooled data on *P. gyrina* is 0.28 ( $df=145$ ,  $P<0.0001$ ). Although a significant relationship existed, it appears to be the type of artefact that Crespi (1989) referred to as a right-triangular plot: a random cloud of points with an absence of large-male/small-female matings. Thus, gender expression in physid snails is probabilistic: the smaller of two copulants is more likely to donate sperm, but



there is apparently no fixed size ratio or absolute criterion for sperm donors to be smaller than sperm recipients.

### Contested Copulatory Attempts

Contested copulatory attempts (by shell swinging) occurred in approximately 19% of *P. gyrina* pairs and 38% of *P. heterostropha* pairs in the laboratory, and 28% of *P. heterostropha* in the field. In general, intended sperm recipients rejected larger potential donors (Fig. 1). For *P. gyrina*, I observed too few contested matings to analyse each replicate separately, so I performed a paired *t*-test (paired  $t=4.73$ ,  $df=10$ ,  $P<0.001$ ; Fig. 1a). For *P. heterostropha* in the laboratory, there was no replicate effect within or between pairs ( $F_{1,13}=0.19$  and  $0.74$ , respectively), but the size asymmetry within pairs was significant ( $F_{1,13}=14.26$ ,  $P=0.002$ ; Fig. 1b). I observed too few shell swinging events ( $N=5$ ) for *P. heterostropha* in the field to test whether snails rejected mates larger than themselves. The signed size differences (recipient size – donor size) were less, however, for shell-swinging events than for uncontested interactions (Mann-Whitney  $U=63$ ,  $df=5,13$ ,  $P=0.003$ ). Thus, would-be sperm donors were received agonistically if they were similar in size or larger than their intended recipients (Fig. 1c).

### DISCUSSION

In general, relatively small sperm donors were received amicably, whereas larger would-be sperm donors were received agonistically (i.e. with shell

**Figure 1.** Size-based interactions in physid snails. Solid symbols indicate the size of sperm donors and recipients in uncontested copulations; copulations that were contested by shell swinging are shown as open symbols. (a) *P. gyrina* in laboratory aquaria. Sperm donors generally copulated with larger recipients but copulation attempts were contested by smaller recipients. Data on copulating snails are  $\bar{X} \pm \text{SE}$  for each of the seven samples. Data on contested copulation attempts are presented as a single point, because only 11 contests were observed. (b) *P. heterostropha* observed in the laboratory. The two symbol shapes represent different samples. (c) *P. heterostropha* observed in the field. The laboratory and field studies with *P. heterostropha* concurred with the size-based mating observed for *P. gyrina* in the laboratory. Dashed lines indicate isometric donors and recipients.

**Table I.** Analysis of variance of the pair-wise size relationships of successfully copulating snails (by replicate, after Wilkinson 1992)

Source	Sum of squares	df	Mean square	F	P
<i>P. gyrina</i> in the laboratory					
<b>Between pairs</b>					
Replicate	165.95	6	27.66	24.16	0.0001
Error	159.12	139	1.14		
<b>Within pairs</b>					
Pairing asymmetry	16.36	1	16.36	22.93	0.0001
Pairing asymmetry*replicate	1.39	6	0.23	0.33	0.9227
Error	99.19	139	0.71		
<i>P. heterostrophia</i> in the laboratory					
<b>Between pairs</b>					
Replicate	0.02	1	0.02	0.01	0.9523
Error	101.43	22	4.61		
<b>Within pairs</b>					
Size asymmetry	33.67	1	33.67	25.13	0.0001
Size asymmetry*replicate	0.01	1	0.01	0.01	0.9705
Error	29.48	22	1.34		
<i>P. heterostrophia</i> in the field					
<b>Within pairs</b>					
Size asymmetry	13.33	1	13.33	26.60	0.0002
Error	6.02	12	0.50		

swinging; Fig. 1). Thus, body size influences the value of one or both gender roles. Although the total amount of reproduction through eggs and sperm is equal (Fisher 1930), the costs of performing each sexual function may differ. Animals that have the choice of reproducing through either sexual function should choose the least expensive function (Bateman 1948). This value asymmetry in the cost of reproducing results in sexual conflict (Parker 1979). Similarly, for hermaphrodites there will be gender conflict when individuals prefer the same gender role (Wethington & Dillon, in press). Potential hermaphrodite mates could resolve a conflict over a shared gender preference in a number of ways. Leonard (1990, 1991) argued that reciprocal mating is the expected outcome of such conflict. Leonard's arguments belie the fact, however, that unanimous preference for a gender role is less the issue than is the quantitative value assigned to each role.

It is reasonable to expect value asymmetries between organisms in the net gain (or loss) through a given behavioural alternative (Maynard Smith & Parker 1976). Two questions are at issue for simultaneous hermaphrodites. (1) What is the preferred gender role? (2) What are the probable costs and benefits of each role? The preferred

gender role for physid snails is to act as a male (i.e. to donate sperm). Reproduction via sperm is probably less costly than egg production due to anisogamy (Bateman 1948). More important, however, is that behaving as male (donating sperm) is necessary to physiologically reproduce as such. In contrast, females, once mated, do not need to be reinseminated to continue producing outcrossed progeny (e.g. Wethington & Dillon 1991). In some species there are advantages to continually receiving sperm (e.g. to increase genetic variability among offspring; Madsen et al. 1992). Pulmonate snails do not solicit the female role (e.g. van Duivenboden & ter Maat 1985), however, and seem to avoid being mounted in general. In fact, *P. heterostrophia* without sperm stores are subject to large inbreeding costs, yet they still do not solicit the female role (Wethington & Dillon, in press).

Consider the conflict that occurs when two hermaphrodites each wish to donate sperm. The value of the male role will depend on the number of eggs that can potentially be fertilized. Because larger snails are more fecund (e.g. DeWitt 1954b, 1991), the smaller snail in an encounter stands to gain more by donating sperm to the larger, more fecund, snail. Such value asymmetries often

determine the outcome of animal contests simply because the contestant with more to gain will be motivated to escalate the contest more than the contestant with less potential gain (Maynard Smith & Parker 1976). Indeed, snails in this study rarely contested copulatory attempts by smaller would-be sperm donors. When mounted by larger would-be donors, however, shell swinging usually resulted (Fig. 1). Thus, the shell-swinging behaviour patterns appear to be contest escalations. Indeed, Wethington & Dillon (in press) also argued that the rejective behaviour patterns described by DeWitt (1991) occur as a form of conflict because the intended sperm recipient would prefer to donate sperm.

Behavioural ecologists usually define contest escalations in terms of physical attacks or threats (Krebs & Davies 1993), and the cost of such a contest escalation is the risk of injury or death. When animals fight, larger body size is often an advantage. When a small individual stands to gain more in a contest, it is important to escalate the contest in a way that does not cause the escalator a greater risk of injury or death than the other contestant. Thus, a physical attack is less preferred than other forms of escalation. I propose that shell swinging is a contest escalation in which the risk of injury or death is due largely to the risk of predation. This cost of increasing predation risk is less likely than physical attack to place a small escalator at a relative disadvantage, so that contests can be escalated on more of an even basis. Metaphorically, using predation risk as a weapon evens the playing field.

The interpretation of shell swinging as a form of escalation involving predation risk rather than fighting will be important to verify experimentally. Physical coercion is not likely to be the important issue, because shell swinging does not forcibly detach would-be sperm donors. Preliminary studies that I performed with other authors supports the predation-risk interpretation in two ways. (1) Model shells that were magnetically induced to shell swing were attacked more frequently by molluscivorous fish, *Lepomis gibbosus*, than were static models, and (2) shell swinging was strongly reduced in the presence of chemical cues from predation events (T. J. DeWitt, J. B. Wolf, J. D. Arendt & R. S. Wilcox, unpublished data).

In conclusion, when two snails encounter each other, the smaller, to whom the male gender role

is more valuable, is more likely to act as male or escalate the conflict with shell swinging, which increases the risk of predation. Further testing is necessary to elucidate the role of other factors that affect the relative costs and benefits of gender roles (e.g. resource level, predation risk, environmental stochasticity). This study is the first use of the size-advantage model to explain the behaviour of simultaneous hermaphrodite animals separate from allocation issues.

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