Low potential for sexual selection in simultaneously hermaphroditic animals

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Hermaphroditic animals are poorly represented in the sexual selection literature. This deficiency may reflect our inability to come to grips with hermaphroditism or, alternatively, it could be due to an inherent difference between hermaphrodites and gonochorists. Here we provide a number of reasons why sexual selection on traits related to mate acquisition can be expected to be intrinsically weaker in hermaphrodites. We show that the 'male' fitness component, which can be increased by sexual selection in hermaphrodites, is only half that of pure males in a gonochorist population. This component can be reduced even further when hermaphrodites self-fertilize. As a result, the potential for sexual selection (ψ) on male characters in hermaphrodites is at most half that of gonochorists. Given a specific mate handling cost, sperm production cost and rate of encountering receptive mates, we calculate the optimal allocation to mate acquisition and sperm. Since both partners of a hermaphroditic pair invest in mate acquisition, hermaphrodites should optimally invest less in mate acquisition. This can further reduce ψ by up to one-half. A higher readiness to mate and high investment in sperm can lead to a further systematic reduction in P_s in hermaphrodites.

Keywords: hermaphrodite; sexual selection; sperm competition; reproductive allocation

1. INTRODUCTION

Males and females often differ markedly from each other. Males are often more conspicuously coloured or possess exaggerated traits that females lack. Darwin (1871) argued that such sexual dimorphisms can be explained by sexual selection, which is defined as competition between members of one sex for access to mating with the other. Costly secondary sexual characteristics, such as the peacock's tail, can then be explained by the advantage they confer to the carrier through obtaining more matings. Darwin (1871) also argued that, in principle, secondary sexual characteristics cannot exist in hermaphrodites because the sexes are united in the same individual. This misconception has been rectified by Bateman (1948), Charnov (1979), Morgan (1994) and Michiels (1998) who argued that hermaphrodites can also compete to fertilize a finite number of ova. Characters that enable individuals to fertilize a larger portion of these eggs than the average hermaphrodite could then be considered secondary sexual characters. However, as Bateman (1948) has already pointed out, it may just be more difficult to identify such characteristics since they are not unequivocally sexually linked. Indeed, even in plants, it has proven very difficult to determine whether floral traits enhance male or female reproductive success (Queller 1983).

Despite the plausibility of hermaphroditic sexual selection, there are good reasons why we could expect sexual selection to be weaker in simultaneous hermaphrodites (SHs). Charnov (1979) argued that SHs will be stable when fitness through male function is limited in some way. Examples include sessility combined with internal fertilization or limited access to partners in some parasites. He thus felt that, in cases where an SH is stable, limitations on mates would nip sexual selection in the bud. Morgan (1994) used quantitative genetic models to show that sexual selection is possible in SHs, but that simultaneous hermaphroditism hampers certain aspects of sexual selection. For instance, genes that enhance male sexual fitness at the expense of viability will cause exactly the same viability cost on the female function, but without conferring any benefits to the latter. This means that the trait space is restricted when compared to gonochorists and that Fisherian runaway selection will not be established as easily. Greeff & Michiels (1999) argued that, due to severe sperm competition and sperm digestion, fitness through male function could, like that through female function, become resource limited. This means that Bateman's (1948) principle (males' fitness is limited by the number of mates, whereas females' fitness is limited by resources) is reduced and sexual selection weakened. Plant biologists have turned all these arguments on their heads, suggesting that high levels of sexual selection can in fact lead to specialization in male and female roles and, ultimately, lead to dioecy (Willson

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1979). Here too, the feeling is that sexual selection and hermaphroditism are strange bedmates.

Frequently, one of the sexes (often males) invests more time and energy in acquiring mates whereas the other sex invests more in gamete production and caring for young (Trivers 1972). Sutherland (1985, 1987) showed that the proportion of total 'reproductive time' spent on acquiring mates (time in) determines the strength of sexual selection. The proportion of reproductive time spent on other parental activities, such as caring for young or maturing eggs (time out), is thus inversely related to the strength of sexual selection, confirming Trivers' (1972) arguments. This idea that the strength of sexual selection is determined by time-in:time-out ratios has been substantially expanded by Parker & Simmons (1996), who related these ratios to different mating systems. The basic idea is that, when an animal spends most of its time acquiring mates, then a small increase in its mate-acquiring ability will increase its fitness substantially. On the other hand, such a small change would have gone unnoticed in an organism that spends very little time acquiring mates. By equating time with energy, the same arguments can be made from an energetic standpoint. Given that we can predict the strength of sexual selection from an animal's investment budget, it is interesting to ask whether hermaphrodites and gonochorists differ fundamentally in their budgeting.

Here we first show that being an SH implies at least a halving of the potential for sexual selection on traits related to mate acquisition. Furthermore, selfing, which is common in many SHs, is shown to reduce this potential even further. Then we look at the optimal allocation of reproductive energy to mate acquisition (time in) and to handling time and sperm production (time out). Since both partners of a hermaphroditic pair can invest in mate acquisition we find that optimal investment in time in can be less than in gonochorists. Finally, we consider whether there are inherent differences in the parameter space occupied by hermaphrodites and gonochorists that could lead to further differences in the potential for sexual selection.

2. BEING MALE AND FEMALE

Consider males from a gonochoristic population. Within the population animals are identical and all follow the same investment strategy. When investing in (active) mate acquisition they encounter receptive mates at a rate of λ (Parker 1979). λ specifies the number of potential partners the focal animal can acquire per unit of energy. Given this rate, an animal will obtain $F[\lambda]$ matings. Let us assume the population is at equilibrium. Hence, each animal will be replaced and each female will produce two offspring. Weighing these two offspring by their genetic similarity to the mother (0.5), each female has a fitness of 1. Since each offspring has a mother and father (at least in diploid organisms), fitness through male and female function must be equal (Fisher 1930). For this section we assume that all matings result in the same fertilization success; hence, females cannot favour the sperm of one male over the other. Then each mating gives a fitness benefit of $1/F[\lambda]$. Now consider a mutant with an encounter rate n times that of the average animal, $n\lambda$ and which obtains $F[n\lambda]$ matings. This increase in encounter

rate is the result of some secondary sexual characteristic and is therefore what we are interested in. This mutant male will thus have a fitness of

$$w_g = F[n\lambda] \frac{1}{F[\lambda]}. \quad (1)$$

Now consider an SH investing a proportion r of their total resources (R) in the male function, the remainder going to the female function. Let the fitness through female function be $(1-r)^t$, where t determines the rate at which the fitness returns decrease or increase as r changes. For an SH to be stable, t must be smaller than 1 (Charnov *et al.* 1976). We can write the fitness of the mutant as the sum of its fitness through its male and female functions, respectively, as

$$w_h = \frac{F[n\lambda]}{F[\lambda]} \times (1-r)^t + (1-r)^t. \quad (2)$$

When we consider a regular individual of the population ($n=1$), the right-hand side of equation (2) is equal to $2(1-r)^t$. If we again consider a population at equilibrium, each individual will have to be replaced and w_h must be equal to 1. Hence, $(1-r)^t$ must be equal to 0.5. We can thus rewrite equation (2) as

$$w_h = \frac{F[n\lambda]}{F[\lambda]} \times \frac{1}{2} + \frac{1}{2}. \quad (3)$$

By comparing equations (1) and (3) it is clear that the increase in encounter rate can only benefit the SH's male fitness. Hence, a trait resulting in an animal having n times the normal encounter rate will need to be half as costly (or, if the cost is the same, twice as effective) in an SH in order to result in the same selective advantage as in a pure male. If we now consider a hermaphrodite where a proportion s of the ova are reserved for self-fertilization, we can expand equations (2) and (3) to

$$w_h = \frac{F[n\lambda]}{F[\lambda]} \times \frac{(1-s)}{2} + \frac{s}{2} + \frac{1}{2}. \quad (4)$$

Equation (4) clearly shows how the reservation of a proportion of the ova for the purpose of self-fertilization will further reduce the pool of ova that can be capitalized on by an increase in encounter rate. Morgan (1994) mentioned but did not explicitly consider these two effects.

3. OPTIMAL BUDGETS FOR SIMULTANEOUS HERMAPHRODITES AND MALES

In internally fertilizing SHs, such as snails, flatworms or nudibranchs, which often occur in high densities, male function is not limited by mating opportunities. Hence, fitness through male function could potentially increase linearly with investment in male function. We want to compare this SH to a pure male in a gonochoric population. We will not search for the optimal allocation to the male function in the SH (r), but, rather, we ask how resources allocated to male function are further divided into the activities of acquiring mates, producing sperm and handling mates. In fact, for this model, the exact value of r does not matter since it cancels out. This cancelling allows us to consider males of a gonochoric species as

a special case of hermaphrodite. Since Sutherland (1985, 1987) did not consider sperm competition, we include it to see whether it affects the applicability of time-in:time-out ratios as a surrogate measure of the strength of sexual selection.

(a) Number of matings

Once an animal has acquired a mate and rendered it willing to copulate, it needs to make some further investments we will call handling costs. These costs may be the energetic costs of guarding a mate or caring for young and is equal to H per mating. Handling costs exclude the sperm transferred. In our notation we use an asterisk to indicate the population evolutionary stable strategy (ESS) and normal notation usually refers to a mutant. Let a mutant SH (or male) allocate g of its Rr (or R) resources to male gametes with the remaining $(1 - g)$ resources being used to acquire mates and to pay for handling costs. We have to find the ESS allocation to gametes, g^* . However, first we need to relate a g strategy to a specific fitness. If we first consider a male, the cost of one mating (excluding the sperm) is thus $1/\lambda + H$ since it takes an average of $1/\lambda$ units of energy to acquire one mate. Given that the total amount of energy available for acquiring and mating with mates is $R(1 - g)$, the total number of matings obtained by a male (F), is

$$F = \frac{R(1 - g)}{1/\lambda + H}. \quad (5)$$

In the case of a hermaphrodite, we need to construct the equivalent equation to equation (5) carefully, because, whereas we assumed that only males were acquiring mates, all individuals in a hermaphroditic population are acquiring mates. This means that if λ involves some searching cost, then both individuals in a pair may contribute to paying this cost. To avoid unnecessary complications we simply assume that an animal can benefit from a proportion K of the mate acquiring investment of other conspecifics. Hence, when animals invest g^* in gametes, each animal can be expected to be acquired by another individual $F_{\text{extra}} = K(Rr(1 - g^*) - HF_{\text{extra}})/(1/\lambda + H)$ times. Notice that, for these extra matings, an individual only needs to pay the handling costs and, hence, we subtract HF_{extra} from $Rr(1 - g^*)$. Moving terms around we find $F_{\text{extra}} = KRr\lambda(1 - g^*)/(1 + H\lambda(1 + K))$. The mutant's total number of matings is thus

$$F = \frac{Rr(1 - g) - HF_{\text{extra}}}{1/\lambda + H} + F_{\text{extra}} = \frac{Rr\lambda((1 - g)(1 + H\lambda(1 + K)) + (1 - g^*)K)}{(1 + H\lambda)(1 + H\lambda(1 + K))} \quad (6)$$

Notice that, when $K=0$ and $r=1$, equation (6) simplifies to equation (5), indicating that gonochorists can be treated as a special case of hermaphrodites.

(b) Value of each mating and sperm competition

We have now defined how the number of matings depends on the gamete investment strategy and the other variables. Next, we need to specify the value of each of these matings. An animal that invests less in gametes will be able to mate more frequently, but it does so at the cost of transferring less sperm and, as a result, it will be less

able to outcompete other males' sperm. A general phenomenon with sperm competition is that the fitness return per ejaculate shows diminishing returns as the ejaculate size increases (Parker 1998). We will consider an organism that reproduces continuously and mates at regular intervals. During each mating, sperm already in store in the receiving animal is displaced from the spermatheca according to a certain rule, the ϕ function. Here we will just use one of many possibilities that ϕ can assume, namely that $\phi = (\text{sperm donated})/(\text{sperm donated} + \text{sperm already in store})$. If c specifies the number of sperm that can be made per unit of resource, then the sperm transferred during one mating, assuming that equal amounts of sperm are transferred during each one of the F matings, is equal to $Rgrc/F$. If there is μ sperm in storage, we can write ϕ as

$$\phi = \frac{Rgrc/F}{Rgrc/F + \mu} = \frac{rg\beta/F}{rg\beta/F + 1} \quad (7)$$

with $\beta = Rc/\mu$. ϕ specifies the proportion of the sperm in the receiver that belongs to the last donor. Assuming that it is a fair raffle the last donor (individual X) will fertilize ϕ of the offspring produced by the receiver, up and until the receiver mates again. Then the sperm of the new donor will displace that of individual X, who will, as a result, fertilize a smaller proportion of the receiver's eggs. With each successive mating of the receiver, X's contribution to the offspring reduces. Charnov (1996) showed that, if this process continues an infinite number of times, X's total fitness received from that one mating can be calculated as $\phi[g]/\phi[g^*]$ when X allocates g to gametes and the remainder of the population allocate g^* . This assumption of an infinite number of matings contradicts our aim of obtaining the optimal number of matings F^* . The error introduced by this assumption is not known for the present model. However, Greeff & Michiels (1999) showed that the infinity assumption is fairly robust for sex allocation models and only leads to an appreciable inaccuracy when F is less than approximately eight matings.

(c) Fitness function and optimal allocation

If we look at the fitness of a mutant male or the 'male fitness' of a mutant hermaphrodite investing g in a population allocating g^* , we can write it as

$$w = F \times \frac{\phi[g]}{\phi[g^*]} \times \frac{\alpha}{F^*}, \quad (8)$$

with α equal to 1 for a male and $(1 - s)/2$ for a hermaphrodite. Note that we only consider that part of the hermaphrodite's fitness that can be enhanced by sexual selection. F^* indicates the number of matings of a non-mutant individual. Using equation (8) we will now solve for the optimal allocation to gametes. Since α is a constant, we can safely set it equal to unity for the moment. If we insert equation (7) into equation (8) we obtain

$$w = \frac{gF(\beta rg^* + F^*)}{g^*F^*(\beta rg + F)}. \quad (9)$$

To find the ESS g^* we insert equation (6) into equation (9) and then solve for g^* in $dw/dg|_{g=g^*} = 0$. One of the two roots gives the optimal strategy as

$$g^* = \frac{(1+K)\sqrt{x(1+y)}}{(1+K)\sqrt{x(1+y)} + 1 + y(1+K)}, \quad (10)$$

with $x = \lambda\mu/c$ and $y = H\lambda$. In other words, we can explain x and y as follows. x is the number of mates that can be acquired with the energy equivalent of the sperm stored in the spermatheca. Here we need to specify that it is not just the cost of the sperm inside the spermatheca but that it also includes the cost of sperm that were transferred during a mating but which never reached the spermatheca because the sperm receiver digested them. y is the number of mates that can be acquired with the handling cost of one mating. Notice that neither R nor r affects the optimal male gamete allocation.

(d) Time in, time out

We can now calculate the proportion of the total energy allocated to male function (Rr) that will be used as time in or the energy invested in acquiring mates (s) as

$$s = \frac{F - F_{\text{extra}}}{Rr\lambda} = \frac{1}{1 + (1+K)(y + \sqrt{x(1+y)})}. \quad (11)$$

(e) Potential for sexual selection

Let us now consider a mutant with an encounter rate n times that of the normal animal ($n\lambda$) in a population allocating g^* to gametes, as specified in equation (10). Following the same lines of analyses we can find the equivalents to equations (6) and (9) as

$$F_n = \frac{Rr\lambda(1-g^*)(K + n(1 + H\lambda(1+K)))}{(1 + H\lambda(1+K))(1 + nH\lambda)}, \quad (12)$$

and

$$w_n = \frac{F_n(\beta rg^* + F^*)}{F^*(\beta rg^* + F_n)}, \quad (13)$$

respectively. Following Sutherland (1987), we can now see how the fitness of the mutant changes as a function of n by inserting equation (12) into equation (13) and looking at dw_n/dn . If we assume that most mutations resulting in an increased encounter rate have small effects, then we can simplify matters by looking at dw_n/dn at its limit where n approaches 1. This gives us the potential for sexual selection (ψ) as

$$\psi = \left. \frac{dw_n}{dn} \right|_{\lim(n \rightarrow 1)} = \frac{1}{(1+K)(1+y + \sqrt{x(1+y)})} \quad (14)$$

We can look at how well time in reflects the potential for sexual selection by looking at ψ/s . When K is zero, as is the case with gonochorists, then this fraction is 1, showing that time in exactly reflects the potential for sexual selection. When K is more than zero this fraction is less than 1, indicating that time in actually overestimates ψ . The overestimation reaches its maximum of 2 when x and y approach zero and K is 1. This overestimation rapidly decreases as x and y increase. Hence, we can confirm

Figure 1. The potential for sexual selection (ψ) as a function of x and y when K in equation (14) is set to zero, i.e. $\psi = 1/[1 + y + (x(1+y))^{0.5}]$. The heavy arrows show how x and y change if λ increases. The short and long thin arrows show the effects of increases in H and m/μ on y and x , respectively. See §4 for explanations of x and y .

that, at least for gonochoristic species, time in gives an accurate reflection of the potential for sexual selection.

4. DISCUSSION

Our model shows how four factors affect the potential for sexual selection: (i) the cost of sperm stored in the spermatheca, (ii) the handling cost, (iii) the encounter rate and (iv) the extent to which animals can capitalize on the mate acquisition efforts of conspecifics. The last factor is probably not unique to hermaphrodites, but is certainly more probable to occur in them. In hermaphrodites, where the searching mate is also the mate being searched, animals can, under certain circumstances, rely on being found by partners. As K , a measure of the extent to which animals will be acquired by partners, increases from zero to 1, the ESS is to invest less and less in acquiring mates. To calculate the maximum effect of K on ψ we set K equal to 1 and zero and divide the former by the latter. This yields 0.5 and, hence, the maximum effect of K is a twofold decrease. In other words, the potential for sexual selection can be greatly reduced, as hermaphrodites are more likely to be searched out by partners. Thus, by having to play both the male and female roles, SHs experience an additional reduction in the potential for sexual selection because they invest less in mate acquisition (their optimal time is less). Just as an aside, if most of the mate acquisition costs are the actual searching costs, then the model suggests that hermaphrodites should be rather reluctant to find mates. This is just the opposite of the normal view that animals experiencing difficulties in acquiring mates should evolve to be hermaphroditic, thereby doubling the chance of meeting a sexually receptive partner (Charnov *et al.* 1976). In

other words, the causality of the relationship between hermaphroditism and poor mate attraction may indeed be reversed.

Now we would like to show how each of the three remaining parameters affects the potential for sexual selection. To appreciate the effects of the variables on the potential for sexual selection we have graphed equation (14) (figure 1). Variables x and y are composite variables, both being affected by λ and, thus, need some explanation. $x = \lambda\mu/c$ and $y = H\lambda$. Hence, if species A has a λ , e times more than species B, then A will have an x and y both e times that of B. When the cost of sperm stored in the spermatheca is higher in species A than B, then A will have a larger x than B. When mate handling is more costly in A than in B, then A will have a higher value of y . From figure 1 we can see that, as (i) mates are acquired more easily, (ii) sperm becomes more expensive and (iii) handling becomes more costly, the potential for sexual selection becomes less.

Next, we would like to establish whether hermaphrodites are more likely to have parameter values such that the potential for sexual selection is less than that of what one would expect for a gonochorist. We know of two reasons why, in populations of roughly the same density, hermaphrodites should be able to acquire mates more easily. First, assuming that the gonochoric population's sex ratio is 50:50, a hermaphrodite is twice as probable to meet a compatible partner. Second, of these partners found, a hermaphroditic partner is more likely to mate than a female would, since it is seldom in a female's interest to mate many times (Arnqvist & Rowe 1995; Chapman *et al.* 1995; but see Olsson *et al.* 1996). In particular in hermaphrodites that mate reciprocally, allowing a partner to mate may be the only cost to obtaining a mating oneself. All other things being equal, these behavioural biases could lead to hermaphrodites having a consistently lower potential for sexual selection than gonochorists.

We have shown that, together, sperm competition and sperm digestion can result in sperm being extremely costly to hermaphrodites (Greeff & Michiels 1999). This could also bias hermaphroditic populations towards higher values of x than gonochoric populations.

Hence, systematic biases in λ and the cost of sperm could cause the potential for sexual selection to be less in hermaphrodites than in gonochorists. Whether the cost of mate handling differs systematically between hermaphrodites and gonochorists is unclear at this stage. It is important to note that we have only considered sexual selection with regard to mate acquisition and from a very male-biased perspective, with females serving as mere receptacles for male battles. It is possible that mate choice by the 'female' and even the 'male' function of a hermaphrodite can be high (Michiels 1998). In addition, Charnov (1979) and Michiels (1998) argued that the potential for intersexual conflict can be very pronounced in hermaphrodites and may result in evolutionary arms races that have not been considered here.

To summarize, being male and female at the same time seems to lead to a number of effects that reduce the potential for sexual selection in animals.

- (i) Only male fitness through outcrossing can be boosted by sexual selection.

- (ii) Since animals can be acquired by a partner, as opposed to doing all the acquiring work, optimal investment in time in is reduced and so the P_s is reduced as well.
- (iii) The possibility of exchanging sperm would mean that willingness to mate is probably higher in hermaphrodites than gonochorists. As a result, λ should be less for otherwise equivalent hermaphroditic and gonochoric populations and so too the investment in time in.
- (iv) High investment in sperm could also bias hermaphrodites to invest less in time in.

To test this model, the number of sexually selected traits and the extent to which traits have been exaggerated through sexual selection must be compared between closely related groups of hermaphrodites and gonochorists. We hope this paper illustrates the value of such comparative research.

Finally, it is interesting to consider whether the encounter rate λ itself can evolve. After all, we consider whether mutants with an encounter rate n times that of a normal individual will increase in the population. In cases where λ can increase it will mean that the population will slip down the slopes of figure 1 and that sexual selection itself will erode away the potential for further sexual selection. Although this is a possibility, we feel that, since sexual selection will frequently be frequency dependent, a carrier of an n times mutation advantage will, as the trait becomes more common in the population, drop back to the former value of λ .

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