



## Research

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# Sex allocation and investment into pre- and post-copulatory traits in simultaneous hermaphrodites: the role of polyandry and local sperm competition

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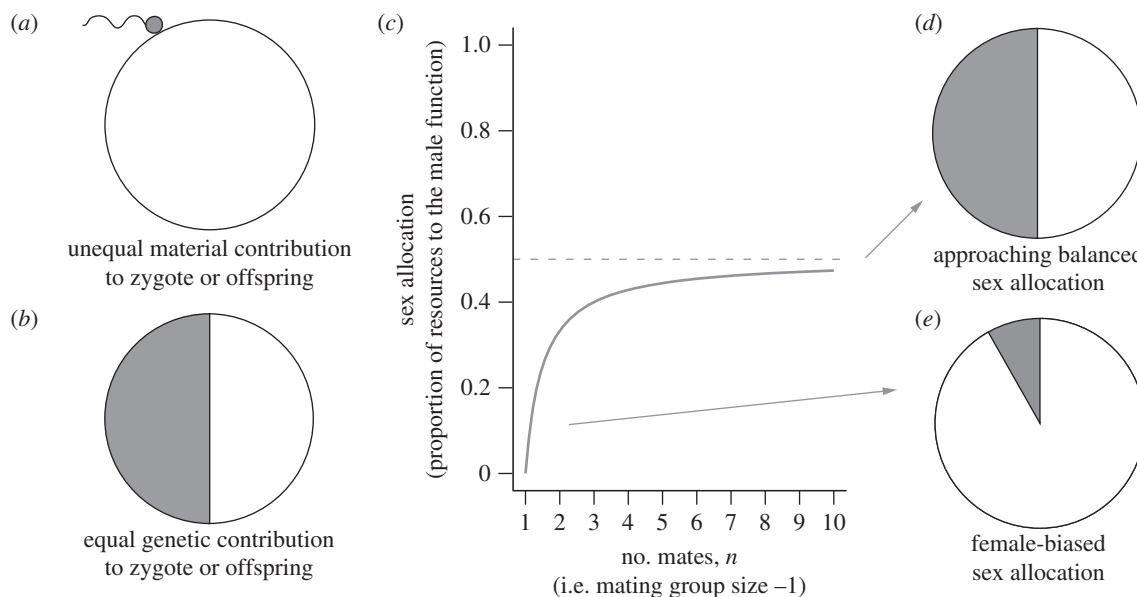
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Sex allocation theory predicts the optimal allocation to male and female reproduction in sexual organisms. In animals, most work on sex allocation has focused on species with separate sexes and our understanding of simultaneous hermaphrodites is patchier. Recent theory predicts that sex allocation in simultaneous hermaphrodites should strongly be affected by post-copulatory sexual selection, while the role of pre-copulatory sexual selection is much less clear. Here, we review sex allocation and sexual selection theory for simultaneous hermaphrodites, and identify several strong and potentially unwarranted assumptions. We then present a model that treats allocation to sexually selected traits as components of sex allocation and explore patterns of allocation when some of these assumptions are relaxed. For example, when investment into a male sexually selected trait leads to skews in sperm competition, causing local sperm competition, this is expected to lead to a reduced allocation to sperm production. We conclude that understanding the evolution of sex allocation in simultaneous hermaphrodites requires detailed knowledge of the different sexual selection processes and their relative importance. However, little is currently known quantitatively about sexual selection in simultaneous hermaphrodites, about what the underlying traits are, and about what drives and constrains their evolution. Future work should therefore aim at quantifying sexual selection and identifying the underlying traits along the pre- to post-copulatory axis.

## 1. Introduction

Sex allocation theory aims to predict relative allocation to male and female reproduction in sexual organisms [1], i.e. the sex ratio in gonochorists (organisms with separate sexes), the timing and direction of sex change in sequential hermaphrodites, and the allocation to male and female function in simultaneous hermaphrodites. Sex allocation is an important parameter in life-history theory, with implications for the cost of sex, population growth rate, and the evolutionary stability of the different reproductive modes [1]. Two books [2,3] have recently synthesized our understanding of sex allocation patterns—with a very strong focus on gonochorists—and concluded that sex allocation theory is a success story in evolutionary biology, by clearly documenting that evolutionary theory can accurately predict evolutionary outcomes.

The general logic of sex allocation theory is based on the insight that, despite the generally unequal paternal and maternal material contribution to the zygote or offspring (figure 1*a*), each sexually produced offspring genetically has exactly one father and one mother (figure 1*b*), and at the population-level total fitness obtained through male and female reproduction must therefore be equal [4,5] (this is sometimes called the Fisher condition [6], although the insight actually goes back to Düsing [4]; see also [7]). Deviations from equal investment should therefore lead to higher fitness returns per unit invested



**Figure 1.** Basic elements of sex allocation theory for hermaphrodites. (a) Unequal male (grey) and female (white) material contribution to the zygote or offspring (assuming no paternal care). (b) Equal male and female genetic contribution to the zygote or offspring (the Fisher condition). (c) Effect of the number of competing hermaphrodites (i.e. mating group size minus unity) on the optimal sex allocation (note that self-fertilizing individuals should be counted as mates, as their sperm can potentially compete with that of a partner). (d) Under random mating and in large populations optimal male and female allocation are equal (balanced or Fisherian sex allocation). (e) With smaller numbers of competing hermaphrodites the optimal sex allocation is increasingly female-biased.

into the rarer sex and should thus favour an evolutionary shift towards an equal sex ratio. These arguments, however, make some strong assumptions, such as random mating and large population size, and it was later shown that biased investment can be adaptive under a range of conditions that violate these assumptions. For example, Hamilton [8] showed that local mate competition (LMC)—a type of competition between related males for mates that can result from spatially structured populations—can favour female-biased sex ratios. LMC often occurs because of ecological constraints, such as when one mother's offspring mate within a local group. From the mother's perspective, competition between her sons is wasteful and she can maximize the number of grandchildren she produces by making fewer sons (thus reducing the competition between them) and instead making more daughters (thus providing more mates to her sons), potentially leading to strongly female-biased sex ratios [8,9]. As more females contribute offspring to the same local group, mate competition occurs less and less among related males and more and more among unrelated males, and as a consequence mothers are predicted to produce more sons and a more balanced sex ratio, an empirically very well-supported prediction [2,3].

Although work on sex allocation has predominantly focused on gonochorists, simultaneous hermaphrodites are also well suited to test sex allocation theory, and recent reviews show that sex allocation research on simultaneous hermaphrodites is making substantial progress, both in plants [10] and animals [11] (for recent reviews on sequential hermaphrodites, which we do not cover here, see [12,13]; for simplicity, we hereafter refer to simultaneous hermaphrodites as hermaphrodites). We primarily focus on copulating simultaneous hermaphrodites, by which we mean animals where the sperm donor engages in some form of direct sperm transfer to a sperm recipient (including itself in the case of selfing). Little focus is placed on either simultaneously hermaphroditic broad- or spermcast mating animals [14,15]

or plants [16,17]. Many of the points we raise here are, however, expected to be relevant also for these organisms.

Sex allocation models for hermaphrodites are based—either explicitly or implicitly—on fitness gain curves that describe the fitness returns for investment into the male and female functions. These models reveal that both the predicted stability of hermaphroditism and the optimal allocation to male and female reproduction are expected to depend on the shapes of these curves [1,18]. For hermaphroditism to be the optimal reproductive mode, at least one of the fitness gain curves needs to show saturating returns, so that it does not pay to invest in this sex function beyond a certain point. Remaining resources are thus predicted to be channelled to the other sex function, which results in sex allocation being biased towards the function with the less strongly saturating fitness gain curve. A recent review [11] concluded that there is currently little evidence to suggest that the female fitness gain curve shows saturating returns over its natural range in hermaphrodites, so that the male fitness gain curve would need to be saturating in order to explain the stability of hermaphroditism in these organisms. We therefore need to investigate which processes might be responsible for a saturating male fitness gain curve.

## 2. Sex allocation and local sperm competition

Classical sex allocation models for hermaphrodites refer to LMC as the reason for the saturating male fitness gain curve [19–21], but this term is very misleading in hermaphrodites. In a recent review, Schärer [11] therefore proposed the term local sperm competition (LSC), in order to better capture the nature of the *local* competition. LSC, analogous to LMC, also leads to a female-biased sex allocation, but it does not in fact require the mates to be related (nor does it require spatial population structure). Instead, LSC results from competition between related sperm, generally from

the same sperm donor, for the fertilization of a given set of ova of a sperm recipient. It can thus be viewed as the mirror image of sperm competition, which represents the ‘competition between the sperm from two or more [unrelated] males for the fertilization of a given set of ova’ [22]. From the sperm donor’s perspective—and analogous to the situation of LMC—competition between its own sperm in the recipient is wasteful, and it may therefore not pay to produce additional sperm. Models have therefore explored if the sperm donor can maximize its overall fitness by reducing sperm production and reallocating resources towards the production of eggs, leading to a female-biased sex allocation.

Extreme levels of LSC occur under selfing and monogamy (i.e. in the absence of polyandry;  $n = 1$  in figure 1c), where only one donor exists and competing sperm are maximally related, and so the male fitness gain curve is expected to saturate quickly once sufficient sperm have been produced to assure fertility [1,23]. Under selfing and monogamy, the sex allocation is therefore predicted to be highly female-biased (figure 1e), for which there is considerable empirical support [11,20,24,25]. As the number of (generally unrelated) sperm donors ( $n$ ) mating with a sperm recipient increases (i.e. with increasing polyandry, generally termed mating group size in the hermaphrodite literature [1]), sperm competition gets stronger and LSC weaker (i.e. sperm competition occurs less and less among related sperm and more and more among unrelated sperm). Allocation to sperm production thus continues to pay off, predicting a more linear male fitness gain curve and a shift towards a more equal sex allocation (figure 1d). While evidence for the former prediction is still relatively limited [26–28], the latter prediction is increasingly well supported [11,29–32]. The decisive factor for a saturating male fitness gain curve would therefore appear to be the level of LSC resulting from variation in the mating group size (i.e. the level of polyandry).

However, this argument (and the underlying mating group size model [1,19,20]) makes some strong and potentially unwarranted assumptions. Namely, it assumes that the resources that can no longer be profitably allocated towards sperm production owing to the occurrence of LSC are necessarily channelled towards an individual’s own female function, rather than (i) towards potential male-driven pre-copulatory components aimed at either obtaining more mates or gaining exclusive access to mates (such as mate searching, mate attraction, mate assessment, mate guarding, armaments, ornaments, nuptial gifts or coercion; leading to variance in mating success) and/or (ii) towards potential post-copulatory male fitness components other than sperm production, aimed at increasing the fitness returns per unit invested in sperm (such as invasive genitalia, manipulative seminal fluids or copulatory plugs; leading to variance in within-clutch paternity share). As we argue in §3, both of these assumptions seem to be clearly wrong in many hermaphrodites, although the first appears to capture some important aspects of the reproductive biology of these organisms. Moreover, the mating group size model further assumes that (iii) an increased number of mates leads to a fair-raffle sperm competition (where all sperm contributed by the mates count equally for fertilization). As we discuss in §5 this also seems unlikely in many hermaphrodites. The model we then present in §7 explores the consequences of relaxing these three assumptions.

### 3. Pre- versus post-copulatory sexual selection in simultaneous hermaphrodites

In order to explain conspicuous and costly traits in gonochorists—such as massive antlers and flamboyant breeding colorations—Darwin formulated the theory of sexual selection [33]. Since then, many such traits have been shown to indeed help members of one sex (generally the males) to win contests with same-sex individuals for access to opposite-sex individuals or to induce members of the opposite sex (generally the females) to mate with the carriers of these traits [34,35], confirming Darwin’s notion that these traits are sexually selected. In contrast, Darwin [33] explicitly doubted that sexual selection occurs in hermaphrodites, stating that they ‘have too imperfect senses and much too low mental powers to appreciate each other’s beauty or other attractions, or to feel rivalry’. However, this statement needs qualification in that Darwin’s view of sexual selection was restricted to the pre-copulatory level and was primarily focused on secondary sexual traits, as is evident from his statement that ‘with animals belonging to the lower classes, the two sexes are not rarely united in the same individual, and therefore secondary sexual characters cannot be developed’.

While pre-copulatory sexual selection is clearly important—and secondary sexual characters very prevalent—in gonochorists [34,35], evidence from hermaphrodites for choice of mating partners—let alone concrete traits involved in such choice—remains scarce [36], and evidence for competition for access to mating partners may even be lacking entirely. The available empirical examples of mate choice include, on the one hand, preferences for large partners, which can lead to size-assortative mating (e.g. [37–40]; but see [41]). This kind of preference is probably linked to a positive correlation between body size and female fecundity, and may thus represent a preference for more fecund mates. On the other hand, mate choice has been shown to involve pre-copulatory assessment of the mating status or novelty of the partner (e.g. [42–44], but see [45,46]). It seems probable that this kind of preference is linked to assessing cues that can serve as a proxy for the likelihood of encountering sperm competition, and that they are therefore strongly linked to post-copulatory sexual selection. These documented forms of pre-copulatory sexual selection could therefore be seen as a form of male mate choice, where the aim is to maximize the fitness returns per mating (or per unit of resources invested in sperm), rather than at maximizing the number of partners one mates with. While this kind of pre-copulatory sexual selection may lead to elaborate ways of assessing the partner [38], it does not appear to lead to conspicuous armaments or ornaments, as observed in gonochorists. It is important to realize, however, that, while sex-limited expression makes secondary sexual characters very evident in gonochorists, the probable absence of sex-limited expression in hermaphrodites makes it more difficult to identify traits linked to pre-copulatory sexual selection in hermaphrodites [47]. Thus, such traits might be present in hermaphrodites and should be searched for empirically in mate choice studies. The difficulty in detecting such traits may explain why models have assumed an absence of investment towards pre-copulatory male fitness components that we have mentioned above. Alternatively, the general absence of such traits could represent an actual fundamental difference between gonochorists and hermaphrodites.

It was not until Parker's [48] far-reaching realization of the importance of sperm competition—or more generally post-copulatory sexual selection—that the significance of sexual selection in hermaphrodites came into focus [18]. Indeed, much of what we currently know about sexual selection in hermaphrodites appears to occur at the post-copulatory level [36,49–53], including the highly variable allocation to sperm production under different competition scenarios that we mentioned in §2 when discussing LSC. In §5, we discuss a range of additional mechanisms of post-copulatory sexual selection, how they may affect LSC and thus the evolution of sex allocation and how their interaction could potentially lead to sexual conflicts (see also [11]). Together these now provide good evidence for variation, not only in sperm production, but also in other traits involved in post-copulatory sexual selection, such as love darts, genital morphology and different glands [54–56]. These considerations clearly document that the second assumption we mentioned above is wrong: hermaphrodites undoubtedly do allocate towards post-copulatory traits other than sperm production. But before we elaborate on this, we outline what we can learn from the existing sexual selection models in hermaphrodites about why, and indeed if, post-copulatory sexual selection prevails over pre-copulatory sexual selection in hermaphrodites.

#### 4. Models of sexual selection in simultaneous hermaphrodites

Charnov [18] proposed a verbal model that assumed Bateman's principle is transferable to hermaphrodites in that '... fertilized egg production by an individual is limited not by the ability to get sperm, but by resources allocated to eggs', so that '... individuals copulate not so much to gain sperm to fertilize eggs as to give sperm away (to gain access to another's eggs)'. As a consequence, hermaphrodites may often be willing to donate, but not necessarily receive sperm. When two hermaphrodites meet, their interests may thus be incompatible, creating potential for mating conflicts [18,49]. A solution is that individuals accept to receive sperm only if they can also donate sperm to their partner [57], and such conditional reciprocity could be enforced with reciprocal mating, which is very widespread among hermaphrodites [49]. Reciprocal mating may in turn reduce pre-copulatory sexual selection and increase mating rate, leading to intense post-copulatory sexual selection in the form of sperm competition. Moreover, reciprocal mating may lead to receipt of too much sperm or sperm from unattractive sires, favouring post-copulatory mechanisms to remove or choose among sperm of different sperm donors, promoting sperm digestion and cryptic female choice, and probably leading to antagonistic coevolution [18,49] (see also §5). But whether Bateman's principle usually operates in hermaphrodites is of course an empirical question, not a theoretical one [11,53,58]. There is a long-standing debate about this question [49,57,59–62], but the relevant data needed to inform this debate are largely lacking at the moment. Fortunately, there now is some agreement about the kind of data that are needed to inform this debate [58,63] (see also §9).

In addition to Charnov's verbal model, two studies have modelled pre-copulatory sexual selection in hermaphrodites more formally and concluded that it is indeed less likely to

occur, because—in the absence of sex-limited expression—all individuals carry a given ornament thus doubling its cost [64], and because selection was considered to act less strongly on a sexually selected trait [47]; but see [35]. However, these models did not consider two important aspects of hermaphrodite mating systems, namely that sex allocation is often biased [11] and that we can often expect mutual mate choice [65], especially when mating is reciprocal. While sexual selection models that allow for biased sex allocation are still largely lacking (but see the model we present below), a recent model compared Fisherian sexual selection between gonochorists and hermaphrodites, while exploring the effects of unilateral versus mutual mate choice [65]. While the results suggest that the conditions for Fisherian sexual selection are indeed more restrictive in hermaphrodites than gonochorists under unilateral choice—thus confirming earlier results [47,64]—the two reproductive modes do not appear to differ in their propensity for Fisherian sexual selection under mutual choice [65]. Given that mutual choice appears probable in hermaphrodites [18,38,49], this is an important insight, making Fisherian sexual selection, and thus ornaments and preferences for ornaments, more probable in hermaphrodites.

While the sex allocation models that informed Charnov's influential arguments excluded allocation towards pre-copulatory traits [1,18], this may have been founded on the then prevailing view that hermaphrodites are primarily sessile or low motility organisms living at low population densities, with limited competition between rivals, and where partners are expected generally to be willing to mate once an opportunity arises [66,67]. Later work showed, however, that hermaphroditism is widespread also in motile organisms that can occur at high densities, and the highly complex adaptations to post-copulatory sexual selection we observe in hermaphrodites [49,50] clearly indicate that many hermaphrodites live under conditions that are conducive to sexual selection. We therefore next give an overview over the known mechanisms of post-copulatory sexual selection in hermaphrodites.

#### 5. Post-copulatory sexual selection and its effects on local sperm competition

Charnov's mating group size model—in which he explores the influence of the number of sperm donors contributing sperm to a sperm recipient—assumes fair mixing of the sperm contributed by all the sperm donors [1]. It predicts that with increasing mating group size (i.e. with decreasing LSC) the optimal sex allocation quickly approaches equality (figure 1). On the basis of this reasoning, one would therefore conclude that a low population density (i.e. small social group sizes), and a resulting low number of partners, are required for the long-term stability of hermaphroditism in mobile hermaphrodites. However, as we argue in the following, low population density might not be the only source of LSC, but can also result from different processes of post-copulatory sexual selection.

##### (a) Sperm displacement

A later model by Charnov relaxed the assumption of fair mixing of competing sperm and investigated how different sperm displacement rules can affect optimal sex allocation [68]. This suggested that, regardless of the specific



mechanism of sperm displacement explored, efficient displacement of sperm from previous sperm donors can maintain a female-biased sex allocation, even when a large number of sequential sperm donors contribute sperm to the same recipient. The reason for this is that the displacement of sperm from previous sperm donors by the current sperm donor leads to a reduction in the amount and diversity of sperm encountered by the following sperm donor (a scenario more likely to occur when the sperm storage capacity of the recipient is relatively small). Thus, little is gained from investing in the production of additional sperm, as it would simply increase LSC. Sperm displacement can therefore influence the evolution of sex allocation (see also the results of our model in §8).

### (b) Sperm digestion

A different situation occurs when sperm are removed and/or digested by the recipient. Sperm digestion is widespread in hermaphrodites [49,69,70], and although its evolutionary origins and adaptive significance are currently poorly understood, several scenarios are possible. Sperm digestion may be indiscriminate with respect to sperm donor identity, and may primarily serve to remove—and possibly gain resources from—superfluous sperm that have been received as a result of a mutual willingness to mate. It is important to note, however, that there currently exist no data in support of the notion that sperm digestion occurs at a net energetic benefit to the digesting individual, as is often assumed [69,71]. Instead, sperm digestion could occur at a net energetic loss to the digesting individual, while still being beneficial in terms of fitness returns, because it reduces potential harm imposed by, for example, polyspermy [72] or manipulative substances (see §5*d*). In one model, the sperm recipient simply digests a fixed proportion of the sperm transferred by each sperm donor and gains resources from such sperm digestion [69]. Under these conditions sperm digestion can co-evolve with male allocation (i.e. high male allocation leads to a high proportion of sperm digested), and drive sex allocation to equality or even to male bias. A similar conclusion comes from a model that considers s-shaped sperm displacement functions [73], which could also result from sperm digestion, because a minimum investment in sperm may be needed to overcome sperm digestion and begin to displace rival sperm. Viewed from the perspective of the above sperm displacement model, one effect of this type of sperm digestion is that it reduces the efficiency of sperm displacement, leading to reduced LSC and higher sperm competition.

### (c) Cryptic female choice

Alternatively, sperm digestion may represent an adaptation that specifically digests sperm of certain sperm donors (i.e. it may represent a form of cryptic female choice). Until recently, most models of sperm competition have treated the sperm recipients as a passive vessel in which sperm from different sperm donors compete for access to ova. However, as Charnov [18] pointed out in his seminal 1979 paper, reciprocal mating may lead to post-copulatory female choice (later termed cryptic female choice [74,75]; see also [76]). Cryptic female choice is expected to be prevalent in hermaphrodites because reciprocal mating strategies lead to the receipt of sperm from individuals that are unattractive as fathers. Traits that allow the removal of such undesired

sperm are expected to evolve, and sperm digestion may thus be a female trait to retain control over paternity. A recent model has shown that cryptic female choice in hermaphrodites for the sperm of preferred partners can lead to a reduction in the number and/or competitive ability of effectively competing sperm donors, and can thus lead to increased LSC and a female-biased sex allocation [77]. However, the conclusions strongly depend on whether the sperm recipient digests a fixed amount or a fixed proportion of the received sperm. Only if a fixed proportion is removed does the sex allocation become more female-biased, while for the removal of a fixed amount the model can predict high male allocation, and even a male-biased overall sex allocation (a similar effect on variation in the allocation to sperm production has been observed in gonochorists [78]). The reason for this is that the removal of a fixed amount of sperm allows a sperm donor to overcome female choice, as any sperm above the threshold fully count in sperm competition, while the removal of a fixed proportion of sperm penalizes all sperm produced to a similar extent. The latter may appear to contradict the findings of the sperm digestion model discussed in §5*b* (where the digestion of a fixed proportion led to a higher male allocation). However, a fundamental difference between these models is that in the sperm digestion model the individuals obtain an energetic benefit from the digested sperm, whereas this is not the case in the cryptic female choice model. This clearly suggests that we need empirical data, not only on the mechanisms, but also on the costs and benefits of sperm choice and sperm digestion, which are currently not available for any species.

### (d) Antagonistic coevolution

From what we have just outlined, these mechanisms of male and female post-copulatory sexual selection may have a profound impact on LSC and thus on the evolution of sex allocation. These mechanisms may not evolve independently, however, but instead be involved in sexually antagonistic coevolution [35,79]. For example, whereas it is in the interest of the sperm donor to fertilize all the available eggs of the recipient, the recipient may want to retain control over which of the different sperm donors fertilizes its eggs. This can lead to sexual conflict with manipulative persistence traits in the sperm donor, which either influence stored sperm from previous matings or affect the recipient's ability to exhibit cryptic female choice. In response, one can expect defensive resistance traits in the sperm recipient, which allow it to retain control over fertilization. Given the importance of male and female post-copulatory mechanisms in determining the level of LSC, sexually antagonistic coevolution could thus drastically affect the evolution of sex allocation (see also [11]). Such interactions have not yet been modelled in much detail though (but see [80]).

### (e) Random paternity skews

Moreover, a recent model [81] showed that random variation in siring success in hermaphroditic plants, possibly because of stochastic effects in pollination or spatial proximity to mates, may favour a much stronger female-bias in sex allocation than expected based on the nominal number of male competitors alone, because it reduces the effective number of male competitors competing for the same eggs (i.e. it increases LSC). Similar effects may result from other types

of stochastic effects also in other hermaphrodites, such as the order in a mating queue via its effect on sperm precedence or a limited accuracy of sperm allocation to a given mating.

## (f) Empirical evidence

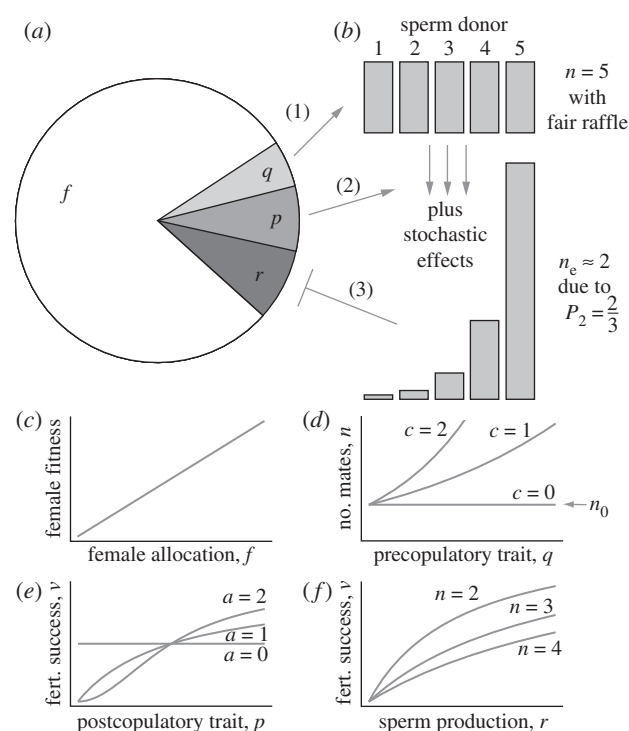
It is clear from the above that stochastic effects, and different mechanisms of post-copulatory sexual selection, such as sperm competition, sperm digestion and cryptic female choice are expected to have profound effects on LSC and consequently on the evolution of sex allocation [11]. However, compared with the massive amounts of data on, for example, sperm competition in gonochorists (e.g. [82] for insects and [83] for reptiles), there are still few quantitative data on hermaphrodites (e.g. reviews by Michiels [49] and Baur [50]). In addition, most data are restricted to gastropods [84,85], and for most of these there are currently few data on sex allocation.

## 6. Sexual selection from a sex allocation perspective

From a sex allocation perspective, we can ask what the fitness gain curve for investment towards a particular sexually selected trait is, whether that investment yields fitness gains on the pre- or post-copulatory level, whether fitness consequences are restricted to either the male or female function, and how such fitness gains compare with fitness gains from reallocating towards own egg production (with presumably linear returns). Recent models have investigated optimal allocation towards different male post-copulatory components in both gonochorists [86,87] and hermaphrodites [80,88], and there are recent empirical studies showing variation in allocation towards traits other than sperm production [56,89]. In contrast, models that integrate pre- and post-copulatory components have until recently been rather simplistic. A model by Parker *et al.* [90] now explores how different types of pre-copulatory processes (ranging from scramble to contest competition) combined with different sperm competition scenarios can affect the optimal split of resources allocated towards pre- versus post-copulatory traits. Similar models are clearly needed for hermaphrodites, but they need to consider an important complication, namely that the often biased sex allocation patterns in hermaphrodites mean that allocation towards the function with the lower investment necessarily yields a higher return per unit investment, because the Fisher condition of course applies also to hermaphrodites [11]. Thus, variation in sex allocation will probably change the shapes of the male and female fitness gain curves with respect to each other. Unravelling the balance between pre- and post-copulatory sexual selection is required for understanding the kinds of traits to which a hermaphrodite will channel its reproductive resources. There is therefore a clear need for quantitative studies of sexual selection in these organisms that explicitly consider variation in sex allocation (see also §9). In the following, we present a first model formulated with these aims in mind.

## 7. The model

Here, we describe the basic set-up of our model and its underlying assumptions. Technical details can be found in appendix A.



**Figure 2.** Logic of the relationships explored in the text and the model. (a) We assume that the total reproductive allocation is partitioned into female allocation,  $f$ , which we assume to yield linear fitness returns (depicted in (c)), and male allocation consisting of a pre-copulatory trait,  $q$ , a post-copulatory trait,  $p$ , and sperm production,  $r$  (we do not imply that the visualized quantities are necessarily representative of a specific biological scenario). (b) Now imagine that a sperm recipient mates  $n_0 = 5$  times. Assuming fair raffle sperm competition, we expect all five sperm donors to contribute equally to the sperm stored in a sperm recipient (top), leading to a number of mates of  $n = 5$ , unless the pre-copulatory trait,  $q$ , leads to an increase in the number of mates (indicated by arrow (1) and depicted in (d)). Owing to the action of the post-copulatory trait,  $p$  (indicated by arrow (2) and depicted in (e)) and possibly additional stochastic events, the contributions to the sperm stored in a sperm recipient can become highly skewed (the depicted example assumes no stochastic events and that allocation to  $p$  leads to a displacement of two thirds of the previously stored sperm). This results in a much lower effective number of mates,  $n_e \approx 2$ , than expected under fair-affle sperm competition, and thus a much lower optimal male allocation to sperm production,  $r$  (indicated by arrow (3) and depicted in (f)) (i.e. because the fitness gain curve for sperm production saturates more quickly with smaller  $n$ ). Note that the parameters  $c$  and  $a$  scale the effects of parameters  $q$  and  $p$ , respectively.

We work with a population of outcrossing simultaneous hermaphrodites with non-overlapping generations. All individuals have an identical amount of reproductive resources that can be differentially allocated to four different traits that affect egg production, sperm production, pre-copulatory mate competition and post-copulatory sperm competition:

- A fraction  $r$  of resources is allocated to sperm production.
- A fraction  $p$  is invested into a post-copulatory trait.
- A fraction  $q$  is allocated to a pre-copulatory trait.
- The remaining fraction  $1 - r - p - q$  is devoted to egg production.

The structure and components of the model are depicted in figure 2. We make no assumptions about the level of reciprocity during matings. Thus, the model applies equally well

to species with strictly reciprocal exchange of sperm, as well as to species that inseminate unilaterally.

We focus on a rare mutant individual in a resident population. Trait values of the resident population are equipped with a hat (^) to distinguish them from trait values of the mutant focal individual.

The focal individual mates on average  $n$  times in the male role, where  $n = n(q)$  increases with the focal individual's pre-copulatory investment  $q$ , as indicated by arrow (1) and in figure 2*d*. Since mutants are assumed to be rare, they mate exclusively with resident individuals that have on average  $\hat{n} = \hat{n}(\hat{q})$  sperm donors, including the focal individual itself. The focal's sperm allocation per mate is then  $r/n$ , and following the approach of Michiels *et al.* [88], this amount is multiplied by an increasing function  $g(p)$  of the investment,  $p$ , into a trait that boosts post-copulatory competitive ability. The resulting quantity is the focal individual's 'effective' ejaculate size

$$m = \frac{r}{n} g(p). \quad (7.1)$$

The focal individual's effective ejaculate size affects its fertilization success, i.e. the proportion of eggs fertilized by its sperm rather than by sperm of the other  $\hat{n} - 1$  sperm donors (figure 2*e*). Importantly, and following the approach of Greeff *et al.* [81], we do not assume that the outcome of sperm competition is given by a 'fair raffle', but we allow for a skewed proportional representation of the sperm of different donors in a recipient. Given that we here do not consider any female influence on sperm storage or usage such skews necessarily result in a paternity skew. We will therefore in the following use the term paternity skew (consistent with [81]), but it is important to acknowledge that the two need not be equivalent. Specifically, we assume that this skew is determined both by random factors and the trait values of competitors. In any particular mating, the paternity share of the focal individual is a random variable  $z$ , with mean  $\bar{z} = 1/\hat{n}$ , and we can write its fertilization success as

$$v = \frac{1}{n} \sum_{i=1}^n \frac{z_i m}{z_i m + (1 - z_i) \hat{n} m}. \quad (7.2)$$

The  $z_i$  are specific realizations of  $z$ , the distribution of which is expected to depend on specific mechanistic details of the sperm competition process. The variance  $V$  of this distribution is closely related to the concept of the 'effective number of mates'  $n_e$ . This is the number of mates such that, if each contributes equally to paternity, i.e. in the absence of paternity skew, the degree of LSC is the same as generated by having  $n$  mates with a paternity skew given by  $V$ . The effective number of mates is given by the formula [81,91]

$$n_e = \frac{1}{\sum_{i=1}^n z_i^2}. \quad (7.3)$$

Clearly,  $n_e = 1$  is the minimal value, obtained if a single donor fertilizes all eggs ( $z_i = 1$  for one particular  $i$  and  $z_j = 0$  for all  $j \neq i$ ), and  $n_e = n$  the maximal value, obtained if all donors have an equal share ( $z_i = 1/n$  for all  $i$ ).

Since a variance is by definition  $V = (1/n) \sum z_i^2 - \bar{z}^2$ , we can also write

$$n_e = \frac{n}{1 + n^2 V}. \quad (7.4)$$

In appendix A2, we derive expressions for  $V$  and  $n_e$  for several different sperm competition scenarios. Moreover, in our model, we want to allow for the possibility that the paternity variance increases with higher mean levels of investment into the post-copulatory trait  $p$ , as indicated by arrow (2) in figure 2*a*. The rationale for this is that such traits will probably affect sperm competition success, probably making the outcome of sperm competition more variable if all individuals invest heavily in these traits. A simple way of accomplishing this is to set

$$V = V_0(1 + b\hat{p}), \quad (7.5)$$

where  $V_0$  is given by a variance expression derived in appendix A2 and  $b$  is a parameter that governs the rate at which  $V$  increases linearly with  $\hat{p}$ . These variance effects are expected to lead to LSC, and thus to a lowered allocation to sperm production  $r$ , as indicated by arrow (3) in figure 2*a*.

In order to derive optimal or evolutionarily stable trait values ( $r^*$ ,  $p^*$ ,  $q^*$ ), we construct an expression for the fitness of a focal individual with trait values ( $r$ ,  $p$ ,  $q$ ) in a resident population with trait values ( $\hat{r}$ ,  $\hat{p}$ ,  $\hat{q}$ ). An individual's total fitness  $W$  is the sum of its fitness  $W_f$  through female function, i.e. how many eggs it produces itself, and its fitness through male function  $W_m$ , i.e. how many eggs it fertilizes in others:

$$W = W_f + W_m. \quad (7.6)$$

We make the standard assumption that female fitness increases linearly with the fraction of resources allocated to eggs (figure 2*c*):

$$W_f = 1 - r - p - q. \quad (7.7)$$

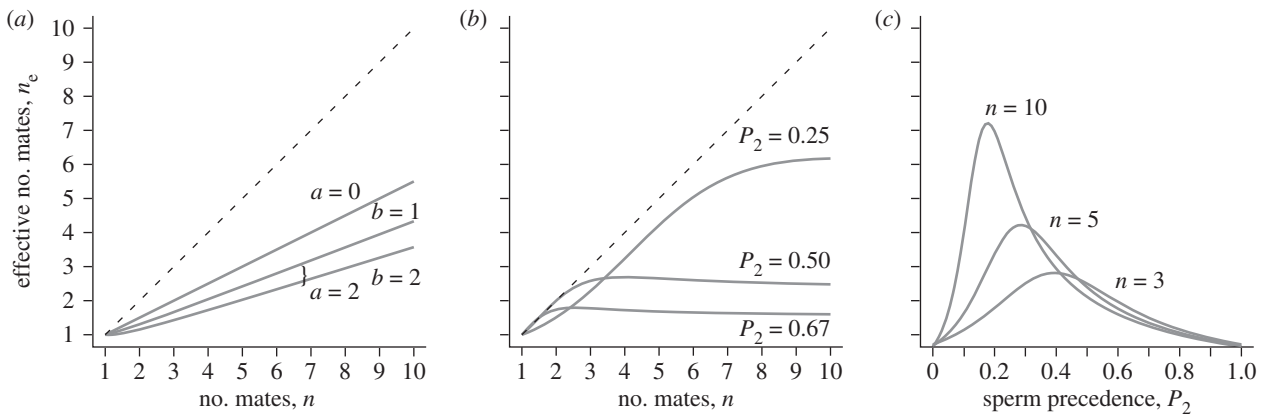
Fitness through the male function is the product of the number of mates  $n$ , expected fertilization success  $v$  and the number of eggs  $\hat{W}_f = 1 - \hat{r} - \hat{p} - \hat{q}$  of a typical mate:

$$W_m = n v (1 - \hat{r} - \hat{p} - \hat{q}). \quad (7.8)$$

At the population level, fitness through female function must equal fitness through male function, i.e.  $\hat{W}_f = \hat{W}_m$ , the so-called Fisher condition [6], which implies the 'consistency requirement' that  $\hat{v} = 1/\hat{n}$ .

Evolutionarily stable values for a trait  $x$  ( $= r$ ,  $p$  or  $q$ ) are found by calculating the selection differential  $\partial W/\partial x$  for  $x$ , evaluated at its population-level value  $\hat{x}$ . Setting the resulting expression equal to zero and solving yield the optimal trait value  $x^*$ . The details for the specific traits can be found in appendix A3.

We were able to find a general solution for the optimal sperm allocation  $r^*$  (equation (7.9)) but solutions for  $p$  and  $q$  require specific assumptions about the functional forms of  $g(p)$  and  $n(q)$ . Like Michiels *et al.* [88], we assume that effective ejaculate size increases in proportion to  $p^a$ , where  $a$  is a positive exponent (figure 2*e* shows the effect of this on  $v$ ). In addition, we assume that a higher pre-copulatory investment,  $q$ , increases the number of mates exponentially, that is,  $n(q) = n_0 \exp(cq)$ , with  $c \geq 0$  and  $n_0$  the number of mates without any pre-copulatory investment (figure 2*d*). Sexual selection models often assume that male secondary sexual traits have this kind of exponential effect on male attractiveness [92].



**Figure 3.** Relationship between the (nominal) number of mates,  $n$ , and the effective number of mates,  $n_e$ . (a) Effect assuming a beta distribution for the paternity share, without ( $a = 0$ ) or with ( $a = 2$ ) an effect of the post-copulatory trait,  $p$ , on ejaculate size, and with a small ( $b = 1$ ) or large ( $b = 2$ ) effect of  $p$  on the variance of the beta distribution. (b,c) Effect of different sperm precedence patterns as a function of different  $P_2$ -values.

## 8. Results and discussion of the model

### (a) Variation in effective number of mates

In figure 3, we show how the effective number of mates,  $n_e$ , varies with the actual number of mates,  $n$ , for different scenarios of sperm competition and different assumptions about the effects of the post-copulatory trait,  $p$ . For figure 3a, we assumed that the paternity share follows a beta distribution, a common generic probability distribution for proportions (see appendix A2). Here, the effective number of mates scales nearly linearly with the actual number of mates and is typically less than half the actual number. A higher level of  $p$ , reduces  $n_e$  even further. In figure 3b, we use the concept of sperm precedence, which in the classical double-mating experiments is often expressed as  $P_2$ , the paternity achieved by the last mate (or the proportion of sperm displaced by the last ejaculate) as a model for sperm competition (see appendix A2). Compared with figure 3a, the relationship is now more strongly nonlinear, and for relatively high but realistic [82,84,93]  $P_2$ -values  $n_e$  remains very low and even decreases slightly with  $n$ . Figure 3c shows in more detail how  $n_e$  varies with  $P_2$ .

### (b) Optimal allocation strategies

The optimal allocation to sperm production  $r^*$  turns out to be

$$r^* = (1 - p - q) \frac{n_e - 1}{2n_e - 1}. \quad (8.1)$$

This result is similar to Charnov's [19] classical result  $r^* = (n - 1)/(2n - 1) - 1/2$ , except that (8.1) is more female-biased because of paternity skew ( $n_e \leq n$ ) and by a reduction in allocation to sperm production proportional to the amount  $p + q$  invested into the pre- and post-copulatory traits. Interestingly, the optimal ratio of investment into sperm and investment into eggs is fully determined by the effective number of mates:

$$\frac{r^*}{1 - r^* - p - q} = \frac{n_e - 1}{n_e}. \quad (8.2)$$

However, that is not to say that this ratio is invariant with respect to  $p$  and  $q$ , since both traits are likely to affect  $n_e$ .

The optimal post-copulatory investment  $p^*$  is simply given by

$$p^* = ar^*. \quad (8.3)$$

In order for selection to favour any investment at all in pre-copulatory traits, it turns out that quite strong selection ( $c > 1$ ) is required. Indeed, the optimal value for  $q^*$  is given by

$$q^* = 1 - r^* - p^* - \frac{\hat{n}_e}{c}. \quad (8.4)$$

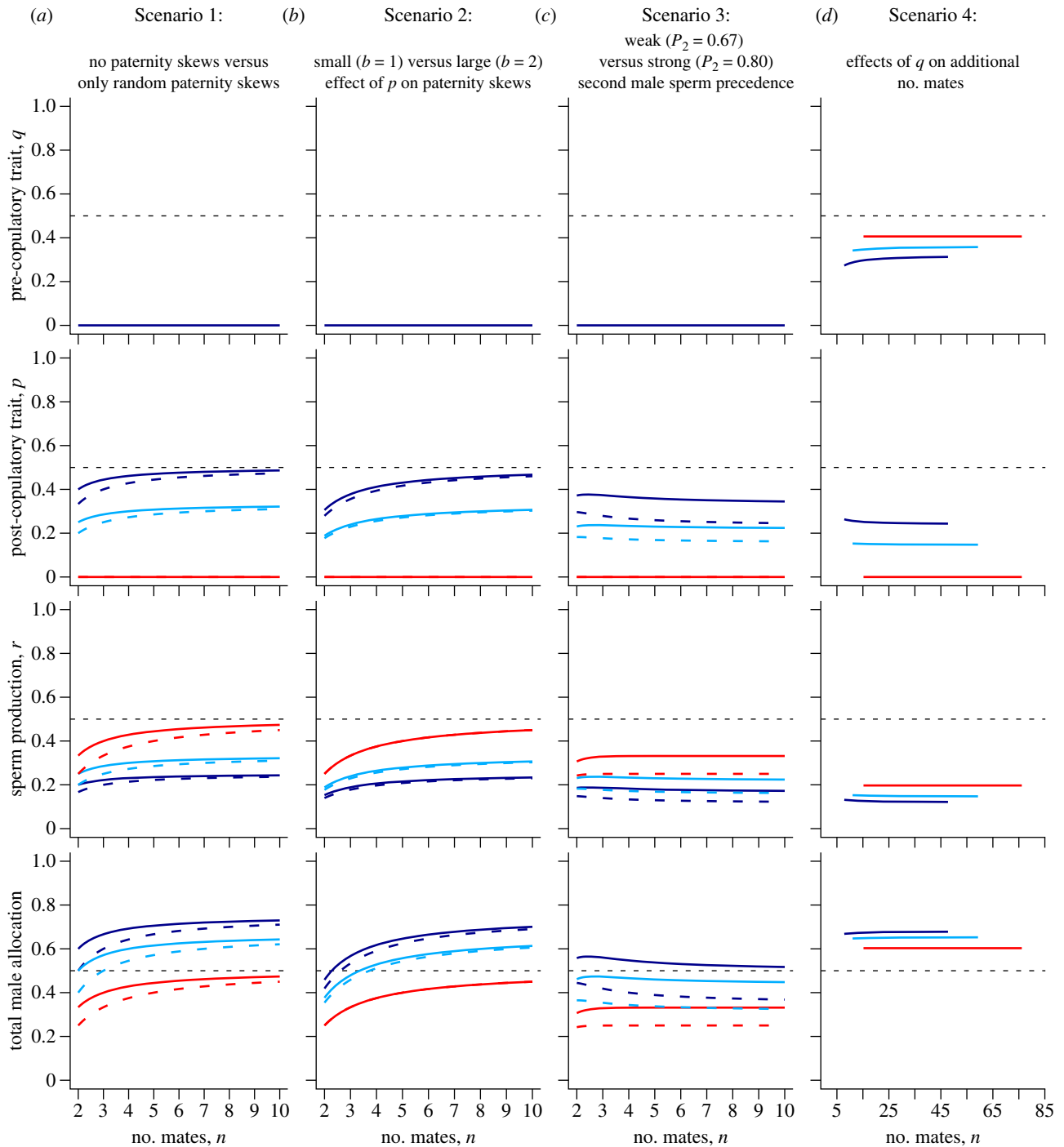
This shows that in order for  $q^* > 0$ , it is necessary that  $c > \hat{n}_e/(1 - r^* - p^*)$ , which is always larger than unity and more so for larger  $\hat{n}_e$ . Thus, in our model, investment into traits that increase the number of mates is not easy to evolve.

These results are illustrated in figure 4. From top to bottom, each column of four panels shows the optimal values of  $q$ ,  $p$ ,  $r$  and their sum (i.e. the total allocation to male traits), plotted against the number of mates,  $n$ . The first three columns correspond to different scenarios regarding skewed paternity, without any pre-copulatory investment, and the last column on the right considers the effect of pre-copulatory investment.

#### (i) Scenario 1

The solid lines in column (a) correspond to the model of Michiels *et al.* [88], which reduces to Charnov's [19] model in the absence of post-copulatory investment ( $a = 0$ ). It shows that investment in the post-copulatory trait,  $p$ , exceeds investment in sperm,  $r$ , when 'effective' ejaculate size increases in an accelerating fashion ( $a > 1$ ) with  $p$ . This is not surprising, since the effect of investment in  $r$  has a linear effect on ejaculate size. What is remarkable is that the overall investment in male traits (bottom panel) typically exceeds investment in the female function, which would tend to make hermaphroditism unstable (see also [88]). The dashed curves in column (a) show the effect of allowing for skewed paternity but without an additional effect of the post-copulatory trait  $p$  on the variance of the paternity distribution (i.e.  $b = 0$ ). Here, we assumed a beta distribution for paternity (see appendix A2), which reduces the effective number of mates by roughly one half (see also figure 3a). It is clear that such 'random skew' reduces investment towards





**Figure 4.** Relationship between the number of mates,  $n$ , and the allocation towards the pre-copulatory trait,  $q$ , the post-copulatory trait,  $p$ , the sperm production,  $r$  and the total male allocation (sum of  $q$ ,  $p$  and  $r$ ) for four different scenarios that we have explored in the model. In all panels the red, light blue and dark blue lines are for values of parameter  $a = 0, 1$ , and  $2$ , respectively, and the solid versus dashed lines are for different values of other parameters explored in each scenario. (a) Scenario 1: nominal number of mates ( $n$ , assuming fair raffle sperm competition, solid lines) versus effective number of mates ( $n_e$ , assuming basic random paternity skews, dashed lines) (for  $b = 0$  and  $c = 0$ ). (b) Scenario 2: small ( $b = 1$ , solid lines) versus large ( $b = 2$ , dashed lines) effect of the post-copulatory trait,  $p$ , on the paternity skews (for  $c = 0$ ). (c) Scenario 3: moderate ( $P_2 = 0.67$ , solid lines) versus strong ( $P_2 = 0.80$ , dashed lines) second male sperm precedence pattern (for  $b = 1$  and  $c = 0$ ). (d) Scenario 4: effect of the pre-copulatory trait,  $q$ , on the additional number of mates (for  $b = 1$  and  $c = 5$ ) (only cases where values of  $q > 0$  evolve are shown, which requires large values of  $c$  and  $n$ ).

both  $r$  and  $p$ , but not dramatically, so that overall investment in male traits is still often larger than investment in eggs.

### (ii) Scenario 2

In column (b), we then allow for a positive effect of  $p$  on the variance of the (beta) distribution of paternity (namely for  $b = 1$  and  $b = 2$ , see also figure 3a). This lowers the optimal investment to  $r$  and  $p$  considerably compared with column (a), since a higher variance in paternity leads to lower

effective numbers of mates. Still, the overall investment in male traits can easily exceed investment in eggs.

### (iii) Scenario 3

In column (c), we show the effects of different strengths of second male sperm precedence ( $P_2 = 0.67$  and  $P_2 = 0.8$ ), including an effect of  $p$  on the paternity variance ( $b = 1$ ). This kind of sperm precedence tends to strongly reduce the effective number of mates (see also figure 3), and therefore

reduce investment in male traits. In this case, overall investment in the male traits is often smaller than investment into eggs. Since for this kind of sperm competition the effective number of mates is very insensitive to the actual number of mates, there is essentially no relationship between actual number of mates and the optimal allocation traits (or the relationship may even be negative).

#### (iv) Scenario 4

In column (d) on the right, we allow for very strong selection ( $c = 5$ ) on pre-copulatory investment,  $q$ , combined with moderate sperm precedence ( $P_2 = 0.67$ ). Smaller  $c$ -values usually lead to selection in favour of no investment ( $q^* = 0$ ) at all. Overall investment in male traits now typically exceeds investment in eggs. Note the expanded scale of the  $x$ -axis, indicating the strong effect of higher  $q$ -values on the actual number of mates. At first, we were surprised that it is so difficult to have selection favour investment in pre-copulatory traits, and speculated that this is because of the fact that hermaphrodites have the option of investing into eggs rather than investing effort into being more successful in fertilizing the eggs of others. However, a similar model for a gonochoristic species, with a trade-off between investment into sperm and the number of mates, gave very similar results (not shown), also requiring very high  $c$ -values. Standard models of sexual selection for gonochoristic species typically assume weak selection, i.e.  $c = 1$  (reviewed in [92]), but those models assume a different kind of trade-off, namely between investment into male traits (e.g. tail length) and survival until adulthood.

## 9. General discussion

In the following, we first briefly discuss some important limitations of the model we have presented, and outline how it should be extended to include important additional factors that are likely to have a strong influence on the evolution of sexually selected traits in hermaphrodites. Then we point to the kind of empirical data that are now required to make progress in our understanding of the evolution of sex allocation and sexual selection in hermaphrodites, and which biological traits are particularly interesting.

### (a) Limitations of the current model

One important caveat of our model is that it explores just a few types of pre- and post-copulatory sexual selection, and that care should therefore be taken not to draw too sweeping conclusions from this model. Specifically, the effect of the pre-copulatory trait,  $q$ , that we have modelled here is that it allows individuals to increase the number of mates they obtain, which if all individuals express that trait, leads to a higher number of mates,  $n$ , more sperm competition, and thus a potentially diminished value of these additional mates (i.e. by simultaneously lowering the fertilization success,  $v$ ). So  $q$  could represent traits such as mate searching, mate attraction or ornaments that exploit pre-existing sensory biases in the partners (or other forms of coercion), but probably not traits such as armaments, mate guarding and nuptial gifts, which may permit the monopolization of mating partners (thus potentially reducing  $n$  and increasing  $v$ ).

Similarly, the way in which we have modelled the post-copulatory trait,  $p$ , suggests that it increases the efficiency of a unit of produced sperm in obtaining successful fertilizations, such as might result from invasive genitalia or substances that manipulate sperm storage success (thus increasing  $v$  without a direct effect on  $n$ ), but not from copulatory plugs or chemical chastity belts that prevent efficient remating (thus reducing  $n$  while increasing  $v$ ). However, as a result of the built-in effect of  $p$  on the sperm competition skews, also the former kinds of traits may in fact have an influence on the number of mates via their effect on the effective number of mates,  $n_e$ .

Given these caveats, it is clear that these other scenarios should also be explored in future models. Moreover, it may be preferable to be explicit about a specific mechanism of sexual selection one has in mind in such models, and if possible to formulate it based on some specific biological properties of a given model system, rather than simply considering them as acting on the pre- or post-copulatory level. This is also important, because it is clear that some traits can act on one level, but have strong effects on the other.

While our model confirms the main finding of Michiels *et al.* [88], namely that certain types of post-copulatory traits can evolve readily and can lead to a male-biased overall sex allocation, we also clearly show that other outcomes are possible when their assumptions are changed. Specifically, we observe that introducing paternity skews clearly reduces the parameter space in which we find male-biased sex allocation. We consider it probable that extreme post-copulatory traits, such as the ones modelled by Michiels *et al.* [88], will lead to at least some level of paternity skews, especially in internally fertilizing species (while fair-raffle sperm competition seems more probable in external fertilizers with simultaneous sperm release). We therefore caution against the conclusion put forward by that paper, that many hermaphrodites are constrained in their sexual mode and are unable to evolve towards gonochorism. Given our results, this conclusion does not seem warranted.

We would also like to point out that some of the scenarios we explored here do not appear to match certain aspects of the biology of hermaphrodites. As we have outlined above, it is now well established that many hermaphrodites show a plastic adjustment in the allocation towards sperm production when exposed to different social situations [11]. This response is not predicted by scenarios 3 and 4, so these therefore need to be treated with some caution.

### (b) Important extensions in future models

While the model we present here is a first step for a set of more general models of sexual selection and sex allocation in hermaphrodites, it is limited in a number of important ways. For one, it currently presents a strongly male-biased perspective, as it does not include female traits, such as female mating preferences, sperm digestion and cryptic female choice, which, as we have outlined above, are expected to be prevalent in hermaphrodites [65,69,77], nor does it include the (direct and indirect) costs and benefits of such traits (about which we currently know little). It seems quite probable that including such 'female' traits in models will shift the overall allocation away from 'male' traits and may therefore contribute to the stability of hermaphroditism.

Moreover, the model treats all individuals as being uniform and having fixed allocation patterns, which clearly does not match the extensive evidence for plastic sex allocation in these organisms (often also linked to the size or condition of an individual) [11]. Similarly, the model assumes that all individuals have an identical amount of reproductive resources (thus not allowing potential trade-offs between growth, maintenance and reproduction). These are strong and probably unrealistic assumptions for many hermaphrodites, and future models should aim at exploring the implications of relaxing these assumption. Finally, recent studies have outlined that hermaphrodites could show some level of sex limitation, for example, if individuals differ in how male and female fitness depends on size and condition [94,95], thus potentially leading to intra-locus sexual conflict.

### (c) Future empirical work

Recent efforts in the hermaphrodite research community have led to the formulation of an approach to quantify sexual selection on the male and female function in hermaphrodites [58]. The approach is based on measures derived from formal selection theory [59,96] which have so far primarily been used in gonochorists [97,98]. It permits assessing the importance of different stages of sexual selection along the pre- to post-copulatory axis and to identify putative underlying traits. Importantly, the approach incorporates specific aspects of hermaphrodite mating systems not fully included in earlier treatments [59,99], e.g. that mating success in one sex function can affect the own reproductive success in the other sex function (cross-sex effects) and that male and female mating success can be highly correlated as a result of reciprocal mating [58].

Briefly, the approach investigates the Bateman gradient, i.e. the strength of the relationship between a measure of mating success and the resulting reproductive success [100]. Specifically, the approach proposes that mating success and possible linked traits are measured at different stages of the pre- versus post-copulatory axis, ranging from mate encounters (e.g. mobility, activity, pheromones), copulations per encountered mate (e.g. armaments, ornaments, coercion, resistance), sperm transferred/stored per copulation (e.g. sperm production rate, sperm quality, genital morphology), fertilizations per transferred/stored sperm (e.g. seminal fluids, sexy sperm traits), hatchlings per zygote (e.g. compatibility, selective abortion) and adults per hatchling (e.g. maternal or paternal effects, differential allocation). It then permits correlations to be identified between different traits and male and female mating and reproductive success by calculating mating differentials and selection differentials for individual traits, and to explore variances and covariances of these traits, thus allowing us to identify possible sexually selected traits and how they may be constrained in their evolution [58,59,63,99]. Specifically, some traits may be under antagonistic selection between the male and female function (e.g. sperm production rate and egg production rate), while others could potentially have positive effects on both sexes (e.g. mate searching or pheromones) and this may be considered shared cost traits (*sensu* [101]). Moreover, some traits are likely to be beneficial only on either the pre- or post-copulatory level (e.g. ornaments and sperm quality), while other traits may be beneficial on both levels (e.g. seminal fluids that mark a partner as already mated). Performing such studies in hermaphrodites with different natural histories is now an important empirical aim [58,63].

## 10. Conclusions

In summary, we have argued that a profound quantitative knowledge of sexual selection is needed to fully understand the evolution of sex allocation in hermaphrodites, and that there are many links between these two concepts that have not yet been explored, either theoretically or empirically. The emphasis should therefore be on developing a broader theory base for sexual selection and sex allocation in simultaneous hermaphrodites, and to measure quantitative aspects of hermaphrodite mating interactions and their fitness consequences.

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## Appendix: details of the model

### A.1. Selection differentials, effective number of mates and LSC

The total fitness of a focal individual is

$$W = W_f + W_m = 1 - r - p - q + nv(1 - \hat{r} - \hat{p} - \hat{q}). \quad (\text{A } 1)$$

The number of mates is  $n = n(q)$  and the expected fertilization success  $v = v(r, p, q)$  is given by equation (7.2) in the main text. For any allocation trait  $x$  ( $= r$  or  $p$  or  $q$ ), the selection differential evaluated at the population level trait value  $\hat{x}$  is given by

$$\frac{\partial W}{\partial x} \Big|_{x=\hat{x}} = -1 + \left( \frac{1}{\hat{n}} \frac{\partial n}{\partial x} \Big|_{x=\hat{x}} + \frac{1}{\hat{v}} \frac{\partial v}{\partial x} \Big|_{x=\hat{x}} \right) (1 - \hat{r} - \hat{p} - \hat{q}). \quad (\text{A } 2)$$

Note that we have employed the Fisherian consistency requirement  $\hat{v} = 1/\hat{n}$ . Working out the derivative of  $v$ :

$$\begin{aligned} \frac{\partial v}{\partial x} \Big|_{x=\hat{x}} &= \frac{1}{\hat{n}} \sum_{i=1}^{\hat{n}} \frac{z_i(1-z_i)}{\hat{m}} \frac{\partial m}{\partial x} \Big|_{x=\hat{x}} \\ &= \frac{1}{\hat{n}\hat{m}} \frac{\partial m}{\partial x} \Big|_{x=\hat{x}} \left( 1 - \sum_{i=1}^{\hat{n}} z_i^2 \right) = \frac{1}{\hat{n}\hat{m}} \frac{\partial m}{\partial x} \Big|_{x=\hat{x}} \frac{\hat{n}_e - 1}{\hat{n}_e}. \end{aligned} \quad (\text{A } 3)$$

The second step follows from the assumption that the mean  $z_i$  equals  $1/\hat{n}$ , hence  $\sum z_i = 1$ , and the last step follows from (7.3). Plugging the final expression back into (A 3) gives

$$\frac{\partial W}{\partial x} \Big|_{x=\hat{x}} = -1 + \left( \frac{1}{\hat{n}} \frac{\partial n}{\partial x} \Big|_{x=\hat{x}} + \frac{1}{\hat{m}} \frac{\partial m}{\partial x} \Big|_{x=\hat{x}} \frac{\hat{n}_e - 1}{\hat{n}_e} \right) (1 - \hat{r} - \hat{p} - \hat{q}). \quad (\text{A } 4)$$

Thus,  $(\hat{n}_e - 1)/\hat{n}_e$  is seen to be the proper LSC discounting factor on the positive effect on male fitness of a larger ejaculate ( $\partial m/\partial x > 0$ ).

### A.2. Modelling paternity skew

Since the paternity shares  $z_i$  are proportions, a generic phenomenological way of modelling them is by assuming that they follow a beta distribution, a flexible method to model probability distributions for proportions ([http://en.wikipedia.org/wiki/Beta\\_distribution](http://en.wikipedia.org/wiki/Beta_distribution)). The probability density

function of a beta distribution with shape parameters  $\alpha$  and  $\beta$  can be written as

$$B(z; \alpha, \beta) = \frac{z^\alpha(1-z)^\beta}{\int_0^1 z^\alpha(1-z)^\beta dz}. \quad (\text{A } 5)$$

The mean and variance of this distribution are

$$\bar{z} = \frac{\alpha}{\alpha + \beta}, \quad V = \frac{\alpha\beta}{(\alpha + \beta)^2(\alpha + \beta + 1)}. \quad (\text{A } 6)$$

Since in our model  $\bar{z} = 1/\hat{n}$ , it follows that  $\beta = (\hat{n} - 1)\alpha$ , and the variance is then given by

$$V = \frac{\hat{n} - 1}{\hat{n}^2(\alpha\hat{n} + 1)}. \quad (\text{A } 7)$$

Clearly,  $V$  increases for smaller values of  $\alpha$ , but there is a lower bound on  $\alpha$ . In fact, the maximal variance in paternity must occur when all eggs of a sperm recipient are fertilized by a single donor. The variance in paternity then equals the binomial variance  $p(1-p)/\hat{n}$ , with  $p = 1/\hat{n}$  being the binomial success probability of fertilizing all the eggs of a given mate. The maximal value of  $V$  therefore equals  $(\hat{n} - 1)/\hat{n}^3$ , which implies  $\alpha > (\hat{n} - 1)/\hat{n}$ . Thus, the effective number of mates is bounded by

$$\frac{\hat{n}}{1 + (\hat{n} - 1)/\hat{n}} \leq \hat{n}_e = \frac{\hat{n}}{1 + (\hat{n} - 1)/(\alpha\hat{n} + 1)} \leq \hat{n}. \quad (\text{A } 8)$$

In numerical examples, we set  $\alpha = 1$ , in which case  $\hat{n}_e = \frac{1}{2} + \frac{1}{2}\hat{n}$ .

A more mechanistic approach to modelling paternity skew is to derive an expression for  $V$  based on an explicit process. One such process is sperm precedence, where each subsequent sperm donor displaces a proportion  $P_2$  of the sperm already present, assuming that a single ejaculate completely fills the sperm storage of the recipient. In a sequence of  $\hat{n}$  donors, the first donor then ends up with paternity share  $(1 - P_2)^{\hat{n}-1}$ , the last one in the sequence with  $P_2$ , and the  $j$ th donor in between with  $P_2(1 - P_2)^{\hat{n}-j}$ . This distribution has variance

$$V = \frac{2\hat{n}(1 - P_2)^{2\hat{n}-1} + (\hat{n} + 1)P_2 - 2}{\hat{n}^2(2 - P_2)}. \quad (\text{A } 9)$$

The corresponding effective number of mates is

$$\hat{n}_e = \frac{2 - P_2}{P_2 + 2(1 - P_2)^{2\hat{n}-1}}. \quad (\text{A } 10)$$

For relatively large  $P_2$ -values, this expression rapidly tends to  $(2 - P_2)/P_2$  with increasing  $\hat{n}$ . For example, if  $P_2 = \frac{2}{3}$ , the effective number of mates is effectively 2 for all  $\hat{n} > 1$  (see also figure 3b).

### A.3. Evolutionary equilibria and special assumptions for numerical examples

The selection differential for sperm allocation  $r$ , evaluated at the population value, is obtained by setting  $x = r$  in (A 4):

$$\left. \frac{\partial W}{\partial r} \right|_{r=\hat{r}} = -1 + \frac{1}{\hat{r}} \frac{\hat{n}_e - 1}{\hat{n}_e} (1 - \hat{r} - \hat{p} - \hat{q}). \quad (\text{A } 11)$$

Setting  $\hat{r} = r^*$  and solving for  $r^*$  yields the optimal sperm allocation in equation (8.1) of the main text.

Likewise, the selection differential for the post-copulatory trait  $p$  is

$$\left. \frac{\partial W}{\partial p} \right|_{p=\hat{p}} = -1 + \frac{g'(\hat{p})}{g(\hat{p})} \frac{\hat{n}_e - 1}{\hat{n}_e} (1 - \hat{r} - \hat{p} - \hat{q}). \quad (\text{A } 12)$$

Solving for  $p^*$  and combining with (A 11) gives the simple equilibrium condition

$$\frac{g'(p^*)}{g(p^*)} = \frac{1}{r^*}. \quad (\text{A } 13)$$

In numerical examples, we follow Michiels *et al.* [88] and use  $g(p) = p^a$ . This yields the solution in equation (8.3) in the main text.

Finally, the selection differential for the pre-copulatory trait  $q$  is

$$\left. \frac{\partial W}{\partial q} \right|_{q=\hat{q}} = -1 + \frac{1}{\hat{n}(\hat{q})} \left. \frac{\partial n}{\partial q} \right|_{q=\hat{q}} \frac{1}{\hat{n}_e} (1 - \hat{r} - \hat{p} - \hat{q}). \quad (\text{A } 14)$$

A positive solution to (A 14) requires that  $n(q)$  has a steep slope at  $q = q^*$ , so we take an exponential function  $n(q) = n_0 e^{cq}$  in numerical examples. This gives the solution in equation (8.4) in the main text.

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