Opinion piece

Sex allocation and sexual conflict in simultaneously hermaphroditic animals

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Links between sex allocation (SA) and sexual conflict in simultaneous hermaphrodites have been evident since Charnov's landmark paper published 30 years ago. We discuss two links, namely the potential for sexual conflict over SA between sperm donor and recipient, and the importance of post-copulatory sexual selection and the resulting sexual conflict for the evolution of SA. We cover the little empirical and theoretical work exploring these links, and present an experimental test of one theoretical prediction. The link between SA and sexual conflict is an interesting field for future empirical and theoretical research.

Keywords: cryptic female choice; sex allocation; sexual conflict; sexual selection; simultaneous hermaphrodites; sperm competition

1. INTRODUCTION

Charnov (1979) provided the foundation for sex allocation (SA) theory in simultaneous hermaphrodites (hereafter called hermaphrodites). He focused on optimal resource allocation towards male and female reproduction, given specific male and female fitness gain curves describing the relationships between resource allocation and fitness returns. SA theory has been very successful in predicting SA patterns in both hermaphroditic animals (Schärer 2009) and plants (Campbell 2000).

SA in hermaphrodites differs from that in gonochorists (species with separate sexes), in that it concerns a life-history decision about an individual's current reproduction, rather than the future reproduction of its offspring, as is generally the case in gonochorists. In support of this idea there is considerable evidence that SA is phenotypically plastic in hermaphrodites, i.e. the effort allocated to male and female reproduction (e.g. production of ejaculates versus eggs) varies with the social or nutritional context (Schärer 2009).

Charnov (1979) was the first to recognize the importance of sexual conflict (he called it male–female conflict) to understand diverse and complex reproductive adaptations in copulating hermaphrodites, and he concluded that some of these ideas 'should hold even in

[gonochorists]'. Remarkably, his contribution was published in the same year as Parker's influential paper on sexual selection and sexual conflict (Parker 1979). Sexual conflict is now a thriving research field (e.g. Arnqvist & Rowe 2005; Chapman 2006; Parker 2006), with several spectacular and well-understood examples in hermaphroditic animals (e.g. Koene & Schulenburg 2005; Chase & Blanchard 2006; Anthes *et al.* 2008).

Here, we (i) argue that plasticity in SA offers potential for sexual conflict over SA between the mating partners, (ii) present an experimental test of a prediction resulting from this, and (iii) explain how post-copulatory sexual selection and resulting sexual conflicts can affect the evolution of SA in hermaphrodites.

2. SEXUAL CONFLICT OVER SEX ALLOCATION

Charnov (1979) proposed that sperm donors (hereafter donors) should be selected to transfer ejaculates that 'turn on egg maturation and deposition', thus increasing the number of eggs fertilized by the donor. Moreover, 'counter selection would favour the recipient's attempting to stop this influence', and resulting sexual conflicts may affect the evolution of 'neuro-hormonal control of egg maturation and deposition'.

However, in multiply mating species, such a manipulation of the recipient may also increase the number of eggs available to competitors. Donors may thus also attempt to prolong the recipient's 'interval until [the] next copulation' by reducing mating motivation, e.g. by 'destroying the [recipient's] ejaculatory organ' (Charnov 1979). Disrupting the recipient's male mating motivation is particularly effective if mating occurs 'mostly to give sperm away'. This is because mating of the recipient increases the strength of sperm competition that the donor experiences in that recipient, particularly with reciprocal mating. In addition, by disrupting male mating motivation in the recipient, the donor may obtain a benefit by weakening that individual as a future sperm competitor. However, such a benefit would only materialize under specific conditions, e.g. where the same individuals interact repeatedly.

Finally, the recipient's male allocation may use reproductive resources that, assuming a trade-off between male and female function, might otherwise be allocated to the female function. Disruption or down-regulation of the male function, or direct upregulation of the female function in the recipient, may thus increase the fitness of the donor. These ideas were later fleshed out and extended to generate predictions about sexual conflicts over SA (Michiels 1998; Schärer 2009).

Empirical support for such manipulations is currently weak. Numerous studies have shown that, when exposed to more mating partners, individuals increase rather than decrease male allocation, as predicted by standard SA theory, while their female function either remains unchanged or decreases (reviewed in Schärer 2009). By contrast, a study on the pond snail (*Lymnaea stagnalis*) suggested that male allocation was lower and female allocation higher in snails that mated more often (Koene *et al.* 2006), lending support to the manipulation hypothesis. However, follow-up experiments now

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One contribution of 16 to a Special Feature on 'Sexual conflict and sex allocation: evolutionary principles and mechanisms'.

suggest that there is a trade-off between egg size and egg number, which can be affected by prostate secretions transferred during mating (Koene *et al.* in press; J. M. Koene 2009, personal communication). As female allocation was estimated by egg number only, it needs to be clarified whether this actually represents a change in female allocation.

3. A TEST OF THE 'A PRIORI BIAS' HYPOTHESIS

(a) Introduction

Michiels (1998) predicted that a consequence of the expected manipulation by the donor is that recipients may anticipate feminization, by *a priori* biasing their SA towards the male function before mating, so that they achieve optimal SA once they have been feminized. He speculated that this might partly explain the importance of prostate glands and the widespread occurrence of protandry (i.e. an earlier maturation of the male function) among hermaphrodites. Here, we test a qualitative prediction of this hypothesis by comparing the SA of virgin and mated individuals in the free-living flatworm *Macrostomum lignano*.

(b) Materials and methods

Juvenile worms hatching from eggs laid within 2 days (starting on day 1) were obtained from mass cultures, and distributed on day 11 to 24-well plates either alone (virgins, $n=56$) or in sets of two (pairs, $n=62$) in the usual conditions (Schärer & Ladurner 2003; Janicke & Schärer 2009). Worms were allowed to mature and transferred to fresh plates on days 21, 28 and 35. Body, testis and ovary size were measured according to standard procedure (Schärer & Ladurner 2003) on days 36–41 in one individual per replicate. Testis size/(testis size + ovary size) was used to estimate SA (Schärer 2009).

(c) Results

Virgins were somewhat smaller than worms from pairs ($t_{116}=2.29$, $p=0.023$), did not differ in the size of their ovaries ($t_{116}=0.24$, $p=0.81$), but had highly significantly smaller testes ($t_{116}=8.16$, $p<0.0001$) (conclusions unaffected when correcting for body size); leading to a more male-biased SA in pairs ($t_{116}=9.21$, $p<0.0001$) (figure 1).

(d) Discussion

Our results do not support the *a priori* bias hypothesis. Virgins are more female rather than more male biased compared with worms from pairs, and investment in ovaries does not change in response to mating status. Instead, the results agree more with a phenotypically plastic response to mating group size (i.e. the number of mates), where little allocation is channelled into sperm production when no mating can occur. Contrasts between pairs and larger groups were previously tested and show that male allocation increases (Schärer & Ladurner 2003) and female allocation, at least sometimes, decreases (Schärer *et al.* 2005; Janicke & Schärer submitted) in larger mating groups. The higher male allocation in pairs compared with virgins suggests that these worms spend
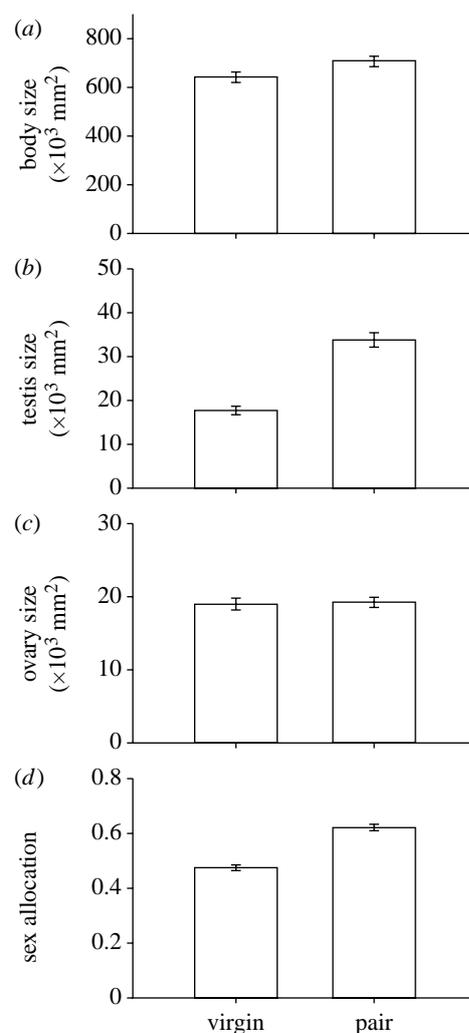

Figure 1. Effect of growing up as a virgin or in a pair in the flatworm *M. lignano* on (*a*) body size, (*b*) testis size, (*c*) ovary size and (*d*) sex allocation (testis size/(testis size + ovary size)). See text for statistics.

considerable effort on male allocation even in the absence of sperm competition, in agreement with the recent finding that worms appear unable to distinguish novel from familiar mates (P. Sandner & L. Schärer unpublished data). The slight protandry in *M. lignano* is thus probably not due to an *a priori* bias, but rather linked to resource-dependent SA (Vizoso & Schärer 2007).

4. POST-COPULATORY SEXUAL SELECTION, SEXUAL CONFLICT AND THE EVOLUTION OF SEX ALLOCATION

Charnov (1979) also explored the implications that Bateman's principle (Bateman 1948) may have had for the evolution of reproduction in hermaphrodites. Specifically, he assumed that 'fertilized egg production by an individual is limited not by the ability to get sperm, but by resources allocated to eggs', and concluded that 'this suggests that sperm competition […] and a form of male–female conflict have played important roles in the evolution of hermaphroditism'. Insights that Charnov drew from this view are that in hermaphrodites, 'individuals copulate not so much to gain sperm to fertilize eggs as to give sperm away

(to gain access to another's eggs)' and that 'fitness through male function depends upon the ability to have one's sperm used as gametes (instead of perhaps food [...])'.

Thus, Charnov (1979) recognized the potential for conflict between donor and recipient over the fate of the transferred ejaculate. He thereby not only clarified the role of sperm competition (explored more deeply in Charnov 1996), but also recognized the importance of post-copulatory female choice (later termed cryptic female choice, Thornhill 1983), and the potential for sexual conflict and sexually antagonistic coevolution resulting from their interaction. Specifically, post-copulatory sexual selection often leads to sexual conflict (Parker 2006), because donors that have managed to transfer sperm to a recipient should be under strong selection to prevent the recipient from removing that sperm from the fertilization set (see also Koene & ter Maat 2001; Chase & Blanchard 2006).

The outcome of sexually antagonistic coevolution can strongly affect the shape of the male fitness gain curve, and thus the evolution of SA. As outlined in detail elsewhere (Schärer 2009), the reason for the often saturating male fitness gain curve is local sperm competition (LSC, i.e. competition between related sperm, termed in analogy to local mate competition in gonochorists). Small mating group size is not the only process that leads to LSC; so does efficient sperm displacement (Charnov 1996). Even if recipients have many partners the donor will only compete against few other donors, if the sperm of earlier mates are efficiently removed. Moreover, cryptic female choice can have a similar effect by also removing sperm of some donors from the fertilization set. In hermaphrodites the effect on male allocation strongly depends on how the recipient chooses (as was previously shown for gonochorists, Greeff & Parker 2000). If a fixed proportion of a donor's sperm is removed, this leads to a more female-biased SA than expected based on mating group size alone. Conversely, if a fixed amount is removed, this can lead to an overall male-biased SA, because high allocation to male function can pay to overcome this barrier (E. van Velzen, L. Schärer & I. Pen, unpublished data).

Given that sperm displacement and cryptic female choice can strongly limit the fitness return from male allocation, it is not surprising that a male strategy that (at least initially) allows to bypass both processes should spread, as predicted by Charnov (1979) and discussed in more detail by Michiels (1998). This may explain the widespread occurrence of hypodermic impregnation (which Charnov called haemocoelic insemination) among hermaphrodites. Here, sperm is injected directly into the body of the partner, rather than deposited in the sperm-receiving organ, where it may be available for manipulation by both the other donors and the recipient. A possible consequence of a spread of hypodermic impregnation is that sperm of different donors will again compete in a way that approximates a fair-raffle-type sperm competition, leading to a SA that should more closely match the mating group size.

5. CONCLUSIONS

There are several evident links between SA and sexual conflict in hermaphrodites, most of which were pointed out by Charnov exactly 30 years ago. Unfortunately, empirical tests of these ideas are still scarce, but the coming of age of research on the evolutionary reproductive biology of hermaphrodites offers exciting opportunities to do justice to Charnov's landmark contribution.

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