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REVIEW

Reproductive strategies in hermaphroditic gastropods: conceptual and empirical approaches[1]

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Abstract: An individual optimizes its reproductive success by adopting a particular reproductive strategy. Studying the details of a reproductive strategy leads to an understanding of how sexual selection acts, as the former is the process via which the individual reproduces successfully. Hermaphroditic gastropods display a bewildering diversity of reproductive strategies, which may be due to their mode of gender expression, when compared with well-studied separate-sexed species. Extensive theoretical, observational, and experimental research has been conducted on this topic. However, despite our knowledge about the reproductive system of hermaphroditic gastropods, we still need to fill the gap between pre- and post-copulatory processes and reproductive success. Here, we review and propose conceptual and empirical approaches aimed at understanding reproductive strategies of hermaphroditic gastropods. In sum, our suggestions are (*i*) to focus on sex-biased traits, (*ii*) to take biologically reliable measurements at both the pre- and post-copulatory level that relate to reproductive success, and (*iii*) to examine the fitness consequences of biased sex allocation.

Key words: hermaphrodite, paternity longevity, reproduction, sperm competition, sperm storage, sex allocation, sexual selection.

Résumé : Les individus optimisent leur succès de reproduction en adoptant des stratégies reproductives qui leur sont propres. L'étude des détails d'une stratégie de reproduction permet une meilleure compréhension des mécanismes de sélection sexuelle, puisqu'il s'agit du processus par lequel l'individu se reproduit avec succès. Comparativement à des espèces bien étudiées dont les sexes sont distincts, les gastéropodes hermaphrodites présentent une extrême diversité de stratégies de reproduction qui pourrait être le fait du mode d'expression du sexe. De nombreux travaux théoriques, expérimentaux et d'observation sur ce thème ont déjà été réalisés. Cependant, malgré les connaissances acquises sur le système reproducteur de gastéropodes hermaphrodites, le lien entre les processus pré- et post-copulatoires et le succès de reproduction n'est pas encore bien établi. Nous passons en revue et proposons des approches conceptuelles et empiriques visant à mieux comprendre les stratégies de reproduction des gastéropodes hermaphrodites. Nous suggérons (*i*) de mettre l'accent sur les caractères dont la distribution dépend du sexe, (*ii*) de prendre des mesures fiables sur le plan biologique aux stades pré- et post-copulatoires, qui sont reliées au succès de reproduction et (*iii*) d'examiner les conséquences d'une détermination asymétrique des sexes sur l'aptitude. [Traduit par la Rédaction]

Mots-clés : hermaphrodite, longévité de la paternité, reproduction, concurrence des spermatozoïdes, stockage des spermatozoïdes, détermination du sexe, sélection sexuelle.

Introduction

A reproductive strategy is defined as a set of (behavioural, morphological, physiological) traits that optimize reproductive success of an individual under given local conditions. Basically, for sexually reproducing organisms, there are two different reproductive strategies: a male one and a female one. This is also true for hermaphrodites, though they optimize their overall reproductive success as an individual by using both male and female reproductive strategies (Morgan 1994; Anthes et al. 2010). This trivial, yet crucial, difference makes their reproductive strategies interesting, complicated, and sometimes extreme (reviewed in Baur 1998; Michiels 1998; Koene 2006; Anthes and Michiels 2007*a*; Jordaens et al. 2007). As a matter of fact, some of the arguably most bizarre reproductive strategies are found in hermaphroditic animals, such as stabbing mating partners with accessory reproductive organs (see below). Their extreme reproductive habits primarily attract researchers interested in sexual selection, albeit hermaphrodites were initially overlooked in evolutionary biology due to the focus on sexual dimorphism as the main consequence of sexual selection (e.g., Darwin 1871). Given this background, in this review, we propose the need for proper empirical approaches to unveil the reproductive strategies of hermaphrodites and their evolutionary trajectories. We open by describing conceptually why reproduction of hermaphrodites is fascinating. Then, we summarize three main complications to studying their reproductive strategies. In the subsequent sections, we then focus on these complications and put forward potential empirical solutions.

Why are hermaphrodites interesting and important in the study of reproductive strategies?

One of the exemplary bizarre acts of mating in hermaphrodites is found in many land snail species that stab their mating partners with calcareous needles, called love darts, during mating. Detailed research on the garden snail, *Cornu aspersum* (O.F. Müller, 1774) (previously referred to as *Cantareus aspersus* (O.F. Müller, 1774) or *Helix aspersa* (O.F. Müller, 1774)), has found that mucus on the love dart contains an allohormone which manipulates the female reproductive tract of the partner (Koene and Chase 1998; Rogers and Chase 2001; Koene and Ter Maat 2001). By introducing the allohor-

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mone into the partner's blood, the snail obtains higher paternity success with the sperm that it subsequently donates, i.e., it fertilizes more of its partner's eggs (Landolfa et al. 2001; Chase and Blanchard 2006). As illustrated by this example, such eccentric reproductive strategies of hermaphrodites require detailed study to understand sexual selection processes in such animals. Moreover, the vast majority of sexual selection research has concentrated on species with separate sexes, while hermaphroditism is present in 24 of the 34 animal phyla (Jarne and Auld 2006; Michiels 1998; Anthes 2010) and is present in approximately 5% of animal species and most plant species (respectively, Jarne and Auld 2006; Eppley and Jesson 2008).

It is noteworthy that hermaphrodites provide unique opportunities to test pertinent hypotheses about sexual selection, which are impossible to test in gonochorists (separate sex species). For instance, one of the essential questions is "what are the necessary ingredients for evolution of sex differences or sexual dimorphism via sexual selection"? The fundamental difference between males and females lies in the size and number of gametes produced, which is referred to as anisogamy (Parker et al. 1972). Though anisogamy alone could be sufficient for sexual selection to produce sexual dimorphism, we cannot examine this hypothesis using gonochorists because they already exhibit sexual dimorphism (Schärer et al. 2012). In contrast, because simultaneous hermaphrodites, by definition, do not have sexual dimorphism, it here becomes testable whether anisogamy is necessary and sufficient for sexual selection to act. By using a hermaphroditic freshwater snail species, Pélissié et al. (2012) revealed that in the freshwater snail *Physa acuta* Draparnaud, 1805 (= *Physella acuta* (Draparnaud, 1805)), the male function seems to be under stronger sexual selection than the female function. This indicates that, in this species, sexual dimorphism is not required for sexual selection to act. This clearly illustrates that studies of reproduction in hermaphrodites can contribute greatly to expand our general understanding of evolution on reproductive life history.

Three main complications of investigating reproductive strategies of hermaphrodites

Despite the above, there are some complications when studying reproduction of hermaphrodites, compared with gonochorists. First, a crucial aspect of hermaphroditism is that many traits of an individual, e.g., body size or colour, influence both male and female reproductive success (Arnold 1994*a*; Morgan 1994). Clearly, in gonochoristic animals, one can measure body size of males and females independently, but this is not possible in simultaneous hermaphrodites. Therefore, to investigate the male or female reproductive strategy of a hermaphroditic species, one has to be careful in the choice of target traits, which should preferably be highly biased for either sex function. For instance, love darts in land snails are obviously "male" traits, whereas ovulation is a clear "female" trait. With such sex-biased traits, one can detect not only which individual is successful as male or female, but also speculate on the mechanisms behind it (e.g., in *C. aspersum*, good "shooters" gain higher male reproductive success because their successful injection of allohormone would lead to more of their sperm being stored). This can then be followed up by investigating the relationships between these sex-biased traits and (or) other traits (e.g., whether good shooters are larger: Chase and Vaga 2006). Thus, to unravel their complex reproductive strategies, we think it is a promising starting point to identify and focus on male- or female-biased traits of hermaphrodites.

A second difficulty in investigating reproductive strategies of hermaphrodites is the quantification of reproductive success at a reasonably high resolution. Obviously, reproductive success is one of the fundamental variables for the theoretical framework of sexual selection (e.g., Bateman 1948; Anthes et al. 2006*a*; Anthes et al. 2010), and empirically crucial when one wants to identify successful males or females. However, reproductive success can be surprisingly demanding to quantify even in gonochorists, because many species are promiscuous, have internal fertilization, and can store and use sperm after copulation (Birkhead and Møller 1993; Neubaum and Wolfner 1999). Moreover, many simultaneous hermaphrodites have the additional complication that they can self-fertilize (selfing). This means, even if a hermaphroditic individual mates only once, it already possess two types of sperm for fertilization of eggs: allosperm (its mating partner's sperm) and autosperm (its own sperm). Although it is difficult to quantify reproductive success and its variation, it is necessary and highly rewarding because it provides us with detailed insight into sexual selection.

The third main difficulty is the flexible sex allocation of hermaphrodites, as this can severely interfere with the investigation of their reproductive strategies. In this review, we discuss sex allocation of simultaneous hermaphrodites in terms of their internal decision of distributing reproductive resources between their male and female functions (Charnov 1982; Schärer 2009; Schärer and Pen 2013). They alter their sex allocation flexibly depending on various factors, e.g., group size (Schärer and Ladurner 2003) or external environmental factors (Ter Maat et al. 1983, 2012). The implication of such changes in sex allocation is that even if one found successful "males" under a specific, controlled condition, one has to be careful with generalizing that conclusion; these successful "males" might not be successful at all under different, more natural, and (or) realistic conditions.

Here, we review these complications in hermaphroditic gastropods and propose empirical approaches aimed at a better understanding of their reproductive strategies. First, we describe the wide distribution of hermaphroditism in gastropods and briefly summarize the theoretical framework of sexual selection in hermaphrodites. Then, we focus on each of the three complications above (target traits, quantification of reproductive success, sex allocation) to explain why they are problematic and what would be a useful approach to take. Lastly, we summarize our suggestions and provide a more precise definition of the goal in studies of sexual selection in hermaphrodites.

Hermaphroditism in gastropods

Gastropoda is the largest class of the Mollusca, which is the second largest phylum in the animal kingdom. There are three main orders: Prosobranchia (sea, freshwater, and land snails), Opisthobranchia (sea slugs), and Pulmonata (land and freshwater snails and slugs), but note that their phylogenetic relationships are still under debate (e.g., Jörger et al. 2010). Hermaphroditism is widespread in all of these three groups, particularly in the Opisthobranchia and Pulmonata (Baur 1998; Jarne and Auld 2006; Jarne et al. 2010; Valdés et al. 2010). Pulmonata has two suborders, Basommatophora (freshwater snails) and Stylommatophora (land snails and slugs). Most mature snails are simultaneous hermaphrodites, although a few species show sequential hermaphroditism (Jarne and Auld 2006).

Reproductive modes of gastropods are highly diverse. Most gastropods have internal fertilization, but some prosobranch species are external fertilizers (Jarne and Auld 2006). Although a few sea slug species inseminate hypodermically, copulation (with a copulatory organ) is the most common mode of sperm transfer. Within those copulating, many species copulate unilaterally, meaning that one individual plays the male role, while the other plays the female role (e.g., sea slugs, and land and freshwater snails). Other species usually copulate via reciprocation, which can occur simultaneously (both play male and female at the same time; e.g., many land snails and slugs: Davison et al. 2005) or sequentially (the male and female roles are alternated once or repeatedly; e.g., sea slugs: Leonard and Lukowiak 1984; Anthes and Michiels 2007*a*). Moreover, as they are simultaneous hermaphrodites, they possess both types of gametes and can potentially self-fertilize. The ability to self-fertilize shows considerable variation across species. For example, most sea slugs are obligatory outcrossers (Baur 1998), while in snail species, this varies between extremely high selfing rates and strong preference for outcrossing due to inbreeding depression (Escobar et al. 2009, 2011). The diversification of reproductive modes is a fruitful and challenging context in which to study reproductive strategies in hermaphroditic gastropods.

In this review, we focus on hermaphroditic gastropods that transfer their sperm via copulation or hypodermic injection, as our main interest lies in post-copulatory processes and sperm competition (Parker 1970). In addition, we included sequentially hermaphroditic gastropods in this review because changing sex does not mean reproductive success via the first sex role ends (Dupont et al. 2006; Proestou et al. 2008; Brante et al. 2011). That is, after a sequential hermaphrodite becomes female, it can still obtain male reproductive success due to sperm stored in its previous mating partners.

Brief theoretical background of sexual selection in hermaphrodites

Historically, researchers believed that hermaphroditic animals could not undergo sexual selection, owing to the limited sensory ability of lower animals (Darwin 1871). In addition, since simultaneous hermaphrodites are both male and female at the same time, it was believed that they would have lower potential for the evolution of sexually selected traits (Darwin 1871; Morgan 1994; Arnold 1994*a*; Greeff and Michiels 1999*a*).

In contrast to these beliefs, hermaphroditic animals show extraordinary reproductive behaviours, attracting researchers to investigate these in the context of sexual selection. One of the early comprehensive reviews about reproductive strategies in hermaphroditic animals was done by Ghiselin (1969). He pointed out the reproductive advantages of hermaphroditism from a theoretical and systematic point of view. Subsequently, Charnov et al. (1976) greatly extended the theory to explain maintenance and evolution of hermaphroditic reproduction. This, in turn, suggests that hermaphrodites do compete to fertilize as many ova as possible, just like gonochorists (Charnov 1979). Subsequently, many theoretical studies have been carried out on sexual selection in hermaphrodites, even given their limitations compared with gonochorists (Arnold 1994*a*; Morgan 1994; Greeff and Michiels 1999*a*, 1999*b*; Anthes et al. 2006*a*, 2010). Recent work even proposed that the action of sexual selection in hermaphrodites can be more extreme than that in gonochorists (Michiels and Koene 2006; Bedhomme et al. 2009; Michiels et al. 2009). Furthermore, many empirical researchers have provided sufficient circumstantial evidence of the act of sexual selection (reviewed in Leonard 1991, 2006; Baur 1998; Michiels 1998; Koene 2006; Chase 2007; Jordaens et al. 2007; Abbott 2011). Thanks to the developed theoretical frameworks and many empirical reports, it is now clear that hermaphrodites are under sexual selection, and as a consequence, possess reproductive strategies to achieve higher reproductive success.

However, conclusive empirical evidence demonstrating sexual selection in hermaphroditic animals is scarce. We are still far removed from understanding how different sexual selection acts in hermaphrodites in comparison with gonochorists. A recent exciting advancement is the generalization of the Bateman gradient theory to also encompass hermaphrodites (Anthes et al. 2010). The Bateman gradient is the regression between relative mating success and relative reproductive success, and characterizes the overall intensity of sexual selection (Jones 2009). The extension to hermaphrodites provides theoretical background to systematically investigate if hermaphrodites are under selection and, if so, how it acts (Anthes et al. 2010; Schärer and Pen 2013; Shuster et al. 2013). To date, a few empirical surveys have tried to quantify the action of sexual selection in hermaphrodites (Lorenzi and Sella 2008; Anthes et al. 2010; Pélissié et al. 2012; J.N.A. Hoffer and J.M. Koene, unpublished data). Yet, there is still a considerable potential to improve our resolution of the measurement of sexual selection and reproductive strategies in hermaphrodites. To encourage further empirical studies, in the following, we refer to the three main complications identified above and propose approaches to deal with them.

Target traits: a choice between sex-biased and shared cost traits

Since hermaphrodites have male and female interests to satisfy with their reproductive strategies, successful individuals would maximize the number of offspring produced by optimally balancing those produced via the male and female function (Arnold and Duvall 1994; Arnold 1994*a*; Morgan 1994; Jordaens et al. 2007; Anthes et al. 2010). To study these strategies in hermaphrodites, one would have two fundamental questions: (1) who has successfully reproduced and (2) how did they achieve this? To deal with these questions, one has to select and measure target traits related to their reproduction and reproductive success.

As target traits, we argue that the most promising traits in hermaphrodites are sex-biased ones. Obviously, hermaphrodites have various traits that could affect male and female reproductive success differently (Arnold and Duvall 1994; Morgan 1994). For instance, dart shooting of *C. aspersum* affects male reproductive success (Landolfa et al. 2001; Chase and Blanchard 2006), but it is not expected to influence the shooter's female reproductive success. Also, the traits relating to gametes (egg, ovulation for female function; sperm, seminal fluid, traumatic mating behaviour for male function) are sex-specific, or highly sex-biased, and to a large extent, determine male or female reproductive success (e.g., Table 1 in Anthes et al. 2008; Table 9.1 in Jarne et al. 2010). Focusing on these sex-biased traits makes things relatively straightforward. Pointing out who is successful as male and (or) female will also allow us to investigate the mechanisms via which they obtain their high reproductive successes. As such, the approach to use sex-biased traits can be fruitful for disentangling the network of reproductive strategies in hermaphrodites.

This approach, however, has some drawbacks. First, sex-biased traits are not abundant, by definition, in hermaphrodites. Except for the traits listed above, almost all traits are shared, or at least considerably influence reproductive success via both functions. Second, sex-biased traits are sometimes difficult to measure. For instance, seminal fluid proteins of hermaphrodites would be interesting sex-biased traits of the male function, as shown in various separate sexed animal groups (e.g., Swanson and Vacquier 2002; Gillott 2003; Chapman 2008). To quantify the variation of these proteins between individuals, detailed knowledge is required and appropriate techniques need to be developed (e.g., Sirot et al. 2011). To date, however, few studies on seminal fluid proteins in hermaphrodites have been carried out (but see Koene et al. 2009*a*, 2010). Therefore, the current limited availability of sex-biased traits, as well as the technical difficulties with their quantification, can hamper the investigation of hermaphroditic taxa.

To investigate reproductive strategies of hermaphrodites, it is also interesting to target shared traits (e.g., body size, body colour), or traits that influence both male and female reproductive success (e.g., mating success, mate searching). Here, we refer to these as "shared cost traits" (see Charnov et al. 1976; Schärer and Pen 2013). Shared cost traits are abundant and easy to measure. In particular, mating success is one of the most important reproductive characters, because it is considered a causality of sexual selection (Arnold 1994*b*). Moreover, body size has received extensive attention in sex allocation studies (Ghiselin 1969; Angeloni et al. 2002; Schärer 2009). Given this theoretical background, the availability and measurability of shared cost traits

Table 1. Summary of sperm precedence (P_2) or paternity of last sperm donor (P_n) value reports in hermaphroditic gastropods.

	Type of								
Order and species	Hermaphroditism	Insemination	Range	P_2 (mean ± SD or SE)	No. of recipients tested (*N*)	P_2 monitoring time per recipient	Sperm storage duration	Source of variance	References
Prosobranchia									
Crepidula coquimbensis Brown and Olivares, 1996	Sequential	Copulation	0.27–0.46	0.35±0.91 (SD)	5	3 capsules, 30 days	>360 days	*a*	1
Opisthobranchia									
Alderia modesta (Lovén, 1844)	Simultaneous	Hypodermic	0.00–0.88	0.40±0.06 (SE)	13	3 egg masses	13–16 days PL50	*b*	2
Aplysia californica	Simultaneous	Copulation (unilateral)	0.00–1.00	0.73±0.09* (SE)	20	1 egg mass, 7 days	41 days at max.	*c*	3
Pulmonata									
Bulinus africanus (Krauss, 1848)	Simultaneous	Copulation (unilateral)	—	0.49	10	4 days	123 days at max.	*d*	4
Bulinus cernicus	Simultaneous	Copulation (unilateral)	0.00–1.00	0.52±0.33 (SD)	27	?	70 days at max.	*d*, *e*	5
Lymnaea stagnalis	Simultaneous	Copulation (unilateral)	0.10–1.00	0.60±0.28 (SD)	8	1st egg mass	116 days at max.	*d*	6
Cornu aspersum (*Helix aspersa*, *Cantareus aspersus*)	Simultaneous	Copulation (reciprocal)	0.00–0.72	0.27*	35	1st clutch?	1460 days	*f*, *g*	7
			—	0.23±0.04 (SE)	38	1st clutch		*f*, *h*	8
			0.00–1.00	0.40±0.37 (SD)	22	1st clutch		*f*, *i*	9
			—	0.24±0.06* (SE)	13	1st clutch		*j*, *k*	10
			0.00–1.00	0.48±0.07 (SD?)	19	1st clutch?		*j*, *f*	l, 11
Arianta arbustorum	Simultaneous	Copulation (reciprocal)	0.00–1.00	0.43±0.06 (SE)	35	>3 clutches, >2 years	>360 days	*j*, *k*	12
			0.00–0.94	0.39±0.33 (SD)	9	1st clutch?		*j*, *m*	13
			0.00–0.90	0.27±0.26* (SD)	28	2 clutches?		*c*, *n*	14

Note: Source of variance are as follows—(*a*) extra male supplied to field-collected females; (*b*) laboratory-raised and field-collected recipients are pooled; (*c*) field-collected mating pairs; (*d*) laboratory-reared individuals or strain; (*e*) we pooled data of experiments 1–3 from Rollinson et al. (1989) so that effects of different age and mating intervals are confounded; (*f*) field-collected, mature individuals; (*g*) successful dart shooting increases paternity gain; (*h*) mucus from digitform glands increases paternity gain; (*i*) "good" shooters obtained higher paternity; (*j*) field-collected, immature individuals; (*k*) time interval between two matings affects paternity success; (*l*) mating order and reproductive morphology affect paternity success; (*m*) comparison between different populations; (*n*) young adults showed higher last male precedence. References are as follows—1: Hoagland (1978), Brante et al. (2011); 2: Angeloni (2003); 3: Angeloni et al. (2003), Ludwig and Walsh (2004); 4: Rudolph and Bailey (1985); 5: Rollinson and Wright (1984), Rollinson et al. (1989); 6: Cain (1956), Koene et al. (2009); 7: Rogers and Chase (2002); 8: Taylor (1900), Chase and Blanchard (2006); 9: Landolfa et al. (2001); 10: Evanno et al. (2005); 11: Garefalaki et al. 2010; 12: Baur (1988), Baur (1994*a*); 13: Kupfernagel and Baur (2011*a*); 14: Kupfernagel and Baur (2011*b*).

*Significant difference from a mean P_2 value of 0.5.

seem to provide a promising starting point for trait-based research.

However, when adopting a shared cost trait as a target trait, we have to be aware of the serious constraint, which is the correlation between male and female reproductive success. For instance, in hermaphrodites, male and female mating success seem to be highly correlated to each other, even in unilaterally copulating model systems (Anthes et al. 2010; Pélissié et al. 2012; Minoretti et al. 2011; J.N.A. Hoffer and J.M. Koene, unpublished data), although some general traits might be predominantly selected for via one sex function (e.g., human pelvic bones: Hogervost et al. 2009; Koene 2012). As a consequence, one cannot discriminate if it is a male or female reproductive strategy to mate (as male and (or) female) more often than others (Michiels et al. 2003). In other words, we cannot firmly conclude that a high mating rate might be either beneficial for male reproductive success, as is often the case in separate-sex animals (Bateman 1948), or for female reproductive success (Jones et al. 2000). Probably, both scenarios are plausible in hermaphrodites, and one can pinpoint which individual is successful as male and (or) female. The problem is that one cannot investigate how they achieved high reproductive success if we only focus on shared cost traits.

In summary, we recommend to target sex-biased traits to study the reproductive strategies of hermaphrodites. This allows us to interpret results readily relating to either male or female strategies. Moreover, many sex-biased traits are extreme, making them fascinating to study, such as sexual stabbing behaviour and dart morphology (Koene and Schulenburg 2005; Koene and Chiba 2006) or transferal of seminal fluid proteins (Anthes and Michiels 2007*a*; Koene et al. 2009*a*, 2010; Benke et al. 2010). A second option would be to focus on shared cost traits. They are abundant and easily measureable. However, the interpretation of data would be problematic due to the difficulty of relating them exclusively to either male or female strategies. Of course, the ultimate goal to study reproductive strategies in hermaphrodites is to understand the network of all the significant life-history traits relating to male and female reproductive success (Arnold and Duvall 1994; Arnold 1994*a*). As a first step, it is necessary to carefully consider what such target traits could reveal.

Determinants of reproductive success

Reproductive success is one of the most important variables, not only in terms of the theoretical framework for quantifying sexual selection (Bateman 1948; Arnold and Duvall 1994; Arnold 1994*a*; Morgan 1994; Anthes et al. 2010), but also for investigating reproductive strategies in hermaphrodites. The definition of reproductive success is the number of (successful) offspring produced that survive to adulthood (i.e., next generation). In contrast to this rather simple definition, empirical measurement of reproductive success is often challenging, due to internal fertilization, multiple mating, sperm storage, and nonrandom fertilization between sperm donors. Moreover, in hermaphrodites, there is an additional layer of complexity: self-fertilization (selfing; Jarne and Charlesworth 1993). Although some species are incapable of selfing (Baur 1998), most hermaphroditic gastropods can potentially fertilize their own eggs. It, therefore, is crucial to know such details about the reproductive system of one's study species, and use this knowledge to define a measurement for reproductive success that is as biologically realistic as possible. To guide the decision about which information is most relevant, in this section we review pre- and post-copulatory processes in hermaphroditic gastropods, respectively, and suggest which traits would be significant in terms of reproductive success in this group.

Pre-copulatory processes: sex role preference and mate choice

In internally fertilizing animals, the act of copulation is defined as the moment when sperm is introduced into the recipient's reproductive tract. Anything that happens before that moment is considered pre-copulatory (Koene 2012). Initially, hermaphrodites were mainly characterized as animals with limited, if any, mobility, poor sensory ability, and low population density, which was all suggestive of scarce mating opportunities (Darwin 1871; Ghiselin 1969; Charnov et al. 1976). This view was supported by their selfing ability and general lack of social structure in a population (e.g., territory, social ranking, or parental investment; Baur 1994*b*). All of these aspects did not argue for strong precopulatory sexual selection. However, recent work has convincingly shown that hermaphroditic gastropods are highly promiscuous, often exhibit a nonrandom mating system (reviewed in Baur 1998; Anthes and Michiels 2007*a*; Jordaens et al. 2007), and may even display social interactions with conspecifics (social facilitation: Vernon 1995; Baur and Baur 2000). All of these newly discovered features imply the high potential for pre-copulatory sexual selection in hermaphrodites.

To obtain reproductive success via the male and female function, hermaphroditic gastropods usually copulate, except for a few preferentially selfing species (e.g., Tian-Bi et al. 2008). Prior to copulation, outcrossing hermaphrodites choose whom to mate with (= mate choice) and which sex role they prefer (= sex role preference). Note that these two choices need not be mutually exclusive to each other. For instance, if a hermaphrodite is very eager to mate as a male, it might not care about whom it mates with (Halliday 1983; Jordaens et al. 2007). Thus, we argue that these two choices are part of the same continuum of decision making that occurs prior to copulation. Hence, although we make a distinction between sex role preference and mate choice in the following text, the reader should bear in mind that ultimately these decisions interact with each other and are often very hard to separate clearly.

Aside from reviewing these two pre-copulatory processes, we will also discuss their significance for overall reproductive success. In short, we suggest focusing on the relationship between pre-copulatory processes and reproductive success or fitness for future studies (see also Anthes et al. 2006*a*).

Sex role preference

Hermaphrodites with unilateral copulation clearly have two possible mating roles, male or female. But even in reciprocal mating systems, individuals can choose how much sperm they donate and (or) receive from their mating partners; that is the land snail *Arianta arbustorum* L., 1758 (Baur et al. 1998). Because of the difference in costs and benefits in assuming each mating roles, it has been proposed that hermaphrodites will have a sex role preference. This preference has been studied extensively in theory, with some empirical supports (reviewed in Anthes et al. 2006*a*). There are essentially three proposed hypotheses: (1) female-driven role preference, (2) male-driven role preference, and (3) preference depending on male and female fitness gain (Leonard and Lukowiak 1984, 1991; Leonard 1999; Greeff and Michiels 1999*b*; Anthes et al. 2006*a*).

During the last decades, the expectation was put forward that the female role was preferential in hermaphroditic mating systems with internal fertilization, because the availability of eggs is controlled by the female function. This idea seems to be supported by the mating behaviour of the sea slug California aglaja, *Navanax inermis* (J.G. Cooper, 1863), which swaps mating roles repeatedly (Leonard and Lukowiak 1984). The repeated donation and receipt of sperm within one mating interaction was interpreted as an assurance of paternity (Leonard and Lukowiak 1984, 1991). This process is called sperm trading (or conditional reciprocity), defined as only donating (more) sperm when sperm is also received, which was largely inspired by egg trading in external fertilizing hermaphroditic fish species (Fischer 1980, 1981).

Another school of thought argued that sperm trading is driven by male interest, not female, because of considerable investment in an ejaculate (Greeff and Michiels 1999*a*; Michiels et al. 2003). Although a single sperm cell may be relatively cheap to produce, many spermatozoa (and additional seminal fluid substances) required for a paternity gain can be costly (Dewsbury 1982). Furthermore, as shown by recent studies, many hermaphrodites are highly promiscuous, which leads to sperm competition (Michiels 1998; Baur 1998; Anthes and Michiels 2007*a*; Jordaens et al. 2007). In addition, efficient sperm storage and sperm digestion further enhance competition for paternity gain (Greeff and Michiels 1999*b*; Michiels et al. 2003; Beese et al. 2006, 2009). Indeed, the great pond snail, *Lymnaea stagnalis* (L., 1758), invests considerably in its male function (De Visser et al. 1994; Koene et al. 2009*a*; Hoffer et al. 2010). Thus, sperm trading in hermaphrodites can also be explained by the high cost of ejaculates (Greeff and Michiels 1999*a*; Michiels et al. 2003; Anthes et al. 2006*a*).

Neither of the two hypotheses above seem to find full empirical support for the occurrence of reciprocity in the different investigated systems, as detailed studies often did not support conditional reciprocity (in Opisthobranchs: Anthes and Michiels 2007*a*; in various hermaphroditic animals: Chaine and Angeloni 2005; Anthes et al. 2006*a*; Jordaens et al. 2009). To deal with this intra- and inter-specific diversity in sex role preference and mating behaviours, Anthes et al. (2006*a*) proposed a more flexible model. Their gender ratio hypothesis assumes that the preference depends on male and female potential fitness gain. So, when they can get higher female fitness gain, they prefer to mate as female, and vice versa. Although the landscape of male and female fitness gain needs verification, the large flexibility of this model seems quite appropriate to cover mating strategies of hermaphroditic gastropods.

Of course, there are many factors influencing sex role preference in hermaphroditic gastropods. We, therefore, highlight a few potential factors hereafter. This will also illustrate that, although the gender ratio hypothesis is quite promising, our understanding of reproductive strategies has not yet reached the level to apply it in full to any study system. Therefore, it is essential to consider the various factors involved.

Availability of seminal fluid and sexual isolation

The great pond snail, *L. stagnalis*, has a clear determining factor for its male role preference, which is the availability of seminal fluid in the prostate gland (De Boer et al. 1997; Koene and Ter Maat 2005). After 8 days of sexual isolation, the snails become eager to mate as males, but do not seem reluctant to mate as female (Van Duivenboden and Ter Maat 1985). Intriguingly, this implies different pathways for the motivation of male and female mating preference; we will here focus on the male role. For *L. stagnalis*, on the one hand, it is costly to mate as a male. One elegant piece of evidence comes from experimental work in which male mating behaviour was surgically eliminated; consequently, these snails produced far more eggs than control individuals (De Visser et al. 1994; Koene et al. 2009*a*) even when they are only allowed to perform the male role (Hoffer et al. 2010). On the other hand, they may not be able to stop their gamete and accessory gland substance production completely, which is reflected in their spontaneous egg laying even under unfavourable conditions (Ter Maat et al. 1983, 2012). Although they can re-allocate their resources to growth (Koene et al. 2008), the snails seem to prefer to mate as males when they have plenty of seminal fluid available (De Boer et al. 1997; Koene and Ter Maat 2005). Clearly, using what is available at a given moment is one (opportunistic) way of optimizing gain via male reproductive success.

The availability of ejaculate may be a general determinant of male role preference in Pulmonata, as an increased mating motivation after a period of isolation has been found in some other snails (European ambersnail, *Succinea putris* (L., 1758): Dillen et al. 2008; *Physa heterostropha pomilia* Conrad, 1834: Wethington and Dillon 1996; *Physa gyrina* (Say, 1821): McCarthy 2004; *Biomphalaria glabrata* (Say, 1818): Vernon and Taylor 1996; Table 2 in Anthes et al. 2006*a*). Isolation also seems to influence sex role preference in sea slugs (Table 2 in Anthes et al. 2006*a*), but this was interpreted as a mechanism to either avoid risk of sperm competition or obtain sperm to reproduce (see further details in Mate choice). Interestingly, in the freshwater snail *P. acuta*, an opposite pattern was found: seeming to prefer the female role after 30 days of isolation (Facon et al. 2007). The authors suggest this to be most likely due to depletion of stored allosperm, which is important because this species experiences severe inbreeding depression, and is reluctant to self-fertilize.

Behavioural factors and mate stabbing

The sea slug *Siphopteron quadrispinosum* Gosliner, 1989 shows an intriguing example of sex role being determined by interaction between mates. During the pre-copulatory behaviour, each individual (tries to) stabs its mating partner using the spiny appendage branched from its penis, called penial papilla or “stylet” (Anthes and Michiels 2007*a*, 2007*b*). When they stab each other almost simultaneously, reciprocal sperm transfer takes place. However, if one of them is late or fails to stab, the stabber acts as male only (Anthes and Michiels 2007*b*). In this species, the incidence of unilateral copulation is as common as reciprocal copulation (Anthes and Michiels 2007*a*). This research group is uncovering that too frequent mating is costly for the sea slug *S. quadrispinosum*: when mating rates were higher than their natural rate, their egg production declined (Lange et al. 2012). This cost may be related to the physiological costs and (or) manipulation via hypodermic injection. This example indicates that the details of behavioural interactions can determine the choice of sex role.

The abovementioned traumatic mating behaviour of sea slugs readily reminds us of love dart stabbing of land snails. However, in *C. aspersus*, the size of the spermatophore transferred did not change when they failed to stab properly (Chase and Vaga 2006). This may imply that the quality of stabbing behaviour does not reflect a sex role preference in this species.

Age and body size

When considering sex role preference in hermaphroditic gastropods, one important factor is maturation. Even if conditions are preferable for the female role, animals first need to mature as females to enjoy such benefits. Most hermaphroditic gastropods have a time discrepancy between maturation of their male and female function. The range varies considerably; many simultaneous hermaphrodites mature as males slightly earlier than as females (protandry; Jordaens et al. 2007). In many sequential hermaphrodites, the timing of maturation depends on body size, so the range can be quite long, with some individuals remaining male (or female) their entire life (Baur 1998). Therefore, careful experimentation is needed to see if a species prefers to mate as male or whether it did not mature as female yet, as found in the sea slug *Chelidonura sandrana* Rudman, 1973 (Sprenger et al. 2009).

In addition, because animals with indeterminate growth often show strong correlation between age and body size (Jordaens et al. 2007), one needs to figure out which has prominent influence on sex role preference. For example, Hermann et al. (2009) showed that sex role preference of *L. stagnalis* is mostly determined by age, not size. The snails tend to mate more as males at a relatively young age, their preference gradually shifting towards the female role as they get older (Hermann et al. 2009). The interpretation of these results would be related to mate choice and sex allocation, but it is a nice illustration of possible confounding factors on sex role preference.

Mate choice

In contrast to gonochorists, who can only mate with conspecifics of the opposite sex, hermaphrodites can mate with any other mature conspecific. Nevertheless, they would still discriminate who they mate with. Reasons for being choosy are often found in various costs and risks of copulating (energy expenditure, time investment, resource investment, predation, survival, infection risk, and manipulation or injury inflicted by mates). The optimal reproductive strategy would include optimal mate choice. To date, there is plenty of circumstantial evidence of mate choice in hermaphroditic gastropods. Here, we give an overview of several important factors that affect mate choice.

Pre-copulatory, courting behaviours

Almost all hermaphroditic gastropods have pre-copulatory and (or) courting behaviours that can play a role in the assessment of mate quality. Many stylommatophoran species show long and elaborate pre-copulatory behaviours (reviewed in Tompa 1984; Baur 1998; Leonard et al. 2002; Reise 2007), while freshwater snail species' courtship is usually shorter and simpler (reviewed in Jarne et al. 2010). Also, opisthobranch species have relatively stereotyped pre-copulatory behaviours (reviewed in Anthes and Michiels 2007*a*). These behaviours not only provide chances to detect the species identity of a potential conspecific mate (e.g., Wiwegweaw et al. 2009), but also their quality as mating partners. For example, by determining whether the potential partner is infected by parasites (Webster et al. 2003; Webster and Gower 2006), is genetically related (Facon et al. 2006), has the same handedness (Koene and Cosijn 2012), was previously encountered (Koene and Ter Maat 2007), or has recently mated with a different individual (to avoid intense sperm competition: Haase and Karlsson 2004; Anthes et al. 2006*b*). Despite the above examples, empirical or quantitative evidence for mate choice via pre-copulatory or courting behaviours is limited. Also, the proximate mechanism has never been investigated in detail: they may detect quality via water-borne chemicals, substances in mucus trails, or tactile information.

Mating history and sperm competition

One of the prominent factors on mate choice is mating history. From the male perspective, which is in contrast to the female's, insemination should occur with as many partners as possible to ensure its paternity throughout the population (Bateman 1948). However, this "ideal" situation is rarely reached because there are substantial costs for the production and transfer of ejaculates (Dewsbury 1982). To optimize reproductive strategies, hermaphrodites should choose mates with a high reproductive potential. For instance, by avoiding partners that they have recently mated with or that have recently mated with others. The latter would lead to intense sperm competition. Two sea slug species seem to display such mate choice behaviours (*Aeolidiella glauca* (Alder and Hancock, 1845): Haase and Karlsson 2004; *C. sandrana*: Anthes et al. 2006*b*).

Mate novelty or virginity of mates can also be important for mate choice in hermaphroditic gastropods (as it is in separate-sexed species, e.g., Wilson et al. 1963; references in Häderer et al. 2009). When mating with a virgin, a sperm donor can potentially monopolise the reproductive resources of its mate. When choosing to mate with novel partners, a donor can distribute its sperm widely and possibly overcome the risk of incompatibility with particular mates. In the freshwater snail *L. stagnalis*, male acting snails seem to not discriminate between virgins or not (Koene et al. 2008), but they do prefer to mate with new partners, referred to as the Coolidge effect (Wilson et al. 1963; Koene and Ter Maat 2007). These experiments partially indicate that they may recognise mate novelty via their mucus trails, but this remains to be confirmed (Koene and Ter Maat 2007). In contrast, the Coolidge effect was not found in the freshwater snail *B. glabrata* (Häderer et al. 2009). One of the reasons for this contradictory result is that *B. glabrata* cannot obtain sufficient benefits from discriminating mate novelty. This is partially supported by the high mating rate in *B. glabrata*, which is 4–13 times within 12 h (Vernon and Taylor 1996). Further studies in various other hermaphroditic gastropods are needed to test if mate novelty or virginity is of general importance for mate choice.

Genetic background

A clear example of female mate avoidance depending on genetic background was found in the freshwater snail *P. acuta* (Facon et al. 2006). In experiments with two wild populations, the female acting snails swung their shells and bit the partner's phallus more frequently when these partners were siblings (Facon et al. 2006). Because *P. acuta* shows strong inbreeding depression, this mate avoidance behaviour might shorten unwanted mating attempts and copulation durations (inbreeding avoidance; Facon et al. 2006). In contrast, two freshwater snail species of the genus *Biomphalaria* prefer to mate with sympatric individuals, which was interpreted as a local adaptation against parasitic infection (Rupp and Woolhouse 1999; see also below). *Physa gyrina* also shows more intense avoidance behaviour when they mate with snails from other populations, although the interpopulation pairs had higher mating rates than intrapopulation pairs (McCarthy 2004). As the last study indicates, further studies are required to test consequence of avoidance behaviour, for instance by investigating how efficient the avoidance behaviour of *Physa* is, and whether unwanted mating results in reduced reproductive output. This would require a clearly aimed experimental design combined with application of genetic markers to assess reproductive success.

Parasitic infection

Parasite infection can substantially influence reproduction and growth of hosts, as reviewed for pulmonates in Jordaens et al. (2007). In terms of mate choice, it would be highly beneficial to discriminate between infected and noninfected mates, as the freshwater snail *B. glabrata* has been shown to do (Webster et al. 2003; Webster and Gower 2006). Aside from this study, this type of mate choice and the resulting reproductive strategy after infection has received little attention, even though parasite infection is widespread and severely interacts with the host's life-history traits and evolution (Ballabeni 1995; Sorensen and Minchella 2001).

Body size

Body size seems not to be a general indicator for mate quality. However, there is a general trend of greater egg production in larger animals (Anthes and Michiels 2007*a*; Jordaens et al. 2007), so it may seem beneficial to mate with larger partners. Such a preference would generally lead to size assortative mating. Although this has been found in several groups of sea slugs, it rarely occurs in land and freshwater snails (reviewed in Anthes et al. 2006*a*; Anthes and Michiels 2007*a*; Jordaens et al. 2007; Baur 2010). This pattern is not so surprising. Firstly, body size is a shared cost trait, so it affects both female and male reproductive success. Hence, approaching or copulating with such a large partner might have a trade-off: they might obtain benefits by mating with a large "female" but may, at the same time, experience costs by being exploited (via seminal fluid components) by a large "male" (e.g., Y. Nakadera, C. Blom, and J.M. Koene, unpublished data). Secondly, body size cannot indicate current reproductive potential of a hermaphrodite precisely enough. Given that infection with some parasites leads giant growth of hosts (gigantism), in such species there may actually be relatively strong selection against choice based on large body size (Ballabeni 1995; Sorensen and Minchella 2001). Also, many land snail species with long life spans reach their growth asymptote soon after maturation or have determinate growth. Thirdly, as discussed above, body size often correlates with age, thus confounding conclusions from mate choice experiments (e.g., Norton et al. 2008).

Conclusion

For outcrossing hermaphrodites, pre-copulatory processes are essential for achieving reproductive success. As described above, there are plenty of studies on this subject, but yet some components require further research. Here, we suggest two lines of inquiry. First, sex role preference and mate choice are expected to considerably depend on physiological costs of the male or female function, e.g., costs of ejaculates in terms of egg production. These costs can explain large variation in sex-role preference and (or) mate choice between different species. Second, it is promising to focus on the quantitative relationship with reproductive success or fitness (Anthes et al. 2006*a*).

Post-copulatory processes

With insemination, post-copulatory processes commence and a new set of reproductive strategies come into play (Koene 2012). Post-copulatory processes are expected to be important for reproductive success of hermaphroditic gastropods, as they generally have lengthy matings with multiple partners, can digest and store sperm, fertilize internally, and potentially self-fertilize (Bateman 1948; Michiels 1998; Baur 1998; Michiels et al. 2003; Koene 2012; Parker et al. 2013). Hence, in the post-copulatory phase, sperm donors will be strongly selected to assure their own paternity via sperm competition (Charnov 1979; Schärer and Pen 2013), and sperm recipients should optimize their own reproductive success by (cryptic) female choice (Eberhard 1996). As a consequence, hermaphroditic gastropods are predicted to have evolved elaborate reproductive strategies in post-copulatory processes.

In contrast to their conspicuous and extreme pre-copulatory behaviours, post-copulatory processes are often more covert, mainly due to internal fertilization and therefore more difficult to study. Consequently, conclusive experimental evidence is still limited. For instance, one of the fundamental measurements in sperm competition is sperm precedence, P_2 value, which is the proportion of eggs fathered by the second partner in a controlled double-mating trial (Parker 1970; Simmons and Siva-Jothy 1998). This index provides a brief indication of sperm competition in a study system, as found in insects (Table 10.1 in Simmons and Siva-Jothy 1998). We, therefore, conducted a literature survey for studies reporting P_2 values in hermaphroditic gastropods. To the best of our knowledge, there is a surprisingly limited number of articles published (Table 1), although some general patterns in P_2 values still emerge (see below). This collection of P_2 values is rather disappointing when compared with the extensive number of studies focussing on pre-copulatory processes in hermaphroditic gastropods.

However, this limited research on post-copulatory processes is not entirely unexpected, and seems largely hampered by the particular life history of gastropod species focussed on. For example, reproductive success of sea slug species is difficult to measure because of their planktonic life stage. This also prohibits culturing these species for several generations in the laboratory. In many land snails and slugs, it takes a lot of effort to let them mate under experimental conditions because they generally have long pre-copulatory phases. For instance, pairs of the land slug *Deroceras gorgonium* Wiktor, Vardinoyannis, and Mylonas, 1994 can take up to 9 h until they start copulating (Reise et al. 2007). They also have a long lifespan, requiring much effort to culture further generations. Some snail species, like freshwater snails, are relatively easy to do experiments with, but even they have a pitfall in studies on post-copulatory processes. Due to lack of a good marker for allosperm, it is still unknown where they store received sperm, even though their sperm storage ability has been known since the 1950s (Cain 1956; Koene et al. 2009*a*; reviewed in Jarne et al. 2010). Despite these difficulties and constraints in studying post-copulatory processes in hermaphroditic gastropods, it is a very fruitful area to expand our knowledge of their reproductive strategies.

Here, we highlight several potential aspects of post-copulatory processes in hermaphroditic gastropods. Because most post-copulatory processes have not been directly investigated, we discuss many pre-copulatory behavioural traits affecting post-copulatory processes. Our primary aim is to encourage further research to fill the gap between pre- and post-copulatory processes and reproductive success.

Promiscuity and repeated mating

Hermaphroditic gastropods are typically promiscuous. For instance, in the sea slug genus *Chelidonura*, copulations in the field frequently occur between three or more animals (= chain copulations; Anthes and Michiels 2007*a*). Pulmonates also generally mate promiscuously (reviewed in Baur 1998; Jordaens et al. 2007), but the degree of promiscuity depends on various factors, e.g., inbreeding depression or mate availability (Escobar et al. 2011). Hence, some species mate several times within a short time period, while others do not mate even though mates are available (Wirth et al. 1997). Despite a few exceptions, multiple mating is a general trend in hermaphroditic gastropods and together with internal fertilization creates the conditions for sperm competition (Parker 1970).

Polygamous and repeated copulation can enhance or reduce the female reproductive success of recipients (Sprenger et al. 2008*b*, 2011; Lange et al. 2012; Hoffer et al. 2012; see also review by Jordaens et al. 2007; Shuster et al. 2013). This is highly relevant for the male reproductive success of donors, because even if they outcompete other donors in sperm competition, it is ultimately egg production that determines the number and (or) quality of offspring sired. One of the general explanations for the positive effect of repeated mating is cryptic female choice: fresh allosperm should be preferred for outcrossing, especially just after hibernation (Chen and Baur 1993). Alternatively, recipients can overcome genetic incompatibility with particular donors or may prefer to have high genetic variation in their offspring. Interestingly, Sprenger et al. (2008*a*) observed that the polyandrously mated sea slug *C. sandrana* produces larger veligers than slugs that were repeatedly mated with the same partner. For that particular case, no benefit was found for offspring with larger body size, but the effect of repeated or polygamous mating on both partners, as well as offspring quality, would be interesting to test in other taxa.

One of the explanations for the negative effect of repeated mating for female reproductive output lies in the cost of donating and receiving ejaculates (Hoffer et al. 2010). Hermaphrodites usually play both roles, male and female. Especially reciprocal mating, in which both roles need to be performed, could bring physiological costs caused by extreme pre-copulatory behaviours (Lange et al. 2012). Furthermore, according to sex allocation theory (see also Sex allocation), hermaphrodites will spend their resources on either ejaculates in expense of egg production or vice versa. This is indeed found in the freshwater snail *L. stagnalis*, which produces about 1.6 times more eggs if it does not donate or receive ejaculates (Hoffer et al. 2010). In addition, the reduction of egg mass production can be explained by manipulation of the sperm donors for their own benefits (see Male accessory gland secretions). In summary, repeated mating affects female reproductive outputs, although the exact mechanism still remains to be identified. For further studies, quantification of costs for each mating role and gamete production, quality of offspring for mate manipulation, and paternity assignment for testing cryptic female choice would be informative.

Sperm transfer

Because the number of sperm transferred is an important aspect for sperm competition (Parker 1982; Birkhead and Møller 1998), it is worthwhile to examine this in hermaphroditic gastropods. They have generally two different ways to transfer sperm. For instance, many sea slugs and all freshwater snails transfer an ejaculate in the form of semen (composed of sperm plus seminal fluid), while many land snails and land and sea slugs transfer a special package of sperm or a spermatophore. Spermatophores of land snails are often very species-specific and display a high level of diversity; some being relatively large, calcified, and elaborately spined (Tompa 1984; Baur 1998). The adaptive significance of spermatophores is not entirely clear, but most likely functions to avoid sperm digestion and assist in efficient sperm storage (Lind 1973; Baur 1998, 2010; but see Garefalaki et al. 2010; Kimura and Chiba 2013).

These two ways to transfer sperm could have implications for which sexual role controls the number of sperm that get transferred. Obviously, being a sperm recipient is not a passive role (Eberhard 1996; Sprenger et al. 2008*b*, 2011; Facon et al. 2006), and because insemination is an interaction between the recipient and donor's reproductive organs, the size of the ejaculate could be controlled by both individuals. Spermatophores, in contrast, are made inside the donor's reproductive tract (often before insemination), so the donor predominantly controls its content (although mate manipulation of this process by the recipient is possible).

Experimental research about the number of sperm transferred is quite limited in many hermaphroditic gastropods. The freshwater snail *L. stagnalis* alters the number of sperm transferred depending on its partners mating history; virgin snails transfer and receive more sperm than mated snails (Loose and Koene 2008). Intriguingly, a recent study showed that much more sperm is donated when the mating partner is feminized (i.e., male function eliminated); such recipients produce nearly twice as many eggs as control recipients (De Visser et al. 1994; Hoffer et al. 2010). As indicated by the latter, these results suggest that the number of sperm transferred is one of the crucial factors for successful sperm competition. In contrast, studies on spermatophore-transferring land snails did not support this prediction. The number of sperm they transfer show high variation, but no correlation with mating history, body size, or dart shooting success (*A. arbustorum*: Baur et al. 1998; *C. aspersus*: Rogers and Chase 2001; Chase and Vaga 2006; *Succinea putris*: Jordaens et al. 2005, but see Dillen et al. 2008). Of course, aspects of mate choice remain to be tested, but these results imply other factors could have strong influence on sperm competition, e.g., accessory gland secretions.

Male accessory gland secretions

Several different male accessory glands can be found in hermaphroditic gastropods (e.g., prostate gland, digitform gland, penial gland), and their secretions seem to be used to increase donors' paternity success and possibly manipulate their mates. This suggests that such secretions fulfil an important role in post-copulatory male reproductive strategies, most notably sperm competition.

As shown in various taxa, seminal fluid from a prostate gland is not only essential for fertilization, but also functions in various ways to gain paternity (reviewed in Swanson and Vacquier 2002; Gillott 2003; Chapman 2008). The first seminal fluid protein, ovipostatin, was fully characterized in the freshwater snail *Lymnaea stagnalis* (Koene et al. 2010). This seminal fluid protein is novel, indicating its rapid and dynamic evolutionary history (as has also been shown for separate sexed animals; reviewed in Swanson and Vacquier 2002). Ovipostatin suppresses egg mass production of recipients, consistent with previous observations of reduced egg mass production after multiple mating (Van Duivenboden 1983; Van Duivenboden et al. 1985), as well as with experimental injection of prostate gland products (Koene et al. 2009*b*). Further study showed that repeatedly mated snails invest more per egg than snails with limited mating opportunity, although total egg mass production declines (Hoffer et al. 2012). This implies that the sperm donors' manipulation is aimed at gaining offspring with higher quality. Although the cost of receiving ovipostatin and the fitness benefit of larger eggs and offspring remain to be examined, this experimental evidence indicates a sexual conflict in *L. stagnalis* with a crucial role for seminal fluid proteins in male reproductive strategies of hermaphrodites in general.

The best documented male secretion is the mucus from the digitform glands that are located at the base of the muscular sac containing the love dart in the garden snail *C. aspersum.* Prior to transferring its spermatophore, it stabs its mating partner with a love dart, which is a calcareous needle-like structure. Our current understanding of the function of this behaviour is to transfer mucus to gain higher paternity success, although this traumatic behaviour has evoked quite some speculations (reviewed in Koene 2006; Chase 2007). Successful dart shooting snails do obtain higher paternity (Rogers and Chase 2001; Landolfa et al. 2001) because of the mucus injected and not the physical piercing (Chase and Blanchard 2006). Koene and Chase (1998) found that the mucus from the digitform glands induces changes in the female tract of the recipient that ultimately led to a delay in sperm digestion (in the bursa copulatrix), and results in higher paternity gain. Furthermore, the high diversity of love dart morphology and stabbing behaviour provides fruitful opportunities to study further details (Koene and Schulenburg 2005; Koene and Chiba 2006). For instance, in *Euhadra quaesita* (Deshayes, 1850), injected mucus made recipient snails reluctant to re-mate (Kimura et al. 2013). Nonetheless, all of these results demonstrate that dart shooting is used to influence the sperm recipient to obtain higher paternity success.

Another interesting accessory gland is the elaborate penial gland of the land slug *Deroceras panormitanum* (Lessona and Pollonera, 1882), which is used for cutaneous application of its secretion after they transfer their spermatophore (Benke et al. 2010). Behavioural observations of abundant mucus production during copulations and licking its own body after copulation might imply a potential function of this secretion (Reise 2007; Benke et al. 2010). Although the exact function of this penial gland secretion remains to be revealed experimentally, slugs of the *Deroceras* genus are likely candidate for further studies on this reproductive strategy because of their highly diverse penial morphology, extremely long and elaborated pre-copulatory and courting behaviour, and very short sperm transfer (Reise et al. 2007; Reise 2007).

There is much circumstantial evidence for the important roles that male accessory gland secretions play in obtaining (higher) male reproductive success, but the exact functions and reproductive consequences are mostly unknown. For instance, the sea slug *S. quadrispinosum* seems to hypodermically inject prostate gland secretion into its partner to "force" the recipient to only play the female role (Anthes and Michiels 2007*b*). Clearly, further investigation is needed, not only to determine the physiological functions of the secretions, but also to uncover the reproductive consequences for donors by quantifying paternity gain (e.g., Landolfa et al. 2001; see Sperm competition).

Sperm competition

Paternity success is one of the ultimate parameters of male fitness gain. To date, by using phenotypic (albinims) or genetic markers, double-mating experiments in eight hermaphroditic gastropods have been carried out to measure sperm precedence, P_2 value (Table 1; note that the use of albinism as a genetic marker, if it has not been back-crossed, could lead to a biased estimate of the P_2 value: Vianey-Liaud et al. 1996). According to Parker's (1970) prediction, these data indicate the existence of strong sperm competition since P_2 values lie around 0.5 with considerable variance. Also, in contrast to insects, they do not often show first male precedence (Parker 1970; Simmons and Siva-Jothy 1998).

The variance in P_2 values in this group implies that mating order is not a dominant factor in determining paternity success. For instance, sea slugs have extremely high mating rates, fecundity, and mortality rates in the planktonic stage. Such life-history traits may inhibit a reliable assessment of a P_2 value and paternity success. One possible determinant for paternity success in sea slugs might be quality of eggs (Sprenger et al. 2008*a*), but this needs further investigations. Moreover, as shown for dart shooting in *C. aspersum*, detailed knowledge about the mechanism that determines paternity gain is required (Simmons and Siva-Jothy 1998). Furthermore, because offspring are often genotyped shortly after double-mating experiments, P_2 values may only partially capture paternity success, especially in animals with efficient long-term sperm storage (Baur 1994*a*; Table 1; see Sperm digestion and storage). In summary, in addition to mating order, paternity success in these hermaphrodites might be determined by quality of eggs, dart shooting, or sperm storage duration.

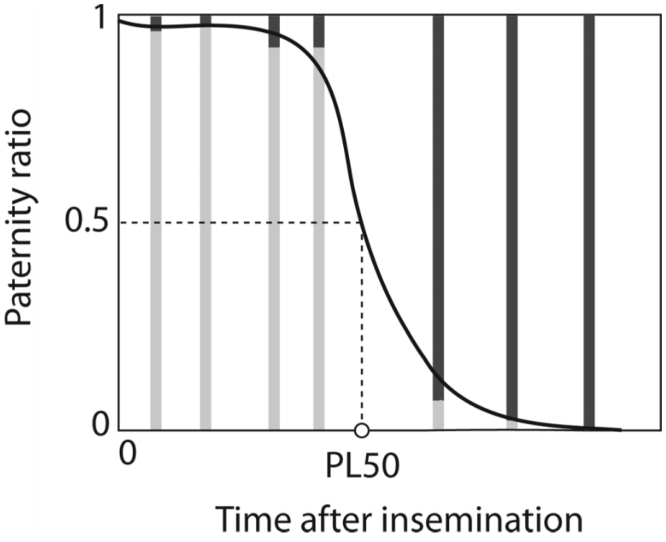
Sperm digestion and storage

Hermaphroditic gastropods often have efficient sperm digestion, which can substantially influence sperm competition and paternity success. After sperm is transferred to a recipient, most sperm is digested in the bursa copulatrix. Only a small amount of allosperm is stored for fertilization in the female sperm storage organ (also referred to as spermathecae or seminal receptacle, depending on study species). For instance, in the land snails of the *Helix* or *Cornu* genus, only 0.025%–0.1% of allosperm reaches the sperm storage organ (Lind 1973; Rogers and Chase 2001). Although it has often been speculated that recipients can extract resources from digested sperm, this has not yet been demonstrated experimentally.

Sperm storage is a common reproductive feature in the animal kingdom (Birkhead and Møller 1993; Neubaum and Wolfner 1999), and crucial for gaining paternity success. First of all, it is the last phase before the fertilization event (Arnold and Duvall 1994). Second, sperm storage provides sperm donors with a prolonged paternity success without additional mating. In pulmonates, next to selfing, one of the best studied reproductive traits is sperm storage (reviewed in Baur 1998; Jordaens et al. 2007). As expected from the complex reproductive morphology of pulmonates (Leonard 1991), it takes hours to move allosperm to the sperm storage organ after insemination (Lind 1973; Rogers and Chase 2001; Koene et al. 2009*a*; Baur 2010; Y. Nakadera, C. Blom, and J.M. Koene, unpublished data). In pulmonates, allosperm goes through the vaginal duct, uterus, and spermoviduct, which is not a proper duct but rather an evaginated ridge (Jarne et al. 2010; Baur 2010). Unfortunately and surprisingly, the exact location of sperm storage in Basommatophora is unknown (Koene et al. 2009*a*), but sperm storage organs in Stylommatophora have been extensively studied. Studies at intra- and inter-species levels have revealed that morphological diversity of sperm storage organs in land snails have been formed by interactions between sperm donors and recipients, as well as life-history traits, such as reproductive modes (Haase and Baur 1995; Baminger and Haase 1999; Davison et al. 2005; Beese et al. 2006, 2009; Koemtzopoulos and Staikou 2007; also in Opisthobranch: Anthes et al. 2008). After allosperm is stored, it can be used for a long time; storage duration of allosperm ranges from a few weeks to more than a year, indicating their efficiency to maintain allosperm viable, even during a hibernation period (Baur 1988). At the same time, their efficient sperm storage indicates prolonged paternity gain.

Given these sperm storage characteristics, one of the biologically realistic metrics for paternity gain would be a combination of P_2 values and sperm storage duration. Usually, except for two studies in *A. arbustorum* and *Bulinus cernicus* Morelet, 1867 with relatively low fecundity, P_2 values were measured in eggs laid just after a second copulation (Table 1). In contrast, all of these species have considerably long sperm storage duration, which implies that the P_2 value may not be the best estimate of paternity success of donors in reproductive system with efficient sperm storage. Here, we propose a new metric for paternity success, which we refer to a paternity longevity 50 (PL50), which is the time point when paternity of a focal donor declines to 50% (Fig. 1). When paternity of a donor declines gradually or abruptly along with time after copulation, one can calculate PL50 from a logistic model with paternity data (focal sired or not). The middle point of the logistic model is the most invariable point (depending on the shape of possible models), so one can compare paternity longevity reliably. Several published data in this group show abrupt or gradual increase or decrease of their paternity ratio (*L. stagnalis*: Cain 1956; *B. glabrata*: Vianey-Liaud et al. 1996; *Aplysia californica* J.G. Cooper, 1863: Ludwig and Walsh 2004; *P. acuta*: Dillon et al. 2005). As an example, we calculated PL50 of *A. californica* from Fig. 1B in Ludwig and Walsh (2004), which resulted in 15.7 ± 5.61 days (mean ± SD). Because the paternity was not identified in the same way in most other studies, this metric can still reveal variation of allosperm storage duration among species. Furthermore, by using the model for PL50, one can quantify paternity success by multiplying the number of offspring produced by recipients. The quantified variation of paternity longevity or paternity gain may then explain diversified and sometimes extreme pre-copulatory processes.

Fig. 1. Hypothetical pattern of paternity longevity. The bars indicate occurrence of egg laying after insemination event(s) at time zero. Light and dark gray colours on the bars show the paternity ratio of different sperm donors, with light gray indicating the focal sperm donor. The solid line is a fitted logistic model to the paternity data. From this line, the paternity longevity 50 (PL50) can be determined, which is at the point when the focal's paternity has declined to 50% of total paternity.



Cryptic female choice

Animals with internal fertilization should have considerable opportunities for cryptic female choice (Eberhard 1996). In hermaphroditic gastropods, recipients may actively choose "good" or "sexy" sperm to fertilize their eggs, to increase their own reproductive success. One possible candidate where such choice can take place is the sperm storage organ, especially in land snails (Bojat and Haase 2002; Bojat et al. 2002). Their complex and partitioned structure has been suggested to allow for cryptic female choice for sperm from particular donors (Haase and Baur 1995). However, experimental support for this is lacking. Further study, including application of molecular techniques to genotype sperm in storage (compartments), would be useful for understanding their reproductive strategies.

Conclusion: filling the gap

In contrast to well-studied reproductive strategies in pre-copulatory processes, post-copulatory reproductive strategies have vast unexplored possibilities for promising future studies, e.g., accessory gland secretion, sperm competition, and cryptic female choice. To unveil post-copulatory reproductive strategies of this taxa, the application of molecular techniques is highly promising to quantify paternity success. Furthermore, the gap between the conventional measurement of sperm competition (P_2 values) and the actual reproductive biology (e.g., sperm storage) is often ignored, but can be remedied quite easily in follow-up work (Table 1). Given detailed knowledge of their efficient sperm storage, paternity longevity or PL50 would be a biologically relevant measure to quantify reproductive success and compare this across hermaphroditic (gastropod) species.

Sex allocation

The last important factor for investigating reproductive strategies in hermaphroditic gastropods is sex allocation. Given that most hermaphrodites can change their sex allocation flexibly, the general applicability of any finding about a mating strategy may be severely limiting. Here, we discuss sex allocation in the sense of an individual's plastic internal decision about how much energy to allocate to either sex function (i.e., not the evolutionary stable condition for reproductive resource investment: Charnov 1982; Schärer 2009).

In contrast to gonochorists, which need at least a generation to alter their sex allocation in terms of sex ratio, simultaneous hermaphrodites are known for their flexible adjustment of sex allocation depending on various factors. In hermaphroditic gastropods, various abiotic or biotic factors influencing sex allocation are known: mating group size and density (Sprenger et al. 2011), rearing condition (Locher and Baur 2000*b*; Koene and Ter Maat 2004; Koene et al. 2008), mating opportunity (Locher and Baur 2000*a*; Karlsson 2001; Koene et al. 2006; Hoffer et al. 2012; Lange et al. 2012), age (Hermann et al. 2009; Sprenger et al. 2009), body size (Angeloni 2003; Chaine and Angeloni 2005; Ter Maat et al. 2007), parasitic infection (reviewed in Jordaens et al. 2007), food availability (Adamo and Chase 1991; Locher and Baur 2002), O_2 contents and cleanness of environment (Ter Maat et al. 1983), light cycle (Ter Maat et al. 2012), and temperature (Dogterom et al. 1984). However, because most studies only investigate the change in allocation towards one sex function, not both simultaneously (Schärer 2009) or growth (Koene et al. 2006), the exact mechanism and fitness consequences of the flexible altering of sex allocation remain to be tested. Nonetheless, given the effects of these various factors on sex allocation, it is clear that allocation of resources to the male and (or) female function is plastic in these animals.

In the context of investigating reproductive strategies in hermaphrodites, one of the serious questions is how realistic a documented strategy is. Usually, experimental biologists try to control everything in the laboratory: light, temperature, medium, food, instruments for measurement, and certainly, animals. Under such controlled conditions (clean medium with absence of pathogens, parasites, and predators), findings about reproductive strategies may be unrealistic in the sense that such conditions rarely, if ever, will be encountered in nature. Although it is entirely appropriate to acclimatize animals to the laboratory conditions, hermaphrodites will most likely adjust their sex allocation to these conditions, even if it is a rare situation in the wild. Hence, if one then identifies "successful males" under the controlled conditions, such individuals may not be successful at all under different, more realistic, conditions. So, this is then clearly something that needs to be tested in follow-up experiments.

To expand the understanding of reproductive strategies in a broad sense, we proposed to examine (*i*) when and how hermaphrodites alter their sex allocation and (*ii*) what the consequence is for male and female reproductive success when sex allocation is biased. Quantification of sex allocation needs to be done carefully (Schärer 2009); particularly in gastropods, due to their ovotestis, one can at least indirectly measure and compare sex allocation of hermaphrodites between laboratory and wild populations. The general expectation is that any target hermaphroditic gastropod (e.g., wild population) will allocate more resources to either the male or female function, because they potentially get higher benefits from this allocation (Schärer 2009; Schärer and Pen 2013). Combining the factors that are known to alter their sex allocation with the benefit to fitness obtained from biased sex allocation will allow for generalization of reproductive strategies in laboratory-kept animals.

For the first issue, altered sex allocation, previous studies already provided a firm background to examine when this takes place. For instance, the freshwater snail *L. stagnalis* immediately lays eggs when transferred from dirty water to a pot with clean O_2-rich water and clean surface (clean water stimulus, CWS: Ter Maat et al. 1983). Such egg laying can be interpreted as immediate allocation to the female function. Including other factors, this reaction may be adaptive in the wild, as it could provide their offspring a favourable condition for development (Ter Maat et al. 2012). This implies that one might predict less female-biased allocation by snails in the wild compared with those in the laboratory, because of the clean environment in laboratory. However, one critical drawback is that the influence of CWS on the male function or growth is still unknown. This again illustrates that measuring changes in male and female allocation at the same time is highly valuable and essential, as the existence of trade-off is a fundamental assumption in sex allocation theory (see Schärer 2009).

The second question concerns fitness consequence of biased sex allocation. Even if we found differences in sex allocation between natural and laboratory populations, the difference might be too small to alter reproductive strategies due to minor additional fitness returns. To investigate how much benefit animals can obtain with biased sex allocation, one can manipulate their sex allocation using factors discussed above. For instance, by using the abiotic factors, one might be able to make sex-biased hermaphrodites, then test if these manipulated individuals are successful in the invested sex function or not. This information would help us to understand the relationship between sex allocation and its fitness consequence.

Finally, as suggested in the context of decision making on sex role preference (Anthes et al. 2006*a*), the investigation of sex allocation would broaden our understanding of reproductive strategies in this group.

Conclusion and perspectives

Hermaphroditic gastropods are expected to have widely diverse elaborate reproductive strategies, as they show extreme pre-copulatory behaviours (e.g., long pre-copulatory phase, injections via dart or penial stylet), as well as complex post-copulatory processes suggestive of strong sperm competition (e.g., variable P_2 values, extensive sperm digestion, efficient sperm storage). This could be due to the fact that they are hermaphroditic (Michiels and Koene 2006; Bedhomme et al. 2009), which also invokes several complexities exemplified in their shared cost traits (e.g., body size, mating success) and flexible sex allocation. In this last section, we summarize our suggestions of each topic discussed above.

When investigating reproductive strategies, one has to be careful in choosing target traits. If one focuses on a sex-biased trait (e.g., egg, sperm, or seminal fluid protein), the interpretation for a reproductive strategy will be straightforward. Or, if a shared cost trait, such as body size, is under examination, one needs to keep in mind that it can affect both sexual functions. Ideally, the aim would be to depict a path diagram of traits for interactions between traits, and ultimately, reproductive success (Arnold and Duvall 1994; Arnold 1994*a*).

Pre-copulatory processes in this group are well investigated in extensive theoretical and experimental studies (Anthes et al. 2006*a*), but fitness consequences still remain to be properly quantified. Although some factors (e.g., parasite infection) already indicate clear sex-role and mate preference, it is recommended to add the scope of paternity gain or reproductive success together with molecular genotyping methods. At this stage, multivariate analysis or statistical model selection on behavioural data would be useful to find out which factors significantly affect reproductive success.

Disappointedly, we have quite limited information about post-copulatory reproductive strategies. One of the reasons is that some life-history traits (e.g., planktonic stage, long life span) hamper experimental surveys of their reproductive strategies on post-copulatory processes. Moreover, application of molecular genotyping methods is limited to a few taxa, despite its necessity, especially for investigating sperm competition. To date, none of the internally fertilizing hermaphroditic gastropods has been fully sequenced (although a few genomes are on their way, e.g., *A. californica*, *B. glabrata*, and *L. stagnalis*), which may cause reluctance to apply genetic methodology. However, given detailed knowledge about sperm storage, it is highly promising to quantify biologically reliable reproductive success. Furthermore, detailed studies of the sperm storage organ can potentially demonstrate cryptic female choice, if paternity assignment can be carried out on the sperm stored within this organ.

Flexible sex allocation is quite interesting, but a difficult aspect of hermaphrodites in the context of reproductive strategies, as our findings in the laboratory may only overlap with a narrow range of the natural (biotic or abiotic) environmental continuum. To generalize our finding on the reproductive strategies, two things are required: (1) factors influencing sex allocation and (2) consequences of biased sex allocation. For the first, various factors are already known that change sex allocation (e.g., mating rate, clean water), but the information is often not complete enough to describe both effects on male and female allocation. The latter issue could be dealt with by manipulating and (or) making sex-biased individuals. For instance, one can test whether male-biased individuals obtain higher paternity success, and if it is in expense of female reproductive output. Such data would lead to depict the trajectory of reproductive strategies of hermaphrodites along with their sex allocation.

In this review, we highlight the flexible, sometimes opportunistic, and complex reproductive features of hermaphroditic gastropods. The understanding of their reproductive strategies would have implications for a broad range of zoological fields. First, the knowledge about their reproductive strategies surely contributes to understanding sexual selection in hermaphroditic animals, because it is the dominant process shaping their strategies. Ultimately, some theories for the origin and maintenance of hermaphroditism could be validated via these studies, as their predictions are based on reproductive success, which is the target to quantify in investigations of reproductive strategies. Second, comparing the findings with other hermaphroditic animals (e.g., flatworms, polychaete worms) or separate-sex animals will be instructive to generalize or contrast reproductive strategies in different reproductive system or sex-determinant system.

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