

Sexual selection and hermaphroditic organisms: Testing theory

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Abstract Sexual selection is widespread if not ubiquitous in hermaphroditic organisms. Although many phenomena that have been described as sexual selection in gonochores, (e.g. harem polygamy, multiple mating, elaborate courtship, even secondary sexual characters) can be found in some hermaphrodites, what is more interesting is the ways in which sexual selection in hermaphrodites may differ from dioecious taxa. In hermaphrodites, an individual's mating success includes its success from both sexual roles. Secondly, in many simultaneously hermaphroditic taxa there is strong evidence of sexual selection and yet the operational sex ratio is 1:1, by definition. Many simultaneous hermaphrodites have elaborate courtship and genital anatomy, suggesting sexual selection plays an important role in reproductive success. Sperm competition and cryptic female choice mean that the number of mates acquired is not necessarily a predictor of reproductive success. Even in simultaneous hermaphrodites with reciprocal mating, variance in reproductive success through the male role and through the female role may differ in a population. Moreover hermaphrodites may choose to emphasize one sexual role over the other. Data suggest that the preferred role varies in hermaphrodites, which creates an opportunity to test fundamental predictions and assumptions of sexual selection theory. Hermaphrodites may vary their emphasis on one sexual role over the other either developmentally or behaviorally in response to environmental or social parameters. How they use this capability in acquiring more or higher quality mates still requires study [*Current Zoology* 59 (4): 579–588, 2013].

Keywords Sexual selection, Hermaphrodites, Mate choice, Reproductive success

Sexual selection has been defined in many ways (see Leonard, 2006 for partial list) but the modern definition most consistent with Darwin's original idea is that sexual selection is selection (i.e. differential reproductive success) through competition to acquire mates or to be chosen as a mate (Andersson, 1994). This definition is useful both because it most closely reflects Darwin's original thinking and also because it includes the possibility of sexual selection acting on the widest possible variety of organisms (see Leonard 2006 for discussion). Famously Darwin (1871) considered that sexual selection would be limited to some of the "higher" animals, considering that among invertebrates only some of the arthropods had the sensory and "mental" powers to discriminate among mates, and that sexual selection could not exist in hermaphrodites. This point of view has changed gradually, with Bateman (1948) realizing in his seminal paper that if sexual selection stemmed from anisogamy it should extend to plants as well as animals. By the 1970's, many authors were including mate choice and sexual selection in their thinking about reproduction in plants, including hermaphrodites (for discussion of the early history of sexual selection thinking

in plants see Charlesworth et al., 1987; Andersson, 1994). More recently it has become clear that even organisms lacking anisogamy may be subject to sexual selection and in fact, anisogamy itself may be, at least in part, a sexually selected trait (see Leonard, 2010 for review). In the last 30 years interest in mating systems and sexual selection in hermaphrodites has become a flourishing field which has been reviewed at intervals (see references below). Here I discuss briefly some unique properties of sexual selection as it pertains to hermaphrodites and point out how thinking about sexual selection in hermaphrodites can provide opportunities to test theory developed for dioecious organisms.

1 In Hermaphrodites, the Opportunity for Sexual Selection Comes through Two Sexual Roles

The first and most obvious difference is that hermaphrodites can achieve reproductive success through both male and female function; i.e., whether they are sequentially or simultaneously hermaphroditic, their lifetime reproductive success can (although it need not)

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come from both sexual roles. That is, in hermaphrodites, the opportunity for sexual selection comes from the lifetime variance in reproductive success for individuals, not the differential reproductive success of the two sexual roles (see discussion in Leonard 2006). This creates a problem in the use of some of the commonly used measures of sexual selection such as I_{mates} (Shuster and Wade, 2003), which focuses on male mating success as a fraction of the total, and Bateman gradients (for a discussion of the difficulties in applying Bateman gradients to hermaphrodites see Arnold, 1994; Arnold and Duvall, 1994 and Anthes et al., 2010), since they focus on comparing the relationship between reproductive success and number of mates in the two sexual roles separately. A fundamental problem with the prevalent indices of sexual selection, particularly Bateman's gradients, is that they focus on the number of mates acquired rather than the quality of the mates. In the *Descent of Man* Darwin (1871) explicitly considered that differences in mate quality could have an important influence on sexual selection and in recent years data has shown that, particularly in females of dioecious taxa, offspring quality is an important component of reproductive success and that it can vary with the number and/or genetic quality of mates [e.g. mallards (Drea, 2005); whitefish (Wedekind et al., 2001); see discussion in Parker and Tang-Martinez, 2005 and Anthes et al., 2010]. It has become clear that in many taxa, including hermaphrodites, individuals choose to mate with many males and that this can have beneficial effects on fitness (see review in Simmons, 2005). In an hermaphroditic opisthobranch, individuals that mate multiply as females invest more in their offspring, leading to higher survival (Sprenger et al., 2010). Multiple mating and multiple paternity has long been known to be common in hermaphroditic gastropods (see review in Leonard, 1991) and are considered to be the rule in spermcast mating systems among sessile hermaphrodites (Bishop and Pemberton, 2006). Multiple paternity and pollen competition are common in angiosperms (Willson and Burley, 1983). The prevalence of multiple paternity and mate choice in both hermaphroditic and dioecious taxa suggests that they have some benefit to individuals and that it would be inappropriate to use measures of sexual selection that exclude quality of offspring. In theory it might be possible to modify Bateman's gradients to accommodate this complexity but the application of Bateman's gradients to hermaphrodites as postulated by Anthes et al. (2010; see also Pélissié et al., 2012) becomes so complex and unwieldy that it seems to be of dubious predictive value.

A crude but perhaps more useful way to look at the opportunity for sexual selection would be to simply use Crow's Index (I): the ratio of the variance in progeny number to the square of the number of progeny (Crow, 1958), as done by Lorenzi and Sella (2008). This is a measure of the upper limit on total opportunity for selection but may be useful in comparing taxa or populations. While it is true that this measure may confound variance in reproductive success through sexual selection with that through natural selection and even random factors (Jennions et al., 2012; Kokko et al., 2012), this is not avoidable without making *a priori* assumptions about the nature of these processes (see discussion in Tang-Martinez and Ryder, 2006).

A problem with all of these measures is that they require knowledge of lifetime reproductive success. Lifetime reproductive success is the critical parameter because it is the ultimate measure of selection and the raw material for evolution. Ideally we want to measure the lifetime reproductive success of individuals, with a given trait suspected to be under sexual selection, in the face of competition for mates and in the absence of competition for mates; the difference will be the measure of sexual selection; not a trivial thing to measure but perhaps feasible in laboratory populations of some model organisms. Another issue is that it seems probable that the relative contribution of sexual vs. natural selection will vary from time to time and population to population according to environmental conditions. For these reasons, a crude measure based on variance in total reproductive success seems the most sensible starting point. While it is important to parse the components of sexual selection to obtain a theoretical view of the process (e.g. Anthes et al., 2010; Kokko et al., 2012; Jennions et al., 2012; Pélissié et al., 2012), what the practical biologist needs when looking at the real world is a framework for understanding what the weird attributes of the species he/she happens to be looking at mean for reproductive success. Measuring sexual selection, as a practical matter, may be best confined to studies of reproductive success through mating vs. costs from natural selection, in individual traits (see discussion in Ghiselin, 2010 and below). After all, Darwin's concept of sexual selection focused on, and applied to traits that seemed inexplicable by natural selection. A measure of the total sexual selection on a population would require measurement of natural vs. sexual selection and chance effects across the suite of characters associated with reproduction. Consideration of sexual selection in hermaphrodites has led to a realization that sexual selection

is not a matter of sex differences but rather a matter of selection on traits that aid in obtaining more and/or better mates in either or both sexual roles.

2 Operational Sex Ratios in Simultaneous Hermaphrodites Are 1:1; Or Are They?

One of the most influential theories of sexual selection is that of operational sex ratio (OSR) (Emlen and Oring, 1977). The premise of OSR theory is that where and when one sex is more numerous than the other, the opposite sex represents a limiting resource and will be competed for. The important feature of this insight is that it is not the absolute sex ratio of the population that is important but the number of individuals of each sex that are available for breeding at a particular time and place (for review see Andersson, 1994; Kvarnemo and Ahensjö, 1996). In simultaneous hermaphrodites on the other hand, the operational sex ratio is, by definition, equal. The OSR hypothesis would suggest that sexual selection should not be a major factor in simultaneous hermaphrodites. However, when we look at taxa such as the euhyneuran gastropods which are simultaneous hermaphrodites and which, in many taxa, have simultaneous reciprocal copulation (Leonard, 1991), we see many of the same phenomena that are associated with sexual selection in dioecious taxa (Table 1; Leonard, 2006). Euhyneuran gastropods, particularly stylommatophorans, often have very complex genital anatomy (Baur, 2010; Jarne et al., 2010; Valdes et al., 2010), and very elaborate courtship and sexual behavior. Although relatively few species have been studied in detail, a variety of striking phenomena have been described including some of the only secondary sexual characters known in simultaneously hermaphroditic animals, including the ‘love dart’ of the garden snail *Cornu aspersum*. The love dart is a small calcareous dart which has been demonstrated to fit the criteria for a secondary sexual character beautifully since it is used during courtship, is absent in immature individuals (Chung, 1986), and receipt of a dart during courtship increases the paternity of the dart shooter (see review by Chase, 2007). This is due to a dart gland product that has physiological effects on the recipient. A similar product has been found in *Euhadra* (Kimura et al., 2013). Darts have evolved many times in the Stylommatophora (Davison et al., 2005). Other secondary sexual characters found in stylommatophorans include the sarcobela or “stimulators” found in *Deroceras* slugs (Reise, 2007)

and used during courtship and the Head Warts and Frontal Organs found in *Euhadra* and other stylommatophorans (for reviews see Takeda and Tsuruoka, 1979; Takeda, 1989; Van Bruggen and de Winter, 1990). More recently emphasis on sperm competition and cryptic female choice has blurred the line between primary and secondary sexual characters (Eberhard, 1996) and there has been increasing interest in the function of the rather baroque genitalia found in euhyneuran gastropods. A rather amazing phenomenon has been described in a nudibranch; individuals autotomize the penis after each copulation and are able to copulate again when the penis regenerates after 24 hours (Sekiwaza et al., 2013). Sperm are observed clinging to the spiny surface of the autotomized penis and it seems probable that the penis is used to remove the sperm of previous mates from the sperm storage organ, reminiscent of the damselfly (Waage, 1979). Further circumstantial evidence for sexual selection in simultaneously hermaphroditic gastropods includes multiple mating and multiple paternity, lengthy and elaborate courtship behavior, mate choice, competition for mates and sexual conflict over a preferred sexual role (see Table 1 and Leonard 2006). Therefore, even with a 1:1 OSR simultaneous hermaphrodites show the same sorts of evidence of sexual selection that are found in animal taxa with separate sexes, indicating that while a skewed OSR may be sufficient to stimulate sexual selection (see below), it is not necessary for sexual selection to occur.

In contrast to simultaneous hermaphrodites, populations of sequential hermaphrodites are often characterized by an OSR, and an overall sex ratio, that is skewed to the sex that is first to mature (but see Collin, 2006). In some coral reef fishes, individuals live in social groups which consist of small individuals of one sex (often female) and a larger dominant male. When the dominant male is removed, often the largest female will change sex and become the new dominant male. The relevance of this behavior to sexual selection was clear early on (Warner et al., 1975; see history by Ghiselin, 2006) and polygamy in sex-changing fish has been well-studied from that standpoint (see reviews in Warner, 1975; Warner et al., 1975; Shapiro, 1979; Munday et al., 2006; Muñoz and Warner, 2003; etc.). Although, for the most part, theory has dealt with sequential and simultaneous hermaphroditism separately (but see St.Mary, 1997; Cadet et al., 2004), empirical studies recognize a variety of intermediate cases. Over the last 30 years, we have come to realize that there is no clear dividing line between sequential and simultaneous hermaphrodites,

Table 1 Circumstantial Evidence for Sexual Selection (modified from Leonard 2006)

Character	Dioecious taxa	Hermaphrodites
Secondary sexual characters	Common	Found in some stylommatophorans, at least; love darts; sexual pheromones; head warts in <i>Euhadra</i> ; frontal organ in <i>Gymnarion</i> ; sarcobelum in <i>Deroberas</i> (see text).
Competition for mates	Common	Documented in sequential and some simultaneous hermaphrodites; sneaker males in serranines, fighting in <i>Ophyrotracha</i> ; position in chains of <i>Aplysia</i> .
Sperm/pollen competition	Common	Pollen competition common and well-documented; sperm competition documented in one flatworm, some serranines and some gastropods; likely to be common ^a .
Mate choice	common	Documented in <i>Biomphalaria glabrata</i> (Webster and Gower, 2006); size-assortative mating reported in nudibranchs and flatworms ^b .
Multiple mating in the female role; multiple paternity	Common	Common in euthyneuran gastropods ^c ; common in angiosperms; see sperm competition above.
Morphological sexual dimorphism	Common	Not uncommon in sequential hermaphrodites, e.g. bluehead wrasse; one report in simultaneous hermaphrodites ^d .
Sexually dimorphic sexual behavior	Most pair-mating taxa	Found in some simultaneous hermaphrodites; i.e. <i>Hypoplectrus nigricans</i> , <i>Navanax inermis</i> , <i>Lymnaea stagnalis</i> ; <i>Achatina fulica</i> ; common in sequential hermaphrodites ^e
Elaborate and/or expensive mating and/or courtship behavior	Common in insects, crustacea, vertebrates; some molluscs	Common in euthyneuran gastropods; e.g. <i>Navanax inermis</i> , <i>Limax maximus</i> , <i>Helix</i> spp.; <i>Ariolimax</i> spp. ^f
Mating systems based on conditional reciprocity	Not applicable?	E.g. <i>Hypoplectrus nigricans</i> , <i>Serranus tigrinus</i> , <i>Navanax inermis</i> , <i>Ophyrotracha</i> spp.; <i>Arianta arbustorum</i> , <i>Schmidtea polychroa</i> , may be widespread ^g .
Rapid evolution of genitalia/flowers; elaborate genitalia/flowers	Common in arthropods, probably widespread ^h	Common in angiosperms, platyhelminths, stylommatophoran gastropods; e.g. <i>Ariolimax</i> spp., probably widespread ⁱ .
Skews in operational sex ratio	Common	Common in sequential hermaphrodites; also found in simultaneous hermaphrodites with sexual polymorphisms and complex sexual systems (phally polymorphisms, complementary males, androdioecy, gynodioecy, etc.). ^j
Skews in breeding sex ratio	Less studied but see review (Shuster and Wade, 2003)	May be common in cases where sperm transfer and egg-laying are widely separated in time or space; sequential hermaphrodites, internal fertilization w/ sperm storage; spermatcast mating systems; animal pollination, etc., see (Leonard, 2006).
Harem defense polygamy	Well-documented in some vertebrates; arthropods	Common in sequentially hermaphroditic fish; e.g. bluehead wrasse (Warner 1975); documented in two species of simultaneously hermaphroditic serranine fish (see Petersen, 2006).
High variance in reproductive success in either or both sexual roles.	Data from red deer, elephant seals, damselflies, etc. ^k	For plants see Delph and Ashman, 2006; few data for animals, but see Pélissié et al., 2012.
Self-fertilization	Not applicable	Common in simultaneous hermaphrodites; consequences for sexual selection largely unexplored.

^aReviews in Leonard (2006), Anthes (2010), Willson and Burley (1983), Delph and Ashman (2006), Thomson (2006). ^bCrozier, 1918; Vreys and Michiels, 1997; Lüscher and Milinski, 2003; Milinski, 2006. ^cLeonard, 1991; Leonard and Lukowiak, 1991; Sprenger et al., 2010; reviews in Baur (2010), Jarne et al.(2010). ^dWarner, 1975; Petersen, 2006; McLauchlan (1951) reports dimorphic shell morphology associated with differing sex roles in a stylommatophoran. ^eFischer, 1980; Leonard and Lukowiak, 1991; Sella, 1985; Lorenzi et al., 2008; Anthes, 2010 ; hypothesized to be widespread by Charnov (1979); see also Axelrod and Hamilton (1981); Leonard, 1990; reviews in Leonard (1993, 2005; 2006). ^fLeonard, 1991; Baur, 1998; Koene, 2006. ^g see review in Leonard (2005). ^hEberhard (1985) for animals. ⁱEberhard, 1985; for plants Darwin, 1877, 1888; Thomson, 2006; *Ariolimax* spp. see Mead (1943). ^jGhiselin, 1974; Ghiselin, 1969; Willson and Burley, 1983; etc. ^kReview in Andersson (1994).

but a broad continuum between the two extremes (see review in Leonard, 2013). For example in some species, individuals may reach initial sexual maturity in one sexual role and then add on the other sexual function to become simultaneously hermaphroditic [e.g. protandric simultaneous hermaphroditism in the polychaete *Ophyrotracha diadema* (Sella and Lorenzi, 2003) and *Lysmata* shrimps (Bauer, 2006), or protogynous simultaneous hermaphroditism in the anemone *Epiactis prolifera* (Dunn, 1975)]. In some serranines, a subfamily of fish in the family Serranidae, small individuals are simultaneous hermaphrodites and larger individuals may lose female function to become harem-holding males (e.g. *Serranus fasciatus*, Hastings and Petersen, 1986).

These types of sexual patterns should tend to skew the OSR towards a female-bias. Furthermore, there are many examples of “quantitative gender” in which individuals of a simultaneously hermaphroditic species alter their allocation to, or emphasis on, male vs. female function as a function of age, size or environmental variables in both plants (see review in Klinkhamer and DeJong, 2002) and animals [see references in Leonard, 2006; Anthes, 2010; examples from land snails (Tomiyama, 2002); tapeworms (Schärer et al., 2001; Lüscher and Milinski, 2003) and fish (St. Mary, 1997)]. In some species, individuals may be technically simultaneous hermaphrodites but actually not assume one of the sexual roles; e.g. in some gobies individuals are

anatomically simultaneously hermaphroditic but actually function in only one sexual role (St. Mary, 2000). In *Ophyrotrocha* spp. some individuals may have both sperm and eggs but function in only one sexual role (Di Bona et al., 2010; Lorenzi and Sella, 2013). In other simultaneously hermaphroditic species, individuals of a certain size, or age, or status, might, for example, be likely to mate in one sexual role only 20% of the time and 80% in the other role. This would have an effect on the functional OSR, but one that might be difficult to detect.

This diversity of sexual systems, sometimes within genera or families, produces a range of OSRs that should provide opportunities to test the hypothesis that the more skewed the OSR the stronger sexual selection will be. Is it the case that sequentially hermaphroditic taxa tend to have stronger sexual selection than classically simultaneously hermaphroditic species? Sexual selection seems strong in the well-studied coral reef fish that change sex in response to social cues (Munday et al., 2006). However the stacks of sequentially hermaphroditic slipper limpets (Collin, 2006) may be better explained by natural selection through quantitative gender, i.e. a gradual change of sex allocation to the two sexual roles with increasing size and/or age as opposed to an abrupt sex change (see Leonard 2013 for discussion).

3 Males Are Eager, Females Are Choosy, But Hermaphrodites Have A Choice

Interest in sexual selection in simultaneously hermaphroditic animals was stimulated by Charnov's classic paper (Charnov, 1979) discussing how sexual selection should act in simultaneous hermaphrodites. Under the assumption that sexual selection acts according to Bateman's principle; i.e. that reproductive success through female function is limited by the resources available to produce eggs whereas male function is only limited by access to mates or their eggs, Charnov made some bold and startling predictions. He predicted that simultaneous hermaphrodites should mate more to obtain eggs to fertilize than to obtain sperm to fertilize their eggs. That is, as in gonochores, hermaphrodites acting as males should be "eager" whereas hermaphrodites acting as females should be "choosy". This situation would mean that a mating encounter between pairs of hermaphrodites would involve a very direct sexual conflict in that each individual should be attempting to

mate in the male role. Shortly afterwards, accounts of mating systems which involved repeated alternation of sexual roles by pairs of simultaneous hermaphrodites appeared and were interpreted as representing resolutions of conflict over a preferred sexual role as predicted by Charnov (1979). These systems included two serranine fish (Fischer, 1980; Pressley, 1981), and a polychaete worm (Sella, 1985). Axelrod and Hamilton (1981) interpreted the "egg-trading" described for the externally-fertilizing pair spawning serranines *Hypoplectrus nigricans* (Fischer, 1980) as a Tit-for-Tat solution to the sexual conflict created by two individuals who both preferred mating in the male role as predicted by Charnov (1979). Subsequent work on a variety of hermaphroditic serranines has confirmed a preference for the male role (Leonard, 1993; Petersen, 2006) and this is consistent with evidence from externally-fertilizing simultaneously hermaphroditic polychaetes of the genus *Ophyrotrocha* (see Lorenzi et al., 2006; Di Bona et al., 2010). In contrast, on the basis of behavioral evidence Leonard and Lukowiak (1984) suggested that in the internally-fertilizing opisthobranch *Navanax inermis*, in which members of a pair repeatedly alternate sexual roles during a bout of copulations, the male role is preferred, contrary to Charnov's (1979) prediction. The preference for the male role was later supported by experimental data (Leonard and Lukowiak, 1991; Michiels et al., 2003). This behavior, stemming from a preference for the male role was termed sperm-trading (Leonard and Lukowiak, 1984). Since that time sperm-trading has been found in other internally-fertilizing hermaphrodites (see recent review in Anthes, 2010). Leonard and Lukowiak (1984) explained the difference in role preference between the serranines and *Navanax* as attributable to differences in the control of fertilization in the two types of hermaphrodites. That is, in the externally-fertilizing hermaphroditic serranines the male-acting individual releases sperm after eggs have been spawned giving the male-acting individual "confidence" that the sperm released will fertilize eggs. On the other hand, *Navanax* has internal fertilization with sperm storage and a gametolytic gland. Therefore when a male-acting individual gives sperm to a partner it has no certainty that those sperm will be used to fertilize eggs. The gamete-trading model predicted that the sexual role that offered the greatest certainty of parentage in a mating encounter would be preferred in pair-mating hermaphrodites. Subsequent work indicates that there is a rather intense arms race in the reproductive tract of internally-fertilizing hermaphrodites with both sperm com-

petition and cryptic female choice occurring in an attempt to control fertilization (Garefalaki et al., 2010; Kimura et al., 2013; Kimura and Chiba, 2013; reviews in Chase, 2007; Baur, 2010; Jarne et al., 2010). The game of strategy between a pair of mating hermaphrodites with symmetrical interests and conflict over a preferred role is somewhat different from the classical Prisoner's Dilemma and has been termed Hermaphrodite's Dilemma (Leonard, 1990). Subsequent work on a variety of species has shown that sexual conflict is important in shaping mating systems and the opportunity for sexual selection in many hermaphroditic species, although it has become clear that even in simultaneous hermaphrodites, the partners to a mating encounter may be asymmetrical due to differences in size, age, experience, etc. This literature has been reviewed in detail elsewhere (Leonard, 2005; 2006; Anthes, 2010).

Although the preferred role in simultaneous hermaphrodites has been shown to vary among species, and perhaps among individuals within species, Bateman's (1948) principle predicts a consistent preference for the male role in simultaneous hermaphrodites (see Leonard, 2005 for discussion). According to Bateman's principle, the preference for the male role should exist because the male role will in general have greater variance in reproductive success and therefore those individuals in the population with the greatest reproductive success will be males. However, probability theory tells us that where two potential strategies have equal mean (and total) return, as must be the case in outcrossing hermaphrodites where each offspring has a mother and a father (Fisher, 1958), the strategy with the lower variance will be preferred because it has the lower risk of reproductive failure (Gillespie, 1977). That is, while the most successful individuals in the population will be those adopting the high variance strategy, usually assumed to be the male role; most of the individuals in the population that experience complete reproductive failure will also be males. On the other hand, individuals adopting the low variance strategy, usually assumed to be the female sexual role, run a much lower risk of reproductive failure and evolution will therefore favor individuals that adopt the lower variance strategy. This has been discussed in detail elsewhere (Leonard, 1999; 2005). The message from probability theory is that if the two sexual roles differ in variance in reproductive success, as would be suggested by Bateman's Principle, then hermaphrodites should prefer the role with the lower variance, not the higher variance. It is true that the higher the variance the greater the opportu-

nity for selection, but that is associated with lower fitness; e.g. a greater number of individuals with no reproductive success in that role (see Pélissié et al., 2012). That is, traits associated with the role with higher variance will be more likely to evolve quickly, but the hermaphrodite should, all else being equal, prefer to mate in the role with lower variance. There is as yet little data on the relative variance of the male and female role in species known to engage in egg vs. sperm-trading but it is clear that in most species mating hermaphrodites respond to a variety of factors including size, age, sexual history, social environment and genotype of the partner when making decisions about mating (see reviews by Leonard, 2006; Anthes, 2010).

4 Selection on Male versus Female Function May not Be Easily Separable or It May Be Synergistic

In hermaphrodites, whether sequential or simultaneous, sexual selection is acting on both sexual roles in the same individual and the individual's choice of how to allocate time, effort and resources between the sexual roles (sex allocation) may play a critical role in its success in competing for and being chosen by mates. Much of the research on reproductive success in hermaphroditic taxa has focused on sex allocation but it is important to remember that in general, sex allocation theory focuses on natural rather than sexual selection (West, 2009). That is, understanding sexual selection is more of a prerequisite for understanding sex allocation than the reverse (Schärer and Pen, 2013). The theory of Local Mate Competition (Charnov, 1980; 1982) predicts that sex allocation will shift from female to male function in hermaphrodites as the number of mates in a local group increases. This prediction has been born out in some, but not all, experimental studies (reviews in Leonard 2006; Delph and Ashman, 2006; Sandner and Schärer, 2010; Lorenzi et al., 2006; Schärer, 2009). Schärer (2009) has suggested that the concept of Local Sperm Competition is more useful, since a critical point is reached when an individual's own ejaculates come into competition in a small mating group, leading to a reduction in allocation to sperm (see also Yamaguchi et al., 2012). Tests of sex allocation theory and Local Mate Competition models have revealed some complications. The first is that the trade-off between male and female function may not be in terms of allocation to gametes or reproductive structures. In the hermaphroditic polychaete *Ophyrotrocha diadema*, individuals responded to

an increase in mating group size by strongly reducing allocation to eggs but increasing allocation to male behavior rather than sperm (Lorenzi et al., 2006). Secondly there may be a synergistic effect between reproductive success in the two sexual roles rather than a trade-off as has been shown in some angiosperms (Delph and Ashman, 2006). That is, as predicted by Charnov's (1979) convex fitness function model, in hermaphrodites, mating success in one sexual role may enhance mating success in the other sexual role through such factors as flower structures attracting pollinators or courtship for a reciprocal mating.

Secondly, many, but by no means all, simultaneous hermaphrodites (Jarne and Auld, 2006) have the option of reproducing through self-fertilization, which can potentially have an impact on processes of mate choice and competition for mates, as well as sex allocation. Theory predicts that self-fertilization will provide fitness advantages, all else being equal, since the individual will contribute all of the genes of the offspring rather than half, the two-fold cost of sex (Maynard Smith, 1978). Reproductive assurance through the possibility of selfing is considered to be an important advantage of hermaphroditism (Ghiselin, 1969) but selfing also has costs associated with such phenomena as inbreeding depression (see discussion in Jarne and Charlesworth, 1993). The consequences for sexual selection via self-fertilization remain largely unexplored in animals. On the one hand where a population reproduces largely by selfing there would be little opportunity for sexual selection; on the other hand, where selfing is an option, all matings involve the possibility of sperm competition and cryptic female choice. Investigation of sexual selection in partially selfing species will likely reveal some fascinating new phenomena of sexual conflict.

5 Conclusions

As more attention has been paid to hermaphroditic mating systems, a variety of spectacular reproductive phenomena have been discovered and interpreted, or reinterpreted, in terms of sexual selection. That is, many of the phenomena that offer circumstantial evidence for sexual selection in gonochores; e.g. harem polygamy, secondary sexual characters, elaborate courtship, complex genitalia, etc. have also been found in hermaphrodites (see Table 1 and review in Leonard 2006). These phenomena demonstrate that sexual selection does happen in hermaphrodites and since sexual selection theory has been largely developed in gonochores, attempts to

apply the theory to understanding and predicting the course of sexual selection in hermaphroditic taxa offers opportunities to test theory. An important insight is that the tactics of individuals with a choice of reproducing through sperm versus eggs, may differ substantially from those with no choice.

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