Sexual selection: lessons from hermaphrodite mating systems

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Synopsis Over the last 130 years, research has established that (a) sexual selection exists and is widespread in the plant and animal kingdoms; (b) it does not necessarily entail sexual dimorphism; even hermaphrodites have it; (c) it does not require intelligence or a sophisticated sense of esthetics; even tapeworms and plants choose mates; and (d) it does not require brawn or even mobility for competition; plants may compete for pollinators, and broadcast spawning invertebrates may also compete for matings. Although discussions of sexual selection often focus on sexual dimorphism, several phenomena that are commonly associated with sexual selection are widespread and highly developed in hermaphrodites. These phenomena include (a) bizarre and expensive courtship and copulatory behavior, (b) multiple mating and sperm competition, (c) rapid evolution of genitalia, (d) special structures associated with courtship, and (e) sexual polymorphism. The skewed breeding sex ratios associated with sequential hermaphroditism have long been recognized as contributory to sexual selection. In many simultaneous hermaphrodites, although the sex ratio at mating may be one to one, the actual reproductive sex ratio may also be skewed, creating a high potential for sexual selection. Reproductive biology in hermaphroditic taxa also involves a lot of complexity unknown in dioecious taxa, such as sex change, facultative sex allocation and conditional reciprocity that offers opportunities to enrich our understanding of sexual selection and to test the assumptions and predictions of theory.

Introduction

Sexual selection has come to be seen as a keystone of Charles Darwin’s theory of evolution by natural selection, being the exception that proves the rule that evolution proceeds through differential reproduction (see Ghiselin 1969b for discussion). Famously, Darwin developed the theory of sexual selection to account for certain traits such as the weapons used in male-male competition (for example, a stag’s antlers) or the ornaments used to attract members of the opposite sex (for example, a peacock’s tail) which seemed to be very important in obtaining mates but unimportant otherwise. That these characters were not important in “the struggle for existence” was made clear, he argued, in cases in which the character in question was limited to adult males. In his view, where females and males share the same habitat, food sources, predators, and so on, sexually dimorphic characters must have evolved as a result of differential mating success. Darwin considered sexual selection to be limited to higher animals (from arthropods on up) on two grounds; first, “it is almost certain that these animals have too imperfect senses and much too low mental powers to feel mutual rivalry, or to appreciate each other’s beauty or other attractions (Darwin 1871, p 321),” and “In the lowest classes the two sexes are not rarely united in the same individual, and therefore secondary sexual characters cannot be developed” (Darwin 1871, p 321). Darwin, then, saw hermaphroditism as incompatible with sexual selection both because of a lack of opportunity for evolution of sexual dimorphism and a lack of capacity for mate choice and/or direct competition for mates in many invertebrates. Much of sexual selection research still focuses on sexual dimorphism (for example, Shuster and Wade 2003) and sexual dimorphism and secondary sexual characters are often used as proxies for evidence of sexual selection (see Table 1; Shuster and Wade 2003; Jones and others 2004; Kappeler and Van Schaik 2004; Mead and Arnold 2004; see discussion in Andersson 1994) and/or as part of the definition of sexual selection (Table 1). The first questions to address, then, are the nature of sexual selection and how it might apply to hermaphrodites.

What is sexual selection?

Sexual selection is a term that has meant different things to different people. In a recent review, Tim Clutton-Brock (2004) listed 9 different definitions of sexual selection and the list is not exhaustive (see Table 1). Of those definitions, 4 involve sexual dimorphism (sex differences) and 2 refer only to males. However, the essence of sexual selection as Darwin

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defined it is selection through competition for mates. Darwin first defined sexual selection early in *On the Origin of Species*: "what I call Sexual Selection. This depends not on a struggle for existence, but on a struggle between the males for the possession of the females; the result is not death to the unsuccessful competitor, but few or no offspring." (Darwin 1859, p 88). Fuller treatment of the theory came in *The Descent of Man* where he defined sexual selection as depending "on the advantage which certain individuals have over the same sex and species, in exclusive relation to reproduction" (Darwin 1871, p 256). As Andersson (1994) has pointed out, this definition can be applied to all organisms, including plants, since as in ecology, the effect of competition will be the same whether it occurs as interference competition (male-male combat, for example), scramble competition (sperm competition, pollen competition), or indirectly such as competition to be chosen by females or by pollinators (see Levitan 1998; Skogsmyr and Lankinen 2002; Delph and Ashman 2006; Thomson 2006). Andersson’s (1994) general definition of sexual selection applies to all forms of hermaphrodites as well as taxa, such as protists, that lack anisogamy, making it appropriate to test hypotheses about the origins of sexual selection (contrary to Grant 1995). Therefore, consideration of hermaphrodites shows us the weaknesses of definitions of sexual selection that are specific to sexually dimorphic traits or to males alone. The next questions concern how to identify and measure sexual selection and what its sources may be in hermaphrodites.

**Sources of sexual selection**

The fundamental question in sexual selection theory has been understanding why it is so often the case that males are “eager,” competing with each other for access to mates, whereas females are “choosy” about whom they mate with. The ultimate explanation for the rule of male-male competition and female choice was seen by Darwin as anisogamy. In surprisingly modern arguments he traced the source of male eagerness and female coyness to (1) the motility of sperm vs. the immobility of eggs; and/or (2) the fact that sperm are generally more numerous than eggs. Interestingly, Darwin evoked an energetic argument to explain what he termed “the greater general variability in the male sex”; “The female has to expend much organic matter in the formation of her ova, whereas the male expends much force in fierce contests with his rivals, in wandering about in search of the female, in exerting his voice, in pouring out odiferous secretions, &c. . . . On the whole the expenditure of matter and force in the two sexes is probably nearly equal, though effected in very different ways and at different rates.” (Darwin 1871, p 219; see also discussion in Ghiselin 1987). Therefore, as is so often the case, in his description and definition of sexual selection, Darwin identified most of the issues that occupy us today. Bateman (1948) hypothesized that males compete for mates and females do not because reproductive success in females is limited by the resources available for egg production, that is, the female gain curve plateaus, whereas the reproductive success of males is limited only by access to females, and the male gain curve is proportional to the number of mates (or eggs) available. This hypothesis has been very influential, but problems with it have begun to be identified (see Hubbell and Johnson 1987; Arnold and Duvall 1994; Gowaty 2004; Leonard 2005; see Tang-Martinez and Ryder 2005 for discussion). The problems identified

**Table 1 Definitions of sexual selection**

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<th>Definition</th>
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<tr>
<td>1. Selection on particular traits arising from intrasexual reproductive competition</td>
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<td>2. Selection on particular traits arising from intersexual reproductive competition</td>
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<td>3. Mating competition between males</td>
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<td>4. Sex differences in traits that confer advantages in competition for mates</td>
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<td>5. Variation in male mating success</td>
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<td>7. “Sexual selection is due to variance in reproductive success among members of the same sex and species.” (Gowaty 2004, p 37)</td>
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<td>8. Consistent patterns of mate choice by members of either sex</td>
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<td>9. Sex differences in the intensity of selection on particular traits</td>
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<td>10. Sex differences in the intensity of selection on particular traits caused by contrasting effects of the trait on mating success in the two sexes</td>
</tr>
<tr>
<td>11. “Sexual selection is selection that arises from differences in mating success (number of mates that bear or sire progeny over some standardized time interval” (Arnold 1994b, p 59)</td>
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<td>12. Selection through competition to acquire mates or be chosen as a mate (Andersson 1994; adopted here)</td>
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have been (a) the weakness of Bateman’s own data from *Drosophila* (Sutherland 1985), (b) evidence that sperm (pollen) can be limiting (Nakatsu and Kramer 1982; Willson and Burley 1983; Shapiro and Giraldeau 1996; Levitan 1998); (c) evidence that female choice may not be based on resources (see Gowaty 2004; Gowaty and Hubbell 2005 for discussion); (d) the suggestion that potential reproductive rate and/or breeding sex ratio may better explain the phenomenon (see discussion in Arnold 1994a; Arnold and Duvall 1994; Parker and Simmons 1996; Gowaty 2004); (e) evidence from hermaphrodites that females may have higher variance in reproductive success; despite larger gametes (see Delph and Ashman 2006), and (f) evidence for a preference for the female role in some hermaphrodites (Leonard and Lukowiak 1991; Michiels and others 2003; see review in Leonard 2005). Another factor that has been used to explain the pattern of male-male competition and female choice in dioecious animals (Alexander and Borgia 1979) and the preferred sexual role in simultaneous hermaphrodites (Leonard and Lukowiak 1984) is the control of fertilization. Alexander and Borgia (1979) argued that a fundamental difference between males and females is that in general, females retain a greater degree of control over the fate of their gametes than do males. The arguments of Bill Eberhard (1996) and Patty Gowaty (2004) suggest that female control of fertilization may represent a form of mate choice. At present, a popular hypothesis is that multiple factors may be at work to set the stage for sexual selection (see Shuster and Wade 2003). Table 2 lists factors that have been considered to be important in determining the strength and direction of sexual selection by producing differences between the sexes (or sexual roles) in variance in reproductive success and consequently skewed breeding sex ratio (BSR). The great difficulty is to determine which differences between the sexes are causes of sexual selection and which are effects. In hermaphrodites each individual acts as both male and female and can act as its own control. Identification of the preferred sexual role in hermaphrodites is one way of testing alternative hypotheses as to the source of sexual conflict (see following sections; review in Leonard 2005).

**The potential for sexual selection in hermaphrodites**

Variance in reproductive success has long been of interest as a measure of sexual selection (Bateman 1948; Payne 1979; Fincke 1988; Raffetto and others 1990; etc.). The theoretical upper limit to the intensity of selection on a population is given by Crow’s Index; the ratio of the variance in progeny number to the square of the mean number of progeny (Crow 1958; Shuster and Wade 2003). The use of Crow’s Index as a basis for measuring the intensity of sexual selection (Wade 1987; Shuster and Wade 2003) is an important development in sexual selection theory but the current usage, $\text{I}_{\text{mates}}$ (Shuster and Wade 2003), is inappropriate for hermaphroditic taxa because it focuses on male mating success as a fraction of the total. With separate sexes, in each generation sexual selection acting on males will be separate from that acting on females. In either sequential or simultaneous hermaphrodites however, sexual selection on an individual comes from the total of its success in both sexual roles. An appropriate measure of sexual selection for hermaphrodites would therefore have to include variance in total reproductive success. Clearly, the intensity of sexual selection cannot be larger than total selection so that Crow’s Index represents a theoretical upper limit to the strength of sexual selection. In reality, sexual selection will seldom or never reach this upper limit since other forces of selection are expected to be in operation, although it might be possible to construct experimental conditions that would bring a population close. Also, it should be emphasized that the magnitude of the variance is a measure of the potential for selection and not a measure of the intensity of selection (see discussion Wade 1987; Grafen 1987); random factors could also produce variance in reproductive success (see Sutherland 1985, 1987). However, differences in variance in reproductive success among populations with similar life histories and biology, would offer a first approximation to the potential for sexual selection.

**Evidence for sexual selection in hermaphrodites**

Defining sexual selection as the product of competition with conspecifics for reproductive opportunities is clear in principle, however identifying and measuring it in practice is far from simple, as Darwin predicted. It can be argued that sexual selection occurs at any or all of a variety of levels from detection and attraction of mates, through sperm competition and/or cryptic female choice, to differential parental investment in progeny from mates of different quality (Møller 1998; Clutton-Brock 2004; Watts and others 2004).

**Circumstantial evidence**

Despite the increasingly sophisticated approaches of quantitative genetics that are beginning to be employed (Holland and Rice 1999; Shuster and Wade 2003; Mead and Arnold 2004), most of sexual selection research still relies on the same sorts of evidence that attracted Darwin’s attention; the morphology, sexual behavior,
and social structure of animals. In general, sexual selection has been identified on the basis of circumstantial evidence, such as sexual dimorphism, behavioral evidence of competition for mates (intrasexual competition, usually male-male), and/or mate choice (usually by females, sometimes termed intersexual competition); and/or the perception that certain traits involved in reproduction are expensive in time or energy and/or represent a source of increased risk. Although the biology of many hermaphroditic taxa, particularly invertebrate animals, remains poorly known, review of the literature on hermaphrodite mating systems shows evidence for a variety of phenomena that are associated with sexual selection in dioecious organisms (Table 3).

Competition for mates
Male-male competition has been the major focus of sexual selection research in dioecious species (see Table 1) and among hermaphrodites has been long studied in plants in the form of pollen competition (see reviews in Willson and Burley 1983; Delph and Havens 1998; Skogsmyr and Lankinen 2002; Delph and Ashman 2006; Thomson 2006). More indirect competition in the form of competition for pollinators has been an important evolutionary force in angiosperms and a very active field of research (see reviews in Skogsmyr and Lankinen 2002; Thomson 2006). Less work has been done in animals, but there is strong circumstantial and some direct evidence to suggest that sperm competition is common and important in many internally fertilizing simultaneously hermaphroditic taxa, especially gastropods and flatworms (see reviews in Baur 1998; Michiels 1998). The sperm-cast mating system of sessile hermaphroditic animals that brood eggs may lead to significant levels of sperm competition (see review in Bishop and Pemberton 2006). Multiple mating and sperm storage are common in hermaphroditic animals, including many androdioecious taxa (see review in Weeks and others 2006). Direct evidence for sperm competition is available from a flatworm (Pongratz and Michiels 2003), a leech (Tan and others 2004), and the gastropods, H. aspersa (Rogers and Chase 2002), Arianta arbustorum (Hänggi and others 2002) and Aplysia californica (Angeloni and others 2003).

Competition for access to mates in the form of “sneaky male” strategies has been documented in several of the sequentially or simultaneously hermaphroditic fish (see reviews in Warner 1982; Adreani and others 2004; Fischer and Petersen 1987; Leonard 1993 and Petersen 2006). Some serranines also have harem polygamy (see following section and Petersen 2006) and an increase in male mating opportunities seems to be associated with social dominance in this group (Leonard 1993). Fighting between males has been reported in a sequentially hermaphroditic polychaete (see discussion in Berglund 1986, 1991; Sella and Ramella 1999). It seems likely that classic interference competition for access to mates occurs in other hermaphrodites, although documented examples are rare. This may reflect either a lack of attention to the phenomenon or a difference in the biology of hermaphrodites. For example, in many androdioecious animals, males are rare relative to self-fertilizing hermaphrodites (see review in Weeks and others 2006) so that competition among males for access to hermaphrodites may seldom occur. The prevalence of conditional reciprocity in mating systems in simultaneous hermaphrodites (see discussion that follows and in Leonard 2005) may inhibit the success of interference competition. If this is true, species with hypodermic insemination, unilateral copulation without reciprocity, or chain copulation may be fruitful sources of evidence for direct interference competition. Competition among hermaphrodites for access to a partner’s sperm or for matings

### Table 2 Sources of sexually dimorphic variance in reproductive success

<p>| 1. Differential per gamete investment (Bateman 1948) |
| 2. Differences in gamete number (Darwin 1871) |
| 3. Differential postzygotic investment (Trivers 1972) |
| 4. Skewed operational sex ratio (Emlen and Oring 1977) |
| 5. Differences in potential mating rate (Baylis 1981; Sutherland 1985; Clutton-Brock and Vincent 1991) |
| 6. Differences in latency between reproductive episodes (Hubbell and Johnson 1987) |
| 7. Skewed breeding sex ratio (Arnold and Duvall 1994) |
| 8. Greater control of fertilization by one sex (Alexander and Borgia 1979; Leonard and Lukowiak 1984) |
| 9. Differential correlation between age/size and fecundity (Size-advantage model; Ghiselin 1969a; Warner 1975) |
| 10. Differential correlation between age/size and success in competition for mates (Size-advantage model; Ghiselin 1969a; Warner 1975) |</p>
<table>
<thead>
<tr>
<th>Character</th>
<th>Dioecious taxa</th>
<th>Hermaphrodites</th>
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<tbody>
<tr>
<td>Competition for mates</td>
<td>Common</td>
<td>Documented in sequential and some simultaneous hermaphrodites; sneaker males in serranines, fighting in Ophytrocha</td>
</tr>
<tr>
<td>Sperm/pollen competition</td>
<td>Common</td>
<td>Pollen competition common and well documented (Willson and Burley 1983, etc.); sperm competition documented in one flatworm, some serranines and some gastropods; likely to be common</td>
</tr>
<tr>
<td>Mate choice</td>
<td>Common</td>
<td>Documented in Biomphalaria glabrata (Webster 2006); size-assortative mating reported in nudibranchs, flatworms, and tapeworms</td>
</tr>
<tr>
<td>Morphological sexual dimorphism</td>
<td>Common (see Darwin 1871)</td>
<td>Not uncommon in sequential hermaphrodites, for example, bluehead wrasse; one report in simultaneous hermaphrodites</td>
</tr>
<tr>
<td>Sexually dimorphic sexual behavior</td>
<td>Most pair-mating taxa</td>
<td>Found in some simultaneous hermaphrodites; that is, Hypoplectrus nigricans, Navanax inermis, Lymnaea stagnalis; Achatina fulica; common in sequential hermaphrodites</td>
</tr>
<tr>
<td>Elaborate and/or expensive mating and/or courtship behavior</td>
<td>Common in insects, crustacea, vertebrates; some molluscs</td>
<td>Common in euthyneuran gastropods; for example, Navanax inermis, Linax maximus, Helix spp; Ariolimax spp. (see Baur 1998; Koene 2006)</td>
</tr>
<tr>
<td>Mating systems based on conditional reciprocity</td>
<td>Not applicable!</td>
<td>For example, Hypoplectrus nigricans, Serranus tigrinus, Navanax inermis, Ophytrocha spp; Ananta arbustorum, Schindera polyocha, may be widespread (see text and review in Leonard 2005)</td>
</tr>
<tr>
<td>Rapid evolution of genitalia/flowers; elaborate genitalia/flowers</td>
<td>Common in arthropods, probably widespread</td>
<td>Common in angiosperms, platyhelminths, stylommatophoran gastropods; for example, Ariolimax spp., probably widespread</td>
</tr>
<tr>
<td>Skews in operational sex ratio</td>
<td>Common (Emlen and Oring 1977; review in Shuster and Wade 2003)</td>
<td>Common in sequential hermaphrodites; also found in simultaneous hermaphrodites with sexual polymorphisms and complex sexual systems (phally polymorphisms, complemental males, androdieocy, gynodieocy, etc.)</td>
</tr>
<tr>
<td>Skews in breeding sex ratio</td>
<td>Less studied (but see review by Shuster and Wade 2003)</td>
<td>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; spermcast mating systems; animal pollination, etc. (see text)</td>
</tr>
<tr>
<td>Harem defense polygamy</td>
<td>Well documented in some vertebrates; arthropods</td>
<td>Common in sequentially hermaphroditic fish; for example, bluehead wrasse (Warner and Swearer 1991); documented in two species of simultaneously hermaphroditic serranine fish (see Petersen 2006)</td>
</tr>
<tr>
<td>High variance in reproductive success in either or both sexual roles.</td>
<td>Data from red deer, elephant seals, damselflies, etc.¹</td>
<td>For plants see Delph and Ashman (2006); few data for animals</td>
</tr>
<tr>
<td>Self-fertilization</td>
<td>Not applicable</td>
<td>Common in simultaneous hermaphrodites; consequences for sexual selection largely unexplored</td>
</tr>
</tbody>
</table>

²Reviews in Michiels 1998; Willson and Burley 1983; Ashman and Delph 2006; Thomson 2006.
³Crozier and Arey 1919; Vreys and Michiels 1997; Milinski 2006.
⁴Warner 1975; Petersen 2006; McLauchlan 1951 reports dimorphic shell morphology allegedly associated with differing sex roles in a stylommatophoran.
⁶Eberhard 1985 for animals.
⁷Eberhard 1985; for plants Darwin 1877, 1888; Thomson 2006; Ariolimax spp. see Mead 1943.
⁸Ghiselin 1969a, 1974; Willson and Burley 1983, etc.
in the female role has not been studied but is theoretically possible (see discussion in Leonard 2005).

Mate choice
Female choice of mates is a key aspect of classical sexual selection. Mate choice by hermaphrodites on the basis of size and/or age has been documented in such metazoan taxa as the polychaete Ophyrotrocha (Berglund 1986, 1991; Sella 1988; reviews by Premoli and Sella 1995; Lorenzi and others 2006) and the stylommatophoran snail Achatina fulica (Tomiyama 2002). In addition, evidence for assortative mating by size, implying mate choice, exists for a flatworm (Vreys and Michiels 1997) and a tapeworm (Lüscher and Wedekind 2002; review in Milinski 2006) from laboratory studies, an opisthobranch from field data (Crozier 1918; see also Longley and Longley 1984), and in both laboratory and field data for an earthworm (Michiels and others 2001). In an elegant series of studies, Webster and colleagues (see review in Webster and Gower 2006) have demonstrated that Biomphalaria glabrata snails with resistant genotypes discriminate against mates on the basis of parasitic infection. There is also evidence that simultaneous hermaphrodites may discriminate among sperm on the basis of whether spermatophores were exchanged reciprocally, in an opisthobranch (Karlsson and Haase 2002) and in the stylommatophoran Cantareus (Helix) aspersa, on the basis of whether a dart was received (review in Koene 2006) although, in the latter case, it is not clear whether cryptic female choice or sperm competition is involved. In a planarian, individuals gave more sperm to previously isolated individuals, suggesting a preference for lower sperm competition (Michiels and Bakovski 2000). In some simultaneously hermaphroditic serranine fish, individuals with eggs to spawn mate preferentially with larger hareem-holding hermaphrodites or pure males (see reviews in Leonard 1993; Petersen 2006). Data on the number of offspring sired by first vs. second mates shows considerable individual variation in the stylommatophoran Arianta arbustorum (Baur 1994), suggesting that these simultaneous hermaphrodites may be able to exercise cryptic female choice. Selective abortion in plants may represent a form of cryptic female choice (see reviews in Willson and Burley 1983; Skogsmyr and Lankinen 2002), although in plants female choice may be difficult to distinguish from parent-offspring conflict (Skogsmyr and Lankinen 2002). The study of female choice is complicated by the possibility that there may be no “best” male, but that females pick mates on the basis of compatibility with their own genotype (for example, Bluhm and Gowaty 2004).

Sexual dimorphism
Morphological sexual dimorphism is common in sequential hermaphrodites such as the well-studied examples of fish with social control of sex change (for example, Warner and others 1975; Shapiro 1979). Monoecious plants, that is, those with separate male and female flowers on the same individual, may have sexually dimorphic flowers (Barrett 1998). Ectoprocts with morphologically distinct male and female zooids in a hermaphroditic colony also may be considered to have sexual dimorphism (see Bishop and Pemberton 2006). There is one report (McLauchlan 1951) of stylommatophorans with a shell dimorphism that allegedly reflects differences in sexual behavior associated with age and size. What is more common in simultaneously hermaphroditic taxa than morphological sexual dimorphism is behavioral sexual dimorphism. That is, it is sometimes the case that individuals will behave quite differently when mating in one role rather than the other. For example, the opisthobranch sea slug Navanax inermis copulates unilaterally with one individual acting as male and the other female and this is associated with distinct male and female courtship behaviors (Leonard and Lukowiak 1984, 1985). This is also the case in another opisthobranch, Aplysia californica (Leonard and Lukowiak 1986) and in the basommatophorans Lymnaea stagnalis (review in Koene 2006), Physa acuta (Ohbayashi-Hodoki and others 2004) and Biomphalaria glabrata (Webster and Gower 2006). Simultaneously hermaphroditic serranine fish also show sexually dimorphic courtship behavior (Fischer 1980; Petersen 2006) and in both Navanax and the serranines there is a preference for mating in one of the sexual roles with Navanax preferring the female role (Leonard and Lukowiak 1991; Michiels and others 2003) and the serranines preferring the male role (Leonard 1993; Petersen 2006). Such behavioral dimorphism will probably prove to be more widespread when more hermaphroditic taxa have been studied in detail. In contrast, a species of stylommatophoran banana slug with unilateral introgression (Ariolimax californicus) has symmetrical courtship behavior (Leonard and others 2002). The factors that account for asymmetrical vs. symmetrical courtship behavior in unilaterally copulating taxa have yet to be studied.

Elaborate, costly, or bizarre sexual behavior
Perhaps the most basic criterion for suspecting sexual selection in a species is the observation of sexual behavior or other reproductive characters that seem bizarre, or likely to be costly in terms of either energy, time or risk of harm to the possessor. Lengthy, costly,
and/or elaborate courtship and mating behavior has been described for a variety of pair-mating hermaphrodites (see discussion in Baur 1998; Michiels 1998; Michiels and Koene 2006). The elaborate courtship and mating behavior of land snails of the genus Helix (Cantareus) which involves the shooting of the partner with a centimeter long calcareous “love-dart” has been considered in terms of sexual selection only recently (detailed behavioral description in Lind 1976; reviews in Leonard 1992; Koene 2006). Perhaps even more spectacular is the aerial mating of the land slug Limax maximus in which a pair of simultaneous hermaphrodites climb a tree or wall to an overhang, drop down on 10–25 cm of mucus strands and, hanging, exchange spermatophores between entwined penes, without intromission (Gerhardt 1934; Langlois 1965). The energetic cost of locomotion and mucus production in stylommatophorans is high (Denny 1980) and mucus production is a major source of water loss in these terrestrial mollusks (Luchtel and Deyrup-Olsen 2001). The mucus threads are often eaten after copulation, suggesting that the material content of the threads represents an important resource. Limax is one of the many hermaphrodites that will repay investigation from the standpoint of sexual selection. Another bizarre behavior is the apophallation found in two species of Ariolimax slugs, whereby copulation is occasionally terminated by amputation of the penis of one or both individuals; (Heath 1916; Mead 1942; Leonard and others 2002). A similar behavior has been reported for the genus Deroceras (Rymzhanov 1994) with the difference that in this case, individuals are reported to amputate their own penis after a unilateral copulation and present it to the partner. Another spectacular and apparently expensive behavior termed “penis fencing” has been described in Pseudoceros bifurcus, a marine flatworm with hypodermic insemination, in which individuals apparently attempt to ward off damaging penis insertions (Michiels and Newman 1998). Michiels and Koene (2006) argue, on theoretical grounds, that sexual behavior involving damage to the individual acting as a female is particularly likely to evolve in hermaphrodites.

Sexual conflict

One of the most important differences between sexual selection in dioecious vs. hermaphroditic species is that, in gonochorists, sexual conflict is indirect. That is, in each generation males compete with males for their contribution to the next generation, and females compete with females. Sexual conflict is an epiphenomenon. In hermaphrodites, in contrast, each individual competes with all others in the population, including its mates. Since every individual has both a mother and father, in outbreeding populations both total and mean fitness must be equal for male and female functions. However, if the variances in fitness differ for the two sexual roles, then the potential fitness of the two sexual roles also differs, and one would expect that selection would favor individuals that specialize in the preferred role (see Charnov 1979; Fischer 1980, 1988; Leonard 1990, 1999, 2005; Michiels 1998). Based on Bateman’s principle, Charnov (1979) predicted that simultaneous hermaphrodites should be more eager to mate as males than as females because of the potential for increased fitness; that is, simultaneous hermaphrodites should prefer to mate in the high variance sexual role, although data from angiosperms demonstrates that the female role in hermaphrodites may have higher variance than the male sexual role (see Delph and Ashman 2006 for discussion). Charnov’s hypothesis is contrary to predictions from probability theory which demonstrate that where two strategies offer equal mean return, as must be the case for male and female functions in an outcrossing organism, the strategy with the lower variance will offer higher fitness due to the reduced probability of zero fitness (Gillespie 1974; Real 1980; Leonard 1999; for recent review see Leonard 2005). This logic (Gillespie’s principle) predicts that hermaphrodites will prefer the sexual role with lower variance (see Leonard 1999, 2005 for discussion). If one sexual role has a lower variance than the other, that role should, by Gillespie’s principle (Gillespie 1977; contrary to Charnov 1979; see discussion in Leonard 1999, 2005), offer potentially higher fitness. Hermaphrodites able to specialize in that role, then, should have higher fitness and individuals should compete for that sexual role, creating a direct conflict of interest between mates (see discussion in Leonard 1990, 2005). This conflict of interest creates potential for sexual selection because (a) individuals compete for matings in one sexual role and (b) according to the Hermaphrodite’s Dilemma model (Leonard 1990), individuals will choose mates that are willing to reciprocate by mating in both sexual roles (see discussion in Leonard 2005).

If there are systematic and consistent differences between the sexes in variance in reproductive success, then mating between simultaneous hermaphrodites should involve a conflict of interest whereby each individual will attempt to monopolize one sexual role and, since it takes two to tango (or mate), mating systems based on conditional reciprocity represent a cooperative and stable solution to the problem (Fischer 1980; Axelrod and Hamilton 1981; Leonard and Lukowiak 1984; Leonard 1990; see Leonard 2005 for review; discussion in Petersen 2006). The
Hermaphrodite’s Dilemma model (Leonard 1990) predicts that where a consistent preference for one sexual role exists, mating systems will evolve to reciprocity (Leonard 1990; see discussion in Leonard 2005). Many mating systems in pair-mating hermaphrodites involve either simultaneously or serially reciprocal mating. In the few cases that have been studied, these mating systems appear to be based on conditional reciprocity (for review see Leonard 2005). Direct evidence for conditional reciprocity is of two general types; the first is evidence that an individual’s willingness to assume a particular sexual role is contingent on the partner’s willingness to assume the same sexual role, resulting in either simultaneously or successively reciprocal mating (see review in Leonard 2005); the second is evidence that an individual’s readiness to mate in both sexual roles with a particular partner is dependent on the quality of that partner (review in Leonard 2005; experimental data in Milinski 2006; Webster and Gower 2006). The mating systems of Ophryotrocha spp. offer strong conclusive evidence of conditional reciprocity in mating (review by Lorenzi and others 2006; see also discussion in Leonard 2005). Webster and Gower (2006) describe experiments demonstrating that in B. glabrata parasite-resistant individuals will mate reciprocally with uninfected partners but mate exclusively in the male role with infected partners. Petersen (2006) reviews the mating systems of serranines, which are based on conditional reciprocity, from the standpoint of game theory models (see also Axelrod and Hamilton 1981; Leonard 1990; discussion in Leonard 2005).

The available evidence from simultaneously hermaphroditic animals demonstrates a clear preference for the male sexual role in some taxa whereas the female sexual role is preferred in others (see review in Leonard 2005). So far, data to link these role preferences with differential variance in reproductive success are not available (but see Fischer 1981). Also, it seems clear that in some hermaphrodites the preferred sexual role may vary with size, age, or social environment (Charnov 1982; Klinkhamer and de Jong 1997; Klinkhamer and others 1997; Angeloni and Bradbury 1999; Schärer and others 2001; Tomiyama 2002), as assumed by the size advantage model (see Ghiselin 1969a, 2006; Warner 1975). A disadvantage of variance in reproductive success as a measure of potential for sexual selection is the difficulty of obtaining lifetime reproductive success for a large number of individuals. In hermaphrodites an additional problem is that of separating fitness due to male vs. female reproductive success to determine whether role preference is correlated with either variance.

De Facto Reciprocity. Conditional reciprocity is not the only possible form of reciprocity. In non-pair mating simultaneous hermaphrodites, such as plants, and sessile invertebrates, for example, barnacles, ascidians and bryozoans (Levitan 2005; Bishop and Pemberton 2006; Weeks and others 2006), one might expect de facto reciprocity among individuals in a local population, which would satisfy the prediction of Hermaphrodite’s Dilemma. The behavior of pollinators should be an important selective force in angioperms (Thomson 2006). However, the extent to which individuals tend to fertilize the eggs of individuals from whom they receive sperm remains to be established in such taxa (but see Edmands and Potts 1997). The Hermaphrodite’s Dilemma model predicts that such unconditional or de facto reciprocity should be associated with conditions under which the pay-off matrix is such that the cost of failing to mate is higher than the cost of mating exclusively in the less-preferred role (Game of Chicken conditions, Leonard 1990; see also Michiels 1998; Pongratz and Michiels 2003; Connor 1986, discussion in Leonard 2005).

Lack of Reciprocity. It is important to remember that reciprocity is apparently not a universal feature of mating systems in simultaneous hermaphrodites. There are many examples of unilateral mating in simultaneous hermaphrodites (for example, Lysmata shrimp, Bauer 2006, and chain copulation in certain gastropods, review in Leonard 1991; Baur 1998). What is not clear is whether sexual conflict is absent in these systems, making the assumptions of Hermaphrodite’s Dilemma (Leonard 1990) invalid, or whether the model’s predictions are incorrect. If sexual conflict is absent in these systems, it should be because the variance in reproductive success is equal for the two sexual roles. Understanding the factors that lead to equal vs. unequal variance for the two sexual roles in hermaphrodites will be a key step to understanding the origin of the sex differences in intensity of sexual selection that apply to gonochorists (see discussion in Leonard 2005).

Elaborate, bizarre, extravagant, and/or quickly evolving genitalia

Bill Eberhard (1985) made a bold departure from traditional thinking on sexual selection when he pointed out that where genitalia have diverged so rapidly as to be useful taxonomic character distinguishing species, and even subspecies, it is likely that sexual selection has been involved in the evolution of these traits. The last 20 years have seen a burgeoning interest in the relationship between genital evolution and sexual selection in dioecious animals (reviews in
Hosken and Stockley 2004; Méndez and Córdoba-Aguilar 2004). Some of the major groups of hermaphroditic invertebrates included in Eberhard’s (1985) list of taxa with rapidly divergent genitalia, were stylommatophoran gastropods, turbellarian flatworms, leeches, and oligochaetes. These groups would seem to offer very promising opportunities to test Eberhard’s hypothesis but as yet there has been little work done (but see Emberton 1994; Reise and others 1996; Reise and Hutchinson 2001; Leonard and others 2002; Koene and Schulenburg 2005). The lack of interest in genitalia in hermaphrodites is particularly puzzling in light of Charnov’s (1979) prediction that high fixed costs, such as genital morphology, associated with each sexual role would select against hermaphroditism (see discussion in Leonard 2005).

Skewed sex ratios

Mating systems that involve a marked divergence from 1:1 in primary or operational sex ratios (OSR) have long been regarded as especially likely to be under sexual selection (see discussion in Kvarnemo and Ahnesjö 1996, 2002; Shuster and Wade 2003; Wade and Shuster 2004; Wade and others 2003). Koenig and Albano (1986) argued that the mere existence of a skewed sex ratio is not de facto evidence for sexual selection, stating that if mating were at random, sexual selection would not occur even with a skewed sex ratio. However, a skewed sex ratio would certainly create selective pressures for competition among individuals of the majority sex for opportunities to mate with the minority sex and/or for individuals of the minority sex to be choosy about mate quality, and sexual selection would be expected to evolve in such a situation. Although hermaphroditism has been viewed as a means of ensuring a 1:1 sex ratio, there are many instances of skews in primary sex ratio (see following section); OSR (Emlen and Oring 1977), potential reproductive rate (Baylis 1981, Kvarnemo and Ahnesjö 1996), and BSR (Arnold and Duvall 1994) in hermaphrodites that may lead to skewed sex ratios. Below these have been lumped into a few general categories.

*Sequential hermaphroditism.* Sequential hermaphroditism is a term that includes two general phenomena; one where individuals change sex repeatedly over their life history, often in response to environmental factors (alternating sex change), and one in which individuals begin life as one sex, function reproductively as that sex for a time and then change to the other sex as they grow and/or age (adolescent protandry or protogyny) (Ghiselin 1974). Sequential hermaphroditism is taxonomically widespread throughout the Metazoa but apparently rare except in mollusks and fishes (see Policansky 1982). Dichogamy in which male and female functions are separated in time in a given flower is widespread in angiosperms (Barrett 1998, Routley et al. 2004).

In species in which individuals change sex, sex ratios will tend to be skewed toward the sex that comes earliest in the life history; that is protandrous species will tend to have a predominance of males in the population while protogynous species will have a predominance of females. In fact, a highly skewed sex ratio in fish or invertebrate populations is often taken as evidence for sequential hermaphroditism (but see Wenner and Haley 1981 for discussion). Such a skewed sex ratio would tend to create competition for access to individuals of the limiting sex (Ghiselin 1969a; Warner 1975) setting the stage for strong sexual selection. A single sex change associated with age and/or social environment is also found in a variety of taxa (see Ghiselin 1974; Warner 1975; Hoagland 1978; Baur 1998). Ghiselin (1969a) in his size-advantage model, recognized that the age or size of sex change in sequentially hermaphroditic taxa was influenced by sexual selection (see also Warner and others 1975; discussion in Ghiselin 2006).

Alternating sex change is found in many taxa including mollusks (see review in Baur 1998); plants (see review in Policansky 1982); polychaetes (for example, Ophyrotrocha, Berglund 1991) and fishes (Kuwamura and others 1994; Muñoz and Warner 2003). Alternating sex change may be associated with individual condition (for example, sex change as a function of stored reserves in jack-in-the-pulpit, Policansky 1981); brooding (for example, Ostrea oysters produce sperm when brooding embryos, Coe 1932; Ghiselin 1974; Baur 1998), or social environment (for example, fishes, Kuwamura and others 1994); Ophyrotrocha (Berglund 1991). The effects of alternating sex change on sex ratio are not well known, but there is certainly the potential for considerable variation in sex ratio from place to place or from one season to another in such species and therefore the potential for wide variation in the degree of sexual selection.

*Breeding sex ratios and simultaneous hermaphroditism.* Although theoretical treatments of simultaneous hermaphroditism have been based on the concept of a 1:1 sex ratio (Charnov 1979; Leonard 1990; Arnold 1994a; Morgan 1994), the reality may be quite different. First, the dichotomy between sequential and simultaneous hermaphrodites is an artificial one: there are many intermediate cases. Adolescent protandry followed by an adult phase of simultaneous hermaphroditism is found in many taxa, including Ophyrotrocha (see Lorenzi and others 2006) and
Lysmata shrimps (Bauer 2006). Adolescent protogyny has been described in a sea anemone (Dunn 1975). A less common pattern, in which some simultaneous hermaphrodites lose ovarian tissue and become male, is found in a couple of species of serrane fish (Hastings and Petersen 1986; review in Petersen 2006). In addition, hermaphrodites illustrate an important distinction between the OSR, the sex ratio at the time of mating (Emlen and Oring 1977), and the BSR, or sex ratio of male-to-female parents (Arnold and Duvall 1994). For example, although one sees frequent references to protandry in opisthobranch and pulmonate gastropods, this typically refers to the maturation of sperm before eggs in the gonad and individuals that donate sperm to a partner are also receiving sperm from the same or another partner at the same stage of the life cycle, which will be stored, sometimes for months, before eggs are produced. Thus, protandrous maturation of the gonad can result in an OSR of 1:1 but if individuals mate with multiple partners and sperm are stored by the recipient long enough that there is an appreciable mortality between the time of mating and the time of egg-laying, the BSR may be strongly male-biased. This phenomenon has received little attention but is certainly widespread in eutehynuran gastropods and may occur more widely in hermaphroditic invertebrates. Sperm storage seems to be more common in larger, and consequently longer-lived, gastropods (Tompa 1984; Hadfield and Schmitter-Dunlap 1984).

Another common phenomenon in simultaneous hermaphrodites that has been neglected by theory is the dependence of sexual behavior on age and/or size (but see Klinkhamer and de Jong 1997; St Mary 1997; Schärer and others 2001). As assumed by the size-advantage model, fecundity through one sexual role may be more highly correlated with size than is fecundity through the other sexual role. This may be true even in simultaneous hermaphrodites in populations with a large size/age range for example, a tree (Wells and Lloyd 1991); a goby (St Mary 1994); a tapeworm (Schärer and others 2001). If so, one would expect that (a) the role preference of individuals may change with size/age [contrary to the assumptions of current models; (Charnov 1979; Axelrod and Hamilton 1981; Leonard and Lukowiak 1984; Leonard 1990)] and (b) individuals may discriminate among mates on the basis of size and/or age. In the opisthobranch, A. californica, large individuals were more likely to be found copulating as females than expected at random but there was no tendency for individuals to be male more often at smaller sizes (Angeloni and others 2003). In the tapeworm, Schistocephalus solidus large individuals were preferred as mates (Lüscher and Wedekind 2002) and in this species, large individuals produce more eggs (Schärer and Wedekind 1999). In a basommatophoran snail, Physa acuta, small individuals were more likely to play the male role in copulation and preferred large individuals as partners (Ohbayashi-Hodoki and others 2004). Also, in Achatina fulica, a very long-lived species, Kiyonori Tomiyama (2002) has documented a preference by young individuals for large individuals as partners. In a stylommatophoran slug, Donna Fernandes (1988) found protandric gonadal development and that individuals copulated in youth and then, as the gonad began to shift from sperm to egg production, started to avoid conspecifics and began to lay eggs. These patterns of development and behavior should lead to skewed BSRs creating strong pressure for sexual selection.

Mixed sexual systems. Angiosperms are known for a variety of complex sexual systems; androdioecy, gynodioecy, etc. (see Barrett 1998 for review). In animals, taxa with hermaphroditism may also have complex sexual systems. Most metazoans with androdioecy seem to involve simultaneous hermaphrodites that either self-fertilize or outcross with males (see review by Weeks and others 2006) but there are exceptions. For example, some taxa of barnacles have both simultaneous hermaphrodites and complemental males (see review in Ghiselin 1974; Weeks 2006). In some Ophyrotrocha species, juveniles are males, capable of outcrossing and larger individuals are simultaneous hermaphrodites capable of mating in both sexual roles (review in Lorenzi and others 2006). In two species of simultaneously hermaphroditic serranines with harem polygamy large individuals may lose ovarian function and become male. Hermaphrodites may mate as males with other hermaphrodites or as females with either males or hermaphrodites. The same sexual system, which has been termed protandric simultaneous hermaphroditism (PSH), has recently been discovered in shrimp of the genus Lysmata which had been previously considered to be sequentially hermaphroditic (see review in Bauer 2006). A sexual polymorphism involving hermaphrodites and individuals that are male-sterile has been reported from corals (Chornesky and Peters 1987).

Sexual polymorphisms. Another phenomenon associated with potentially skewed sex ratios in hermaphroditic taxa is the existence of sexual polymorphisms in a population. In tanaid crustaceans, one species appears to consist of females and two types of males, primary males and secondary males, the latter having reproduced as females earlier in their lives (see discussion in Ghiselin 1974). Similar phenomena have been described in sequentially hermaphroditic fish...
(Warner 1975). Another form of sexual polymorphism, phally polymorphism, seems to have evolved multiple times in pulmonate snails (Schrag and Read 1996). In phally polymorphism, a population may consist of hermaphrodites which are euphallic (having a fully developed penis), aphallic (lacking a penis) and/or hemiphallic, having a reduced penis (see reviews in Tompa 1984; Pokryszko 1987; Gómez 2001; Doums and others 1998). Euphallic individuals may self-fertilize or outcross as males and/or females. Aphallic individuals may outcross as females or self-fertilize. In the best studied case, the basommatophoran *Bulinus truncatus*, all individuals prefer to self-fertilize regardless of phally status but the incidence of out-crossing was no lower in aphallic than euphallic individuals (Viard and others 1997). The role of phally polymorphism in mating systems and sexual selection is not as yet understood but it seems probable that these sexual polymorphisms are associated with sexual selection. In *Bulinus*, the evolution of aphally may reflect a reduction in sexual selection due to the prevalence of selfing. The wide variation in the incidence of aphally among populations of *B. truncatus* suggests that this hypothesis can be tested and the factors that promote or inhibit sexual selection in this hermaphrodite can be identified and measured. Further forms of morphological sexual polymorphism such as heterostyly are well known in angiosperms, such as many primrose species, where it is considered an adaptation to promote outcrossing; that is, mating success.

**Harem polygamy.** Among the mating systems that are typically associated with strong sexual selection in dioecious taxa are those that involve polygamy. Examples are found in hermaphrodites. The harem defense polygyny found in a variety of taxa of sequentially hermaphroditic reef fishes, in which individuals are females early in life and the largest individual of a group becomes male (terminal-phase male) and defends the group as a harem, has been a very active field of research in sexual selection (Ghiselin 1969a; Warner 1975; Shapiro 1979; Warner 1982). Harem defense polygyny has also been described in simultaneously hermaphroditic serranines, in which, under high density conditions, large individuals defend harems of simultaneous hermaphrodites and may even lose ovarian tissue to become male (Hastings and Petersen 1986; see review in Petersen 2006). Comparable systems in invertebrate hermaphrodites have not yet been described. In contrast, monogamy is well known in both fish and invertebrates with either sequential or simultaneous hermaphroditism (Pressley 1981; Kuwamura and others 1994). In the polychaete genus *Ophyrotrocha* which has both sequentially and simultaneously hermaphroditic species (as well as gonochorists), the mating system of some species involves serial monogamy of variable fidelity (reviews in Premoli and Sella 1995; Lorenzi and others 2006).

**Differential reproductive investment**

Since Trivers’ (1972) seminal paper, sexually dimorphic patterns of reproductive investment have been seen as a root cause of sexual selection. Differential patterns of reproductive investment in terms of differential size and number of sperm (or pollen grains) vs. eggs are also the rule in hermaphrodites. Parental care is also found in hermaphrodites. Maternal care in the form of brooding eggs and embryos has long been known to be associated with simultaneous hermaphroditism in invertebrates (see reviews in Ghiselin 1969, 1974; Clark 1978; Bishop and Pemberton 2006) and Charnov (1979) argued that brooding was a condition that favored the evolution of simultaneous hermaphroditism. Other forms of parental care in hermaphrodites include maternal care by leeches (Kutschera 1984; Kutschera and Wirtz 1986; Tan and others 2004), communal defense of egg masses in a nudibranch (Rose and Hoegh-Guldberg 1982), biparental care of egg masses in *Ophyrotrocha* (review in Sella and Ramella 1999) and there is one report of paternal care in a polychaete (see Sella and Ramella 1999). The role of sexual selection in mating systems involving parental care remains to be determined in hermaphrodites. Most of the interest in effect of reproductive investment on mating systems and sexual selection in hermaphrodites has come in the form of interest in Charnov’s (1982) theory of sex allocation.

**Sex allocation.** Sex allocation (Milinski 2006; Lorenzi and others 2006; Delph and Ashman 2006; Thomson 2006; Klinkhamer and de Jong 2002) is a trait subject to sexual selection in hermaphrodites (Charnov 1979; 1982; see following discussion) and has been the focus of a great deal of attention over the last 20 years. The fundamental question has been that of determining how a hermaphrodite should partition resources between male and female functions to maximize its fitness. Eric Charnov (1982) made a variety of predictions as to sex allocation under various environmental and social conditions. In this volume, three reviews (Thomson 2006; Delph and Ashman 2006; Lorenzi and others 2006; see also Klinkhamer and de Jong 2002) discuss the problems encountered in attempting to identify and measure trade-offs between male and female functions in hermaphrodites. In all cases, the authors find that the utility of predictions from sex allocation theory is greatly limited by the
difficulties encountered in actually measuring sex allocation. In Klinkhamer and de Jong’s words, “Measuring exact sex allocation in hermaphroditic plants is difficult or perhaps even impossible given the fact flowers serve both male and female functions [see review in Weeks and others 2006].” For that reason, Thomson (2006) suggests that pollen presentation theory is a better source of testable hypotheses about sexual selection in angiosperms than is sex allocation theory. Lorenzi and colleagues (2006) attempted to measure sex allocation in the polychaete O. diadema under varying social conditions, in order to test predictions of local mate competition theory, and found many of the effects seemed to be in the form of changes in behavior that were difficult to quantify. In a review of the results of several studies looking at pollen donation vs. pollen receipt as a measure of male vs. female reproductive success, Delph and Ashman (2006) found that in several studies on hermaphroditic angiosperms, selection did not result in a trade-off between male and female reproductive traits, but rather selection acted in “harmony” on male and female functions. Although not all traits involved “harmony” between male and female functions, these data provide strong support for Charnov’s (1979) prediction that flowers in hermaphrodites would act to link male and female reproductive success. Charnov (1979) predicted that trade-offs between male and female functions would favor the evolution of separate sexes. According to this analysis, simultaneous hermaphroditism would only be favored if success through female and male functions were linked (see discussion in Leonard 2005) and Charnov cited flowers attracting pollinators that would both deposit and remove pollen as an example of a trait that could promote male and female fitness simultaneously. Although the difficulties in actually measuring sex allocation make these predictions difficult to test (see Thomson 2006), the available data may be consistent with Charnov’s prediction that where trade-offs between male and female functions are necessary, simultaneous hermaphroditism will not be stable.

Self-fertilization
The evolution of self-incompatibility mechanisms has been well documented both in plants (see Delph and Havens 1998; Routley and others 2004 for reviews) and in animals (see discussion in Bishop and Pemberton 2006); but many simultaneous hermaphrodites have the ability to self-fertilize. In many animal taxa, such as nematodes, the only known hermaphrodites are self-fertilizing or androdioecious (see review in Weeks and others 2006). Weeks and colleagues (2006) describe an entire genus of clam shrimps which is androdioecious, a very rare sexual system in either plants or animals. The effect of self-fertilization on the evolution of mating systems has received considerable attention from a theoretical standpoint (for example, Jarne and Charlesworth 1987; Pannell and Barrett 2001; Tsitrone and others 2003a). The relationship of self-fertilization to sexual selection in hermaphrodites has received less attention (but see Tsitrone and others 2003b). At one level, it seems clear that where self-fertilization is a possibility, individuals giving sperm (or pollen) to a partner will always be facing a situation of sperm competition. Also, where an individual has the option of fertilizing its own eggs, one might expect it to be more than usually choosy about sires for its offspring. These considerations would suggest that the ability to self-fertilize might tend promote sexual selection by reducing the need for fertility assurance. The importance of these factors will vary with the degree of inbreeding depression associated with selfing, which is highly variable among species. In general, there is evidence that individuals in most species prefer to outcross when mates are available (see Milinski 2006; Weeks and others 2006) although there are many exceptions (see Milinski 2006; Doums and others 1996). In an elegant series of experiments involving laboratory culture of the simultaneously hermaphroditic tapeworm, S. solidus Milinski and co-workers demonstrated that individuals produced more selfed offspring when paired with a partner of dissimilar size than when the pair were of the same size, suggesting that in this tapeworm, selfing may represent a way of cheating on a Hermaphrodite’s Dilemma game (Milinski 2006). Interestingly, even pairs matched in size continued to produce some selfed offspring. This may represent an adaptation to a predominantly Game of Chicken matrix (Leonard 1990) under natural conditions where the tapeworms may often lack a partner (see Milinski 2006 for discussion). The relative fitness of selfed vs. outcrossed offspring can be variable; inbreeding depression is often severe but in S. solidus selfed offspring performed as well as outcrossed offspring, except under competition (Milinski 2006).

Direct evidence for sexual selection
As this discussion demonstrates, there is abundant circumstantial evidence for sexual selection in hermaphrodites in both forms that are familiar from dioecious taxa and forms that are unique to hermaphrodites (for example, socially mediated sex change; mating systems based on conditional reciprocity). While the circumstantial case for sexual selection as an important force in hermaphrodite
mating systems is strong, one would like both to obtain more direct evidence of sexual selection and to identify the sources of sexual selection in hermaphrodites, with the goal of using this information to test existing theories of sexual selection and to develop more predictive theories as to the strength and direction of sexual selection. Obtaining direct evidence for sexual selection requires the ability to measure sexual selection.

Measuring Sexual Selection

The definition of sexual selection adopted here (Table 1, definition 12) was put forward by Malte Andersson (1994). It is based on Darwin’s definition of sexual selection in *Descent of Man* (quoted earlier). The key feature of the definition is competition; not just competition for access to mates, but competition to be chosen as a mate, and competition to choose the best (right) mates. As Steve Arnold (1994b) pointed out, using competition as part of the definition of sexual selection virtually mandates manipulative experiments as a means of measuring sexual selection and/or determining definitively whether sexual selection is acting on a particular trait. This problem seems unavoidable. As discussed earlier, sexual selection acts on a wide variety of traits in both dioecious and hermaphroditic species, and the strength and even direction of sexual selection may change with such variables as sex ratio (Jones and others 2005). Arnold proposed the use of Bateman’s gradients, the relationship between number of offspring and number of mates (Arnold 1994a; Arnold and Duvall 1994), as a way of measuring sexual selection, but acknowledged that this measure ignores the issue of mate quality. This seems like a major disadvantage since the prevalent pattern of male-male competition and female choice (at least in dioecious metazoans) suggests that while males can increase their fitness most readily by acquiring more mates, selection acting on females works very strongly through mate quality.

The role of mate quality in determining reproductive success and driving sexual selection has been largely ignored or underappreciated, perhaps for the simple reason that there is no a priori criterion for a biologist to use to determine whether a female is choosing the “best” mate(s) except by offspring performance. Data from carefully controlled experiments in mallard demonstrate that there is no “best” male but rather each female chooses a male that enhances the quality of her own progeny (Bluhm and Gowaty 2004). Whether this is mediated by major histocompatibility complex (MHC) alleles, as has been suggested for humans (Wedekind and Furi 1997), is not clear. However, it is powerful evidence for both the importance and the subtlety of mate choice. While much of the data from hermaphrodites on mate choice suggests more proximal cues such as size and/or reciprocity (Table 1) as the basis for mate choice in hermaphrodites, the elegant experiments presented here by Webster and Gower (2006) demonstrate that individual basommatophoran snails can discriminate among mates on the basis of their own genotype and the infection status of the partner. Also, data from a stylommatophoran snail demonstrate that the degree of first male advantage varies substantially among females (Baur and others 1998). In angiosperms, the ability of females to abort embryos on the basis of sire genotypes has long been known and this certainly represents a form of cryptic mate choice (Willson and Burley 1983; Eberhard 1996; Skogsmyr and Lankinen 2002), Mate choice is not a negligible aspect of sexual selection, arguing against the sufficiency of Bateman’s gradients as a measure of sexual selection. There seems to be no alternative to rather elaborate experimentation to assess definitively the magnitude and direction of sexual selection.

Lessons from Hermaphrodites

Since sexual selection theory has been very heavily biased toward assumptions and predictions from dioecious taxa, hermaphrodites offer a new perspective (Table 4), a wealth of new observations, and an opportunity to test theory. The first insight hermaphrodites offer is, as just discussed, one of definition. Definitions of sexual selection that are based on sexual dimorphism and/or comparisons between the two sexes are not suitable for general use. In hermaphrodites, sexual selection may (and often does) act on male and female functions simultaneously or “in harmony” (see Delph and Ashman 2006). A second lesson from hermaphrodites is that sexual selection is ubiquitous; evidence for sexual selection has been found wherever it has been sought. Even organisms with little or no brain, such as tapeworms and plants (Bishop and Pemberton 2006; Delph and Ashman 2006; Milinski 2006), can exercise choice; and even organisms without muscle or the power of movement can compete for mates (see Thomson 2006).

Hermaphrodites also offer important insights into the relationship between variance in reproductive success, mate choice, and mating success. Based on Bateman’s principle, a high variance in reproductive success (usually in males) is associated with eagerness to mate due to the “upside potential” available as the number of mates increases. Charnov (1979) suggested that this should translate in simultaneous hermaphrodites into a preference for mating in the male role. However, probability theory tells us that given a choice...
between two investments (or strategies) with equal mean return (as must be the case for the two sexual roles) but unequal variance, the lower variance investment will be the most profitable, because it will be less likely to yield a zero return (see discussion in Gillespie 1974; Leonard 1999, 2005). This predicts that hermaphrodites should prefer the lower variance role (Leonard and Lukowiak 1991; Leonard 1999, 2005 for discussion). This provides an alternative view of the relationship between reproductive success and number of mates in the high variance sex. Perhaps we should think of the “eagerness” or “competitiveness” of males (or the higher variance sex) as a manifestation of desperation to avoid reproductive failure. That is, where sex ratios are equal and monogamy is not the rule, many males may fail to mate at all, or if they do, may still fail to sire offspring due to sperm competition or cryptic female choice. This being the case, the main selective pressure on males is simply to find as many mates as possible in the hope that at least one will provide paternity. That is, the driving force in males may be simply reproductive assurance. In contrast, if variance in reproductive success is low for females, most females may reasonably expect to produce offspring and the difference in fitness among females may come down to offspring quality. For dioecious species, the distinction between “eagerness” and “desperation” might seem moot but it can serve to make falsifiable predictions. For example, if males are “eager” to mate with all possible females as a way of gaining additional fitness, this should be true for all males, including high-ranking males. On the other hand, if males are “desperate” to mate, then high-ranking males would be expected to be more choosy about with whom they mate than are lower-ranking males. Interestingly, the female role has been shown to have higher variance in reproductive success in some studies in hermaphroditic plants (see Delph and Ashman 2006). Data on variation in the relative variances of reproductive success through male and female functions in hermaphrodites may provide insight into the relative contribution of reproductive investment, sex ratio, potential reproductive rate, and control of fertilization to variance in reproductive success.

Another lesson of sexual selection that is reinforced by data from hermaphrodites is that the fact that all offspring are not created equal. Offspring quality varies in ways that are important to the parent’s fitness. In hermaphrodites with the capacity to self-fertilize, outcrossed offspring may be preferred or they may be produced only under special environmental conditions (see Weeks and others 2006; Milinski 2006). Milinski (2006) presents important data suggesting that outcrossed offspring outperform selfed offspring, if and only if, the offspring experience competition. This sort of experiment has important implications for understanding the adaptive significance of sex, perhaps the most important question in evolutionary ecology.

A final lesson from hermaphrodites is that sexual conflict exists and is important. The concept of a conflict of interest between males and females over reproductive decisions and mating behavior has been central to sexual selection and reproductive investment theory for decades. However, sexual conflict is indirect in gonochorines, in that in each generation males compete with males and females with females for a contribution to the next generation. Direct evidence for sexual conflict is therefore hard to obtain (but see Rice 1992). In hermaphrodites, however, each individual competes with all other individuals for its contribution to the population’s next generation and sexual conflict can be direct. In simultaneous hermaphrodites mating systems based on conditional reciprocity have been found to be common as was hypothesized on the assumption that sexual conflict is important (Leonard 1999; see discussion in Leonard 2005). This was a strong prediction since, at the time the prediction was made, very little was known about mating systems in simultaneous hermaphrodites. The apparent lack of reciprocity in the mating systems of some simultaneous hermaphrodites (for example, Lysmata shrimp, Bauer 2006; Lymnaea stagnalis, Koene 2006) suggests that sexual conflict may not be a factor in their mating system. Examination of species with and without
conditional reciprocity may shed light on the sources of sexual conflict and hence sexual selection.

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