SYMPOSIUM

Williams’ Paradox and the Role of Phenotypic Plasticity in Sexual Systems

Janet L. Leonard

Joseph M. Long Marine Laboratory, University of California-Santa Cruz, Santa Cruz, CA 95060, USA

From the symposium “Phenotypic Plasticity and the Evolution of Gender” presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2013 at San Francisco, California.

Synopsis

As George Williams pointed out in 1975, although evolutionary explanations, based on selection acting on individuals, have been developed for the advantages of simultaneous hermaphroditism, sequential hermaphroditism and gonochorism, none of these evolutionary explanations adequately explains the current distribution of these sexual systems within the Metazoa (Williams’ Paradox). As Williams further pointed out, the current distribution of sexual systems is explained largely by phylogeny. Since 1975, we have made a great deal of empirical and theoretical progress in understanding sexual systems. However, we still lack a theory that explains the current distribution of sexual systems in animals and we do not understand the evolutionary transitions between hermaphroditism and gonochorism. Empirical data, collected over the past 40 years, demonstrate that gender may have more phenotypic plasticity than was previously realized. We know that not only sequential hermaphrodites, but also simultaneous hermaphrodites have phenotypic plasticity that alters sex allocation in response to social and environmental conditions. A focus on phenotypic plasticity suggests that one sees a continuum in animals between genetically determined gonochorism on the one hand and simultaneous hermaphroditism on the other, with various types of sequential hermaphroditism and environmental sex determination as points along the spectrum. Here I suggest that perhaps the reason we have been unable to resolve Williams’ Paradox is because the problem was not correctly framed. First, because, for example, simultaneous hermaphroditism provides reproductive assurance or dioecy ensures outcrossing does not mean that there are no other evolutionary paths that can provide adaptive responses to those selective pressures. Second, perhaps the question we need to ask is: What selective forces favor increased versus reduced phenotypic plasticity in gender expression? It is time to begin to look at the question of sexual system as one of understanding the timing and degree of phenotypic plasticity in gender expression in the life history in terms of selection acting on a continuum, rather than on a set of discrete sexual systems.

“Significant variation in reproductive patterns often occurs only at high taxonomic levels… The whole class of oligochaetes are simultaneous outcrossed hermaphrodites. It is unlikely that the forces that led originally to their hermaphroditism are still at work throughout the group.”

G.C. Williams, 1975, p. 123

Introduction

In “Sex and Evolution” George Williams (1975), rather than explaining how sexual phenomena have evolved, presented a problem set on which evolutionary biologists have been working ever since. One of the more intractable of these problems has been that of the discrepancy between the theoretical advantages of various sexual systems and the present distribution of these sexual systems in the animal kingdom. A sexual system is the pattern of distribution of male versus female functions across individuals in a species. Understanding why, in certain species, all individuals are simultaneous hermaphrodites, whereas other species consist of a mixture of males and females (dioecy = gonochorism), or some more complex pattern, is a long-standing problem in evolutionary biology. Williams’ Paradox (Leonard 1990) stems from the brute fact that, in the Metazoa, hermaphroditism and dioecy are, for the most part, characteristic of large, deep clades such as phyla and classes (Table 1; see below) and thus
Table 1. Distribution of dioecy and hermaphroditism in the Metazoa

<table>
<thead>
<tr>
<th>Phylum</th>
<th>Mode(s) of sexuality</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>Porifera</td>
<td>Usually hermaphrodites</td>
<td>No permanent gonads; not clear how often sperm and eggs ripen simultaneously versus sequentially; sessile</td>
</tr>
<tr>
<td>Placozoa</td>
<td>Yes</td>
<td>Very poorly known</td>
</tr>
<tr>
<td>Cnidaria</td>
<td>Either dioecious or hermaphroditic</td>
<td>Either pelagic or sessile</td>
</tr>
<tr>
<td>Ctenophora</td>
<td>Largely hermaphrodites</td>
<td>Pelagic</td>
</tr>
<tr>
<td>Platyhelminthes</td>
<td>Almost exclusively hermaphroditic</td>
<td>Free-living or parasitic</td>
</tr>
<tr>
<td>Nemertea</td>
<td>Dioecious</td>
<td>Free-living</td>
</tr>
<tr>
<td>Rotifera</td>
<td>Dioecious</td>
<td>Free-living</td>
</tr>
<tr>
<td>Acanthocephala</td>
<td>Dioecious, sessile female and dwarf male</td>
<td>Poorly known</td>
</tr>
<tr>
<td>Cyclophora</td>
<td>Protandric or simultaneously hermaphroditic</td>
<td>Sessile</td>
</tr>
<tr>
<td>Entoprocta</td>
<td>Hemaphroditic</td>
<td>Prosnobranchs are an artificial group</td>
</tr>
<tr>
<td>Sipuncula</td>
<td>Dioecious except for one species</td>
<td>Tube-dwelling worms</td>
</tr>
<tr>
<td>Mollusca</td>
<td>Primitively dioecious</td>
<td></td>
</tr>
<tr>
<td>Solenogastres</td>
<td>Hermaphroditic</td>
<td></td>
</tr>
<tr>
<td>Caudofoveata</td>
<td>Dioecious</td>
<td></td>
</tr>
<tr>
<td>Polyplacaphora</td>
<td>Mostly dioecious, some hermaphrodites</td>
<td></td>
</tr>
<tr>
<td>Monoplacaphora</td>
<td>Dioecious</td>
<td></td>
</tr>
<tr>
<td>“Prosobranchia”</td>
<td>Varied sexuality</td>
<td></td>
</tr>
<tr>
<td>Heterobranchia</td>
<td>Almost exclusively simultaneous hermaphrodites</td>
<td></td>
</tr>
<tr>
<td>Cephalopoda</td>
<td>Dioecious</td>
<td></td>
</tr>
<tr>
<td>Bivalvia</td>
<td>Largely dioecious; some hermaphrodites; various independent events</td>
<td></td>
</tr>
<tr>
<td>Scaphopoda</td>
<td>Dioecious</td>
<td></td>
</tr>
<tr>
<td>Annelida</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Polychaeta</td>
<td>Mostly dioecious</td>
<td>Both sedentary and errant families</td>
</tr>
<tr>
<td>Oligochaeta</td>
<td>Hermaphroditic</td>
<td></td>
</tr>
<tr>
<td>Hirudinea</td>
<td>Hermaphroditic</td>
<td>Predators and ectoparasites</td>
</tr>
<tr>
<td>Echiura</td>
<td>Dioecious</td>
<td>Burrow-dwellers</td>
</tr>
<tr>
<td>Pogonophora</td>
<td>Dioecious</td>
<td>Sessile tube-dwellers</td>
</tr>
<tr>
<td>Ectoprocta</td>
<td>Hermaphroditic</td>
<td>Sessile</td>
</tr>
<tr>
<td>Phoronida</td>
<td>Either dioecious or hermaphroditic</td>
<td>Sessile tube-dwellers</td>
</tr>
<tr>
<td>Brachiopoda</td>
<td>Dioecious, some hermaphrodites</td>
<td></td>
</tr>
<tr>
<td>Chaetognatha</td>
<td>Simultaneous hermaphrodites</td>
<td>Pelagic predators</td>
</tr>
<tr>
<td>Gastrotricha</td>
<td>Largely hermaphroditic</td>
<td>Interstitial</td>
</tr>
<tr>
<td>Priapulida</td>
<td>Dioecious</td>
<td>Sessile tube-dwellers or mobile predators</td>
</tr>
<tr>
<td>Loricifera</td>
<td>Dioecious</td>
<td>Interstitial</td>
</tr>
<tr>
<td>Kinorhyncha</td>
<td>Dioecious</td>
<td></td>
</tr>
<tr>
<td>Nematomorpha</td>
<td>Dioecious</td>
<td>Parasitic larvae; free-living adults</td>
</tr>
<tr>
<td>Nematoda</td>
<td>Dioecious or (rarely) androdioecious</td>
<td>Both parasites and free-living forms, dioecious</td>
</tr>
<tr>
<td>Onychophora</td>
<td>Dioecious</td>
<td>Terrestrial, tropical</td>
</tr>
<tr>
<td>Tardigrada</td>
<td>Dioecious</td>
<td>Aquatic</td>
</tr>
<tr>
<td>Euarthropoda</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cheliceriformes</td>
<td>Dioecious</td>
<td>Pycnogonida, Merostomata and Arachnida</td>
</tr>
</tbody>
</table>

(continued)
their distribution is not explicable by the ecological factors that are thought to give an advantage to one particular sexual system over another. Williams (1975, p. 123) argued that “...it must be that they lack preadaptations for changing to some other mode of reproduction”. Here I examine the progress we have made in understanding patterns of distribution of sexual systems in the Metazoa and suggest that making further progress in understanding the evolution of sexual systems requires an emphasis on understanding the costs and benefits, as well as the mechanisms, of phenotypic plasticity in gender and sexual system. Furthermore, a survey of sexual systems suggests that theoretical treatments have failed to take into account the complexity of adaptations that are available as evolutionary responses to particular selective pressures. That is, changes in selective pressures on reproduction may not result in the evolution of an overt change in sexual system.

Naturalists have speculated about the origin and advantages of hermaphroditism versus dioecy since the time of Aristotle (see Ghiselin 1974 for discussion). Mike Ghiselin was one of the first to seek explanations for sexual systems in terms of selection acting on individuals in his ground-breaking review of hermaphroditism in animals (Ghiselin 1969) and in his book “The Economy of Nature and the Evolution of Sex” (Ghiselin 1974). In these works he provided an extensive review of sexual systems

Table 1. Continued

<table>
<thead>
<tr>
<th>Phylum</th>
<th>Mode(s) of sexuality</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crustacea</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Remipedia</td>
<td>Hermaphroditic</td>
<td>Marine</td>
</tr>
<tr>
<td>Cephalocarida</td>
<td>Hermaphroditic</td>
<td>Benthic, marine</td>
</tr>
<tr>
<td>Maxillopoda</td>
<td>Dioecious or hermaphroditic according to subclade</td>
<td>Copepods, ostracods, etc. dioecious; Cirripedia (barnacles; sessile, largely hermaphroditic)</td>
</tr>
<tr>
<td>Branchiopoda</td>
<td>Largely dioecious, some hermaphroditic (notostracans) and androdioecious (chonchostracan) taxa</td>
<td>Largely freshwater; females often parthenogenetic</td>
</tr>
<tr>
<td>Malacostraca</td>
<td>Mostly dioecious; some sequential and simultaneous hermaphrodites</td>
<td>Shrimps, crabs and lobsters</td>
</tr>
<tr>
<td>Uniramia</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hexapoda</td>
<td>Dioecious</td>
<td>Insects, 830,075 species</td>
</tr>
<tr>
<td>Myriapoda</td>
<td>Dioecious</td>
<td>Centipedes, millipedes, etc.</td>
</tr>
<tr>
<td>Mesozoa</td>
<td>Hermaphroditic and dioecious</td>
<td>Endoparasites; Rhombozoa are hermaphrodites which may self- or cross-fertilize; orthonectids are dioecious</td>
</tr>
<tr>
<td>Echinodermata</td>
<td>Largely dioecious</td>
<td>Some hermaphrodites among the asteroids, holothurians, and especially ophiuroids</td>
</tr>
<tr>
<td>Hemichordata</td>
<td>Dioecious</td>
<td>Sessile pterobranchs and free-living enteropneust worms</td>
</tr>
<tr>
<td>Chordata</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Urochordata</td>
<td>Hermaphroditic</td>
<td>Sessile or pelagic in colonies</td>
</tr>
<tr>
<td>Cephalochordata</td>
<td>Dioecious</td>
<td>“Amphioxus”</td>
</tr>
<tr>
<td>Myxinoidea</td>
<td>Dioecious; some functional hermaphrodites</td>
<td>Hagfish; poorly known; highly female-biased sex ratios (Powell et al. 2005)</td>
</tr>
<tr>
<td>Petromyzontiformes</td>
<td>Dioecious</td>
<td>Lampreys; environmental sex determination</td>
</tr>
<tr>
<td>Chondrichthyes</td>
<td>Dioecious</td>
<td>Includes teleosts, sturgeons, gars, bowfins</td>
</tr>
<tr>
<td>Actinopterygii</td>
<td>Largely dioecious; some sequential and simultaneous hermaphrodites among teleosts</td>
<td>Includes teleosts, sturgeons, gars, bowfins</td>
</tr>
<tr>
<td>Actiniana</td>
<td>Dioecious</td>
<td>Coelacanth; internal fertilization; live-bearing</td>
</tr>
<tr>
<td>Dipnoi</td>
<td>Dioecious</td>
<td>Lungfishes</td>
</tr>
<tr>
<td>Tetrapoda</td>
<td>Dioecious</td>
<td>Includes amphibians, reptiles, birds, mammals</td>
</tr>
</tbody>
</table>

Modified from Leonard (2010); taxonomy from Lecointre and Le Guyader (2006); reproductive information from Jarne and Auld (2006), Barnes (1984), and Devlin and Nagahama (2002).
and bizarre sexual phenomena and offered very thoughtful explanations of how such phenomena could evolve through natural and sexual selection acting on selfish individuals. Among other insights, Ghiselin (1969) developed the “Size-Advantage Model” of the adaptive value of sequential hermaphroditism (Warner 1975; Munday et al. 2006; and see below) and noted, building on the Low Density explanation for simultaneous hermaphroditism (Tomlinson 1966), that simultaneous hermaphroditism doubles effective population size as well as enhancing reproductive assurance. Borgia and Blick (1981) used a formal mathematical model to establish that the advantage would be even larger in small populations as hermaphrodites can supply the minority sex when sex ratios are skewed; this could occur through stochastic processes alone. In addition, simultaneous hermaphroditism creates the possibility of self-fertilization when mates are unavailable. This insight, that simultaneous hermaphroditism would be advantageous under conditions of low density or low probability of encounter, offers an explanation of the association, noted by many authors, between hermaphroditism and sessility, parasitism, small population size, and frequent founding effects [see reviews by Leonard (1990, 1999) and Clark (1978)]. The relationship between reproductive assurance and other phenomena that have been associated with simultaneous hermaphroditism, such as brooding (Heath 1977, 1979) and small body size (Clark 1978), is less clear.

Eric Charnov and colleagues (Charnov 1982; Charnov et al. 1976) made an important theoretical advance with a mathematical model that predicted that dioecy will be favored whenever organisms experience a trade-off in fitness between male and female reproductive success (Fig. 1), that is, if reproduction through sperm and reproduction through eggs draw from a common pool of resources such that reproductive success via one sexual role must come at the expense of reproductive success via the other, then simultaneous hermaphroditism cannot be stable and dioecy will be the only stable solution. In order for simultaneous hermaphroditism to be a stable solution to sex allocation, the fitness curve must be convex (Fig. 1); that is, reproductive success in one sexual role must be positively correlated with success in the other sexual role. An important question left open in this model is: What determines whether or not there must be a trade-off between male and female reproductive success. Factors that have been suggested to account for a concave fitness curve include: (1) flowers that attract pollinators that both bring and remove pollen; (2) use of different resources in either type or time in the production of sperm versus eggs; (3) restriction of male mating success by lack of available mates (or eggs); and (4) reciprocity in mating system as a result of sexual conflict over a preferred role (Charnov 1979; Charnov et al. 1976; also see discussion by Leonard, 2005). Factors suggested to favor dioecy include (1) high fixed costs, that is, substantial investment in reproductive structures such as genitalia, (2) high population density, or (3) high search efficiency in the male role (see discussion by Puurtinen and Kaitala 2002; Leonard 2005, 2010; Eppley and Jesson 2008; Iyer and Roughgarden 2008). However, as Williams (1975) pointed out, in the Metazoa sexual systems are very often characteristic of large, old, deep clades such as phyla and classes (Table 1) (Williams 1975; Leonard 1990, 2010; Eppley and Jesson 2008) and it is clear that taxonomy is often a better predictor of sexual system than are the types of parameters discussed in such models. Although many hermaphrodites are sessile, sessile animals are also often dioecious (Table 1). Among predominantly sessile taxa, the Porifera are usually hermaphroditic, as are the entoprocts, the ectoprocts, most barnacles (Cirripedia), and the urochordates (sea squirts). On the other hand, the pogonophoran annelids are dioecious, as are most brachiopods, the stalked sea lilies, and the hemichordate pterobranchs. In the Cnidaria, a phylum with diverse sexual systems, the sessile class Anthozoa consists mainly of gonochores brooders and spawners, with the exception of the order Scleractinia, which are largely hermaphroditic spawners (Kerr et al. 2011). In particular, 89% of octocorals are gonochores, with occasional
hermaphrodites scattered across the clades (Kahng et al. 2011). Recent molecular evidence suggests that the Anthozoa may be polyphyletic with the Octocorallia more closely allied with the Medusozoa (Kayal et al. 2013), but in any case, the evidence suggests that the sexual system is very conservative, even in sessile groups with no permanent gonads. Similarly, while hermaphroditism is found in many parasitic taxa such as the cestodes and trematodes among the Platyhelminthes, and the Rhombozoa among the Mesozoa, there are many dioecious parasitic taxa, such as the many parasitic nematodes, the Nematomorpha (only the larvae are parasitic), the Acanthocephala, and the orthonectids among the Mesozoa (Table 1). In the Platyhelminthes the free-living turbellarians are also hermaphrodites and the only known dioecious group are the parasitic family of schistosomes. In the Nematoda, both parasitic and free-living species are dioecious with a few androdioecious species among the free-living groups (see below). Similarly, attempts to explain the distribution of dioecy among the Metazoa, based on motility and ability to search for mates, show too little resolution to explain existing patterns of sexual systems. While there may be a statistical correlation between ability to search for mates and the lack of hermaphroditism (Puurtinen and Kaitala 2002; Epplle and Jesson 2008; see also Iyer and Roughgarden 2008), these models do not explain why the euthyneuran gastropods are all simultaneous hermaphrodites, whereas various other gastropod groups with heavier shells or sessile adults are dioecious. Furthermore, the mate-search hypothesis does not explain the existence of sessile clades that are dioecious. In sum despite 37 years of research, we still have not gone beyond Williams’ Paradox; that is, it is clear that sexual systems in the Metazoa often are very old, dating back tens or hundreds of millions of years and persisting through very extensive adaptive radiations and in very diverse habitats (Williams 1975; Leonard 1990, 2010). It may well be the case that hermaphroditism can only persist when there is no trade-off between male and female reproductive success (Charnov 1979) but these models do not provide enough detail to allow us to understand the current distribution of these sexual systems.

**Variation in sexual systems**

The phylogenetic evidence demonstrates that, once evolved, both dioecy and simultaneous hermaphroditism can be very stable in animals, in contrast to angiosperms in which dioecy seems evolutionarily ephemeral (Lloyd 1982; Charlesworth 2006; Delph 2009). It is noteworthy that other sexual systems such as sequential hermaphroditism, gynodioecy, and androdioecy are much less common and do not seem to be characteristic of major taxonomic groups in the Metazoa. Gynodioecy (a mixture of females and simultaneous hermaphrodites) exists in animals although it is extremely rare, with only a few verified cases, and there is no evidence that it serves as an evolutionary transition stage between simultaneous hermaphroditism and dioecy in animals as it does in angiosperms (Pannell 2002; Caruso and Case 2012; Weeks 2012). In contrast to angiosperms, in animals, androdioecy (males and hermaphrodites) although still very rare, is more common than gynodioecy; although, with the exception of barnacles (Yamaguchi et al. 2012; Yusa et al. 2013, this issue), it involves populations consisting of self-fertile hermaphrodites and males, in basically dioecious taxa. In these cases, outcrossing consists solely of males mating with hermaphrodites; for example, clam shrimps, tadpole shrimps (Mathers et al. 2013), the mangrove killifish, *Kryptolebias marmoratus* (Molloy et al. 2011) and a few nematodes, including the well-known *Caenorhabditis elegans* (see reviews by Pannell 2002; Weeks et al. 2006, 2012). In most androdioecious animal systems, selfing hermaphrodites seem to be added to a fundamentally dioecious sexual system, thereby providing reproductive assurance (Pannell 2002, 2008). In barnacles, the hermaphrodites may outcross as males with neighbors even if they are carrying complemental males, and the hermaphrodites do not self-fertilize (Yusa et al. 2013, this issue). Trioecey, in which populations contain a mixture of males, females, and simultaneous hermaphrodites has also been recorded: e.g. *Hydra viridissima* (Kaliszewicz 2011); papaya (Ming et al. 2007); and a *Rhabditis* nematode (Chaudhuri et al. 2011). Additional examples of sexual systems involving a mixture of simultaneous hermaphrodites and single sexes exist, although these cases involve a developmental or facultative transition between single sexes and hermaphroditism in the life history of individuals. For example, there are many examples of protandrous hermaphroditism in which simultaneous hermaphrodites start reproduction as males and then add female function as they mature; e.g., the polychaetes *Ophyrotrocha diadema* (Sella and Lorenzi 2003; Lorenzi et al. 2006) and *Lysmata* shrimps (Bauer 2006). In some of the hermaphroditic serranine fishes, individuals start life as simultaneous hermaphrodites and, when there is an opportunity to establish a harem, lose ovarian tissue and become pure males (see reviews by Leonard 1993; Petersen 2006). There are also
examples, such as the sea anemone Epiactis prolifera, in which individuals start life as females and become simultaneous hermaphrodites as they grow older/larger (Dunn 1975) and a goby in which all individuals start as females and some, but not all, individuals become simultaneous hermaphrodites as they mature (Cole and Hoese 2001). Cases in which mixed sexual systems arise from developmental changes are sometimes referred to as “pseudo-androdioecy” or “pseudo-gynodioecy” as opposed to true androdioecy or gynodioecy which are considered to involve genetically distinct morphs (see discussion by Weeks et al. 2006; Leonard 2010; Weeks 2012). From a theoretical standpoint, if the distinctions are genetic then we are dealing with a stable polymorphism in which all morphs should have equal fitness, whereas if the genders are phenotypically plastic, this may not be the case (Maynard Smith 1982; Taborsky and Brockmann 2010). The distinction is therefore, important from a theoretical standpoint but the mode of sex determination is uncertain in many cases and genetic and environmental sex determination (ESD) may not be easily separable. For example, in a trioecious Rhabditis species, there is a chromosomal sex determination system in which males are XO and females and hermaphrodites are XX (Chaudhuri et al. 2011). Whether an XX individual becomes a female or an hermaphroditic seems to depend on whether or not it goes through a “Dauerlarva” stage. In barnacles, androdioecy was long thought to be genetically determined, but Yusa et al. (2013, this issue) suggest that males may sometimes develop into hermaphrodites or females. Understanding the role of phenotypic plasticity in the development of genders and sexual systems will usually require extensive experimental work that remains to be done for most animals.

**Sequential hermaphroditism**

In sequential hermaphroditism, an individual initiates reproduction in one sexual role and then changes sex to reproduce in the other sexual role at some point in its life history. In general, sequential hermaphrodites are either protandrous (functioning first as males and later becoming females) or protogynous (beginning as females and later switching sex to become males). In a third pattern, that of alternating hermaphroditism, individuals may switch from male to female to male, or the reverse, several times during their reproductive lives. Sequential hermaphroditism exists in angiosperms but is rare (Policansky 1982; Warner 1988) although dioecious plants may change sex as a result of environmental influences (Richards 1997). In animals, it is not characteristic of major clades, but has evolved many times, most commonly in sponges, polychaetes, crustaceans, bivalves, “prosobranch” gastropods, and teleost fishes (Ghiselin 1974, 1987; Warner 1975; Policansky 1982; Wright 1988; Heller 1993; Premoli and Sella 1995; Devlin and Nagahama 2002; Munday et al. 2006; Bauer 2007; Yusa 2007; Sadovy de Mitcheson and Liu 2008; Hodgson 2010; Leonard 2010; Collin 2013, this issue; Erisman et al. 2013, this issue). Protogyny does seem to be the dominant sexual system in some families of teleosts (Erisman et al. 2013, this issue). The “Size-Advantage Model” (Ghiselin 1969; Warner 1975; Munday et al. 2006) has been the dominant theory as to the advantage of sequential hermaphroditism. According to this model, selection will favor sex change when the size/age fertility curves for the two sexes cross (Fig. 2), that is, when reproductive success (or reproductive value) in one sexual role is more strongly correlated with size/age than the other (Warner 1988; Munday et al. 2006). For example, in many fish and invertebrates with indeterminate growth, the capacity to produce eggs is correlated with the size of the individual, so that larger females are able to produce more eggs than smaller females, whereas even relatively small males are able to produce enough sperm to fertilize even the largest females. In such a case, as shown in Fig. 2b, selection will favor protandrous sequential hermaphroditism, with individuals starting their reproductive lives as males and then becoming females when they grow to a size at which they would have more reproductive success by producing
eggs. Protandrous sequential hermaphroditism is found in many mollusks, including the famous stacking slipper limpets of the genus Crepidula (Wright 1988; Collin 2013, this issue). A less widespread, but even more intensively studied, pattern is the protogynous sequential hermaphroditism found in several groups of marine fishes, particularly coral reef fishes (Munday et al. 2006; Godwin 2009; Erisman et al. 2013, this issue). Typically, these are fish that live in small social groups in which the largest and most dominant individual is a male and the other individuals form a harem of females that spawn with the dominant male. When the dominant male dies, or is removed, the largest female will typically change sex (but see Muñoz and Warner 2003; Yamaguchi et al. 2013), becoming male and taking over as harem holder. In this scenario, only large individuals can achieve reproductive success as males, because of male–male competition for control of the social group, so that small individuals will be more successful as females (Warner 1975; Warner and Swearer 1991). Protogynous sequential hermaphroditism in fish has been intensively studied over at least 40 years and many variations on the pattern have been identified (Munday et al. 2006; Godwin 2009; Yamaguchi et al. 2013). One thing that is very clear is that in fishes, particularly reef fishes, sex change, and sometimes initial choice of sex, involves environmental cues, particularly social cues (Devlin and Nagahama 2002; Godwin 2009). In fact, with a few exceptions (Munday et al. 2006; Collin 2013, this issue), in sequential hermaphrodites sex change occurs in response to social and/or other environmental cues. In fishes, ESD is widespread taxonomically and is found in many of the same taxa that demonstrate some form of hermaphroditism (Devlin and Nagahama 2002).

A third type of sequential hermaphroditism that has been described rarely, both in plants and in animals, is alternating or successive sex change in which an individual changes sex more than once in its reproductive life (Policansky 1982; Premoli and Sella 1995; Munday 2002; de Jong and Klinkhamer 2005; Munday et al. 2010). This can take several forms: for example, in the perennial angiosperm, the jack-in-the-pulpit, individuals are either male or female in one reproductive season but can change sex from season to season, several times in their lives (Policansky 1981; Bierzychuduk 1984), in an adaptive response to environmental conditions, so that the plant can reproduce in a sexual role appropriate to its current size. In some fishes, often in protogynous species, individuals will change sex after loss of a partner and create a mixed-sex pair, that is, if a female dies, the smaller of a pair of males in a social group may revert to the female sex and create a functional dioecious pair (Munday 2002; Wittenrich and Munday 2005; Kuwamura et al. 2011). The selective advantage seems to be reproductive assurance in cases in which moving to find a mate of the opposite sex would be dangerous. The phenomenon is apparently more common in aquaria than in the field but it does occur in nature (Munday et al. 2010; Kuwamura et al. 2011). In some gobies, individuals are histologically and anatomically simultaneous hermaphrodites but behaviorally they are dioecious with males defending a nest which attracts multiple females (St. Mary 1993). In the famous case of oysters of the genus Ostrea, individuals begin reproduction as females, and then while brooding the fertilized eggs, the gonad turns to the production of sperm (Coe 1932; Chaparro and Thompson 1998), and then back to egg production after the eggs hatch. Thus, Ostrea oysters are only male while pregnant. The advantage here stems from a saturating female-gain curve (Charnov 1979), that is, if female reproductive success is limited, not by the energy available for egg production but rather by space in the brood chamber, then additional energy can be profitably used to produce sperm during the brooding period. Theory would, therefore, predict that, in this case, simultaneous hermaphroditism would be adaptive but what has evolved is alternation between production of eggs and sperm by the gonad. Alternating sex change may be rather widespread in bivalves (Collin 2013, this issue). Another well-studied instance of alternating hermaphroditism is the sequentially hermaphroditic polychaete Ophryotrocha puellaris. In this genus, mating occurs in pairs and females have a preference for large males. After a pair forms, the male grows more slowly than the female does and when the male becomes as large as, or larger than the female, both individuals change sex and then resume mating until the new male has again become as large as the female, whereupon they change again (Premoli and Sella 1995; Sella and Ramella 1999). Established pairs alternate sex more frequently as they do not differ greatly in size and in some cases, both members of the pair may eventually become simultaneous hermaphrodites and alternate egg-laying in the egg-trading behavior characteristic of the simultaneously hermaphroditic species in the genus (Berglund 1990; Premoli and Sella 1995). Alternating sex change appears to represent an intermediate between simultaneous and sequential hermaphroditism, not only in these worms but in many other cases that have been described. How common alternating sex change is in...
nature is unknown as detection requires long-term observation on individuals and often sex can only be determined histologically.

Although sequential hermaphroditism is much more varied and complex than was thought 40 years ago, the size/age advantage model remains a viable explanation of the timing and direction of sex change in most animals. A more perplexing question is why sequential hermaphroditism is not more common, that is, why is it that differences in reproductive value as a function of size/age do not lead to sex change in more taxa (Policansky 1982; Kazancioglu and Alonzo 2009) Theory can explain sex change when it occurs but does not seem to be able to predict in which taxa it will occur, for example, the conditions favoring sequential hermaphroditism in shrimp seem to be more common than actual sequential hermaphroditism (Bauer 2007). One possibility is simply that sequential hermaphroditism is more common than it appears to be, but that it is overlooked because it is hard to detect (Bieler and Hadfield 1990). Again, sequential hermaphroditism is often only detected when histological examination of the gonads shows a transitional state, a rather ephemeral event. Such histological evidence, however, may not be definitive evidence of a functional transition (Sadovy de Mitcheson and Liu 2008; Lorenzi and Sella 2013, this issue). Another explanation of the limited distribution of sequential hermaphroditism is that it may only rarely be more adaptive than the gradual changes in sex allocation associated with age/size that are seen in what Peter Klinkhamer and Tom de Jong have termed "quantitative gender" (Lloyd 1982; Klinkhamer and de Jong 2002; Cadet et al. 2004; de Jong and Klinkhamer 2005). In the theory of size-dependent sex allocation (SDS) for simultaneous hermaphrodites (Klinkhamer et al. 1997), a distinction is made between what are termed "direct" size effects, which are benefits of size per se, such as dominance in fishes that live in groups, or the ability of a tall wind-pollinated tree to spread pollen over a larger area, and "budget" effects of size, in which the benefit of size is due simply to greater energetic resources such as the ability of a larger fish or bivalve to produce both more sperm and more eggs or to devote more resources to reproduction as opposed to growth or maintenance. The argument is that when "direct" effects of size differ for male versus female functions, sex change will be expected to be adaptive, but if "budget" effects are more important, one might expect to see a gradual change in sex allocation between the two sexual roles over the life of a hermaphrodite. That is, when budget effects dominate, one would expect that as individuals get larger the gain curve through sperm might saturate more quickly than the gain curve through eggs and therefore, sex allocation should become increasingly female-biased in hermaphrodites as they get larger. Similar arguments can be made for the effect of investment on mortality, leading to predictions about sex allocation changing with age. A complete sex change would only be predicted when budget effects are absent and direct effects are strong (de Jong and Klinkhamer 2005).

Changes in sex allocation as a function of size and age are often observed in simultaneously hermaphroditic animals. Adolescent protandry, or less often, protogyny is not unusual in simultaneously hermaphroditic animals, for example; Lysmata shrimps (Bauer 2006), Ophryotrocha polychaetes (Sella and Ramella 1999; Lorenzi et al. 2006), a tapeworm (Schärer et al. 2001), and Epiactis sea anemones (Dunn 1975). Many euteuthan gastropods have been described as protandrous because sperm develop and mature before the eggs do, even though copulation may be reciprocal (Leonard 1991; Baur 2010; Jarne et al. 2010). Many species have sperm storage so that pairs of individuals may exchange sperm before either has matured eggs in the gonad (Leonard 1991; Baur 2010; Jarne et al. 2010). A similar situation exists in leeches, in which it has been described as alternating sex change, although individuals play both sexual roles during mating (Kutschera and Wirtz 1986). There is an extensive literature on changes in sex allocation in angiosperms as a function of size (Klinkhamer and DeJong 2002; Ishii and Harder 2012). Review of the diversity of hermaphrodites in the Metazoa shows clearly that there is no sharp dividing line between simultaneous and sequential hermaphroditism and therefore, it may be more productive to think of simultaneous and sequential hermaphroditism, as being two points on a continuum rather than discrete phenomena. A new body of theory that incorporates this fact is being developed by various authors (St. Mary 1997; Angeloni et al. 2002). In addition to phenotypic plasticity in sex allocation as a function of size/age, hermaphrodites may also alter their sex in response to social or other environmental factors (Charnov 1982; Schärer 2009; Schärer and Pen 2013). Such phenotypic plasticity may provide a major evolutionary advantage to hermaphroditism (Leonard 2010).

**Dioecy**

A striking feature of the Metazoa, as opposed to angiosperms, is that dioecy is widespread and very
stable evolutionarily (Table 1). Jarne and Auld (2006) in a recent review, estimated that only about 5–6% of animal species are gynodioecious, which makes 95% of animal species dioecious; this is almost exactly the reverse of the situation in angiosperms in which ~90% are hermaphroditic (Barrett and Hough 2013). The dominance of dioecy in animals can be explained by its prevalence among a few large and prominent taxa, particularly the Arthropods, in which hermaphroditism is rare overall and absent in the huge clade of insects. If the arthropods are excluded, the prevalence of gynochores drops to about two-thirds (Jarne and Auld 2006). It is also unknown in the Tetrapoda (amphibians, reptiles, birds, and mammals) meaning that most familiar terrestrial animals are dioecious, perhaps accounting for the perception among zoologists that dioecy is normal and hermaphroditism a strange phenomenon in need of explanation. In angiosperms on the other hand, dioecy has evolved frequently but is relatively rare and evolutionarily short-lived (Bawa 1980), and consequently is the sexual system that has seemed to require the most explanation (Thomson and Brunet 1990; Delph 2009). A key selection pressure in the evolution of dioecy in angiosperms, is that female function may be under strong selection to avoid inbreeding (Ashman 2006). Delph (2009) provided an attractive scenario for evolutionary transitions between dioecy and hermaphroditism in angiosperms, whereby selection for outcrossing leads to spread of a male-sterile (female) mutant in hermaphroditic populations which then favors increased male allocation by the hermaphrodites, ultimately favoring loss of female function in the hermaphrodites, thereby leading to a dioecious population. Conversely, in this scenario, if mating opportunities become scarcer in a dioecious population, selection will favor any females that can produce a small amount of pollen for selfing, thereby creating androdioecy. Stochastic loss of males will then lead to evolution of a population of hermaphrodites (Delph 2009; Wolf and Takebayashi 2004). This is an appealing hypothesis and in principle it seems that it should be applicable to animals as well. However, gynodioecy is vanishingly rare in animals, with only about six known cases (Keshavmurthy et al. 2012; Weeks 2012) and androdioecy, while commoner than gynodioecy, is much rarer than transitions between hermaphroditism and dioecy, and while it may lead to all-selfing populations of hermaphrodites (Weeks et al. 2009), it has not led to populations of outcrossing hermaphrodites except perhaps in barnacles (Weeks et al. 2006; Weeks 2012; Yusa et al. 2013, this issue). Weeks (2012) attributed the failure of outcrossing hermaphrodites to evolve from androdioecy in animals to the fact that androdioecy has evolved from dioecious taxa with strong sexual dimorphism, so that the evolution of a functional male anatomy and behavior in hermaphrodites, derived from females of these taxa, is too improbable.

In barnacles (which as a clade are generally simultaneously hermaphroditic), dioecy and androdioecy have evolved several times (Kelly and Sanford 2010). In general, the evolutionary transitions have been from hermaphroditism, often protandric simultaneous hermaphroditism, to dioecy through androdioecy. This transition is apparently driven by decreasing mating opportunities. Barnacles are not usually selfers but rather reproduce by pseudocopulation among members of a cluster. In the pattern described by Yusa et al. (2013, this issue), larger clusters consist of hermaphrodites but as clusters become smaller, hermaphrodites allocate less to male function, sperm competition is reduced, and dwarf (=complemental) males can invade the population and thereby create an androdioecious sexual system. As hermaphrodites are often protandrous, the initial stages of this process may simply involve failure of settling hermaphrodites to mature to the hermaphroditic stage (Yusa et al. 2013, this issue). As group size becomes very small and/or food resources become scarce, the system evolves to dioecy with strong sexual dimorphism in which much reduced, dwarf, males often settle on larger, feeding females. Mating systems in dioecious or androdioecious barnacles may be strongly polyandrous with many dwarf males settled on one female (Kelly and Sanford 2010). This pattern of dioecy at low population densities and hermaphroditism at high densities would appear to contradict both the Low Density model of the advantage of hermaphroditism (see above) and the Local Mate Competition model (Charnov 1982) but the possibility of dwarf males changes the predictions of those models (Yamaguchi et al. 2012), demonstrating that life-history variables can complicate predictions of simple models of the advantages of hermaphroditism versus dioecy (see below). Whether sex determination in barnacles is genetic or occurs in response to social cues (i.e., the presence or density of conspecifics) is as yet unclear (Kelly and Sanford 2010; Yusa et al. 2013, this issue). In other cases of dioecy with dwarf males, larvae have been shown to become females when settling in the absence of conspecifics and males when settling in the presence of a female [e.g., the echiuuran Bonellia viridis (Berec et al. 2005); siboglinid worms of the genus Osedax (Vrijenhoek et al. 2008)], as in classic cases of ESD.
Environmental sex determination

ESD, whereby the sex of a developing animal is determined by environmental cues, whether social or physical, is widespread in the Metazoa and is found in many invertebrate clades as well as in fishes and reptiles among the vertebrates (Charnov and Bull 1977; Korpelainen 1990; Devlin and Nagahama 2002; Mank et al. 2006; Ospina-Alvarez and Piferrer 2008; Rhen and Schroeder 2010; Mankiewicz et al. 2013, this issue; Walsh 2013, this issue). ESD is normally associated in the literature with dioecy but obviously for ESD to occur, there has to be a genetic potential for a developing individual to become either male or female. Charnov and Bull (1977), in discussing the circumstances under which ESD would be adaptive, clearly included cases of sequential hermaphroditism in response to social cues and changes in sex allocation in response to environmental variables in simultaneous hermaphrodites. ESD, then, involves phenotypic plasticity in gender, at least early in development, and in many ways represents an intermediate stage between hermaphroditism and dioecy. An interesting example of ESD comes from cyclical parthenogenesis, in which populations of parthenogenetic females persist until an environmental cue stimulates the production of males and sexual females. Examples of cyclical parthenogenesis are found in a variety of invertebrates from dioecious taxa, for example, cladoceran crustaceans (Walsh and Post 2012), rotifers (Stelzer 2011), and aphids (Foster 2002; Dedryver et al. 2013). In *Daphnia*, a very wide variety of environmental cues are capable of inducing the production of males and hence sexual reproduction (Walsh 2013, this issue). In *Daphnia* cyclical parthenogenesis is associated with alternation of asexual reproduction in stable environments, with sexual reproduction through resting eggs, which undergo dormancy, when ponds dry up or otherwise become unsuitable for these zooplankters (Walsh 2013, this issue). The population is then re-established by hatching of these resting eggs when the pond re-fills or conditions again become suitable for growth and reproduction. These same conditions, of alternation of wet and dry periods in ponds, are associated with a high degree of selfing in basommatophoran gastropods (Jarne et al. 2010; Lamy et al. 2012), which is interpreted as allowing populations to re-establish after periods of decimation. In vertebrates, ESD is associated with social cues in fish (Godwin 2009; but see Yamaguchi et al. 2013) and temperature cues in a variety of species of fish and reptiles (Devlin and Nagahama 2002; Mank et al. 2006; Rhen and Schroeder 2010; Luckenbach et al. 2009). That is, in a variety of these ectothermic species the temperature experienced during development determines whether the developing embryo will become male or female as an adult. The theoretical advantage of temperature-dependent sex determination (TSD) is that as: (1) growth rate will be a function of environmental temperature, and (2) male and female life histories differ with respect to the advantage of size, TSD will allow individuals to convert to the sex that offers the best reproductive success under prevailing environmental conditions (Warner and Shine 2008; Luckenbach et al. 2009; Mankiewicz et al. 2013, this issue; but see Valenzuela 2004).

Other sex-determining mechanisms

Although ESD offers a degree of phenotypic plasticity to some dioecious taxa, in other groups, such as many nematodes, insects, and vertebrates (Cook 2002; Kraak and Pen 2002) sex is genetically determined. Sex chromosomes are one of the common mechanisms of genetic sex determination both in vertebrates and in invertebrates (Cook 2002; Kraak and Pen 2002) and is also found in plants (Richards 1997; Diggle et al. 2011). In invertebrates, the exact mechanism of sex determination is unknown in many cases but haplodiploidy occurs in insects and some nematodes, and loss of the paternal genome is the mechanism in some other insects, and in some mites (Cook 2002). A unique genetic sex-determining mechanism, the doubly uniparental mitochondrial DNA (mtDNA) inheritance system, has been found in dioecious freshwater mussels (Breton et al. 2011). The advantage of genetic sex determination, particularly with sex chromosomes, is thought to be maintenance of a 1:1 sex ratio (Fisher 1958; Kraak and Pen 2002) in the face of environmental perturbations. It also has been hypothesized that when there are chromosomal differences between the sexes, the evolution of sex-specific traits may be easier (Karlin and Lessard 1986). Adaptive plasticity in gender is usually thought to be confined to variation in the offspring’s sex ratio in species such as amphibians, birds, and mammals, although in birds there may be some degree of environmental influence (Uller and Badyaev 2009). In laboratory studies, TSD has been reported to disrupt the normal sex chromosome/sex-determination system in amphibians but the temperatures involved were so extreme that it seems unlikely that this would occur in nature (Nakamura 2009). However, in many species sex determination involves both ESD and sex chromosomes and it is probably more...
appropriate to think of ESD and genetic sex determination as complementary rather than alternative mechanisms (Kraak and Pen 2002; Mank et al. 2006; Osipina-Álvarez and Pferrer 2008; Crews and Bull 2009; Luckenbach et al. 2009; Rhen and Schroeder 2010; Dingle et al. 2011). For example, in flatfishes, XY individuals are always male but XX individuals may develop either as females or males, depending on temperature (Luckenbach et al. 2009) or other environmental variables (Mankiewicz et al. 2013, this issue). Cortisol may be the common mechanism for sex determination in XX individuals (Mankiewicz et al. 2013, this issue). Similarly, in a nematode, males are XO and XX individuals become either females or hermaphrodites depending on whether or not the individual undergoes a “Dauerlarva” stage during development (Chaudhuri et al. 2011). Overall then, there seems to be a substantial degree of phenotypic plasticity in sex determination in many animals, even when sex chromosomes are present. Mechanisms of sex determination in dioecious animals seem to span a continuum from quite labile forms of ESD to quite deterministic chromosomal sex determination in some insects and vertebrates.

**Understanding the distribution of sexual systems in Metazoa**

Review of sexual systems across the Metazoa suggests that there are two general sexual systems, hermaphroditism and dioecy, both of which are very stable evolutionarily. However, the diversity of sexual systems is such that it is perhaps not appropriate to think of dioecy and hermaphroditism as well-defined, discrete phenomena (Ah-King and Nylin 2010). Rather, if we look at the diversity of sexual systems across the Metazoa we see a spectrum of plasticity in gender from simultaneously hermaphroditic taxa in which male and female are simply behavioral choices in a mating encounter, for example, the opisthobranch *Navanax inermis* (Leonard and Lukowiak 1984), the polychaete *O. diadema* (Sella 1985), some serrane fishes (Petersen 2006), or *Lythrypnus* gobies (St. Mary 2000) at one end, to rigidly dioecious taxa in which gender is decided at fertilization and phenotypic plasticity in gender is associated only with a reduction in reproductive success, rather than an enhancement, for example, in mammals (Jimenez et al. 2013) and some examples from invertebrates (Cook 2002). Between these two extremes is a very wide array of intermediate cases, from simultaneous hermaphrodites that alter their relative allocation to the two sexual roles as a function of social environment, age, size, or physical factors, for example, *Ophyrophrota* (Lorenzi et al. 2008), the stylommatophoran *Achatina fulica* (Tomiyama 2002), a tapeworm (*Schärer et al.* 2001), general review by Schärer (2009); to taxa that change physiologically from one sex to the other multiple times, for example, some fishes (Munday et al. 2010), the polychaete *O. puerilis* (Berglund 1990), *Ostrea* oysters (Coe 1932); to taxa that change sex once and only once in their lives, for example, *Crepidula* gastropods (Collin 2006), the blue-head wrasse (*Warner and Swearer* 1991), general reviews by Munday et al. (2006), Godwin (2009), Collin (2013, this issue); to taxa that establish their gender once in their lives on the basis of environmental cues (ESD), for example, the echinarian *B. viridis* (Berec et al. 2005), the bone worm (*Vrijenhoek et al.* 2008), or turtles (Rhen and Schroeder 2010). Somewhere in the ESD range are also found taxa with cyclical parthenogenesis, in which environmental cues determine a switch from parthenogenesis to the production of males and sexual females (see above and Walsh 2013, this issue). Included in this group are aphids in which parthenogenetically produced clones may produce males and sexual females in response to an environmental cue; these then may mate with each other in a form of dioecious selfing or “distributed hermaphroditism” (Foster 2002). Neighboring the taxa in which gender is fixed at fertilization is another group of dioecious taxa in which environmental factors interact with sex chromosomes to determine the gender of an individual for one or both sexes, for example; flatfish (Luckenbach et al. 2009; Mankiewicz et al. 2013, this issue); a *Rhabditis* nematode (Chaudhuri et al. 2011).

Understanding the distribution of metazoan taxa along this gradient of phenotypic plasticity will require assessment of the costs and benefits of both phenotypic plasticity in gender and fixity in sex determination. Phenotypic plasticity in gender and sex allocation is one of the major characteristics of hermaphroditism and may be one of its biggest adaptive advantages (see Leonard 2010 for discussion). Since the pioneering theoretical work of Charnov (1982), a flourishing field has developed that is dedicated to understanding patterns of sex allocation both over the course of evolution, and over the life of individuals (Angeloni et al. 2002; Klinkhamer and de Jong 2002; de Jong and Klinkhamer 2005; Lorenzi et al. 2008; Schärer 2009; Schärer and Pen 2013). The advantages of rigidly genetically determined dioecy have not been explored in animals to any great extent, from either a theoretical or an experimental...
standpoint (Valenzuela 2004). In an early discussion of ESD, Charnov and Bull (1977) discussed the advantage of genetic sex determination by saying (p. 829): “When sex is determined at conception, the individual...can begin ‘developing into’ its sex immediately. Early development of sex allows an individual to become a better male or a better female and is probably the major advantage of genotypic sex determination.” This seems like a hypothesis that could, and should, be tested, particularly in taxa in which the degree of ESD versus genetic sex determination varies among species and even among populations. Valenzuela (2004) stated that while formation of intersexes has been suggested to be a disadvantage with ESD, intersexes are very rare in vertebrates and do not appear to be more common in species with ESD than in those with genetic sex determination. The standard explanation for the advantage of sex chromosomes is that they produce a 1:1 sex ratio, which has been shown by Fisher (1958) to be adaptive under most circumstances. Sex chromosomes and ESD both have been shown to occur in dioecious plants (Richards 1997; de Jong and Klinkhamer 2005) but the seed sex ratios, even in plants with sex chromosomes, do not necessarily correspond to the Fisherian sex ratio (de Jong and Klinkhamer 2002).

“One is left with the feeling that some essential feature of the situation is being overlooked.”

(Maynard Smith 1976, p. 257)

The advantages of dioecy in plants have been hypothesized to be: (1) avoidance of selfing, (2) adaptation to low availability of resources (Ashman 2006; Delph 2009), (3) increased resistance to “enemies” (Ashman 2006; Williams et al. 2011), and (4) advantages through sexual selection (Bawa 1980; Pannell 2006; Artieri et al. 2008). In animals, dioecy has been assumed to be the default condition (Leonard 2010) and there has been less attention to its benefits, but, in addition to the avoidance of inbreeding and increased fitness of offspring through outcrossing, hypothesized benefits of dioecy include (1) increased efficiency through “division of labor” for which there is an example in schistosomes, the one dioecious clade in the hermaphroditic phylum Platyhelminthes (Despres and Maurice 1995), (2) the ability to avoid a trade-off of male and female reproductive success (Charnov 1979), which should also apply to plants, and (3) increased opportunity for sexual selection (Artieri et al. 2008; Schärer and Pen 2013; but see Leonard 2013). Conversely, the advantages of hermaphroditism (Ghiselin 1974; Leonard 2005, 2010) have been predicted to be: (1) reproductive assurance through the possibility of selfing, (2) increased effective population size (Ghiselin 1969; Borgia and Blick 1981), (3) increased efficiency through shared function or division of resources (convex fitness function) (Charnov 1979, 1982), (4) reduced covariance of fitness of the offspring, that is, survival of offspring through eggs and sperm should be more independent than if all of the offspring came through one type of gamete (Lloyd 1982; Leonard 1999), (5) reduced variance in fitness (Wilson and Harder 2003), and (6) phenotypic plasticity in sex allocation (Ghiselin 1969; Charnov 1982; Lloyd 1982; Cadet et al. 2004), for example, the Size-Advantage Model or quantitative gender concept. Experimental evidence from a polychaete indicates that plasticity in sex allocation need not incur significant costs (Lorenzi et al. 2008).

It is evident that these advantages of dioecy versus hermaphroditism are quite general and one would expect that it would be possible for evolution through natural selection to arrive at solutions other than a change of sexual system, in response to the selection pressures listed above. For example, avoidance of selfing is a clear advantage of dioecy but after reviewing the selfing in hermaphroditic animals (Jarne and Charlesworth 1993; Jarne and Auld 2006; Lamy et al. 2012), it becomes clear that there are many taxa that do not self. The opisthobranch gastropods are a very diverse group that is overwhelmingly simultaneously hermaphroditic, and yet selfing is extremely rare (Leonard 1991). Even in pulmonates, which exhibit high levels of selfing, the incidence of selfing can range from very high to 0% within a genus or even a species (Heller 2001; Baur 2010; Jarne et al. 2010; also see Johnston et al. 1998 for a study of a bivalve). Barnacles are another large, simultaneously hermaphroditic group in which selfing, although it has been detected, is very rare (Kelly and Sanford 2010; Leonard 2010; Yusa et al. 2013, this issue). Self-incompatibility genes have also evolved in invertebrates (Grosberg and Hart 2001; Bishop and Pemberton 2006) and selfing can also be avoided by asynchronous release of eggs and sperm during broadcast spawning (Lotterhos and Levitan 2010). Settlement patterns have been implicated in promoting outcrossing in hermaphroditic bryozoans (Johnson and Woollacott 2010). It therefore, seems clear that selection can lead to the evolution of avoidance of selfing without dioecy. Similarly, although hermaphroditism may be an effective means of reproductive assurance in the face of sessility or low density, there are other mechanisms that achieve the same end. In barnacles, low density is associated with dioecy with dwarf males, whereas hermaphrodites are associated with...
higher densities (Yusa et al. 2013, this issue; also see discussion above). Dwarf males are also found in other dioecious taxa with low density (Ghiselin 1974; Bieler and Hadfield 1990). Coloniality, gregarious settlement, and sperm attractants are also mechanisms that achieve reproductive assurance in sessile animals (Bieler and Hadfield 1990). In pair-mating taxa, enhanced search for mates (Puurtinen and Kaitala 2002; Eppl ey and Jesson 2008;); long-term monogamy (Bauer 2007), storage of sperm, or facultative parthenogenesis (Walsh 2013, this issue), which has been recently found in tetrapods (Booth et al. 2012), are other mechanisms for improving reproductive assurance in dioecious taxa. Enhanced longevity, as seen in many dioecious trees, also aids reproductive assurance (Ashman 2006). The other selection pressures that would favor dioecy versus hermaphroditism, for example, adaptation to limited resources and reduced covariance of offspring, would seem to have even more alternative life-history solutions. The Metazoa seem to indicate that sexual systems, whatever their advantages, are merely one component of an organism’s life history. Evolution is capable of responding by a variety of novel solutions to almost any selective pressure. Aphids, a strictly dioecious insect group, have evolved a way of achieving self-fertilization through cyclical parthenogenesis (Foster 2002). Therefore, understanding hermaphroditism and dioecy as dichotomous solutions in evolution is probably not a useful way of looking at the distribution of sexual systems. One suspects that the essential aspect of the situation that has been overlooked, as was said in a different context (Maynard Smith 1976) to create Williams’ Paradox, is the complexity of metazoan life histories and the degree of phenotypic plasticity associated with many sexual systems.

The way forward

“Critical evidence on such theories... are more likely to come from studies of groups in which reproductive patterns vary widely at the level of species and genera.”

Williams (1975, p. 123)

It is clear that Williams’ Paradox is still with us; that is, we do not have a theory that explains the distribution of hermaphroditism versus dioecy in the Metazoa. However, we have moved far beyond Williams’ explanation of a lack of preadaptations for change. Real progress over the past 40 years has been made in: (1) understanding the stability of hermaphroditism as a sexual system (Leonard 1999, 2010), (2) understanding the sexual system and reproductive biology of a wide variety of organisms, (3) realizing that gonad morphology and histology do not necessarily reflect reproductive function (Sadovy de Mitcheson and Liu 2008; Lorenzi and Sella 2013, this issue), and (4) understanding the diversity of mechanisms of sex determination and sexual differentiation in organisms (Rhen and Schroeder 2010; Diggle et al. 2011; Mankiewicz et al. 2013, this issue; Marsh-Hunkin et al. 2013). It remains possible that there are taxa that have evolved themselves into a corner in terms of their sexual system; perhaps, for example, the mammals with their strict dichotomy of sexual development (Jimenez et al. 2013), but it does not seem likely that it will be possible to draw those sorts of conclusions from a broad phyletic survey. It seems clear that, as Williams (1975) suggested, in order to test hypotheses about the relative advantages of dioecy versus hermaphroditism or simultaneous hermaphroditism versus sequential hermaphroditism, it will be important to compare closely related taxa that differ in sexual system and/or life history. Fortunately, in recent years these sorts of studies have started to become available. In this issue, Erisman et al. (2013, this issue) present a phyletic survey of those families of teleost fishes with hermaphroditism and show that within these families the sexual system correlates well with the mating system and with the level of sperm competition. In a similar study of the teleost family Labridae, the occurrence of protogynous sequential hermaphroditism was found to be very consistent with the Size–Advantage Hypothesis although transitions from dioecy to sex change were more common than the reverse, contrary to expectations (Kazanciglu and Alonzo 2010). In a similar study in scleractinian corals, Kerr et al. (2011) identified four reproductive modes, gonochorism with brooding, gonochorism with free spawning, hermaphroditism with brooding, and hermaphroditism with free spawning, and found that in both sexual systems, transitions from brooding to spawning were more common than any transition between hermaphroditism and gonochorism, but that the most common transition between sexual systems involved changes from gonochorism with brooding to hermaphroditism with brooding. Changes from spawning to brooding were less common than the reverse although changes from gonochorism with spawning to gonochorism with brooding were as common as changes from gonochorism with brooding to hermaphroditism with brooding. Interestingly, with the postulated association between brooding and hermaphroditism, hermaphroditic brooders were just as likely to make the transition to free spawning as were gonochoristic...
brooders. As molecular tools allow the creation of more detailed phylogenies, these sorts of studies are becoming more common and should provide a clearer picture of the types of transition that occur between sexual systems in animals and how common those transitions are.

Yusa et al. (2013, this issue) show a clear correlation between group size and sexual system in pedunculate barnacles, demonstrating that dwarf males evolved as a mechanism achieving reproductive assurance in which individuals are likely to be isolated, and that, in barnacles, androdioecy with complemental males is a transitional step between an ancestral state of hermaphroditism and dioecy with dwarf males. In the polychaete genus *Ophryotrocha*, which includes dioecious, sequentially hermaphroditic, and simultaneously hermaphroditic species, a comparative study of life-history parameters among a dioecious, a sequentially hermaphroditic, and a simultaneously hermaphroditic species showed that the sexually dimorphic gonochore, *Ophryotrocha labronica* had a higher fitness, \( \lambda \), than did the other species because it had earlier sexual maturity (Prevedelli et al. 2006). *Ophryotrocha labronica*'s sexual system has been the subject of debate because many individuals have been found with both eggs and sperm, a trait that varies among populations. Lorenzi and Sella (2013, this issue) have shown, through experiments in cross-breeding, that this species is dioecious regardless of whether individuals carry both types of gamete, thereby emphasizing the pitfalls of using anatomical data to infer sexual system. In recent years there have been an increasing number of studies comparing closely related taxa that differ in sexual systems, for example, freshwater mussels (Hoeh et al. 1998), fucoid seaweeds (Ladah et al. 2003), and extensive and very sophisticated work with the model system, the nematode *C. elegans*. Androdioecy has evolved twice in this genus (Kiontke et al. 2004), in each case as a distinct single mutation (Braendle and Félix 2006; Pires-daSilva 2007), suggesting that there is no phyletic inertia maintaining the dominant sexual system of dioecy. The factor hypothesized to be maintaining dioecy in nematodes is sexual selection (Artieri et al. 2008). Other studies of nematodes have elucidated the determination of sex by a combination of sex chromosomes and ESD in a trioecious species (Chaudhuri et al. 2011) and the mechanisms of formation of dimorphic sperm in androdioecious taxa (Baldi et al. 2011). There has even been an effort to understand the natural history of *C. elegans* (Félix and Braendle 2010).

Not only do these various studies provide important insight into the evolution and reproductive biology of the taxa examined, but it seems probable that within a few years, meta-analysis of such studies will begin to allow us to make generalizations about the importance of particular selective pressures in transitions between sexual systems. Similarly, the detailed molecular studies of sex determination and differentiation that are under way both in nematodes and vertebrates (Rhen and Schroeder 2010; Mankiewicz et al. 2013, this issue; Marsh-Hunkin et al. forthcoming), will someday make it possible to make informed hypotheses about the existence or absence of phylectic constraints on transitions between sexual systems. The way forward in understanding the distribution and adaptive value of different sexual systems will require both an understanding of the costs and benefits of phenotypic plasticity in gender versus fixity of gender, and a more detailed and sophisticated understanding of how other life-history parameters interact with the sexual system. What are the evolutionary consequences of facultative parthenogenesis versus facultative self-fertilization? Do gonochores generally mature earlier than hermaphroditic congeners? Is sperm competition a major factor in stabilizing dioecy as a rule? Is ESD an evolutionary intermediate between sequential hermaphroditism and dioecy? Someday soon we will be able to review these issues. At present, we can conclude that there is a continuum between dioecy and hermaphroditism in the Metazoa and that the diverse life histories in animals make predicting sexual system across major taxa more complex than is accounted for by current models.

**Acknowledgments**

I would like to thank the participants of this symposium: Malin Ah-King, Andrea Case, Rachel Collin, Pamela Diggle, Brad Erisman, John Godwin, Cristina Lorenzi, Matt Walsh, and Yoichi Yusa, for making the symposium so successful and for offering very stimulating views on the subject. SICB provided a venue and financial support for this symposium, for which they deserve thanks. Thanks are also due to the reviewers and editor whose comments have helped to improve this article.

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