Hermaphrodites
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Glossary
Anisogamy Literally meaning ‘unequal marriage,’ a condition where the fusing gametes are of unequal size, with the male sex by definition producing the smaller and the female sex the larger gametes, leading to an often highly unequal resource contribution to the zygote; more strictly, an additional distinction is sometimes made between anisogamy, where both gametes retain at least some motility, and ‘oogamy,’ where the larger gamete has lost motility entirely.
Dioecy See Gonochorism.
Gonochorism A term mainly used for animals: a sexual system where individuals only ever exhibit either the male or the female sexual strategy throughout their lives (synonymous with ‘dioecy’ used for plants and ‘heterothallism’ used for algae and fungi).
Hermaphroditism A term mainly used for animals: a sexual system where individuals usually exhibit both the male and female sexual strategy, either at different times of their lives (sequential hermaphroditism) or at the same time (simultaneous hermaphroditism) (synonymous with ‘monoecy’ used for some forms of hermaphroditism in plants and ‘homothallism’ used for algae and fungi).
Heterothallism See Gonochorism.
Homothallism See Gonochorism.
Isogamy Literally meaning ‘equal marriage,’ a condition where the fusing gametes are of equal size and make an equal resource contribution to the zygote, although they may exhibit different ‘mating types.’
Local sperm competition Results from competition between related sperm, generally from the same sperm donor (or also from related sperm donors), for the fertilization of a given set of ova of a sperm recipient. It can thus be viewed as the mirror image of sperm competition, which represents the competition between the sperm from two or more (unrelated) males for the fertilization of a given set of ova.
Mating conflict It occurs when two potential mating partners have incompatible sex role preferences, owing to asymmetries in the benefits of mating versus its costs between acting as a sperm donor or sperm recipient (so that both individuals may preferentially adopt the same sex role).
Mating types A genetic compatibility system that only permits gametes that have a different mating type to fuse with each other, possibly in order to avoid self-fertilization; often individuals are thought to produce gametes of only one type and in many organisms there are only two mating types, often called plus (+) and minus (−).
Monoecy See Gonochorism.
Oogamy See Anisogamy.
Protandry In sequential hermaphrodites, sex change from male to female; in simultaneous hermaphrodites, when the male function matures before the female function.
Protogyny In sequential hermaphrodites, sex change from female to male; in simultaneous hermaphrodites, when the female function matures before the male function.
Reproductive value Expected future reproductive success of an individual, of key importance in predicting sex-change decisions made by sequential hermaphrodites.
Sex allocation A decision about the amount of investment channeled toward the two sex functions; for example, the number of sons vs. daughters in gonochorists (the sex ratio), the timing of sex change in sequential hermaphrodites, or the investment toward the production of male vs. female gametes in simultaneous hermaphrodites.
Sexual conflict A conflict between the evolutionary interests of a sperm donor and a sperm recipient.
Size-advantage model A model to describe the idea that the sex-specific fecundity (or reproductive value) of an individual might change as it is growing, for example, being higher for the female function when small and higher for the male function when large, thus favoring sequential hermaphroditism with ‘protogyny.’

Introduction
Hermaphroditism is common, occurring in >90% of plant genera (Renner and Ricklefs, 1995). >70% of animal phyla (Jarne and Auld, 2006), and being present also in many other multicellular taxa, such as volvocine algae (Coleman, 2012) and arguably also in the fungi (Nieuwenhuis and Aanen, 2012) (see ‘Glossary’ for related terms used in diverse organismal groups). The key distinguishing feature of hermaphroditism is that each individual can (at least potentially) gain fitness through both male and female reproduction, either by adopting the two sexes sequentially or simultaneously.

We first outline the evolutionary context for thinking about hermaphroditism, focusing on (1) it being a frequent outcome following the evolution of ‘anisogamy,’ (2) what might be the evolutionary advantages of maintaining two individual routes to fitness, and (3) how local competition drives individual investment decisions between the two sex functions (i.e., ‘sex allocation’). We then apply this framework to highlight some of the key differences in the evolutionary biology of sex in hermaphrodites compared to gonochorists, firstly for sequential hermaphrodites and then for simultaneous hermaphrodites. Finally, we provide an outlook, and argue that studying sex in hermaphrodites is important for gaining a
comprehensive general picture of the consequences of the evolution of anisogamy.

**Hermaphroditism in Context**

**The Evolution of Anisogamy and Its Consequences**

Sexual reproduction usually involves the union of two haploid gametes stemming from two different parental individuals, leading to a diploid zygote in which each parent obtains an equal genetic representation. A common, but far from universal, observation among sexually reproducing eukaryotes is that the two fusing gametes differ substantially in size, a condition termed ‘anisogamy.’ A phylogenetic perspective suggests that anisogamy has evolved from ‘isogamy’ at least half a dozen times independently (Kirk, 2006), with well-known examples including land plants, some red, brown and green algae, malaria parasites, and animals. These multiple origins of anisogamy point to a fundamental phenomenon linked to sexual reproduction and suggest that common selective pressures are at work. In the following we focus largely on animals, but this simply reflects our own expertise and many of the points we raise have parallels in other organismal groups (see also Charnov, 1982; Lloyd, 1982; Charlesworth and Morgan, 1991; Bernasconi et al., 2004).

The evolution of anisogamy probably results from a primordial ‘sexual conflict’ over which parent provides more of the resources needed for the successful development of the zygote, given that larger zygotes may often be fitter and develop into fitter individuals (Parker et al., 1972; Lessells et al., 2009; Parker, 2011). By making large gametes a parent can increase its probability of having fit offspring, but given limited resources, it will also make relatively fewer offspring (i.e., gamete size and number trade-off). Conversely, by making many small gametes, a parent may instead aim at finding and (preferentially) fusing with (more) large gametes, so that its genes also end up in large zygotes (thus exploiting other parents’ gametic investment). Under broad conditions evolutionary models show that this leads to disruptive selection on gamete size, yielding two fundamentally different sexual strategies (Parker, 2011, 2014). By convention, making many small gametes is called the male strategy and making fewer large gametes is called the female strategy, resulting in a type of sexual reproduction – anisogamous sex – in which there are two fundamentally different routes to fitness, male and female reproduction.

When thinking about sexual reproduction, biologists (and especially zoologists) often presuppose that these two sexual strategies already exist and also that they are stably associated with two particular types of individuals, namely males and females, a sexual system called ‘gonochorism.’ But an important challenge for a more complete understanding of anisogamous sex is to acknowledge (1) that it has evolved multiple times independently and that the male and female sexual strategies are therefore convergent phenomena in different organismal groups, and (2) that these strategies can be distributed over individuals in a population in diverse ways, often involving ‘hermaphroditism.’ We therefore argue here that beyond the fact that hermaphrodites show striking sexual adaptations that are interesting in their own right (see below), they are also worth studying because they force us to reevaluate preconceived ideas about what we consider male and female, which – at root – is about anisogamy, and not about courtship dances, huge antlers, or colorful plumage (Schärer et al., 2012).

**The Adaptive Significance of Having Two Routes to Fitness**

Arguably the biggest difference between gonochorists and hermaphrodites is that in the latter each individual has (at least potentially) access to both the male and female routes to fitness (Figure 1). It is currently unclear whether the evolution of anisogamy originally leads to gonochorism or hermaphroditism (Schärer et al., 2014), and the answer may well depend on the specific organismal group. Despite this, many existing models for the evolution of anisogamy make assumptions that necessarily link to the evolution of gonochorism (e.g., Lehtonen and Kokko, 2011; Parker, 2011), so broadening this theory base remains a significant challenge (as does conducting empirical work in extant groups where ongoing evolution of anisogamy can be studied). From a hermaphroditic perspective, it could be argued that gonochorists are a special case, where some individuals have lost (or given up) their ability to reproduce via one of the two routes, and an important aspect of understanding hermaphroditism is therefore to understand the conditions under which it may or may not be advantageous for individuals to maintain two routes to fitness.

Current thinking about the evolution of sequential hermaphroditism considers that the male and female functions may

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**Figure 1** The two routes to fitness in hermaphrodites. In hermaphrodites, survivorship, fecundity, and mating success will often contribute to fitness separately via the male and female sex functions. Nevertheless, we can expect important feedback effects between these different fitness components, only some of which are illustrated here. For example, mating success in one sex function may impact upon reproductive success in the other sex function (so-called cross-sex effects; stippled arrows), as can occur if mating is reciprocal such that additional matings in the male role automatically correspond to more additional matings in the female role. Modified from Schärer, L., Janicke, T., Ramm, S. A., 2014. Sexual conflict in hermaphrodites. Cold Spring Harbor Perspectives in Biology doi: 10.1101/cshperspect.a017673, based on an original figure for gonochorists in Arnqvist and Rowe (2005).
have differing optimal body sizes, such that an individual may maximize its total fitness by first exhibiting one sex and later changing to the other (the ‘size-advantage model’; Ghiselin, 1969; Figure 2). Stated more broadly, the size-advantage model predicts that an individual should want to change sex whenever it can increase its ‘reproductive value’ by doing so, emphasizing that social and ecological factors come into play in determining the optimal sex-change strategy (Warner, 1975, 1988; Charnov, 1982; Munday et al., 2006). We consider the rationale of the size-advantage model in more detail in Section ‘Local Competition and Sex Allocation,’ and then provide examples in Section ‘Sex in Sequential Hermaphrodites’ below.

For simultaneous hermaphrodites, the benefits of dual sexuality may stem from reproductive assurance when the rate of encountering potential mates is low, for example under low population density (Ghiselin, 1969; Schärer, 2009). In contrast to gonochorists, for a simultaneous hermaphrodite each encountered conspecific is a potential mating partner (Tomlinson, 1966). Moreover, even in the complete absence of access to mating partners, exhibiting both sexes simultaneously – or in short sequence, such as in some Caenorhabditis nematodes – has the additional benefit of permitting self-fertilization (Charlesworth and Morgan, 1991; Jarne and Charlesworth, 1993; Jarne and Auld, 2006). However, simultaneous hermaphroditism is clearly not restricted to only organisms occurring at low density, and more generally, this sexual system is expected to be stable whenever there are strong diminishing fitness returns on investment into one of the sex functions (Charnov, 1982; Schärer, 2009), an argument that we develop more fully in Section ‘Local Competition and Sex Allocation.’

Whilst these adaptive explanations for hermaphroditism are undoubtedly important in understanding how it can evolve, the current taxonomic distribution of the different sexual systems among animals also reveals a strong degree of phylogenetic inertia (see Renner and Ricklefs, 1995 for data on plants). While some groups are (almost) entirely hermaphroditic (e.g., flatworms, arrow worms, and gastrotrichs) there are other groups that are (almost) entirely gonochoristic (e.g., insects, nematodes, and acanthocephalans), while yet other groups show more variable sexual systems (e.g., coelenterates, polychaetes, and molluscs) (see also Ghiselin, 1969; Schärer, 2009; Weeks, 2012; Collin, 2013).

Irrespective of the exact conditions under which hermaphroditism is favored or maintained, once two routes to fitness are present in the same individual, this leaves open the possibility of strategically varying the amount of resources invested into the two sex functions, both in terms of overall quantity and with respect to the timing during an individual’s life history (i.e., simultaneously vs. sequentially). These are questions about ‘sex allocation,’ which we discuss next.

**Figure 2** The size-advantage model for sequential hermaphroditism. If the expected fitness returns on operating as either a male or a female change predictably with size (or age), this may – provided that it is physiologically possible and the costs of doing so are not too high (see Kazancioglu and Alonzo, 2009) – favor reproductive strategies that involve sex change. (a) Protogyny (female-to-male sex change) is favored when the relationship between size and fecundity is shallower for females than males, for example, because large males are more successful at holding a territory in which they can mate with multiple females. By contrast, if the size–fecundity relationship is steeper for females, for example, because larger females are more fecund, while a male’s size is relatively unimportant for its fecundity, this may favor protandry (male-to-female sex change). Modified from Munday, P. L., Buston, P. M., Warner, R. R., 2006. Diversity and flexibility of sex-change strategies in animals. Trends in Ecology & Evolution 21, 89–95.

**Local Competition and Sex Allocation**

In anisogamous species, every zygote results from the fusion of one male and one female gamete, and so every individual in the population has exactly one father and one mother. This means that at the level of the population, the amount of fitness that can be obtained via the male and the female reproductive strategy is necessarily equal (despite the male gamete’s usually minimal material contribution to the zygote). Under frequently made simplifying assumptions of random mating (i.e., any male gamete in the population has the same probability of fusing with any female gamete) and large populations size (i.e., mates and competitors are always unrelated) this then predicts equal resource investment in male and female reproduction (Düssing, 1884; Fisher, 1930; Charnov, 1982). However, in nature local competition between related entities often results from imperfect mixing of gametes, clustering of gametes into ejaculates and clutches, and limited dispersal of offspring leading to mate competition between relatives, meaning that these simplifying assumptions are probably broken more often than not. As a result the optimal resource allocation can differ drastically from equality, leading
to strongly biased individual and population sex allocation patterns (Hamilton, 1967; Charnov, 1982; Frank, 1987). Local competition can also affect the optimal distribution of the two sexual strategies over individuals in the population, so understanding the consequences of the evolution of anisogamy requires an understanding of the logic of sex allocation theory. While we cannot give a detailed account of sex allocation theory here (see Charnov, 1982; Schärer, 2009; West, 2009), we will highlight those aspects most relevant to the study of sex in hermaphrodites.

Local competition between related gametes means that investment toward making more gametes shows diminishing returns. If local competition is sex-specific, say affecting male more than female gametes, then there comes a point at which additional resources would be better invested in the alternative sex function: such individuals benefit from investing less than half of their resources into the production of male gametes, resulting in simultaneous hermaphroditism with a female-biased sex allocation (Figure 3(a)). Such 'local sperm competition' may regularly occur under conditions such as low population density, monogamy or in small groups (Charnov, 1982; Schärer, 2009), but it can also result from different processes of sexual selection, such as strong first or last male sperm precedence, cryptic female choice, or random paternity skews (Charnov, 1996; Greef et al., 2001; Schärer, 2009; Van Velzen et al., 2009; Schärer and Pen, 2013). Exclusive selfing is an extreme example, involving maximal local sperm competition and thus strongly diminishing returns on male reproductive investment.

In a similar way, local competition between socially interacting individuals may curtail the reproductive opportunities more strongly for one than the other sex function. If this effect depends on, for example, body size, then reproducing in one sex early in life and later switching to the other sex, i.e., being a sequential hermaphrodite, might be the optimal sex allocation strategy (Figure 2; Charnov, 1982; Munday et al., 2006). Conversely, if investment toward one sex function shows accelerating returns (say because a higher fighting ability or more attractive ornament makes winning in mating competition much more likely), then permanently specializing on one sex role may be the best strategy, thus favoring gonochorism (Figure 3(b); Charnov, 1982). Here individuals can still optimize their sex allocation by producing offspring with biased sex ratios (although under a fairly broad range of conditions the optimal sex ratio may remain close to equality). Note, however, that a gonochorist's sex ratio adjustment is less direct than the sex allocation adjustment within an individual hermaphrodite's lifetime, as the former is played out only in the next generation.

**Sex in Sequential Hermaphrodites**

**The Role of Ecology and Social Interactions**

Recall that the size-advantage model predicts that an individual should want to change sex whenever it can increase its fecundity (or reproductive value) by doing so (Section 'The Adaptive Significance of Having Two Routes to Fitness'). Here we emphasize that ecological and social factors combine in interesting ways to generate predictable sex differences in the size–fecundity relationship favoring sex change, but also that they can constrain individual sex-change decisions.

'Protandry' (male-to-female sex change) is often observed if the habitat leads to very small and stable groups of locally interacting individuals, such as is observed in slipper shells that form stable stacks of individuals (Figure 4(a); Collin, 2006) or in anemone fishes that inhabit individual sea anemones (Figure 4(b); Fricke and Fricke, 1977). In both cases, female fecundity is highly body size-dependent, whereas male fecundity is not, because the particular ecological conditions constrain the opportunity for male–male competition (Figure 2(b)). In the case of slipper shells, the number of mates that a male can obtain is inherently limited to only the neighbors in its stack (Collin, 1995) and paternity is biased toward the closer neighbors (Proestou et al., 2008). In anemone fishes, there is a stable dominance hierarchy among the group members in which the highest ranking individual, a large female, uses aggression to constrain the reproductive decisions of the lower-ranking individuals, which comprise a smaller male (her only sexual partner) and a variable number of even smaller reproductively suppressed immature individuals (Fricke and Fricke, 1977). It is important to acknowledge, however, that such ecological constraints may also favor bidirectional sex change, as observed in some coral gobies.
Figure 4  Sequential hermaphrodites. (a) In the protandrous common slipper shell, *Crepidula fornicata*, individuals form stacks in which the smaller (and younger) individuals closer to the top of the stack are males (the arrowheads indicate very small individuals), while the larger (and older) individuals toward the bottom of the stack are females (note that the individual in the bottom-most shell on the right has already died). Intermediate-size individuals that are in the process of changing from male to female often occur in the middle of the stack (see also Collin, 2006; image ‘Stack of Crepidula’ by Paul Morris from https://www.flickr.com/photos/aa3sd/5044549409/ licensed under CC BY-SA 2.0). (b) In the protandrous twoband anemonefish, *Amphiprion bicinctus*, many individuals live in stable pairs that inhabit and jointly defend a sea anemone (here the bubble-tip anemone, *Entacmaea quadricolor*). Pairs usually consist of two sexually mature individuals, a smaller male individual and a larger female individual, the latter has previously functioned as a male. Moreover, in some cases there are additional immature individuals that are cueing to take the place of the resident male and female (see also Fricke and Fricke, 1977; image by Lukas Schärer). (c) and (d) The protogynous sea goldie, *Pseudanthias squamipinnis*, shows considerable sexual dimorphism, with females (c) being much smaller and largely orange in coloration and males (d) being larger, more variably colored, and carrying a long dorsal fin ray. Males are territorial and can pair spawn with multiple individual females per day; all males start their life as females (see also Shapiro, 1979; images by Lukas Schärer). (e) Like most grouper species, the Red grouper, *Epinephelus morio*, is protogynous and mates in pairs where males experience low sperm competition, while (f) its sibling species the Nassau grouper, *Epinephelus striatus*, is gonochoristic and mates in groups where males experience high sperm competition, supporting the idea that strong sperm competition can make protogyny unstable (see also Erisman et al., 2009; the public domain images are, respectively, from http://www.photolib.noaa.gov/bigs/fish3131.jpg and …/fish3129.jpg).
(Kuwamura et al., 1994; Munday, 2002), or simultaneous hermaphroditism with strongly female-biased sex allocation (Baeza, 2010).

Conversely, in less ecologically restricted conditions that permit the formation of larger groups, male fecundity may strongly depend on an individual’s ability to hold a territory, in which it can gain exclusive access to multiple females. Even if female fecundity is still strongly dependent on body size (as is often the case), a large body size may benefit males more than females, thus favoring ‘protogyny’ (Figure 2(a)). This sexual system is frequently encountered in a diversity of different fish families (Munday et al., 2006; Avise and Mank, 2009; Erisman et al., 2013), including some serranid reef fishes (Figures 4(c) and 4(d)), and many labrid and scarid reef fishes (Robertson and Warner, 1978; Warner and Robertson, 1978; Warner, 1991; Schärer and Vizoso, 2003; Kazancoğlu and Alonzo, 2010). Note that in such species only relatively few individuals may actually reach a size where they change sex and obtain significant reproductive success as male, leading to highly biased population sex ratios (Warner and Hoffman, 1980).

From a mating systems perspective, protandry is expected under conditions where sexual selection is weak, as individuals are often essentially living under monogamy. In contrast, there is ample scope for the evolution of sexual ornaments under protogyny, with multiple males vying for the attention of females. Indeed, males and females often look drastically different in protogynous species (Figures 4(c) and 4(d)), while they often look very similar in protandrous species (Figure 4(b)).

Extensions to the Basic Theory

More recently the theoretical foundations of the size-advantage model have been extended in an attempt to explain some apparently counterintuitive empirical observations (see also Munday et al., 2006), one of which is that in some protogynous species large females sometimes do not change sex when the opportunity arises. The Expected Reproductive Success Threshold model (Muñoz and Warner, 2003) incorporates variation in (1) sperm competition intensity (which reduces the payoffs that can be expected from changing to the male sex) and (2) female fecundity (which considers how much fecundity a female gives up when changing sex compared to the aggregate fecundity of the remaining females). In support of the sperm competition scenario, which may result from group spawning or small males that interfere in pair spawns, a recent comparative phylogenetic study showed that protogyny has shifted to gonochorism at least four times independently among groupers, and that these shifts were always associated with the evolution of group spawning (high sperm competition) from the ancestral pair spawning (low sperm competition) character state (Erisman et al., 2009) (Figures 4(e) and 4(f)). Moreover, the same study showed that relative testis size was much larger in gonochoristic than protogynous species, which also matches this scenario very well. Support for the female fecundity scenario stems from a study on the bucktooth parrotfish, Sparisoma radians, that initially motivated the extended theory (Muñoz and Warner, 2004; but see critique by Clifton and Rogers (2008) and response by Warner and Muñoz (2008)), and arguably also from a study that shows that in the bluehead wrasse, Thalassoma bifasciatum, females that become infected with an ovarian parasite – and thus have a lower female fecundity – change sex earlier and at a smaller size (Schärer and Vizoso, 2003).

Finally, a recent study in the protogynous sandperch, Parapercis cylindrica, suggested that there might be a role for intralocus sexual conflict in sequential hermaphrodites (Sprenger et al., 2012), in that individuals were shown to exhibit a similar aggression level before and after sex change. Given the species’ mating system, the authors argued that high aggression may be good when male, but potentially deleterious when female, which would make any allele affecting aggression sexually antagonistic (for a more detailed discussion of both intra- and interlocus sexual conflicts in sequential hermaphrodites, see Abbott (2011) and Schärer et al. (2014)). If such antagonistic alleles are widespread in sex changers, this could also affect the stability, expression, and timing of sex-change strategies, a field that would greatly benefit from further theoretical work.

Sex in Simultaneous Hermaphrodites

Pre- versus Post-Mating Sexual Selection

As originally conceived, sexual selection sought to account for conspicuous, sexually dimorphic traits that were difficult to attribute to natural selection for survival (Darwin, 1859, 1871). Given the absence of male and female individuals, sexually dimorphic traits cannot really exist in simultaneous hermaphrodites. Nevertheless, there are clearly many traits that might differentially influence reproductive fitness through one or the other sex function. An interesting question is whether the fact that all individuals in a simultaneously hermaphroditic population would have to express a (presumably costly) sexually selected trait and preference fundamentally alters the operation of sexual selection, or whether it just means that such traits are harder to identify (Morgan, 1994; Schärer and Pen, 2013). The conditions that were originally thought to favor hermaphroditism – low mate availability etc. – might tend to favor relatively indiscriminate mating, obviating the need for elaborate pre-mating mate choice mechanisms. Accordingly, most evidence of mate choice in hermaphrodites to date appears to relate instead to indicators of female fecundity or likely fertilization returns on male investment (Schärer and Pen, 2013).

The importance of post-mating sexual selection (Parker, 1970; Eberhard, 1996) in hermaphrodites is much more clearly established. Indeed, some of the earliest insights about how sperm competition, cryptic female choice, and sexual conflict would play out were those in the hermaphroditic-specific treatment of Charnov (1979). Many of the familiar post-mating sexually selected traits found in gonochorists have also been well described in various hermaphroditic taxa. Some of these adaptations even appear to be especially common in hermaphrodites, as is for example the case for devices that inject manipulative substances into the mating partner, for example, the love darts of various land snails (Figure 5(a))

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Sex Role Preference as a Unique Pre-Mating Arena of Conflict

Applying Bateman’s principle (Bateman, 1948) to simultaneous hermaphrodites, Charnov (1979) realized that hermaphroditic individuals may often wish to ‘copulate not so much to gain sperm to fertilize [the own] eggs as to give sperm away,’ basically because the female sex function is typically more limited by access to resources and the male sex function by access to eggs (Figure 6) (for a more thorough review see Anthes et al., 2010). If two potential mating partners are then both male and female, this may often create a conflict over which of them adopts the male and female sex role in any particular mating interaction, i.e., a ‘mating conflict’ (Charnov, 1979; Michiels, 1998; Schärer et al., 2014) (Figure 7). This need not always be the case, however, since the expected male preference refers to the average situation, not to a specific interaction in which the individuals may or may not have compatible mating interests; for example, for a virgin individual there may be a considerable fitness gain to be had from mating in the female role (Figure 6), so a virgin and a non-virgin individual might readily agree over their different, preferred sex roles. Whenever there are incompatible mating interests, these could be resolved in various ways, either resulting in realized conflict or not (Charnov, 1979; Michiels, 1998; Schärer et al., 2014). In the former category would clearly be behaviors such as penis fencing exhibited by some polyclad flatworms, in which each individual attempts to stab and hypodermically inject sperm into the partner whilst simultaneously avoiding the same fate itself (Michiels and Newman, 1998; Figure 8(a)). More peaceful resolutions occur in those species that agree to reciprocally exchange gametes, meaning they consent to adopt both the preferred and non-preferred roles through either conditional sperm receipt or conditional sperm donation. This could involve interactions during which two individuals may exchange sex roles, but each mating itself is unilateral (e.g., Figure 8(b)). For example, empirical evidence suggests that such a resolution of mating conflict manifests as egg trading in serranid reef fishes (Figure 8(c)). In one case of proposed sperm trading – in the sea slug Chelidonura hirundinina – the predicted conditionality of gamete trading has also been experimentally demonstrated: individuals are more reluctant to mate with non-reciprocating partners (Anthes et al., 2005). In other cases, reciprocal exchange of gametes is achieved by both individuals acting simultaneously as sperm donor and sperm recipient, as in some land snails (Figure 8(d)) and flatworms (Figures 8(e) and 8(f)).

Sex Allocation Manipulation as a Unique Post-Mating Arena of Conflict

It was again Charnov (1979) who first suggested that a common target of manipulation by a simultaneously hermaphroditic sperm donor might be the sex allocation of the corresponding sperm recipient. This could occur in two distinct ways, either by boosting the female function of the mating partner, or else by attacking its male function. The former mechanism should normally be straightforwardly
Figure 6  Bateman gradients in hermaphrodites. (a) Hypothetical plot showing the expected fitness returns (measured as reproductive success) on obtaining mating success in the male or the female sex function in hermaphrodites. As in gonochorists, it is often expected that the ‘Bateman gradient’ (i.e., the slope of the regression of reproductive success on mating success; Bateman, 1948; Arnold, 1994a) is steeper for males (solid green line) than for females (solid orange line). The dotted line illustrates a scenario whereby for the male sex function there is a large increase in fitness from an initial mating (where the individual’s state switches from virgin to mated) but further matings then have little impact on fitness (e.g., because once mated the individual has access to stored sperm) (see also Anthes et al., 2010; Schärer et al., 2014). Recent empirical studies in two simultaneously hermaphroditic snails, (b) Biomphalaria glabrata and (c) Physa acuta (here engaged in a unilateral mating), confirm that the male sex function indeed exhibits a steeper Bateman gradient than the female sex function (see Anthes et al., 2010; Pélissié et al., 2012). (Images of B. glabrata and P. acuta courtesy of Nils Anthes and Tim Janicke, respectively.)

Figure 7  Potential mating conflicts over sex roles in simultaneous hermaphrodites. Two simultaneously hermaphroditic individuals that must decide, not just whether they wish to mate, but also which sex role or roles they wish to play: donate sperm, receive sperm, or both. Mating conflicts arise whenever the two individuals have incompatible mating interests and they are strongest when both individuals either want to only donate (green-shaded square) or to only receive sperm (orange-shaded square), but they also occur wherever there is partial disagreement (lighter-shaded squares). Modified from Schärer, L., Janicke, T., Ramm, S. A., 2014. Sexual conflict in hermaphrodites. Cold Spring Harbor Perspectives in Biology doi: 10.1101/cshperspect.a017673, based on an original figure in Michiels (1998).

Outcrossing versus Self-Fertilization

As we already mentioned above, another unique aspect of sex in simultaneous hermaphrodites (and indeed certain sequential hermaphrodites, namely if the gamete type produced first can be stored prior to use) is the phenomenon of self-fertilization. Despite potential negative effects resulting from inbreeding depression, this may still offer a better alternative than being unable to reproduce at all, and current evidence of so-called delayed selfing bears this out: upon reaching sexual maturity, in the absence of outcrossing opportunities many simultaneous hermaphrodites at first wait for such an opportunity to arise (especially if inbreeding costs are high; Tsigutina et al., 2003a; Escobar et al., 2011), and if an opportunity does not materialize they later switch to selfing (e.g., Tsigutina et al., 2003b; Escobar et al., 2011; Ramm et al., 2012). Note, however, that by far not all simultaneous hermaphrodites are capable of selfing, as there may be morphological constraints that prevent ready selfing (cf. Ramm et al., 2012; Ramm et al., 2015) or self-incompatibility systems that normally guard against it (Bishop, 1996; Bishop et al., 1996) that would need to be overcome, and the precise costs and benefits of outcrossing versus selfing will depend strongly on the previous history of selfing within a population (Jarne and Auld, 2006; Escobar et al., 2009; Escobar et al., 2011).
Outlook

Even from this brief account, it should be clear that questions about the sexual system, sex allocation, and sexual selection are inextricably linked, and that we therefore need to learn more about how these processes operate in hermaphrodites compared to the much better investigated gonochorists. In a similar vein, it should be evident that there are important parallels between sex changers, simultaneous hermaphrodites, and gonochorists, and it is worth pointing out that these broad categories gloss over a much richer diversity of sexual systems, including for example mixtures of males and hermaphrodites (such as androdioecious clam shrimp; Weeks et al., 2006), dwarf males with both gonochorists and hermaphrodites (as in barnacles; Yusa et al., 2013), cyclical parthenogenesis in which one clone can make both male and female offspring (as in cladocerans; Innes and Singleton, 2000), and asexual propagation and fissioning in hermaphrodites (as in many...
Hypotheses for sex allocation manipulation in simultaneous hermaphrodites. For a sperm donor, manipulating the reproductive allocation of the sperm recipient could be adaptive for a number of reasons. Most straightforwardly, the donor could divert resources toward the recipient’s female function, and thereby gain from fertilizing a greater number of eggs ((a) and (b)). Depending on from where these resources are diverted, this may (b) or may not (a) result in a corresponding reduction in the recipient’s male allocation (i.e., it may or may not affect the individual’s sex allocation in the strict sense). Alternatively, it may pay the donor to directly target the recipient’s male sex function, either because doing so results in a reallocation of resources toward the female function due to a sex allocation trade-off (c), or because reducing the recipient’s male allocation is by itself beneficial (d). Possible adaptive scenarios for the latter include that it may constrain the ability of the recipient to re-mate (thus reducing the likelihood that the donors faces sperm competition to fertilize the recipient’s eggs); that it may limit the costs when a donor re-mates as a recipient with that same mating partner (e.g., if fewer costly substances are transferred, or costly mating duration is reduced); or that the sperm competitive ability of a potential rival donor in other recipients in the population would be reduced.

For further discussion, see also Schärer et al. (2014) and Schärer (2014).

**Figure 9** Hypotheses for sex allocation manipulation in simultaneous hermaphrodites. For a sperm donor, manipulating the reproductive allocation of the sperm recipient could be adaptive for a number of reasons. Most straightforwardly, the donor could divert resources toward the recipient’s female function, and thereby gain from fertilizing a greater number of eggs ((a) and (b)). Depending on from where these resources are diverted, this may (b) or may not (a) result in a corresponding reduction in the recipient’s male allocation (i.e., it may or may not affect the individual’s sex allocation in the strict sense). Alternatively, it may pay the donor to directly target the recipient’s male sex function, either because doing so results in a reallocation of resources toward the female function due to a sex allocation trade-off (c), or because reducing the recipient’s male allocation is by itself beneficial (d). Possible adaptive scenarios for the latter include that it may constrain the ability of the recipient to re-mate (thus reducing the likelihood that the donors faces sperm competition to fertilize the recipient’s eggs); that it may limit the costs when a donor re-mates as a recipient with that same mating partner (e.g., if fewer costly substances are transferred, or costly mating duration is reduced); or that the sperm competitive ability of a potential rival donor in other recipients in the population would be reduced.

For further discussion, see also Schärer et al. (2014) and Schärer (2014).

**Figure 8** Types of mating in simultaneous hermaphrodites. Mating conflicts can be resolved in a number of ways, which may or may not result in realized conflict. (a) Two polyclad flatworms of the species *Pseudobiceros bedfordi* engage in penis fencing, which involves the attempt to traumatically inseminate sperm into the mating partner using paired copulatory stylets (double arrowheads), while trying to avoid being stabbed oneself (see also Michiels and Newman, 1998 for data on *Pseudoceros bifurcus*; image ‘Two Individuals of *Pseudobiceros bedfordi* About to Have a Sperm Battle’ by Nico Michiels from doi:10.1371/journal.pbio.0020183.g001 licensed under CC BY). (b) Unilateral mating in the freshwater snail *Lymnaea stagnalis*, with the male role individual at the top inundating the female role individual below using its penis-carrying organ, the preputium (see also Koene et al., 2010; image courtesy of Joris Koene and Cathy Levesque). (c) Two black hamlets, *Hypoplectrus nigricans*, engaged in an egg trading exchange in which the male role individual (the egg releaser) is facing downwards and the female role individual (the sperm releaser) has clenched jaws and is curled around the former. Roles are then usually exchanged multiple times in an iterated way (see also Fischer, 1980; Henshaw et al., 2015; still image from a video by the BlyenWatcher.com website hosted at http://www.youtube.com/watch?v=5d2dXRNKcBg and courtesy of Ned and Anna DeLoach). (d) Two garden slugs *Cornu aspersum* (formerly *Helix aspersa*) involved in a reciprocal mating, during which they assume a head to head position and reciprocally insert their male copulatory organs (see also Koene, 2006; Garefalaki et al., 2010; image courtesy of Alexandra Staikou). (e) Two free-living flatworms of the species *Macrostomum lignano* engaged in a reciprocal mating, during which they curl around each other in the shape of two interlocking ‘G’s (see also Schärer et al., 2004; Vizoso et al., 2010; still image from a video by Lukas Schärer). (f) An *M. lignano* individual engaged in the postcopulatory ‘suck’ behavior, during which it places its pharynx over its own female genital opening and appears to be sucking, presumably to remove ejaculate components that it received during the preceding reciprocal mating (see also Schärer et al., 2004; Vizoso et al., 2010; still image from a video by Lukas Schärer).
References


