Diversity and flexibility of sex-change strategies in animals

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Here, we review recent empirical advances that have improved our understanding of why and when sex change occurs. We show that sex-changing animals use a greater diversity of strategies to increase their reproductive success than was previously recognized: some individuals change sex early, others change sex late, some individuals change sex more than once, and others do not change sex at all. These different strategies can be unified by the principle that individuals change sex when it increases their reproductive value. The breeding tactics (male, female or non-breeder) adopted by individuals often appear to be adaptive responses to their own social–ecological context and variation in these conditions results in significant differences in the timing of sex change within and between species.

Introduction

Sex allocation theory explains the way in which organisms allocate resources to male and female function [1]. The theory encompasses issues ranging from offspring sex-ratio adjustment by gonochores (which have fixed sexes) to allocation to male and female function by hermaphrodites (which can have both sexes during their lifetime). Hermaphrodites are typically classified as either simultaneous, where individuals function as male and female at the same time, or sequential, where individuals first function as one sex and then swap to the other sex at some later stage (sex change; Box 1). For simultaneous hermaphrodites, sex allocation theory is used to predict the optimal allocation an individual should make to male and female function. For sequential hermaphrodites, sex allocation theory focuses on explaining why individuals change sex and predicting when they should do so.

Sex change occurs in animals as diverse as annelids, echinoderms, crustaceans, molluscs and fishes [2]. One part of sex allocation theory, the size-advantage hypothesis (SAH) [3,4], is widely used to understand sex change [1,4]. The SAH predicts that sex change is favoured when an individual reproduces most efficiently as one sex when young or small, and most efficiently as the opposite sex when old or large [3,4]. In its simplest form,

the hypothesis is often presented as a plot of expected fertility against body size for males and females (Figure 1). Sex change is favoured where fertility increases more quickly with size (or age) for one sex compared to the other, assuming that growth and mortality rates are approximately the same for both sexes. Sex change is predicted to occur at the size or age where the fecundity gain curves of the sexes intersect [4] (Figure 1).

In an attempt to understand variation in the timing of sex change, Warner [5] suggested that the SAH be framed in terms of the reproductive value of each sex rather than in terms of fertility. Reproductive value (RV) is expected future reproductive success, taking into account effects of growth and mortality. By using RV, the SAH can take into account sex-specific differences in expected growth, mortality and chances of obtaining high levels of reproductive success later in life. The size-advantage prediction then becomes that sex change should occur at the size where the male and female RV curves intersect (even if current fertility declines). Framing predictions in terms of sex-specific RV helps explain why the timing of sex change does not always correspond with predictions based solely on sex-specific fertility [6]. It also predicts that individuals from the same population might change sex at different sizes because of the different ways that they can trade off sex-specific fertility, growth and mortality [7].

The first mathematical formulations of the SAH were population genetic models, where the direction and timing of sex change were viewed as evolutionary responses to demographic parameters of the entire population (i.e. size-specific fecundity, mortality and growth) [4]. These models predict a single optimal size at sex change within a population. However, the SAH can also be applied at the scale of the local mating group. This is applicable in situations where sex change is a phenotypically plastic response to local conditions [5], which is evidently the case in the many species where sex change is socially controlled [8,9]. In this situation the advantage of sex change for any individual is based on its RV as male or female relative to the size of the other individuals in the mating group. Expectations of sex-specific growth, mortality and fertility can vary from one local social group to another, and changes in circumstances can rapidly alter these expectations. Consequently, we expect to find adaptive variation in the timing of sex change within populations as a result

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Box 1. What is sex change?

Adult sex change occurs when an individual changes from one functional sex to the other. Although this definition is relatively simple, the sexual patterns of hermaphroditic animals are often complex and difficult to categorize [61,62]. For example, small fishes from the genus *Lythrypnus* can have mature gametes of both sexes in the gonad, but individuals appear to function exclusively as one sex or the other [63]. Anatomically, they resemble simultaneous hermaphrodites, but functionally they are sequential hermaphrodites. The distinction between anatomy and function is important because sex allocation theory considers the way that fertility curves of the sexes scale with size, age, or available resources [1]. Thus, it is reproductive output (function) of each sex that really counts when assessing the adaptive significance of hermaphroditism.

From an ontogenetic perspective, adult sex change is just one part of the sex determination process. Individuals of many species can also make choices about being male or female before maturation. Consider a classic protogynous (female first) hermaphrodite: individuals begin life as juvenile females, they mature into adult females, some of which change sex to become adult males. In some species, such as the bluehead wrasse *Thalassoma bifasciatum* [12] (Figure I) and the humbug damselfish *Dascyllus aruanus* [64,65], a proportion of the juveniles become males without first breeding as a female (these are usually called primary males). Even more complex patterns exist: juvenile *Gobiodon* can mature directly into either adult males or adult females [66], both of which are capable of subsequent sex change [50].

Importantly, recent research has shown that the decision to become a primary male might be a plastic response to local social conditions [47], just as adult sex change is in many species. It now seems that there could be a continuum in the timing of sexual differentiation in some species that transcends ontogenetic boundaries. In this perspective, individuals choose to become male or female at various crucial stages throughout their lives, with adult sex change simply being the last stage in the process.
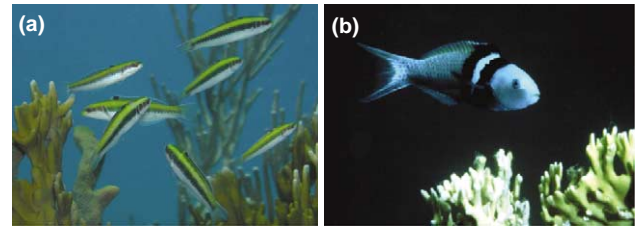
Figure I. Complex life histories of sex-changing animals. This is illustrated by the bluehead wrasse *Thalassoma bifasciatum* where individuals can mature as either a female or a primary male. Females and primary males look almost identical **(a)**. Adult females change sex when they have the opportunity to take over the territory of a large male. Females that change sex and become a territorial male take on a distinct, bright colouration **(b)**. Primary males can also become brightly coloured if they reach a size large enough to defend a territory, even though they have not changed sex. Photographs reproduced with permission from Will White and Ken Clifton.

of variation in the size structure and dynamics of different mating groups.

Here, we review recent empirical developments that have improved our understanding of why and when sex change occurs. We show that sex-changing species exhibit a greater diversity of sexual strategies than previously recognized, and that individuals appear to tailor the timing and direction of sex change to maximise their RV. We also show that variation in the timing of sex change among species, populations and individuals can often be traced back to differences in the structure of the local mating group. Our conclusions contrast with recent analyses that have proposed that sex change occurs at the same relative size across species [10,11] and demonstrate that understanding the scale at which individuals gather information on RV is crucial to our understanding of the selective advantage of sex change.

The mating system and variation in the timing of sex change

The mating system provides the opportunity for the RV of males and females to increase with size at different rates. In polygynous mating systems, where large males monopolize matings with many females, male RV is strongly dependent on size. This favours female–male sex change (protogyny). When the mating system is known, most species exhibiting protogyny have a polygynous mating system [12,13]. By contrast, in monogamous systems or where mating is random, female RV tends to be more strongly dependent on size than does male RV. This favours male–female sex change (protandry). Although the mating systems of most protandrous sex changers are not well described, species for which the mating system is known are either monogamous [14] or appear to mate approximately

randomly with regard to size [6,15–17]. The message from the empirical data is that interspecific differences in the direction of sex change (protogyny versus protandry) are often associated with differences in the mating system.

Empirical evidence also suggests that the mating system, or mating group structure, influences the relative timing of sex change between species. In a recent study, Collin [18] found significant variation in the relative size at sex change (average size at sex change divided by maximum size) of 19 species of protandrous gastropods. This result contrasts with earlier reports that the relative size at sex change is the same (i.e. invariant) in all sex-changing species [10,11]. At least part of the reason for these conflicting results appears to lie in the method that has been used to test invariance (Box 2), which obscures
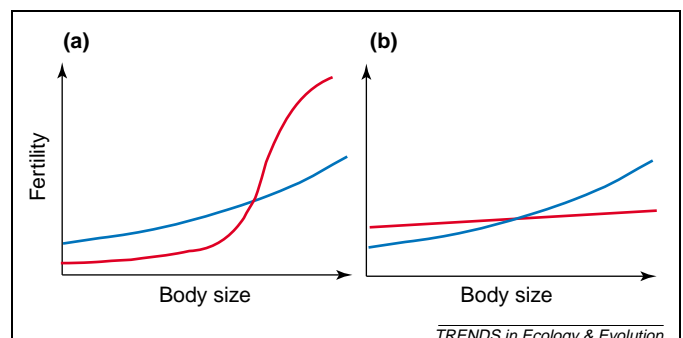
Figure 1. The size advantage hypothesis. Expected female offspring production (blue line) increases with body size if large females can lay more eggs. Expected male offspring production (red line) increases strongly with body size if, for instance, large males breed with many more females than do small males. Sex change is favoured when the size- (or age-) specific fertility curves of the sexes cross. Female–male sex change [**(a)** protogyny] is favoured when the fertility of an average male increases more rapidly than the fertility of an average female. Male–female sex change [**(b)** protandry] is favoured when fertility of an average female increases more rapidly than fertility of an average male. Fitness functions can be applied at the scale of the breeding group or at the scale of the breeding population (as appropriate).

Box 2. An invariant size at sex change?

The life-history invariant approach to the study of life-history evolution [67] has generated much interest. The approach tests hypotheses that dimensionless ratios of life-history traits are invariant across populations or taxa. The existence of invariance is interesting because it suggests that there is a general explanation for the evolution of the invariant trait. Recently, two studies [10,68] have suggested that the relative size at sex change is invariant across taxa. An ensuing debate has questioned the validity of these claims and, indeed, the whole approach used to detect life-history invariance [19–21,69].

The claim that relative size at sex change is invariant is based on the observation that a log-log plot of average size at sex change against maximum size produces a slope of 1 and a high R^2 [10]. However, null models, in which size at sex change is randomly distributed between size at maturity and maximum size, produce the same apparent invariance in relative size at sex change [19,20,69] (Figure I). This seems to be a general problem for claims of invariance in which one life-history trait constrains the other [21]. So, how do we identify invariance? One suggestion is to compare variation in potentially invariant traits to variation in other traits [20]; however, what sort of traits could be compared, and what range of variance would qualify for invariance, has yet to be defined.

Another question is when will an invariant pattern be informative? Allsop and West [10,68] suggested that, across species, average size at sex change divided by maximum size of the species is invariant. This implicitly assumes that there is a single optimal size at sex change in each species. Although this assumption is probably valid for some populations [70], it is probably not true for populations with distinct mating groups. Populations are often subdivided into breeding groups and optimal size at sex change varies among these groups, depending on the size structure and social conditions experienced in each group. In such cases, the sex-change rule (or invariant) will probably be found by comparing groups rather than whole populations or species.
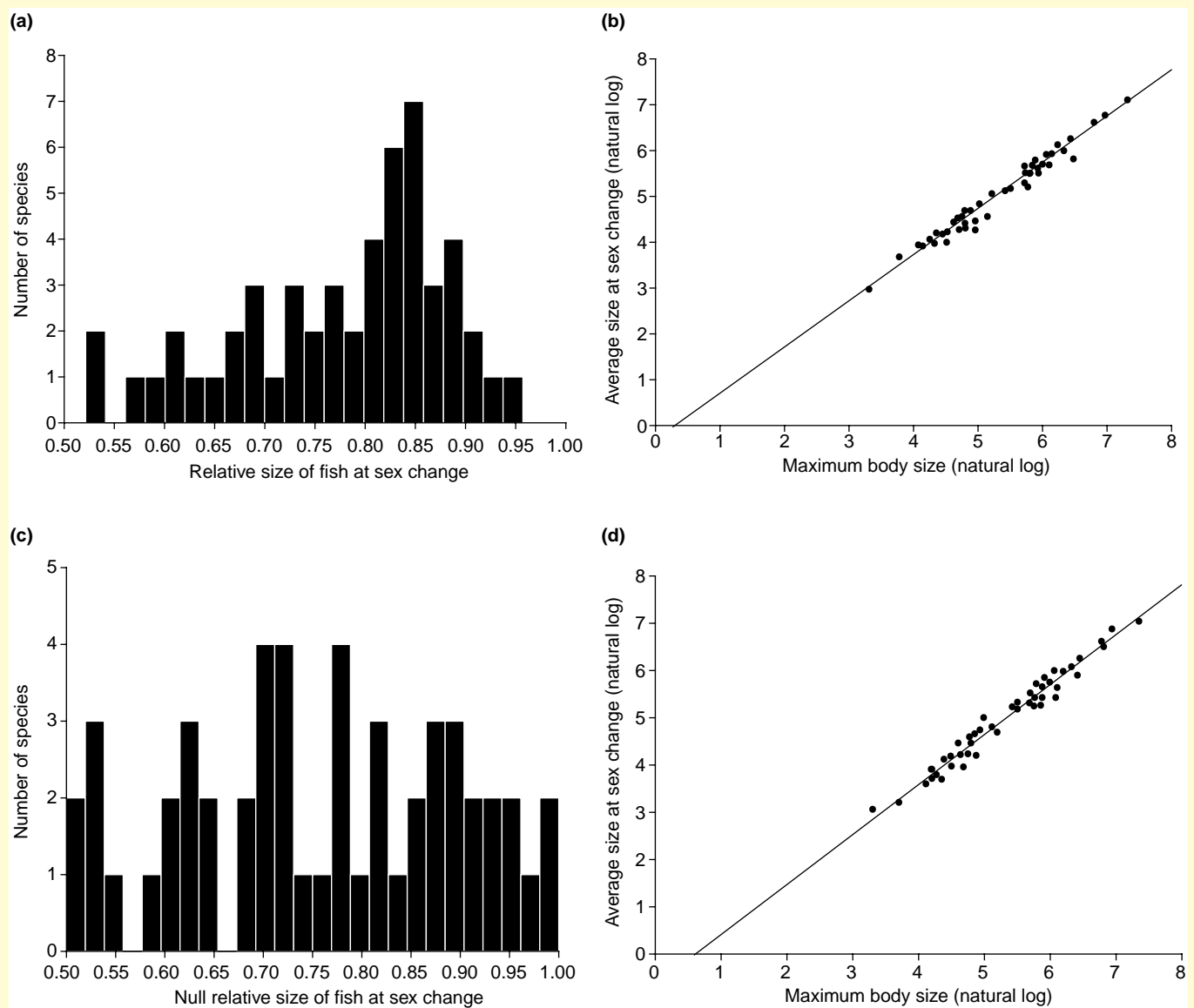

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Figure I. Variation in the relative size at sex change among species. **(a)** Relative size at sex change for 52 species of fishes. Relative size at sex change is the average size at sex change recorded for a species divided by maximum body size of the species. **(b)** These data appear invariant (slope of 1 and high R^2) when the average size at sex change is plotted against maximum size on a log-log scale. However, null data, where the relative size at sex change is randomly distributed **(c)** also produce an apparently invariant relationship when plotted on a log-log scale **(d)**. Data taken from [68] (a).

much of the interesting variation in the timing of sex change [19–21]. Importantly, a large amount of the variation in size at sex change among species observed by Collin [18] was associated with variation in mating group structure. This indicates that variation in social structure can indeed drive differences in the timing of sex change between species.

One of the most dramatic effects of the mating system on the timing of sex change is seen in species with alternative male tactics, such as the bluehead wrasse *Thalassoma bifasciatum*. Where local conditions favour resource defence polygyny, most males are derived by adult sex change [12,22]. By contrast, when high densities make resource defence polygyny uneconomic, individuals usually choose to become male before maturation (so-called primary males; Box 1) [12,22] and never change sex as adults. Differences in the relative frequency of sex change can occur on neighbouring reefs, indicating that individuals are choosing a life-history tactic that involves adult sex change, or not, depending on the mating conditions that they experience in that habitat patch.

Between-population variation in the timing of sex change

The SAH predicts that sex change will occur earlier in populations with slower growth rates and/or higher mortality rates [5]. This pattern has been documented in a range of protogynous [23–25] and protandrous species [26,27], and recent analyses are uncovering the mechanisms responsible for this variation. The mean age at sex change and demographic rates co-vary in genetically connected populations of fishes [25,28] and shrimp [26], indicating that the timing of sex change in these populations is a flexible response by individuals to local conditions. This conclusion is supported by the relatively rapid changes (within a few years and less than one generation) in the age or size at sex change in some fish populations following a change in the mortality rate [29]. It is unknown if individuals in any of these populations are responding directly to demographic rates (growth or mortality), or to the size distribution of other individuals in the population (a pattern generated by growth and mortality rates). However, the results demonstrate that individual plasticity in the timing of sex change can generate significant structure in the mean size or age of sex change at large spatial scales.

Although individual plasticity explains variation in the size of sex change among populations of some species, evidence suggests that other species have a relatively fixed size at sex change. In at least one protandrous shrimp [30] and one protandrous limpet [31], there was no variation in size at sex change despite considerable short-term variation in age structure and mortality rates within and between populations. The apparent absence of sex-ratio compensation following selective removal of males by fishing in some large protogynous fishes [32] suggests that they also have a relatively fixed size at sex change. Why the timing of sex change should respond strongly to local environmental conditions in some species, but not others, deserves further attention.

Within-population variation in the timing of sex change

Not all individuals in a population of sex-changing animals follow the same life history. In some species, a proportion of the population matures directly into the second sex (Box 1). Other individuals never change sex because favourable conditions do not arise. More intriguing are individuals that change sex when there is no immediate advantage in doing so, dominant individuals that do not change sex when the opportunity arises, and individuals that change sex more than once. RV provides the key to understanding this variation in the timing and direction of sex change.

No sex change

In haremic species, the largest female in a group usually changes sex following the disappearance of the dominant male [5,12,13,33] because she can increase her RV by spawning with all the remaining females. Some females even change harems to advance their position in the size hierarchy, and in doing so increase their RV because they end up monopolizing a harem sooner [34]. Similarly, in species that exhibit resource defence polygyny, a large female will usually change sex following the disappearance of a territorial male [35] because it greatly increases her RV. Territorial males can spawn with > 50 females per day [22], so the advantage to changing sex when a dominant position becomes available can be significant.

It is not always the largest female that changes sex following the disappearance of a dominant male. This appears non-adaptive, because the largest female could spawn with all the remaining females if she did change sex. However, a recent modification of the SAH [36] shows that the largest female in a group would not increase her RV by changing sex if the combined fecundity of the other females in the group is less than her current fecundity, and/or if sperm competition was intense. Under these circumstances, the larger individual would do better to remain female and one of the smaller females might gain the most by changing sex. These predictions were borne out in a manipulative experiment with the bucktooth parrotfish *Sparisoma radians*, where the largest female usually declined to change sex following the removal of the dominant male, and it was one of the smaller females that became male [37]. It remains to be seen whether a similar response occurs in other species where size–fecundity skew and sperm competition might favour large individuals that do not change sex. Nevertheless, this example suggests that individuals of some species make precise assessments of RV and refrain from changing sex when it is not beneficial.

Early and late sex change

Females sometimes change sex at a size where they appear to have little chance of breeding as a male (early sex change) and thus experience no immediate gain in reproductive success [38,39]. Early sex change might be a viable alternative strategy if non-reproductives have decreased mortality rates or increased growth rates [7], so that a small decrease in current reproductive success results in a much larger gain in RV. Early sex change in the spotlight parrotfish *Sparisoma viride* appears to be

favoured because non-reproductive males grow faster than do territorial males [40] and do not appear to suffer markedly higher mortality rates [41]. Simple multiplications of size-based fecundity and number of spawns per year indicate that the lifetime fecundity of early sex changers is similar to that of individuals that change sex later in life [41]; thus, early sex change can be a viable alternative breeding tactic in this species.

An alternative reason for early sex change is that these individuals have the best chance of taking over a harem, or breeding territory, following the loss of a territorial male [42]. Here, there is not necessarily a growth or survival advantage to early sex change; individuals are simply positioning themselves to take over from a territorial male [43]. The probability of encountering a vacant territory increases in circumstances where many such territories can be sampled, and it is in these circumstances that large females of some species of angelfish and parrotfish abandon reproduction, change sex and become roving bachelor males. Where opportunities are more restricted, large females remain in a harem and do not change sex before the dominant male position becomes vacant [44].

In some cases, individuals delay sex change to increase their RV. The protandric hermaphroditic shrimp *Lysmata wurdemanni* lives for <18 months and individuals reproduce in only one or two breeding seasons [45]. Males that recruit to the population early in the season change sex to female after a few months. By contrast, males that recruit later in the season do not sex change until the start of the next breeding season. Late recruiters apparently delay sex change because they have a growth or survival advantage as males during the winter non-reproductive period [45].

Repetitive sex change

It has been known for a long time that repetitive sex change can occur in some invertebrates [1,2], but sex change in vertebrates was thought to occur just once, either because there were physiological constraints on sex reversal, or because there was no advantage in reverting to the original sex. This assumption has been overturned by an increasing list of fish species in which multiple sex reversals can occur ([13,46–48] and references therein) and by the recognition of ecological conditions that favour repetitive sex change [49,50].

The polychaete worm *Ophryotrocha puerilis* forms breeding pairs. In each pair, the largest individual functions as a female, enabling individuals to take advantage of the female size–fecundity relationship. Males grow more quickly than do females and reciprocal sex change occurs when the male becomes larger than the female. This enables the pair to continue to maximize their reproductive success over multiple breeding bouts [51]. In this system, the fact that the relative size of individuals in a pair changes over time creates a benefit for repetitive sex change.

Monogamous coral gobies also exhibit repetitive sex change, but the benefit of this strategy is not related to the relative size of individuals in the pair, and reciprocal sex change has not been observed. In coral gobies, when one of
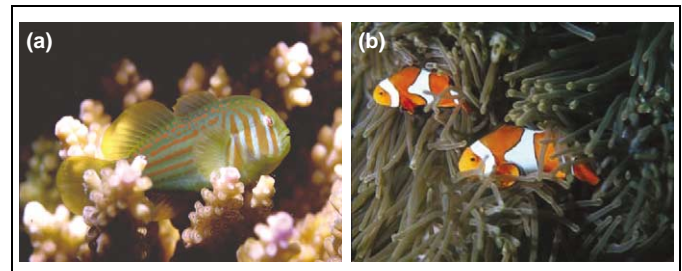

Figure 2. Examples of fish that change sex. Monogamous coral gobies and anemonefishes are ecologically similar but exhibit different sexual patterns. **(a)** Bidirectional sex change is beneficial in the coral goby *Gobiodon histrio* because movement between corals might be required to form a breeding pair following the loss of a partner. The ability to change sex in each direction enables an individual to breed with any other single adult encountered, and thus reduce the risk of searching for a new partner [49,50]. **(b)** Bidirectional sex change does not occur in the anemonefish *Amphiprion percula*, because the replacement mate is always from non-breeders within the anemone [14]. Movement to find a new partner is an option for coral gobies because the habitat patches that they occupy tend to occur in much higher density than those used by anemonefishes. (b) reproduced with permission from Shane Paterson.

the breeding pair dies (or the host coral dies) the survivor might move to find a new partner. Searching for a new mate is, however, risky [49,50]. When new partnerships form, one individual will change sex if the new partners are the same sex. The advantage of bidirectional sex change is that an individual maximizes its RV by searching as little as possible for a new mate [49,50] (Figure 2).

Repetitive sex change also occurs in polygynous species. In the small reef fish *Trimma okinawae*, protogynous sex change occurs when a female becomes the largest individual in a social group. Males can change back to female if they change social groups and find themselves subordinate to a larger male [52]. Unpredictable changes in group structure are likely to occur in species such as *T. okinawae*, because their small size (they are among the smallest vertebrates) makes them highly vulnerable to predation. Furthermore, the short life span of small gobies (sometimes just a few months [53]) means that any delay in finding a breeding partner might seriously diminish the RV of an individual. Thus, the expense (mortality risk and lost mating opportunities) incurred by a single male waiting for a dominant position to become available following loss of a harem is likely to exceed the cost of changing sex and breeding as a female in an existing group.

In some species, repetitive sex change has not been observed in the wild, despite the capacity for sex change in each direction being demonstrated in laboratory experiments [54]. Future research should concentrate on elucidating where and when repetitive sex change occurs in nature.

Proximal cues and variation in the timing of sex change

We have shown that individuals generally change sex when it increases their RV. What cues do they use to assess the RV of being male or female, and how does this influence variation in the timing of sex change?

Experiments have confirmed that the timing of sex change is sensitive to the immediate social environment in limpets [9,55], snails [56], shrimp [17] and many species of

fish [8,12,13,33]. The size of an individual relative to others in the social group [14,35,55], the sex ratio of the social group [9,50,57] and local density [58,59] have all been shown to influence the timing of sex change. Clearly, each of these factors can provide reliable information on the probable success of an individual as one sex or the other.

Selection could favour simple decision rules for sex change, based on a single cue such as relative size, sex ratio, or density, if one cue is a reliable predictor of sex-specific RV. For example, anemonefish have highly predictable social hierarchies, where changing sex to female is advantageous when a male becomes the largest individual in a social group. In this circumstance, a simple rule of thumb about when to change sex (e.g. when largest in a group) will usually lead to an increase in RV. Selection could, however, favour a more complex decision algorithm based on multiple cues, if several factors have a major influence on sex-specific RV. In the basslet *Pseudanthias squamipinnis*, the largest individual adopts male sex in small groups, but as group size grows (and sex ratio becomes female biased) additional individuals might benefit from becoming male [57]. In this situation, relative size and sex ratio act as cues to sex change. As the social situations that individuals encounter become more varied, selection might favour more complex algorithms governing the timing of sex change.

Variation in the cues that individuals use to make decisions about sex change will influence variation in the timing of sex change, within and among populations. The greatest variation should occur in populations where the size structure, sex ratio, or density of local social groups varies greatly. Even the simplest algorithms about when to change sex can generate significant variation in the timing of sex change if there is variation in the structure of local social groups.

Conclusions

Empirical studies are revealing surprising variation in the timing of sex change within and between species. In most cases, these strategies appear to be adaptive when viewed in the context of the local social and ecological environment of an individual. This suggests that individuals are often able to assess the reproductive value associated with functioning as one sex or the other, and to adopt the appropriate breeding tactic.

Elucidating the proximal mechanisms that control sex change is important because these mechanisms indicate the scale at which individuals are assessing RV. In many species, the timing of sex change varies at the scale of local social groups, and this is the scale at which we should examine the selective advantage of sex change. Some other species appear to have a relatively fixed size at sex change, and in these species the advantage of sex change could be examined at the population level. Other species are likely to exhibit interactions between genetic and environmental sex determination, and will be particularly beneficial to study because they could provide a deeper understanding of the multiple scales over which factors influencing RV can operate.

Understanding the benefits of sex change to individuals is key to understanding its adaptive significance. This will require detailed information about sex-specific fecundity, growth, mortality and movement patterns at the individual level. Only then can we really assess how RV is affected by the different breeding tactics (male, female or non-breeder) that individuals can use. We predict that a multiplayer game theoretic approach (e.g. [60]) will prove useful for modelling the advantage of sex change in species where this trait is under social control. Such models could compare the RV of different breeding tactics for a range of different social and ecological conditions. Models that can be applied at the scale of individuals and that can incorporate a diversity of factors that influence current and future reproductive success are the way of the future.

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