

The evolution of sex-change timing under environmental uncertainty: a test by simulation

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ABSTRACT

Background: Life-history theory predicts that selection for changing from an initial sex to a second sex exists when the size- or age-specific reproductive-rate curves for males and females cross. The optimal timing of sex change will be the size or age at which the curves cross. But wild populations of many sex-changing fishes do not follow this prediction; individuals generally change sex at a size or age at which the sex that they become cannot yet reproduce. This phenomenon is termed ‘early sex change’.

Question: Does uncertainty in the advent of successful reproduction in the second sex favour the evolution of early sex change?

Method: Genetically explicit simulation to track the evolution of sex change timing.

Key assumption: Reproduction in the initial sex (female) is assured but of low value, whereas reproduction in the second sex (male) is uncertain but of high value.

Organisms: Our model is primarily based on the natural history of the bluehead wrasse, *Thalassoma bifasciatum*, but is designed to apply to many other species of sex-changing fishes.

Results: Early sex change rapidly evolved under the conditions of the model. Moreover, the timing of sex change became highly variable within a population. The mean age of switching from female to male depended on the ratio of male to female reproductive rates: the higher the ratio, the earlier the mean age at which females switched. A second mechanism for early sex change arose from the asymmetrical fitness surface of females: those that switch earlier than the optimum time pay a smaller fitness penalty than those that switch later.

Keywords: asymmetric fitness surface, early sex change, genetic algorithm, probabilistic size-advantage

INTRODUCTION

The size-advantage model of sex change (Ghiselin, 1969) proposes that selection for sex change will exist if the size- or age-specific reproductive rates increase at a faster rate for one sex than for the other, holding the other vital rates equal between the sexes. In such a system, the functions describing male and female reproductive rates must cross, and a sex-changer

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adopting whichever sex has the higher payoff across the life history will have higher fitness than either a pure-male or pure-female strategy (Warner, 1975; Warner *et al.*, 1975; Leigh *et al.*, 1976). For example, imagine a system in which female reproductive output increases with size as a function of an individual's physiological capacity to produce eggs. If females mate at random, there is no reproductive advantage to being a large male, and protandrous (male-to-female) sex change is favoured (Fig. 1). Alternatively, if females prefer large males, or if large males exclude smaller males from access to mates, protogyny (female-to-male sex change) is favoured (Fig. 1).

In addition to explaining the adaptive significance of sex change and its direction, the size-advantage model further predicts the timing of this event: the optimal size- or age-at-sex-change is the point at which the reproductive functions cross (Warner, 1975). Thus, the expectation that the reproductive rate should immediately increase upon sex change is implicit to the size-advantage model (Ghiselin, 1969; Warner, 1975). However, in protogynous fishes, a group in which sex change has been especially well studied, there are many examples where this is not the case. In protogynous fishes, an individual changing from the initial to the second sex often enters a protracted non-reproductive period before successful reproduction in the second sex is resumed. Hoffman *et al.* (1985), who refer to this phenomenon as 'early sex change' in their own study of *Thalassoma* (Labridae), note work by Thresher (1979) documenting early change in two species of *Halichoeres* (Labridae), and by Moyer and Zaiser (1984) in two species of *Centropyge* (Pomacanthidae). Aldenhoven (1986) provides an example in a third species of *Centropyge*, and Warner and Downs (1977) describe early change in their study of *Scarus* (Scaridae).

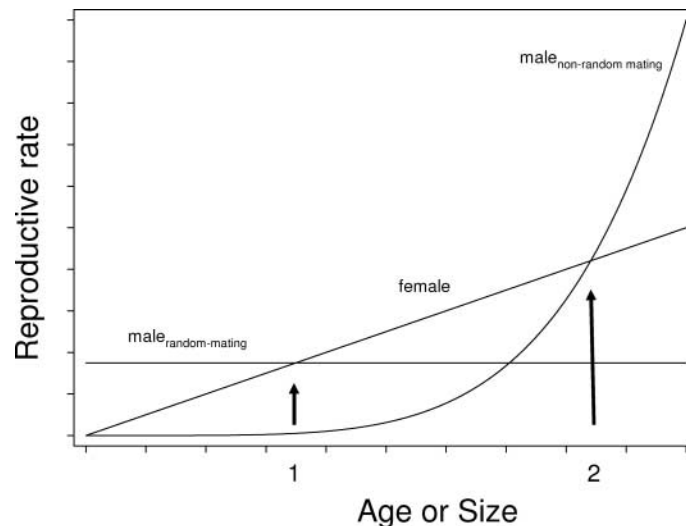


Fig. 1. The size-advantage model of sex change (adapted from Warner, 1975). Female reproductive rate increases with age and/or size, largely as a function of increased capacity to produce eggs. If females mate at random, large males have little or no advantage over small males, and the male reproductive rate is independent (i.e. flat) of age/size. Sex change should be protandrous and is predicted to occur at age/size 1 (the point at which the female function begins to exceed the male function). If large males have a mating advantage over smaller males, either due to mate choice or male-male competition, protogynous sex change is favoured and is predicted to occur at age/size 2.

There are several potential explanations for early sex change. First, the delay between reproduction in the initial and second sexes may simply reflect the time required for an individual to reorganize its gonad. This developmental-constraint hypothesis predicts that reproduction in the second sex would resume very soon after the individual gains the physiological capacity to produce the new gametes. Strong evidence that this is not the case exists for two species: *Scarus iserti* (formerly *S. croicensis*) and *Thalassoma bifasciatum*. Warner and Downs (1977) describe a system in which, upon sex change, female *S. iserti* give up daily reproduction within a large, terminal-phase male's territory to become secondary males in 'foraging' groups. While such males are reproductively active, in that they are producing mature sperm and have testes as large as those of territorial terminal-phase males (Warner and Downs, 1977), they are too small to hold a mating territory and generally do not acquire one for several months after sex change (K.E. Clifton, personal communication). Likewise, in their study of *T. bifasciatum*, Hoffman *et al.* (1985) showed that sex-changed, terminal-phase males that do not yet hold mating territories have a very low reproductive rate – less than half that of an average female – and that the interval between sex change and even sporadic territorial reproduction averages 81 days. This is much longer than required by development, as Warner and Swearer (1991) found that *T. bifasciatum* are capable of producing tailed sperm in as little as 8 days after initiating sex change.

Weaker evidence against this explanation is seen in the remaining species. In his study of *Halichoeres maculipinna* and *H. garnoti*, Thresher (1979) describes a class of what he termed 'celibate' males: small, sex-changed, terminal-phase males that are subordinate to larger, territory-holding, terminal-phase males. These subordinates contest for open territories upon the death of the previous owner. As the winner of this contest now has access to mates, it is territory acquisition, not physiology, which appears to determine the reproductive success of sex-changed males. Studies by Moyer and Zaiser (1984) on *Centropyge interruptus* and *C. tibicen* and by Aldenhoven (1986) on *C. bicolor* reveal a similar system. In these species, large females will often cease mating, undergo sex change, and either leave on their own accord or be driven away from the harem by the dominant male when they attempt to mate with the remaining females. These 'bachelor' males are physiologically capable of reproduction, but are denied the opportunity to do so by larger males.

A second explanation for early sex change is that it is a consequence of trade-offs between components of the life history. Specifically, if by sacrificing current reproduction an individual increases its expected future reproduction to such an extent that its overall fitness is increased, early sex change may be favoured by selection (Thresher, 1979; Moyer and Zaiser, 1984; Hoffman *et al.*, 1985; Iwasa, 1991; Rogers and Sargent, 2001). The critical test here is whether individual growth and/or survival increases with a suspension of reproduction at sex change. Of the species reviewed here, published estimates of size-, sex-, and colour phase-specific growth and mortality rates exist only for *Thalassoma bifasciatum*. Hoffman *et al.* (1985) cite Warner's (1984, Table 9) finding that the growth rate of non-territorial, terminal-phase male *T. bifasciatum* is 1.5 times that of like-sized initial-phase females. Although this would appear to support the trade-off explanation, an increase in growth that is offset by an accompanying decrease in survival could negate the advantage to an early changer. Although Hoffman *et al.* (1985) state that Warner (1984) detected no differences in survivorship between reproductive initial-phase females and non-reproductive terminal-phase males, Warner's Table 9 records a mortality rate for non-reproductive terminal-phase males 1.93 times higher than that of similarly sized females. Using these data, Rogers (2003) showed

that the fitness advantage of high growth in early changers is more than eliminated by the disadvantage of high mortality. Thus, while life-history trade-offs might explain early sex change in some systems, they do not seem to do so in the most well-studied case.

The final explanation for early change reviewed here, and the focus of the current work, is that there is an inherent advantage to being in the right sex at the right time. That is, early-changers may have an increased probability of acquiring a mating territory or harem when one becomes available (Moyer and Zaiser, 1984; Hoffman *et al.*, 1985; Aldenhoven, 1986). For example, Moyer and his colleagues (Moyer and Zaiser, 1984; Moyer and Nakazono, unpublished) report that upon the removal of the dominant male in *Centropyge interruptus*, the harem is inevitably taken over by an unknown male from without, not replaced via sex change by the largest female from within. Parallels are seen in *Thalassoma bifasciatum* and *Scarus iserti*: when a territory-holding male dies, it is replaced from the existing pool of non-reproductive, 'early' changers, and not by immediate sex change by a large female.

Incorporating reproductive uncertainty into the size-advantage model

Rogers' (2003) explanation for early sex change begins by noting that the factors giving rise to the increase in size-specific reproduction are fundamentally different between males and females, and that this difference predicts early sex change in certain systems. The size-specific reproductive rate, b_x , can be represented as

$$b_x = pot_x \times prob_x, \quad (1)$$

where pot_x represents the potential reproductive rate and $prob_x$ the probability of reproduction. For females, the probability of finding a mate may be assumed to be close to 1, and the size-specific reproductive rate increases primarily as a function of the individual's physiological capacity to produce eggs. For males, because sperm are tiny and cheap relative to eggs, even a small individual may produce orders of magnitude more sperm than the largest female produces eggs, and the size-specific reproductive rate is primarily a function of the individual's probability of mating. Female reproduction then increases deterministically, while male reproduction increases probabilistically.

If sex change occurs at the size at which the male and female reproductive functions cross, x^* , then

$$b_{male, x^*} = b_{female, x^*} \quad (2)$$

and

$$pot_{male, x^*} \times prob_{male, x^*} = pot_{female, x^*} \times prob_{female, x^*}. \quad (3)$$

Rearranging equation (3) gives

$$pot_{male, x^*} / pot_{female, x^*} = prob_{female, x^*} / prob_{male, x^*}. \quad (4)$$

If, for simplicity, we rewrite the left-hand term as

$$pot_{male, x^*} / pot_{female, x^*} = Z \quad (5)$$

and assume that the probability of a female finding a mate is 1, we find that

$$prob_{male, x^*} = 1/Z. \quad (6)$$

Under protogyny, because sex change progresses from female to male, the potential reproductive rate of a male must be greater than that of a female, $Z > 1$, and therefore $1/Z < 1$. As $1/Z$ represents the probability of successful male reproduction at sex change at size x^* , $1 - 1/Z$ individuals changing sex at this size will seem to have changed too early.

In protogynous fishes such as *Thalassoma bifasciatum* with an open (i.e. non-haremic) mating system, an individual shifts from a low-risk, low-payoff strategy (female) to a high-risk, high-payoff one (male) upon sex change. If in such a system a territory-holding, terminal-phase male spawns with 10 females per day, a gene causing sex change at the size/age at which she has a 1-in-10 chance of becoming a successful, territory-holding male will be favoured by selection, even though 9 of 10 individuals bearing that gene would seem to have changed sex 'too early'. Rogers (2003) referred to this as 'odds-playing', and noted that it should not be confused with bet-hedging (see Seger and Brockman, 1987). Indeed, the terms odds-playing and bet-hedging describe very different effects. Bet-hedging strategies accept a reduction in the arithmetic mean fitness in exchange for reduced variance in fitness over a sequence of good and bad generations. As such, bet-hedging maximizes geometric mean fitness across time. An odds-playing strategy accepts an increase in payoff variance among good and bad patches in exchange for an increase in arithmetic mean fitness within a generation.

Here, we test Rogers' (2003) explanation that odds-playing effects could be responsible for the evolution of early sex change. One problem is that tests using real-world systems will likely be confounded by the fact that such systems are likely already at, or near, equilibrium. In this case, there is a correlation/causation problem in which one cannot say if early sex change has evolved directly as an adaptation to environmental uncertainty in the timing of territory acquisition, or indirectly as a correlate of some other aspect of the life history. A simulation model, allowing for the *de novo* evolution of a character over successive generations, does not have the same constraint. Below, we describe a simulation model examining the evolution of sex-change timing under male reproductive uncertainty, and some conclusions that may be drawn from it.

METHODS

The natural history imposed on the simulation is adapted from the biology of *Thalassoma bifasciatum*, the bluehead wrasse. The reproductive biology and life history of this species is described elsewhere (e.g. Warner and Robertson, 1978; Warner, 1984; Hoffman *et al.*, 1985; Warner and Schultz, 1992; Rogers, 1998; Petersen *et al.*, 2001), so here we note only those aspects relevant to the model. *Thalassoma bifasciatum* exhibits two colour-morphs: a small initial phase, and a large terminal phase. Initial-phase fish may be either male or female but terminal-phase fish are always males. Terminal-phase males are the result of colour phase-change by large initial-phase males, and sex- and phase-change by large initial-phase females. Spawning occurs daily throughout the year at sites defended as mating territories by terminal-phase males, or occupied by large groups of initial-phase males. Terminal-phase males generally spawn with females as a pair, and a successful, territory-holding male may mate with many females per day. Warner *et al.* (1975) report a range of less than 5 to as many as 80 matings per day, with a mean (± 1 s.d.) of $35.7 (\pm 21.0)$ for terminal-phase fish of this species. However, as there are two to three times as many terminal-phase males as there are mating territories (Schultz and Warner, 1991), most terminal-phase fish of this species are non-reproductive (this is the definition of early sex change). Initial-phase females produce a clutch on most days (Schultz and Warner, 1991; Rogers, 1998).

Simplifying this biology for the simulation, we modelled only two sexes/phases, initial-phase females and terminal-phase males, across a life span from $t = 0$, the age at first reproduction, to $t = 1$, the age at death. There are two critical points in time: the genetically determined age at which the individual changes sex from female to male, A , and the environmentally determined age at which a male secures a mating territory and thus may begin reproduction in that sex, T . For symmetry, we set the mean of the normally distributed random variable T at the midpoint of the lifetime, and, as it produces a distribution that is easily visually interpreted, we arbitrarily assigned a variance of approximately 0.02. There is no growth or mortality in the model. The reproductive rate for a female is the variable t , $0 \leq t \leq 1$, and the reproductive rate for a successful male is r . For tractability, we set r to 2.5 in the default case; that is, a successful male reproduces at a rate 2.5 times that of the oldest (largest) females. If $A < T$, then the fitness, w_A , of a fish changing at A is

$$w_A = \int_0^A t \, dt + \int_T^1 r \, dt = \frac{A^2}{2} + r(1 - T), \quad (7)$$

and the cost of early change is the non-reproductive interval between ages A and T . Alternatively, if $T < A$,

$$w_A = \int_0^A t \, dt + \int_A^1 r \, dt = \frac{A^2}{2} + r(1 - A), \quad (8)$$

and the cost of late change is the loss of high-rate reproduction as a male between ages T and A . To simplify, equations (7) and (8) may be rewritten as

$$w_A = \frac{A^2}{2} + r(1 - \max\{A, T\}). \quad (9)$$

We used an explicit, stochastic genetic model, a genetic algorithm, to solve equation (9). A genetic algorithm is an iterative model with differential reproduction of favoured forms. As such, a genetic algorithm mimics the process of evolution by natural selection across generations. As in organic evolution, individuals in a genetic algorithm vary in phenotype, that phenotypic variance generates variance in fitness, and phenotype is heritable (for a review, see Holland, 1975). Selectionist systems, whether real-world or simulated, tend to result in populations of well-adapted, but seldom perfectly adapted, individuals (Darwin, 1859; Holland, 1975). The strength of such a stochastic evolutionary simulation is that the outcome arises within the confines of the model, but is not preordained by it as is the case in deterministic models. As modelled here, there are no environmental or error contributions to the phenotype, and thus phenotype and genotype are interchangeable. Individuals are haploid, and the genotype is a single allele specifying the age-at-sex-change. The number of offspring produced by each genotype is a function of an individual's relative fitness (as determined by equation 9). The individual with the highest fitness within a generation has a 100% chance of producing each of four offspring. Genotypes with lower fitness have a proportionally reduced likelihood of reproduction. For example, an individual with a relative fitness of $w = 0.8$ has an 80% chance of producing each of four offspring. As this scenario results in an overproduction of offspring, the original population size of 1000 genotypes is restored

by drawing the adults for the next generation at random from the large pool of offspring. New genetic variation enters the model by adding a relatively small random term ($\mu = 0$) to the genotype at reproduction. Offspring thus closely resemble their parents (inheritance), but this resemblance is imperfect ($V_G > 0$).

A data set consists of 100 replicate runs of the model. Although the simulation appeared to reach equilibrium in less than 50 generations, the model was permitted to run for a total of 100 generations to ensure that directional selection was no longer acting on the population. Each replicate was randomly seeded with a new set of sex-change timing alleles with a uniform distribution between 0 and 1 at generation-0. The model was written in Microsoft Excel. Because many individuals within a replicate are close relatives, only one, randomly chosen allele from each replicate was used in the statistical analyses to avoid pseudoreplication.

RESULTS

Early sex change readily evolves under the conditions set out in Rogers (2003). That is, when the potential male reproductive rate is high relative to the female reproductive rate, and the onset of successful reproduction as a male is predictable but not knowable, selection favours a timing of sex change at a point in the lifetime at which an individual is not assured to be in a position to reproduce successfully (Fig. 2). For example, in the default version of the simulation in which the potential reproductive rate for a male is 2.5 times the maximum of a female, the average age-at-sex-change after 100 generations is approximately (0.32). At this

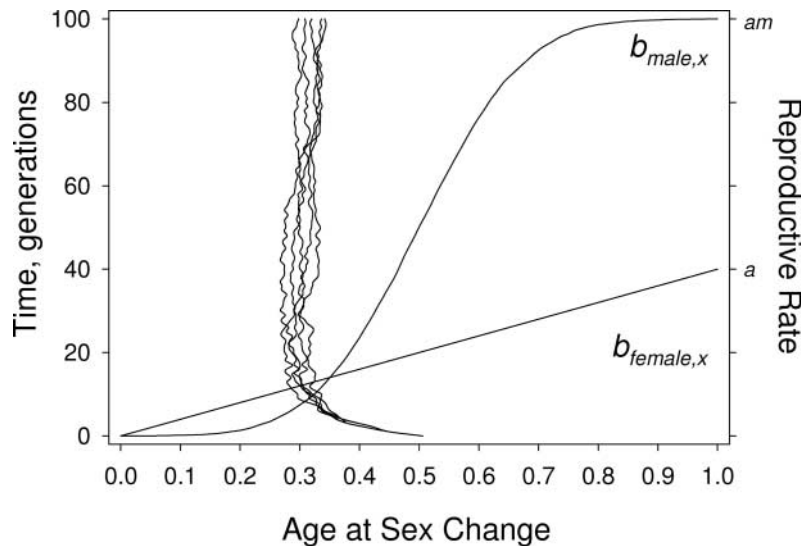


Fig. 2. Evolution of the age-at-sex-change under reproductive uncertainty. Expected male reproduction, $b_{male,x}$, increases to am as a sigmoid function over age as the cumulative probability of acquiring a mating territory increases over time. Realized female reproduction, $b_{female,x}$, increases over age as a linear function of physiological capacity. The squiggly vertical lines trace the mean age-at-sex-change over 100 generations for five example replicates. Note that the timing of sex change evolves quickly from 0.5, the mean of the uniformly distributed alleles at generation-0, to an age that precedes the point at which the male and female reproductive functions cross (approximately age (0.35)).

age, an individual has less than a 9% chance of having acquired a territory; viewed the other way, more than 90% of individuals changing at this age will experience a non-reproductive interval (i.e. early change).

Although the general evolution of early sex change was predicted (Ghiselin, 1969; Warner, 1975; Warner *et al.*, 1975; Leigh *et al.*, 1976), the specific timing of the change differs from expectations. Following Warner (1975), Rogers (2003) predicted that sex change would evolve to the age at which the expected-male and realized-female reproductive functions cross. Under the model's default parameters, this occurs at approximately age (0.35). In contrast, the equilibrium age-at-sex-change is significantly earlier in the lifetime than this age ($H_0 = 0.35$, mean = 0.3194, s.d. = 0.0852, $Z = -3.061$, $P = 0.0022$, $n = 100$). This suggests that there is a fitness peak to the left of age (0.35) (i.e. at an earlier age). We used a quadratic regression of fitness on age-at-sex-change from a randomly selected run of the model at generation-0 to test this (Phillips and Arnold, 1989; Brodie *et al.*, 1995) (Fig. 3a: generations > 0 have been subject to selection, and thus have a reduced x-axis range). While the regression analysis does show a fitness peak at approximately age (0.25), this result is an artifact of the quadratic function. First-order linear regressions fit only through the 'early' changers, that is, age (0.0) through age (0.35) (Fig. 3b) show no relationship between age-at-sex-change and fitness. In contrast, a first-order regression fit through the late-changers shows strong, directional selection against late change. Thus, the apparent peak at age (0.25) in the full data set is generated by the very low fitness of very late changers.

Increasing the ratio of potential-male to realized-female reproductive rates results in the evolution of ever earlier sex change (Fig. 4). Under a null version of the model in which the male reproductive rate is equal to the maximum of a female, the age-at-sex-change is predicted to evolve to age (0.5), and this is confirmed by the simulation (1:1 $H_0 = 0.5$, mean = 0.4964, s.d. = 0.0573, $Z = -0.361$, $P = \text{N.S.}$, $n = 100$). However, when this ratio is increased to 5:1 and to 7.5:1, the equilibrium ages-at-sex-change evolve to 0.235 (s.d. = 0.0998) and 0.205 (s.d. = 0.1072), respectively. As in the default (2.5:1) case above, these ages-at-sex-change are even earlier than predicted (5:1: $H_0 = 0.28$, $Z = -4.488$, $P < 0.0001$, $n = 100$; 7.5:1: $H_0 = 0.24$, $Z = -3.495$, $P = 0.0005$, $n = 100$).

DISCUSSION

In many sex-changing species, particularly those with open (i.e. non-haremic) mating systems, individuals enter a protracted non-reproductive period upon sex change before resuming reproduction in the second sex. This phenomenon, known as early sex change, is not predicted by the simplest theoretical treatments of the size-advantage model (e.g. Ghiselin, 1969; Warner, 1975; Warner *et al.*, 1975; Leigh *et al.*, 1976). However, two modifications to the original model provide explanations of the adaptive significance of early change. Hoffman *et al.* (1985) and Iwasa (1991) note that trade-offs between current and future reproduction can in theory generate a life history including a non-reproductive period (but see Rogers and Sargent, 2001). For example, if resources that might be allocated to current reproduction are instead directed towards survival, the resulting benefit to future reproduction could balance the current costs.

Alternatively, early sex change could be favoured if there is a fitness advantage to being in the right sex at the right time (e.g. Aldenhoven, 1986; Rogers, 2003). In protogynous angelfishes of the genus *Centropyge*, large females change sex to become small, non-reproductive males (Moyer and Zaiser, 1984; Aldenhoven, 1986), which bide their time in groups of such bachelors, and begin

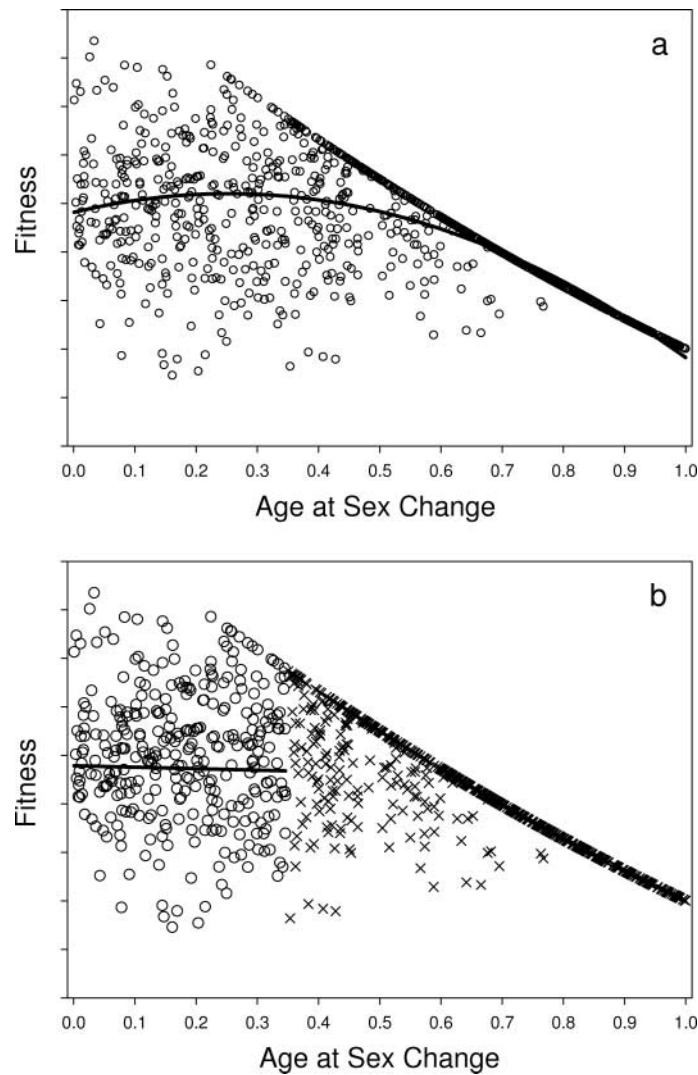


Fig. 3. Scatterplots of fitness as a function of age-at-sex-change. Data are for a single replicate at generation-0, as post-selection generations do not show the full range of genotypic variance. Early changers (age < 0.35) show great variance in fitness, while late change is a uniformly bad strategy. (a) A quadratic regression shows an apparent fitness peak at age (0.25), a much earlier age than predicted. (b) However, a regression through only the early changers shows no relationship between age-at-sex-change and fitness (i.e. the variance in fitness is a result of random chance, not genotype). Thus there is directional selection against changing too late, but not against changing too early.

reproduction in the second sex only upon the death of a harem-holding male. Females from within a harem certainly have the physiological capacity to change sex and take over the harem; however, this does not appear to happen because the male is replaced more quickly from the pool of non-reproductive bachelors. There is, therefore, an inherent advantage to simply being a bachelor male when a harem opens. Similar dynamics are seen in the

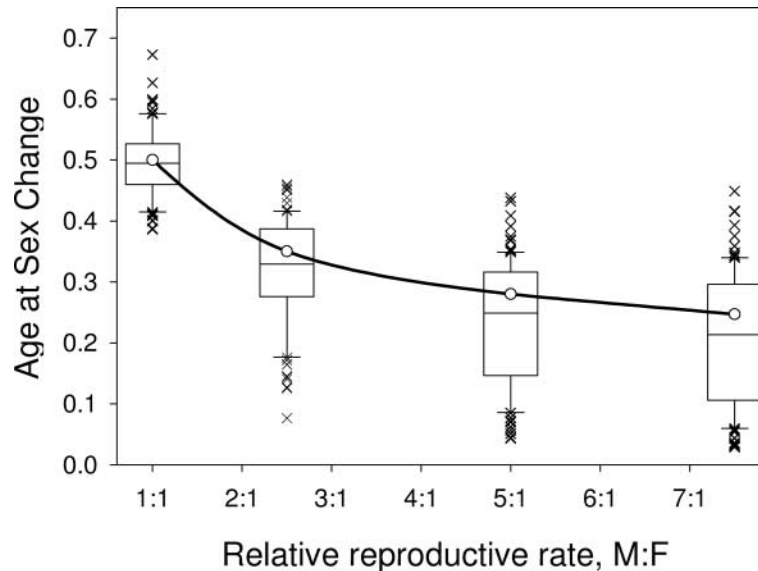


Fig. 4. The evolution of sex-change timing as a function of the relative male and female reproductive rates. The logarithmically decaying function describes the predicted age-at-sex-change, as potential male reproduction, am , increases relative to female reproduction ($b_{female, x}$). The boxplots represent the mean and variance (10th, 25th, 75th, and 90th percentiles) for the evolutionary equilibrium age-at-sex-change. In all cases where $m > 1$ (i.e. where the maximum male reproductive rate is greater than the maximum female rate), the equilibrium age is significantly earlier than that predicted under deterministic conditions (see text for analysis).

parrotfish *Scarus isterti* (Warner and Downs, 1977) and in the wrasses *Halichoeres maculipinna*, *H. garnoti* (Thresher, 1979), and *Thalassoma bifasciatum* (Hoffman *et al.*, 1985).

Each of these early sex-change systems is characterized by two key features: the reproductive rate of the second sex is much higher than that of the initial sex, and the timing of the onset of successful reproduction in the second sex is predictable, but not certain. Rogers (2003) proposed that early, or rather seemingly early, sex change is expected in such systems and, following Warner (1975), that the age-at-sex-change will be the point at which expected-male and realized-female reproductive rates cross. In such cases, sex change should always occur at an age at which successful reproduction in the second sex is unlikely. This is an example of selection maximizing fitness at one level, that of the gene, while increasing the variance in fitness among individuals bearing that gene. As the variance in fitness between lucky winners and unlucky losers increases, an increasing proportion of individuals carrying this gene suffer reduced fitness.

A test by simulation of this hypothesis confirms that sex change under uncertainty evolves as expected (Fig. 2). Starting from a uniformly distributed population of alleles at generation-0, the mean timing of sex change rapidly evolves to an age very close to the point at which the expected male and realized female reproductive rates cross. However, the simulation also shows that selection for a specific age or size, a prediction of both the deterministic (Warner, 1975) and probabilistic (Rogers, 2003) interpretations of the size-advantage model, is locally weak or non-existent. The flat fitness surface in the early-change region

(Fig. 3b) suggests that individuals should exhibit broad variation in the age/size at sex change, not simply among but within populations in natural systems.

The simulation also confirms a prediction that systems in which males have a much higher reproductive rate than females should change sex at an age/size at which they have a proportionately low chance of success (i.e. earlier in life), and will thus have longer non-reproductive periods (Fig. 4). There are two effects acting here. First, as the ratio of potential male to potential female reproduction (represented as Z in equations 5 and 6) increases, the degree of risk that a sex-changer is expected to sustain by changing early ($1 - 1/Z$) also increases (Aldenhoven, 1986; Rogers, 2003). This effect is seen in the predicted ages-at-sex-change in Fig. 4.

The second effect favouring early sex change results from the asymmetrical shape of the fitness surface (Fig. 5). Using Fig. 5, imagine an individual in generation-1 that changes sex at exactly the optimal time. The offspring of this individual will resemble their mother, but because of new genetic variation entering the system, some offspring will change sex a little earlier and others a little later than their mother. Because of the asymmetry, the slightly earlier changing offspring will on average have higher fitness than their slightly later changing siblings. That difference pushes the age-at-sex-change distribution towards younger ages in generation-2 [for examples of a similar effect, see Ruel and Ayers (1999) and Martin and Huey (2008)]. This effect is seen in the deviations between the observed and predicted ages-at-sex-change in Fig. 4.

The correlation between relative male and female reproductive rates and the length of the non-reproductive interval was noted by Hoffman *et al.* (1985) in their study of *Thalassoma bifasciatum*, *Bodianus rufus*, and *B. diplotaenia*. Large, sex-changed male *T. bifasciatum* and *B. diplotaenia* have very high mating success, spawning with 26 and 50 females per day,

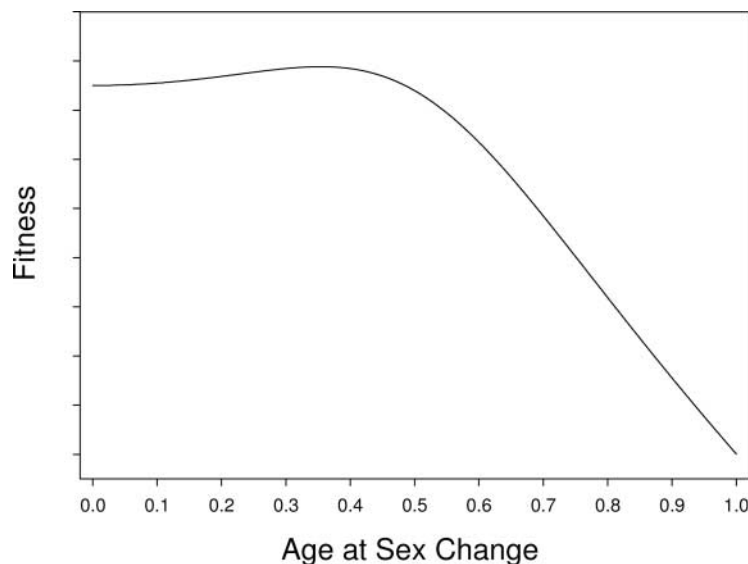


Fig. 5. Expected fitness as a function of age-at-sex-change. The optimal timing of sex change in a deterministic system is approximately age (0.35), the age at which the male and female reproductive rate functions cross. However, the distribution of fitness around this peak is asymmetric, which favours early-changing offspring over their late-changing siblings. See text for discussion of this effect.

respectively. Although a specific period is not given for non-reproductive *B. diplotaenia*, Hoffman *et al.* note that intermediate colour-phase individuals have very low reproductive rates – indeed, lower than that of females – and may remain in this phase for years. While not as protracted, the mean non-reproductive interval for sex-changing *T. bifaciatum* was found to be roughly 80 days; approximately 10% of the lifetime. In contrast, the non-reproductive period for *B. rufus*, a species in which successful males mate with no more than 12 females per day, was found to be about one week (all data from Hoffman *et al.*, 1985). Note that although a sustained non-reproductive period is permitted by a high second-sex reproductive rate, it is not expressly predicted by the trade-off models (Hoffman *et al.*, 1985; Iwasa, 1991). The trade-off models require only that the costs of early change be balanced by a larger benefit elsewhere in the life history. So, a high cost requires a high payoff, but a high payoff does not require a high cost. For that matter, the large cost of a protracted non-reproductive period could be balanced by either an increase in longevity or an increase in the reproductive rate. The models of Aldenhoven (1986) and Rogers (2003) expressly predicted this relationship.

CONCLUSIONS

In many species of protogynous fishes, the timing of two crucial events interact to determine fitness. The first, the timing of sex change, is a property of the individual and is taken to have some genetic basis. The second, the timing of territory acquisition, is a result of environmental happenstance. When the timing of this second event is predictable, but not precisely knowable, early sex change is expected to evolve (Rogers, 2003). A test of this prediction by simulation confirms that the timing of sex change evolves to a point in the lifetime at which an individual is not assured to be in a position to reproduce successfully when the potential reproductive rate is greater than the current reproductive rate. The simulation also suggests that the size/age-at-phase-change will not evolve to such a sharp point; rather, it will be diffuse and asymmetric around the point at which the male and female reproductive rate functions cross, reflecting the asymmetry between the huge potential benefits of changing early, versus the relatively trivial costs of early change. Finally, the model suggests that as this asymmetry increases, the degree of earliness will increase. Each of these findings closely mirrors that which is observed in natural systems.

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