

Costs of Changing Sex Do Not Explain Why Sequential Hermaphroditism Is Rare

Erem Kazancıoğlu* and Suzanne H. Alonzo

Department of Ecology and Evolutionary Biology, Yale University, New Haven, Connecticut 06520

Submitted April 8, 2008; Accepted October 3, 2008; Electronically published January 27, 2009

ABSTRACT: Sex change is a relatively rare phenomenon among animals. While classic theory has been successful in assessing the adaptive significance of sex change and predicting within-species patterns, it does not explain why more animals are not sex changers. A possible explanation for the rarity of sex change is that costs such as decreased reproduction due to gonadal reconstruction favor separate sexes, or dioecy. These costs, however, have not been studied empirically or theoretically. Here, we investigate whether costs of changing sex can favor dioecy. Our analyses suggest that dioecy is favored only when costs of changing sex are large. Moreover, the fitness effect of costs and the strength of male size advantage are not static but change with the population composition, resulting in a dynamic evolutionary game between sex change and dioecy. We conclude that costs of changing sex alone are unlikely to explain the observed rarity of sex changers. Instead, assessing mating systems comparatively and quantitatively and identifying correlates selecting for and against sex change are necessary to understand why some species change sex while others do not.

Keywords: dioecy, evolutionarily stable strategies, game theory, sequential hermaphroditism, sex allocation, sex change.

Introduction

The allocation of resources to male and female reproductive function (i.e., sex allocation) is an important theme in life-history theory (Charnov 1982*b*). A striking example of sex allocation strategies is sequential hermaphroditism, often referred to as sex change or sex reversal. This reproductive strategy has been documented and studied in diverse groups of animals ranging from mollusks and crustaceans to teleost fishes (Charnov 1982*b*; Policansky 1982; Wright 1988; Heller 1993). The definitive phylogenetic distribution of sequential hermaphroditism and how it originated along the tree of life is not yet elucidated. Nevertheless, while sex change is common in some taxonomic groups, it is rare or absent in most. Teleostei, for example, harbors the majority of sequentially hermaphroditic ani-

mals studied so far; however, only 19 out of about 450 teleost families include sex-changing fishes (Helfman et al. 1997; Sadovy de Mitcheson and Liu 2008). Similarly, many species in the teleost family Labridae are known to be able to change sex (e.g., Okada 1962; Dipper and Pullin 1979; Warner and Swearer 1991; Gillanders 1995), while it seems to be very rare in a closely related freshwater family, Cichlidae (e.g., Carruth 2000). Such disparities between groups of animals raise the question of why some species evolved to be able to change sex while other closely related species did not.

If this question were analogous to a coin, one side of it would focus on the presence of sequential hermaphroditism and ask why some species evolved to be able to change sex, and the other side would focus on the absence of sequential hermaphroditism and try to understand why other species did not evolve to become sex changers. Research using the first side has contributed most to our understanding of the adaptive significance of sex change. Early theoretical work on this subject was motivated by the “size-advantage hypothesis” (SAH; Ghiselin 1969), which argued that sequential hermaphroditism would be adaptive if sexes differ in the relationship between size or age and reproductive fitness. Numerical as well as analytical studies (Warner 1975; Warner et al. 1975; Leigh et al. 1976; Charnov 1982*b*) predicted conditions that would select for protogynous (“female-first”) and protandrous (“male-first”) hermaphrodites, investigated the appropriate timing for sex change, and laid a strong theoretical foundation to understand sequential hermaphroditism. Further empirical and theoretical research (reviewed in Munday et al. 2006*a*) led to suggestions to incorporate stochastic processes (Aldenhoven 1986; Rogers and Sargent 2001; Rogers 2003) and skewed female fecundity distribution (Muñoz and Warner 2003; but see Clifton and Rogers 2008; Warner and Muñoz 2008) to better explain the observed pattern and timing of sex change. In answering the main question of why some species evolved to change sex, however, the SAH has not been seriously

* Corresponding author; e-mail: erem.kazancioglu@yale.edu.

challenged in the almost 4 decades since Ghiselin proposed it.

While existing theory has been very successful in explaining the presence, pattern, and timing of sex change, we still have little understanding of why sequential hermaphroditism is absent in the majority of animals. Assuming no differential growth or mortality between sexes, the SAH predicts that sex change would be absent only if the relationship of size or age with reproductive fitness is identical for both sexes (i.e., if there is no size advantage; Leigh et al. 1976). In this scenario, a strategy of changing sex at an age that yields maximum fitness returns (i.e., optimal age of sex change) would have just equal fitness as a dioecious strategy. However, as the optimal age of sex change would change with mortality from one generation to another, the optimal sex-changing strategy for one generation would be suboptimal in the next (i.e., would have lower fitness than the dioecious strategy). Therefore, Leigh et al. argued, this “genetic penalty” would disfavor sequential hermaphroditism in the lack of a size advantage in fitness.

The prediction of the SAH that hermaphroditism would be favored in any case except when the size/age-fecundity relationship is identical for both sexes suggests that sex change should be more common. Dioecious organisms with differential male and female size-specific fitnesses, therefore, indicate that current theory does not convincingly explain why more animals are not sex changers (Warner and Lejeune 1985; Charnov 1986; Shapiro 1987; Warner 1988*a*, 1988*b*). Several potential explanations were proposed, all of which involved a different kind of cost decreasing the fitness of sex-changers relative to dioecious individuals. Charnov (1986) predicted that sex-specific costs associated with reproduction, such as mortality or growth cost, could result in trade-offs, offset the reproductive gains of sex changers, and select for a dioecious life history even in the presence of a size advantage. Charnov’s conclusions were later challenged by Iwasa (1991). Iwasa, however, investigated whether trade-offs could result in an early sex-changing strategy and did not explicitly analyze how trade-offs affect the stability of sequential hermaphroditism against dioecy. Based on their observations of mating systems of four wrasse species, Warner and Lejeune (1985) suggested that in addition to trade-offs, paternal investment to reproduction, such as nest construction and egg care, could weaken the size advantage and reduce the selection for sequential hermaphroditism.

Finally, sex change per se may involve costs that only hermaphrodites have to pay, such as physiological and hormonal complications of restructuring gonads and reproducing as both sexes (Bull and Charnov 1985; Hoffman et al. 1985). Though it has been suggested that costs of changing sex could explain the rarity of hermaphrodites

(Warner 1978, 1988*b*; Charnov 1986), these costs and how they might disfavor hermaphroditism have not been investigated, theoretically or empirically. In this article, we use an extended version of Charnov’s life-history model (1986) to investigate how reproductive costs of changing sex alter predictions of the classic theory on the evolutionary stability of sequential hermaphroditism against dioecy, and we examine how these results change across different scenarios.

The Model

We extend Charnov’s model (1986), as it provides a simple way to test for the evolutionary stability of sequential hermaphroditism in a variety of scenarios by using a single framework for both hermaphroditic and dioecious reproductive strategies. In this framework, hermaphroditic individuals start reproducing as females, do so until they change sex at a later age a , and reproduce as males from that age on (fig. 1*A*). Here, the reproductive allocation of hermaphrodites changes with a . The evolutionarily stable strategy (ESS) value for a represents the evolutionarily stable protogynous life history. In contrast, a dioecious life history is composed of pure females (analogous to never changing sex; $a = \infty$; fig. 1*B*, *left*), and pure males (analogous to immediately changing sex; $a = 0$; fig. 1*B*, *right*). In this case, the reproductive allocation of dioecious individuals changes with the offspring sex ratio. The ESS value for the sex ratio r represents the evolutionarily stable dioecious life history.

Here, we extend this model to build a theoretical framework, which we use to calculate the fitness of a sex-changing mutant in a dioecious population (and vice versa), while ensuring “self-consistency,” that is, equality of total male and female fitnesses (Fisher 1930; also see Houston and McNamara 2002). We first investigate a baseline scenario with a size advantage in fertility for males and no

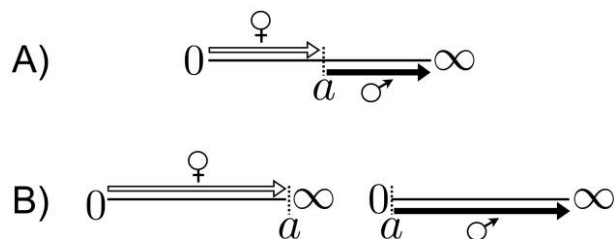


Figure 1: A basic model of sequential hermaphrodites (*A*) and dioecious individuals (*B*). *A*, A sequential hermaphrodite starts its reproduction as female, changes sex at age a , and reproduces as a male until the end of its reproductive lifetime. *B*, A female and male dioecious life history is obtained by shifting a to very late or very early, respectively, in reproductive lifetime.

cost of changing sex, where current theory predicts the evolutionary stability of hermaphrodites. Then we impose various types of fitness costs on sex changers to see how predictions of the baseline scenario are altered.

The Baseline Model: No Cost of Changing Sex

This model investigates the fate of a rare protogynous hermaphroditic mutant in a dioecious population and of a dioecious mutant in a hermaphroditic population. Key variables used in the model are given in table 1. We assume that the period before maturation affects hermaphroditic and dioecious fitness similarly and therefore focus our analyses exclusively on the postmaturation period (“reproductive lifetime”). Ages 0 and t denote the beginning and the end of an individual’s reproductive lifetime, respectively. Protogynous hermaphrodites reproduce as females until age a and then switch to reproducing as males until t . On the other hand, dioecious individuals reproduce either as females or as males during their entire reproductive lifetime and give birth to offspring with a female to male ratio of r . In this evolutionary game between sex changers and dioecious individuals, the age of sex change a and the primary sex ratio r are free to evolve, and stable strategies are found as a function of a and r .

We implement a simple male size advantage through sperm competition, where larger males produce more sperm and fertilize a greater proportion of eggs compared with smaller competitors. We link an individual’s size to its age and assume that growth is deterministic (i.e., older individuals are also larger) and that male fertility increases with age. We denote the age-specific male fertility by mx^b , where m is the male fertility constant, x is age, and b is the shape parameter. For simplicity, we assume that female fecundity remains constant throughout the reproductive lifetime; this is denoted by f . With constant female fecundity, male fitness increases with age at a faster rate than does female fitness, resulting in male size advantage. Here, the shape parameter for the age-specific male fertility, b , determines the strength of size advantage. Finally, we assume that the age-specific probability of survival is equal for both sexes, denoted by e^{-zx} , where x is age and z is the mortality constant.

With these assumptions, in a population with a proportion s of protogynous hermaphrodites that change sex at age a and a primary sex ratio of r for dioecious individuals, the average number of eggs, E , and sperm produced, S , are found:

Table 1: Key variables used in the model

Variable	Definition
m	Male fertility constant
f	Female fecundity constant
r	Primary sex ratio of offspring (female/male) of dioecious individuals
a	Age of sex change
t	Final age of reproduction
z	Mortality constant
b	Shape parameter for age-specific male fertility and the size advantage
s	Proportion of sex changers in a population
p	Length of the period of ceased reproduction following sex change
l	Decrease in reproduction
E	Average number of eggs produced in the population
S	Average number of sperm produced in the population
F_h	Average female fitness of a sex-changing individual
F_d	Average female fitness of a dioecious individual
M_h	Average male fitness of a sex-changing individual
M_d	Average male fitness of a dioecious individual

$$E = s \int_0^a e^{-zx} f dx + (1-s)r \int_0^t e^{-zx} f dx, \quad (1)$$

$$S = s e^{-za} \int_a^t e^{-z(x-a)} m x^b dx + (1-s)(1-r) \int_0^t e^{-zx} m x^b dx, \quad (2)$$

where the terms before and after addition are the contributions of sex changers and dioecious individuals, respectively, to egg and sperm pools.

The average female fitness of a protogynous mutant changing sex at age a' is given:

$$F_h(a', a, r) = e^{-[E/(S+1)]} \int_0^{a'} e^{-zx} f dx, \quad (3)$$

where $e^{-[E/(S+1)]}$ denotes the proportion of the egg pool that is fertilized. Again, the exponential function is chosen for mathematical convenience and ensures that the term approaches 0 (i.e., very few eggs are fertilized), if there are

too few sperm relative to eggs, and 1 (i.e., almost all eggs are fertilized), if the total number of sperm greatly exceeds egg production.

Similarly, the average male fitness of a protogynous mutant changing sex at age a' is

$$M_h(a', a, r) = e^{-za'} \int_d^t \frac{E}{S+1} e^{-z(x-a')} mx^b e^{-[E/(S+1)]} dx, \quad (4)$$

where $E/(S+1)$ is the number of eggs a male fertilizes per sperm he produces.

For a dioecious mutant with a primary sex ratio r' , fitness through male and female functions are found:

$$F_d(a, r', r) = r' e^{-[E/(S+1)]} \int_0^t e^{-zx} f dx, \quad (5)$$

$$M_d(a, r', r) = (1 - r') \int_0^t \frac{E}{S+1} e^{-zx} mx^b e^{-[E/(S+1)]} dx. \quad (6)$$

To find the evolutionarily stable age of sex change and primary sex ratio, we use the ESS criterion (Maynard Smith 1982), which states that a strategy β is evolutionarily stable if no other strategy has higher fitness when rare in a population composed of individuals that adopt β . That is, a^* and r^* are the stable age of sex change and the stable primary sex ratio, respectively, if

$$\left[\frac{\partial W_h(a', a^*, r^*)}{\partial a'} \right]_{a'=a^*} = 0, \quad (7)$$

$$\left[\frac{\partial W_d(a^*, r', r^*)}{\partial r'} \right]_{r'=r^*} = 0,$$

where

$$W_h(a', a^*, r^*) = F_h(a', a^*, r^*) + M_h(a', a^*, r^*), \quad (8)$$

$$W_d(a^*, r', r^*) = F_d(a^*, r', r^*) + M_d(a^*, r', r^*). \quad (9)$$

The values a and r that satisfy equation (7) are the ESS age of sex change and the ESS primary sex ratio, respectively. We find the ESS set (a^*, r^*) for both $s = 0$ (i.e., a rare sex changer in a dioecious population) and $s = 1$ (i.e., a rare dioecious individual in a sex-changing population). Using a^* and r^* in each scenario, we calculate and compare the fitness of sex changers and of the di-

oecious, $W_{h,s}(a^*, a^*, r^*)$ and $W_{d,s}(a^*, r^*, r^*)$, respectively, to investigate the stability of sex change against dioecy.

Sex change is stable against dioecy if

$$W_{h,s=0}(a^*, a^*, r^*) > W_{d,s=0}(a^*, r^*, r^*),$$

$$W_{h,s=1}(a^*, a^*, r^*) > W_{d,s=1}(a^*, r^*, r^*). \quad (10)$$

Dioecy is stable against sex change if

$$W_{h,s=0}(a^*, a^*, r^*) < W_{d,s=0}(a^*, r^*, r^*),$$

$$W_{h,s=1}(a^*, a^*, r^*) < W_{d,s=1}(a^*, r^*, r^*). \quad (11)$$

Partial satisfaction of these conditions implies the coexistence of sex change and dioecy in the population, either in a stable proportion or in a cycling fashion. While coexistence frequencies of dioecy and hermaphroditism and respective reproductive allocation strategies yields interesting results, we do not explore coexistence conditions in this study.

Below, we modify equations (1)–(4) to incorporate costs of changing sex into the baseline model. The analyses proceed identically in all subsequent steps that investigate the stability of sex change against dioecy.

The Effect of Costs of Changing Sex

We focus on three scenarios where sex change inflicts a reproductive cost on hermaphrodites. First, sex change involves a transitory period of gonad degradation and reconstruction (Hoffman et al. 1985; Iwasa 1991; Warner and Swearer 1991), during which reproductive activity may decrease. We assume that reproduction ceases in this period and term it the “nonreproductive period” of length p . Second, a sex-changed individual may have decreased reproduction compared with a dioecious individual of the same condition, due to hormonal complications of reproducing as both sexes in a lifetime (e.g., Bull and Charnov 1985) or potential inefficiencies of the process of gonad reconstruction. We incorporate this scenario in our model by decreasing the fertility of a sex-changed male by the factor of l_m . Finally, a decrease in reproduction due to hormonal complications of reproducing as both sexes may expand to a sex changer’s entire reproductive lifetime. For example, sex changers may also have a decreased fecundity by the factor of l_r before sex change, in addition to a decrease in fertility after sex change. In our analyses of this scenario, we assume a uniform decrease in reproduction throughout an individual’s reproductive lifetime (i.e., $l_r = l_m$).

We translate these biological scenarios into mathematical notations by changing equations (1) and (2) to

$$E = s \int_0^a e^{-zx} f(1 - l_r) dx + (1 - s)r \int_0^t e^{-zx} f dx, \quad (12)$$

$$S = s e^{-z(a+p)} \int_{a+p}^t e^{-z(x-a-p)} m x^b (1 - l_m) dx + (1 - s)(1 - r) \int_0^t e^{-zx} m x^b dx \quad (13)$$

and equations (3) and (4) to

$$F_h(a', a, r) = e^{-[E/(S+1)]} \int_0^{a'} e^{-zx} f(1 - l_r) dx, \quad (14)$$

$$M_h(a', a, r) = e^{-za'} \int_{a+p}^t \frac{E}{S+1} e^{-z(x-a'-p)} \times m x^b e^{-[E/(S+1)]} (1 - l_m) dx. \quad (15)$$

We investigate these different cost scenarios, and combinations thereof, by assigning 0 to one or more of the cost parameters, p , l_r , and l_m . For instance, choosing $l_r = l_m = 0$ and $p > 0$ corresponds to a scenario with a nonreproductive period alone, while assigning $0 < l_r$, $l_m < 1$, and $p = 0$ corresponds to a lifetime decrease in reproduction.

We implemented the model with versions 5.2 and 6 of Mathematica (Wolfram Research 2005, 2007). The Mathematica code we used in our analyses is available on request. In a population of sex changers and dioecious individuals, the ESS value for r depends on the ESS value for a , and vice versa (eq. [7]), and the analytical solution is recursive. Therefore, we analyzed the model numerically using various parameter values. We investigated different shapes for the size advantage by assigning different values to b : 0.5 for size advantage with diminishing returns, 1.0 for linear size advantage, and 1.5 for size advantage with increasing returns. Furthermore, we investigated values for the decrease in reproductive performance, l , and the length of the period of decreased reproduction, p , from 0.0 to 1.0 in intervals of 0.1 and from 0.0 to t in intervals of 10.0, respectively. Also, we used a range of instantaneous mortality constants, z , from very small values (i.e., $z = 5 \times 10^{-4}$, which translates to about 0.05% mortality per time unit) to very large values (i.e., $z = 0.2$, which translates to about 20% mortality per time unit). Expanding

this range did not significantly alter our results. It is important to note that biologically relevant mortality values lie toward the lower end of this range, where survival rate is high, individuals have a long reproductive lifetime, and the size advantage provides sex changers with a substantial fitness advantage. Similarly, we used various large values for the length of the reproductive lifetime (i.e., $t = 200.0, 500.0, 750.0$) and the female fecundity constant (i.e., $f = 10^2, 10^3$) to investigate biologically relevant scenarios with a large number of opportunities to gain fitness, for which the two life histories (i.e., sex change and dioecy) compete. We ensured that there are many more sperm produced than eggs by assigning values for the male fertility constant m that are greater than f (i.e., $m = 10^4, 10^5$). Different values for t , f , and m yielded identical results. Thus, we present only results of analyses with $t = 500.0$, $f = 10^3$, and $m = 10^5$.

Results

In figures 2–4, the area between the Y-axis and a line (e.g., the shaded area in fig. 2A) denotes the parameter space, for which the model predicts sex changers to have greater fitness than dioecious individuals. We refer to this parameter space as “the parameter space favoring sex change” and to the rest as “the parameter space favoring dioecy.” Accordingly, sex change is evolutionarily stable in the parameter space favoring sex change when sex change is common in the population (i.e., $s = 1.0$). Conversely, dioecy is evolutionarily stable in the parameter space favoring dioecy when dioecy is common in the population (i.e., $s = 0.0$).

The baseline version of the model with no cost of changing sex agrees with the size-advantage hypothesis and predicts that sex change is always favored in the presence of a size advantage, both as a rare mutant ($s = 0.0$) and the native strategy ($s = 1.0$; fig. 2, $p = 0.0$, $l = 0.0$; figs. 3, 4, $l = 0.0$). We find, however, as we intuitively expected, that reproductive costs of changing sex can cause dioecy to be favored despite a size advantage (figs. 2–4). It is important to emphasize that different scenarios for the cost and different numerical values for parameters yield quantitatively different results. Nevertheless, our analyses point to several common qualitative patterns.

First, in biologically relevant cases (e.g., smaller mortality values), costs of changing sex have to be large for dioecy to be evolutionarily stable (figs. 2–4). In the numerical scenario reported in figure 2C, 2D (with $l = 0.0$), for example, the nonreproductive period following sex change has to span more than about 34% of the reproductive lifetime for dioecy to be stable. Second, reproductive costs have a stronger effect on sex change not only when the size advantage is weaker (i.e., smaller values of

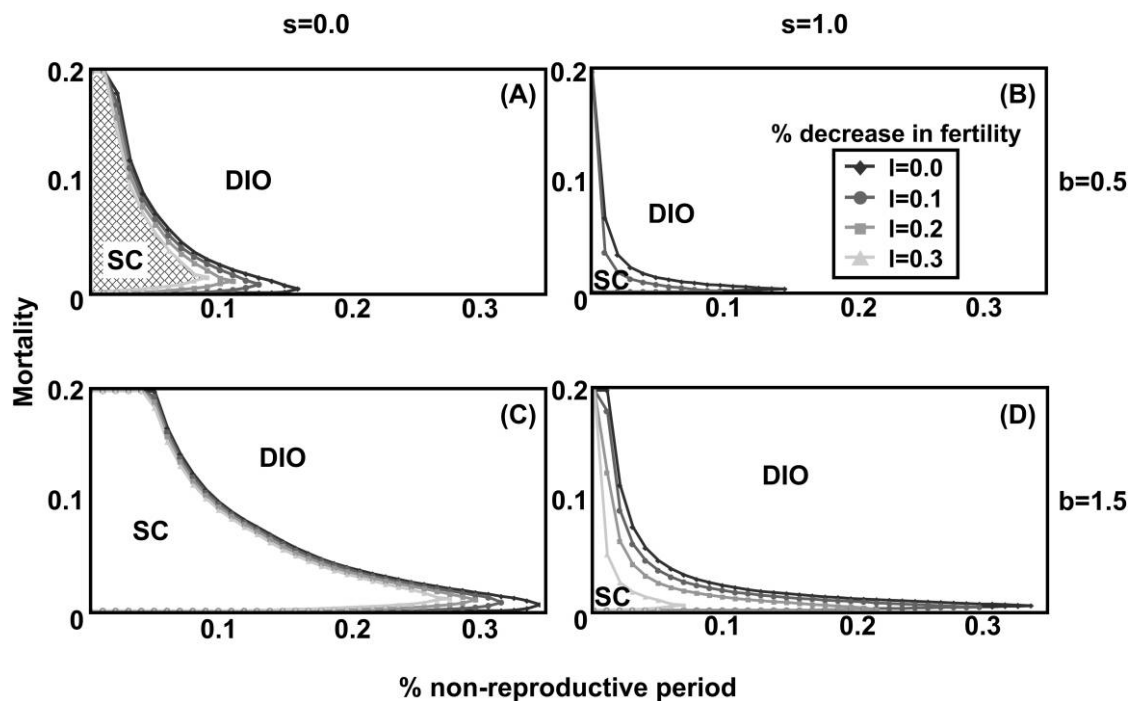


Figure 2: Effects of the nonreproductive period following sex change alone ($l = 0.0$) and combined with a decrease in male fertility ($l > 0.0$) on the parameter space, where the model predicts sex change (SC) to be favored over dioecy (DIO; parameter space favoring sex change). Individual graphs represent predictions when sex changers are rare ($s = 0.0$; A, C) or common ($s = 1.0$; B, D) and at weaker ($b = 0.5$; A, B) or stronger ($b = 1.5$; C, D) size advantage. The area between a line and the Y-axis represents the parameter space favoring sex change for the respective scenario (e.g., the shaded area for $s = 0.0$, $b = 0.5$, and $l = 0.3$). The pattern that dioecy is favored for very small mortality values when the cost is sufficiently large is caused by the structure of our model that imposes a final age on reproduction.

b) but also when sex changers are very common in the population (i.e., $s = 1.0$). Accordingly, in all scenarios, the parameter space favoring sex change decreases with increasing frequency of sex changers in the population as well as with the strength of size advantage (figs. 2–4). The degree of decrease in the parameter space favoring sex change with increasing frequency of sex changers, however, depends on the type of reproductive cost involved. In the case of a lifelong decrease in a sex changer’s fecundity and fertility, the parameter space favoring sex change is nearly identical when sex changers are very rare or common (fig. 4). When the cost of changing sex involves a decrease in fertility following sex change, on the other hand, the parameter space favoring sex change decreases dramatically with increasing frequency of sex changers in the population (fig. 3). In sum, costs of changing sex have a weak effect on the evolutionary stability of dioecy against sex change, and the fitness effect of a cost depends on the strength of size advantage, the type of cost, and the frequency of sex changers.

Discussion

Here, we formally confirm the prediction that reproductive costs of changing sex can outweigh the selection for hermaphroditism through size advantage and favor a dioecious life history. We find, however, that these costs favor dioecy only when very large. Accordingly, we have frequently encountered scenarios where sex change is favored despite a large cost (see “Results”; figs. 2–4). These results indicate that costs of changing sex alone are not likely to explain the observed rarity of sex change. Central to explaining why costs of changing sex have a weak effect on the presence of sequential hermaphroditism is the biological fact that every offspring has exactly one mother and one father, and therefore, the total fitness through male and female functions in a population must be equal (Fisher 1930). Our model demonstrates that this requirement of self-consistency (Houston and McNamara 2002) is crucial not only to building a biologically sound model but also to capture an accurate picture of how different components (e.g., costs of changing sex, size advantage) interact

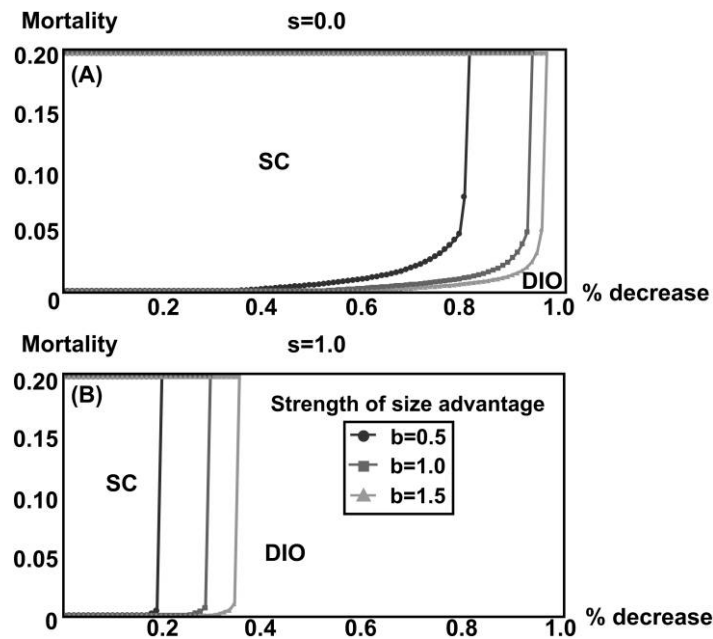


Figure 3: Effect of a decrease in male fertility following sex change on the parameter space favoring sex change (SC) over dioecy (DIO), when sex changers are rare (A; $s = 0.0$) or common (B; $s = 1.0$), for various values for the strength of size advantage ($b = 0.5$ to 1.5). The area between a line and the Y-axis represents the parameter space favoring sex change for the respective scenario (see fig. 2 for an example).

within a system. Self-consistency affects the selection consequences of a cost of sex change in two ways.

First, in a self-consistent scenario, age-specific fitness returns of a sex-changed male are not static but increase with the cost, depending on the type of cost involved. In the case of a nonreproductive period following sex change, for example, reproductive opportunities lost in this period create greater opportunities for those who survive beyond it (i.e., sex-changed males; fig. 5). Consequently, while a nonreproductive period causes a sex changer to lose fitness, increased fitness returns following sex change diminish the decrease in total fitness. The cost of changing sex, however, affects the age-specific fitness in a frequency-dependent way, and the increase in age-specific male fitness becomes limited, as sex changers get rarer in the population (not shown).

Second, the effect of a cost on sex change is also not static but changes in a frequency-dependent way and is weakest when sex changers are rare in the population. Accordingly, the parameter space favoring sex change is greatest when sex changers are rare and smallest when sex changers are common (figs. 2–4). A reproductive cost affects the presence of sex change not only directly by decreasing a sex changer's total fitness but also indirectly by creating an opportunity for dioecious individuals, who do not pay the cost of sex change, to do better where sex changers do worse. In a population composed of sex

changers, for example, a reproductive cost that reduces male fertility after sex change increases the fitness returns for a dioecious male that does not pay such costs. Consequently, a rare dioecious mutant increases its fitness by adopting a male-biased primary sex ratio (not shown). However, as sex changers become rarer in the population and there are fewer individuals that pay the reproductive cost of changing sex, the effect of a cost on the presence of sex change becomes weaker, helping sex change to persist in a population.

It is important to note that in this study, we analyzed whether a sex-changing or dioecious mutant could initially spread in a dioecious or sex-changing population, respectively, given a reproductive cost of changing sex, but we have not explicitly investigated the evolutionarily stable population composition. We encountered scenarios where dioecy (or sex change) is predicted to spread as a rare mutant and to be as stable as the native strategy and, therefore, be the evolutionarily stable strategy in the population. In all versions of the model we investigated, however, the parameter space favoring sex change is greater when sex changers are very rare than when they are very common (figs. 2–4). This implies that there is a parameter space where sex changers are favored when rare but disfavored when common. Here, the model predicts dioecy and sex change to coexist in the population. Conditions leading to coexistence of a dioecious strategy with sex

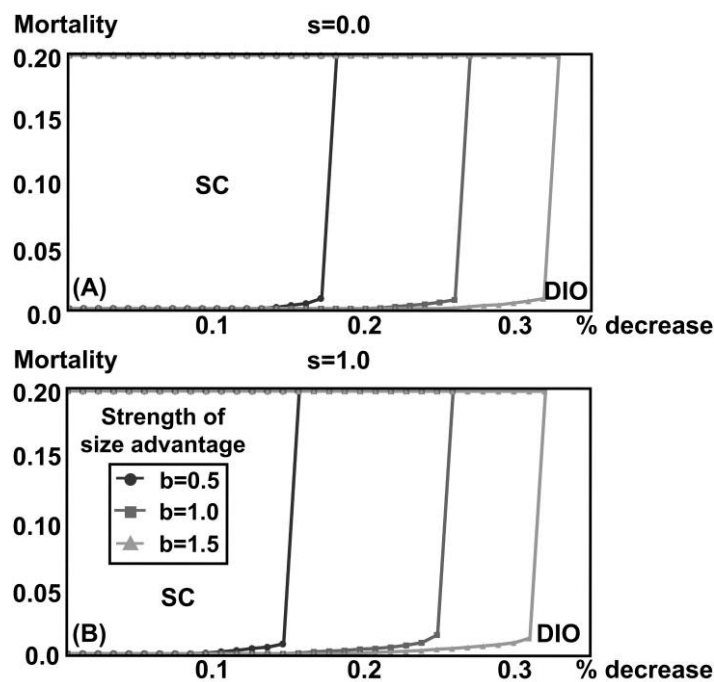


Figure 4: Effect of a lifetime decrease in female fecundity and male fertility on the parameter space favoring sex change (SC) over dioecy (DIO), when sex changers are rare (A; $s = 0.0$) or common (B; $s = 1.0$), for various values for the strength of size advantage ($b = 0.5$ to 1.5). The area between a line and the Y-axis represents the parameter space favoring sex change for the respective scenario (see fig. 2 for an example).

changers have been empirically and theoretically studied in the context of alternative dioecious male strategies in protogynous species (Warner and Hoffman 1980; Charnov 1982a; Munday et al. 2006b). We will explore this aspect of our model in further studies.

A clear message from this study is that the effect of a cost on the selection for sex change depends on the type of cost. Therefore, it is essential to identify these costs in nature. Furthermore, the evolutionary stability of sex change depends on the strength of size advantage, the amount of cost, and its fitness consequences, which indicates that we have to quantitatively and comparatively assess these components if we are to understand why sex change is absent in most animals but present in some. To this end, more empirical work is needed. There are, however, several difficulties associated with studying the effects of costs on the selection for sex change. First, quantifying the size advantage and comparing the strength of selection for sex change across species can be challenging. To detect the size advantage in protogynous coral reef fishes with male alternative reproductive behavior, some researchers have compared the reproductive success of small mature males to that of females of similar size (Warner and Lejeune 1985) or of large territorial males (Hoffman et al. 1985). In other sex-changing species, smaller males that

adopt alternative reproductive behavior can be rare or missing (e.g., Jones 1981; Warner 1988a). In these species with limited opportunities to make meaningful inter- and intrasexual comparisons of reproductive success, detecting and quantifying the size advantage can be very difficult.

Second, determining the types of reproductive costs of changing sex and quantifying their fitness effects are inherently difficult, since there are no known animals with dioecious and hermaphroditic populations, where the costs associated with sex change can be directly measured. There are, however, other systems that can potentially be used to explicitly study costs of sex change. Some hermaphroditic species exhibit two ways of becoming a large, territorial male: maturing as a female and changing sex when sufficiently large or maturing as a small male and attaining territorial status later in life (for references, see Charnov 1982a). Comparisons of reproductive success of these two types of males at similar sizes may help to detect and quantify reproductive costs of sex change. Additionally, some types of costs, such as the period of decreased reproduction, can be relatively easily detected, measured, and compared across sex-changing species. Accordingly, a period of decreased reproduction during and after sex change has been documented in a variety of species, and its length varies from days to years (Hoffman et al. 1985).

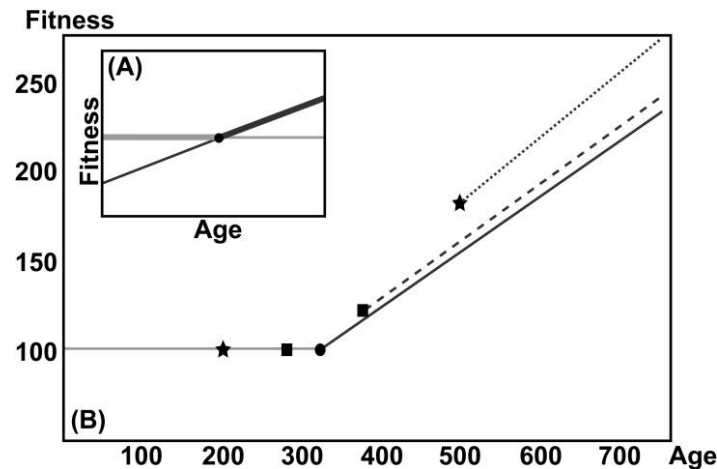


Figure 5: A, Classic visual representation of the size-advantage hypothesis (modified from Warner 1975). If female (gray) and male (black) age-specific fitness trajectories intersect, a sex-changing life history (thick gray followed by thick black) is favored. B, Effect of a nonreproductive period following sex change on the age-specific fitness trajectory of a sex changer in a self-consistent framework. Gray and black correspond to female function and male function, respectively. A hermaphrodite follows the female trajectory changes sex at the age that corresponds to the solid circle (no cost), square (higher cost), or star (highest cost), resumes reproduction at the age that corresponds to the respective symbol, and follows the solid (no cost), dashed (higher cost), or dotted (highest cost) male trajectory. (Parameter values: $z = 0.002$; $p = 0.0, 100.0, 300.0$; $t = 750.0$; $f = 100.0$; $m = 100,000.0$; $b = 1.0$; $s = 1.0$; $r = 0.5$.)

An important caveat, however, is that life-history theory predicts that an extended period of decreased reproduction could also result from stochastic changes in the optimal timing of sex change (Rogers 2003) or from investment to growth to avoid a mortality cost of reproduction (Iwasa 1991) or to quickly attain a larger size under intense competition for good territories (Hoffman et al. 1985) and therefore be adaptive. Clearly, it is crucial to tease apart the costly period of gonad reconstruction from adaptive changes in the timing of sex change in order to understand its effect on the fitness of sex changers.

Costs of changing sex always select against sequential hermaphroditism and could result in a dioecious life history. Our analyses confirm this intuitive prediction but indicate that costs of changing sex alone are not likely to explain why more animals are not sex changers. Alternatively, while some mating system correlates such as territorial behavior or harem social structure select for sex change, it has been suggested that others such as parental care (Warner and Lejeune 1985) may select against it. We suggest that it is essential to quantitatively assess hermaphroditic and dioecious mating systems through comparative, experimental, and theoretical studies and identify correlates that select for and against sex change in order to understand the rarity of sex changers in nature. Finally, a hermaphroditic or dioecious life history is the result of a dynamic evolutionary game between sex change and dioecy, where the fitness effects of costs (figs. 2–4) and the strength of size advantage (fig. 5B) change with the

population structure due to self-consistency. It is important to emphasize that self-consistency is not only an indispensable property of a biologically sound model but is also crucial to capture interesting and relevant dynamics within a system. Here, understanding these dynamics is essential to explain why costs of changing sex have a relatively weak effect on sex changers and therefore cannot explain the rarity of sequential hermaphroditism in nature.

Acknowledgments

We thank R. R. Warner and an anonymous reviewer for their critical comments on an earlier draft of this article and members of Alonzo Lab for their helpful suggestions. This study was supported by Yale University Department of Ecology and Evolutionary Biology Graduate Student Supply Fund to E.K. and National Science Foundation grant IOB-0450807 to S.H.A.

Literature Cited

- Aldenhoven, J. M. 1986. Different reproductive strategies in a sex-changing coral-reef fish *Centropyge bicolor* (Pomacanthidae). *Australian Journal of Marine and Freshwater Research* 37:353–360.
- Bull, J. J., and E. L. Charnov. 1985. On irreversible evolution. *Evolution* 39:1149–1155.
- Carruth, L. L. 2000. Freshwater cichlid *Crenicara punctulata* is a protogynous sequential hermaphrodite. *Copeia* 2000:71–82.
- Charnov, E. L. 1982a. Alternative life histories in protogynous fishes: a general evolutionary theory. *Marine Ecology Progress Series* 9: 305–307.

- . 1982*b*. The theory of sex allocation. Princeton University Press, Princeton, NJ.
- . 1986. Size advantage may not always favor sex change. *Journal of Theoretical Biology* 119:283–285.
- Clifton, K. E., and L. Rogers. 2008. Sex-specific mortality explains non-sex-change by large female *Sparisoma radians*. *Animal Behaviour* 75:e1–e10.
- Dipper, F. A., and R. S. V. Pullin. 1979. Gonochorism and sex-inversion in British Labridae (Pisces). *Journal of Zoology* 187:97–112.
- Fisher, R. A. 1930. The genetical theory of natural selection. Clarendon, Oxford.
- Ghiselin, M. T. 1969. Evolution of hermaphroditism among animals. *Quarterly Review of Biology* 44:189–208.
- Gillanders, B. M. 1995. Reproductive biology of the protogynous hermaphrodite *Achoerodus viridis* (Labridae) from south-eastern Australia. *Marine and Freshwater Research* 46:999–1008.
- Helfman, G. S., B. B. Collette, and D. E. Facey. 1997. The diversity of fishes. Blackwell Science, Oxford.
- Heller, J. 1993. Hermaphroditism in molluscs. *Biological Journal of the Linnean Society* 48:19–29.
- Hoffman, S. G., M. P. Schildhauer, and R. R. Warner. 1985. The costs of changing sex and the ontogeny of males under contest competition for mates. *Evolution* 39:915–927.
- Houston, A. I., and J. M. McNamara. 2002. A self-consistent approach to paternity and parental effort. *Philosophical Transactions of the Royal Society B: Biological Sciences* 357:351–362.
- Iwasa, Y. 1991. Sex change evolution and cost of reproduction. *Behavioral Ecology* 2:56–68.
- Jones, G. P. 1981. Spawning site choice by female *Pseudolabrus celidotus* (Pisces, Labridae). *Behavioral Ecology and Sociobiology* 8: 129–142.
- Leigh, E. G., E. L. Charnov, and R. R. Warner. 1976. Sex ratio, sex change, and natural selection. *Proceedings of the National Academy of Sciences of the USA* 73:3656–3660.
- Maynard Smith, J. 1982. *Evolution and the theory of games*. Cambridge University Press, Cambridge.
- Munday, P. L., P. M. Buston, and R. R. Warner. 2006*a*. Diversity and flexibility of sex-change strategies in animals. *Trends in Ecology & Evolution* 21:89–95.
- Munday, P. L., J. W. White, and R. R. Warner. 2006*b*. A social basis for the development of primary males in a sex-changing fish. *Proceedings of the Royal Society B: Biological Sciences* 273:2845–2851.
- Muñoz, R. C., and R. R. Warner. 2003. Alternative contexts of sex change with social control in the bucktooth parrotfish, *Sparisoma radians*. *Environmental Biology of Fishes* 68:307–319.
- Okada, Y. K. 1962. Sex reversal in Japanese wrasse, *Halichoeres poecilopterus*. *Proceedings of the Japan Academy* 38:508.
- Policansky, D. 1982. Sex change in plants and animals. *Annual Review of Ecology and Systematics* 13:471–495.
- Rogers, L. 2003. Odds-playing and the timing of sex change in uncertain environments: you bet your wrasse. *Behavioral Ecology* 14: 447–450.
- Rogers, L., and R. C. Sargent. 2001. A dynamic model of size-dependent reproductive effort in a sequential hermaphrodite: a counterexample to Williams's conjecture. *American Naturalist* 158: 543–552.
- Sadovy de Mitcheson, Y., and M. Liu. 2008. Functional hermaphroditism in teleosts. *Fish and Fisheries* 9:1–43.
- Shapiro, D. Y. 1987. Differentiation and evolution of sex change in fishes. *BioScience* 37:490–497.
- Warner, R. R. 1975. Adaptive significance of sequential hermaphroditism in animals. *American Naturalist* 109:61–82.
- . 1978. The evolution of hermaphroditism and unisexuality in aquatic and terrestrial vertebrates. Pages 77–101 in E. S. Reese and F. T. Lighter, eds. *Contrasts in behavior*. Wiley, New York.
- . 1988*a*. Sex change in fishes: hypotheses, evidence, and objections. *Environmental Biology of Fishes* 22:81–90.
- . 1988*b*. Sex change and the size-advantage model. *Trends in Ecology & Evolution* 3:133–136.
- Warner, R. R., and S. G. Hoffman. 1980. Population density and the economics of territorial defense in coral reef fish. *Ecology* 61:772–780.
- Warner, R. R., and P. Lejeune. 1985. Sex change limited by paternal care: a test using four Mediterranean labrid fishes, genus *Symphodus*. *Marine Biology* 87:89–99.
- Warner, R. R., and R. C. Muñoz. 2008. Needed: a dynamic approach to understand sex change. *Animal Behaviour* 75:e11–e15.
- Warner, R. R., and S. E. Swearer. 1991. Social-control of sex-change in the bluehead wrasse, *Thalassoma bifasciatum* (Pisces, Labridae). *Biological Bulletin* 181:199–204.
- Warner, R. R., D. R. Robertson, and E. G. Leigh. 1975. Sex change and sexual selection. *Science* 190:633–638.
- Wolfram Research. 2005. *Mathematica*. Version 5.2. Wolfram Research, Champaign, IL.
- . 2007. *Mathematica*. Version 6. Wolfram Research, Champaign, IL.
- Wright, W. G. 1988. Sex change in the mollusca. *Trends in Ecology & Evolution* 3:137–140.

Associate Editor: David Waxman
 Editor: Michael C. Whitlock