Condition Dependent Effects on Sex Allocation and Reproductive Effort in Sequential Hermaphrodites

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Abstract

Theory predicts the optimal timing of sex change will be the age or size at which half of an individual’s expected fitness comes through reproduction as a male and half through reproduction as a female. In this way, sex allocation across the lifetime of a sequential hermaphrodite parallels the sex allocation of an outbreeding species exhibiting a 1:1 ratio of sons to daughters. However, the expectation of a 1:1 sex ratio is sensitive to variation in individual condition. If individuals within a population vary in condition, high-condition individuals are predicted to make increased allocations to the sex with the higher variance in reproductive success. An oft-cited example of this effect is seen in red deer, Cervus elaphus, in which mothers of high condition are more likely to produce sons, while those in low condition are more likely to produce daughters. Here, we show that individual condition is predicted to similarly affect the pattern of sex allocation, and thus the allocation of reproductive effort, in sequential hermaphrodites. High-condition sex-changers are expected to obtain more than half of their fitness in the high-payoff second sex and, as a result, are expected to reduce the allocation of reproductive effort in the initial sex. While the sex ratio in populations of sequential hermaphrodites is always skewed towards an excess of the initial sex, condition dependence is predicted to increase this effect.

Introduction

Sex change theory proposes that when size-specific reproduction increases at one rate for males and at another rate for females the functions describing these rates will inevitably cross, and sex change will be favored by natural selection [1–5]. This, Ghiselin’s size-advantage hypothesis [1], simply and elegantly predicts both the direction and the timing of sex change. The direction of sex change is predicted by the relative reproductive rates: If small females have higher reproductive rates than small males, but large males have higher rates than large females, then protogyny, female-to-male sex change, is favored; if this relationship is reversed, then protandry, male-to-female sex change, is favored [1,2]. The optimal timing of sex change is the age or size at which the reproductive rates cross [2–4] (Fig. 1a), holding the size-specific survival and growth rates equal across the sexes [5,6], as a male.

Incorporating variance in condition

Implicit to Leigh et al.’s solution is the assumption that individuals do not vary in condition. While individual condition or quality is often made tangible by measures such as body mass, nutritional state, experience, or genetic load [8,9], the most coherent definition of condition is that offered by Rowe and Houle [10], who regard condition as simply that which positively correlates with future fitness.

Trivers and Willard [11] modified Fisher’s model to propose that condition-dependence might influence the sex allocation of parents in species providing parental care. Specifically, they suggested that if an offspring’s condition is correlated to that of its mother, and if condition affects male reproductive success (RS) more strongly than it affects female RS [12,13], large, high-condition mothers would benefit from producing sons, while smaller, low-condition mothers would benefit from producing seemingly common condition, particularly in species exhibiting external fertilization and no parental care, the primary sex ratio at equilibrium is 1:1. Leigh et al. realized that Fisher’s solution to the problem of optimal sex allocation across generations must also apply to a sequential hermaphrodite across its lifetime. Their analysis shows that the optimal age at sex change will be the age at which exactly half an individual’s expected fitness will come through reproduction as a female and half through reproduction as a male.
Figure 1. Changes in the age-specific distribution of reproductive value under sex change. a. Idealized male (red) and female (blue) reproductive rates as described in the classic interpretations of the size-advantage model [1–6]. The optimal size at sex change is at age 1, as such an individual has the higher reproductive rate at all ages. b. The probabilities of survival \( l(y-x) \), for individuals of ages 0 (bold), 0.25, and 0.5. The remaining survival time is independent of current age (i.e., the survival function is said to be memoryless). In this example, an individual at age 0 has a 5% likelihood of reaching age 1, the age at sex change. c. The expected reproductive payoff, \( E(y-x|m(y)) \), plotted against age. Figures 1a and 1b give rise to Leigh et al.’s [4] result in which half of the lifetime fitness comes through function in the initial sex (here, female), and half through function in the second sex (i.e. the areas under the blue and red curves are equal). As an individual ages, the expected fitness contribution through reproduction in the high-payoff second sex increases relative to expected contribution via the initial sex.

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detail
RRV\textsubscript{max}(x), must exist, they are inherently unmeasurable. That is, a researcher can measure the realized reproductive rate, \( m(x) \), which she knows to be the product of potential and allocation, \( R_{\text{max}}(x) \times E(x) \), but the underlying values of \( R_{\text{max}}(x) \) and \( E(x) \) cannot be directly measured. Nevertheless, it seems reasonable that one may infer the general form of \( R_{\text{max}}(x) \) from \( m(x) \), and here we make this assumption. The age-/size-specific reproductive rate for a protogynous sex-changer is often modeled by a pair of intersecting functions: a linearly increasing function describing reproduction as a female, and an exponentially increasing function describing reproduction as a male (e.g., Figure 1a of [2]). While such a pair of functions captures the essence of the size-advantage model in the vicinity of the age/size at sex change, they are not mathematically realistic as they imply increases to infinity for both sexes. In reality, the potential reproductive rate of Labroid fishes is best described by a logistic function [22]. For simplicity, we here use a step-function,

\[
R_{\text{max}}(x) = \begin{cases} 
1, & 0 < x < 1 \\
M, & x \geq 1 
\end{cases} \quad (\text{eq.} 6)
\]

in place of the logistic to describe the age-maximal reproductive rate across both the female (\( x < 1 \)) and male (\( x \geq 1 \)) segments of the life history in which male reproduction is \( M \) times that of a female (\( M > 1 \)). While this is a gross approximation of a logistic curve, particularly near the discontinuity, it does mimic the asymptotic behavior of such a curve while making the mathematics tractable.

Having dealt with the first complication, we turn to the second. Finding the level of allocation which maximizes \( V(x) \) requires that we know \( R_{\text{RRV}}(x) \), which in turn requires that we know the optimal level of reproductive allocation at all future ages \( y > x \). Such optimization problems are often solved numerically by the method of backwards iteration in a dynamic programming model [24–27]. In the current work we adopt a different method. We consider a system in which (i) individuals vary in condition, (ii) high-condition individuals have high survival rates, and (iii) the survival rate for an individual is independent of its age. This gives

\[
l(x) = e^{-x/\beta} \quad \text{(eq.} 7)\]

where \( l(x) \) is the probability of surviving to \( x \) from age 0 and \( \beta \) is the life expectancy which varies based on the condition of the individual. The simplified life history described by equations 6 and 7 allows us to approximate equation 5, and solve for the optimal life history analytically (see [28] for a similar approach).

If individuals within the population do not vary in condition, the m:f sex ratio will be

\[
\int_{x=1}^{\infty} l(x)dx = \int_{x=0}^{1} l(x)dx \quad \text{(eq.} 8)\]

As total male fitness must equal total female fitness [7],

\[
\int_{x=0}^{1} l(x)E'(x)dx = \int_{x=1}^{\infty} l(x)E'(x)Mdx \quad \text{(eq.} 9)\]

equation 9 gives rise to Leigh et al.’s [4] condition that half of an individual’s expected fitness is fitness will come through reproduction as a female and the other half through reproduction as a male (Fig. 1c). It is interesting to note here that an individual’s 1:1 expectation changes as it ages. For individuals reaching ages \( > 0 \), the expected contribution to fitness through reproduction in the high-payoff, second sex (here, male) increases relative to the expected contribution through the initial sex (female) for two reasons. First, as individuals grow older, an increasing fraction of initial-sex fitness has fallen in the past and thus no longer exerts an influence on the optimal allocation of effort. At the same time, the probability of reaching the high-payoff, second-sex phase of the life history has increased, increasing the reproductive value of this phase (Fig. 1c).

**Incorporating variance in condition - the effect on sex allocation**

Given this, we now consider the fate of an individual of high condition within a population exhibiting variance in condition. As high-condition individuals have high survival rates, such individuals have higher reproductive value at all ages (eq.7 and eq.a14; see Appendix S2). However, the effect of the high survival rate on the initial- and second-sex components of the life history is not equal: the gains in expected fitness to a high-condition individual through the high-payoff second sex are greater than the gains in the initial sex (Fig. 2a). Likewise, an individual of low condition will have relatively low reproductive value across the lifetime, with the expected reproductive payoffs in the second sex again being disproportionately affected (Fig. 2b). Thus, as condition dependence is expected to alter the sex ratio of a parent’s offspring in an outcrossing species [5,15], it is similarly expected to alter the sex allocation of a hermaphrodite.

**Incorporating variance in condition - the effect on the allocation of reproductive effort**

As noted above, we are here viewing sex allocation as a subcomponent of the optimal allocation of resources over the lifespan. To solve for the optimal schedule of allocation analytically, we must adapt the discrete-time interpretation of reproductive value (implied by equations 1 and 2 above) to a continuous-time interpretation. With \( m(x) \) defined in eq.3, the analogue of eq.2 is

\[
V(x) = \int_{x}^{\infty} l(y-x)E'(x)R_{\text{max}}(x)dx \quad \text{(eq.} 10)\]

Note that the division between current and future components of reproductive value vanishes in a continuous-time description of \( V \). Since our survival rate function is memoryless, the reproductive value beyond age 1, the age at sex change, is a constant, \( MC \), where \( C \) is

\[
C = \sqrt{\frac{(-1 + \sqrt{1 + 4\beta^2})}{2}} \quad \text{(eq.} 11)\]

(see Appendix S2). For all ages \( x \geq 1 \), the reproductive value is the constant

\[
V(x) = MC \quad \text{(eq.} 12)\]

thus the realized reproductive rate is

\[
m(x) = \beta^{-1}MC \quad \text{(eq.} 13)\]
and the optimal allocation of reproductive effort is, by equation 5,

$E^*(x) = \beta^{-1} C$  \hspace{1cm} (eq. 14)

On the other hand, $E^*(x)$ varies for ages $x < 1$. The reproductive value across this phase of the life history is an increasing function satisfying

$MCe^{\frac{x-1}{\beta}} \leq V(x) \leq \beta + (MC - \beta)e^{\frac{x-1}{\beta}}$  \hspace{1cm} (eq. 15)
Figure 3. Condition-dependent effects on reproductive value and reproductive effort. a. Age-specific reproductive value for individuals of normal (blue), high (black), and low (red) condition. For any given age, the true value of the function lies within the limits of the thick lines; see text and Appendix S2. Reproductive value increases as individuals approach age 1, the age at sex change. b. The optimal allocation of reproductive effort, $E^*(x)$ between age 0 and age 1 for individuals of high, normal, and low condition. Allocation to current reproduction decreases as future, expected reproduction increases in value with the approach to the age at sex change [27]. Low-condition individuals exhibit increased allocations to current reproduction, as the value of future reproduction is reduced by low survival rates.

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while the optimal level of effort, \(E'(x)\), is a decreasing function satisfying

\[
\frac{1}{1+\beta\left(MC - \beta \frac{x}{\beta}ight)^2} \leq E'(x) \leq \frac{1}{1+\left(MC^2 - \beta^2\right)^2} \quad (eq.16)
\]

(see Appendix S3).

Recalling that the survival rate, and thus the lifespan, \(\beta\), is a function of condition, we see from eq.16 that high-condition individuals are predicted to have lower allocations of reproductive effort at all ages, while having higher lifetime fitness, than lower condition individuals (eq.15; Fig. 3). This leads to the somewhat counterintuitive result that a low-condition female may produce more eggs than does a high-condition female in a given reproductive bout [16–18] (but see [27]).

**Discussion**

Eighty years ago, Fisher [7] explained why the sex ratio in an outbreeding species without post-zygotic parental care may be expected to be 1:1. Extending Fisher’s logic to sequential hermaphrodites, Leigh et al. [4] showed that the optimal timing of sex change will be the age or size at which half of an individual’s expected reproductive success arrives through function as a female, and half through function as a male. However, these results [4,7] hold only if the individuals within the population have equal fitness expectations; that is, if they are equal in condition (sensu [10]). Trivers and Willard [11] relaxed this assumption to consider the effects of condition dependence on the evolution of the sex ratio. High-condition individuals may be larger, have greater fat reserves, fewer parasites, or control a territory richer than average. The specifics of what endows an individual with ‘high condition’ are immaterial – what is important is that such individuals have higher than average fitness expectations [10].

Here, we apply the Trivers-Willard argument to Leigh et al.’s analysis in order to investigate the effects of condition dependence on both sex allocation and the optimal schedule of reproductive effort across the lifetime in a sequential hermaphroditic. To do so, we model an age-specific life history in which the survival rate, and thus the lifespan, varies with individual condition, but the growth rate is constant. Doing this would be challenging to test in nature, this leads to the prediction that fish with the highest lifetime fitness expectations might reproduce at a lower rate, albeit over a longer lifespan, relative to low-condition fish.

**Supporting Information**

**Appendix S1** Computing the optimal realized reproduction.

**Appendix S2** Modeling the behavior after sex change.

(TDOCX)
Appendix S3  Modeling the behavior before sex change.

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Author Contributions

Conceived and designed the experiments: LR AK. Performed the experiments: LR AK. Analyzed the data: LR AK. Contributed reagents/materials/analysis tools: LR AK. Wrote the paper: LR AK. Text: LR. Mathematics: AK.