

Odds-playing and the timing of sex change in uncertain environments: you bet your wrasse

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Stochastic events contribute to the distribution of environments experienced by individuals and populations. Such distributions have the interesting property that although the effect random events will have on the phenotype of a given individual is uncertain, at larger sample sizes (e.g., at the level of the population) these effects become approximately deterministic and may be easily predicted. For example, the date on which an ephemeral pond will dry out (a deciding occurrence in the life of a developing tadpole), although uncertain, is predicted by some probability density distribution describing the behavior of ponds over space and time.

In this paper I develop a simple model for considering the effect of environmental uncertainty on the optimal timing of life-history transitions, focusing primarily on the timing of sex change. Specifically, I use this fact to explain the phenomenon of “early sex change” on the basis of deterministic factors alone.

The principal model of sex change, the size-advantage model, notes that selection for sex change exists when an organism has a higher reproductive rate as one sex when small or young, and has a higher reproductive rate as the other sex when large or old, assuming equal size-specific survival and growth rates for both sexes (Ghiselin, 1969). The evolutionarily stable size at sex change is the size at which the functions describing male and female reproductive rates intersect (Charnov, 1982; Leigh et al., 1976; Warner, 1975; Warner et al., 1975).

The simplest interpretations of the size-advantage model

thus do not allow for, and do not predict, a nonreproductive interval falling between periods of reproduction in the initial and second sexes. Nevertheless, a sustained nonreproductive period occurs in a number of species. In such systems, the timing of sex change is seen to be earlier than predicted by the simplest interpretations of the size-advantage model (Hoffman et al., 1985). This condition is known as early sex change.

A well-studied species exhibiting early sex change is the bluehead wrasse, *Thalassoma bifasciatum* (Hoffman et al., 1985; Warner, 1991). In this fish, small, initial color-phase (hereafter, referred to simply as initial phase, or IP) females spawn daily at mating sites on the back-current edges of shallow reefs of the west Atlantic ocean. These mating sites either are occupied by aggregations of small IP males that mate en masse with visiting females or, alternatively, are defended against smaller males by large, terminal-phase (TP) males as semiexclusive mating territories. TP males are derived by phase-change by IP males, and by sex- and phase-change by IP females. Warner and Robertson (1978) note that in *T. bifasciatum* sex- and phase-change are discrete events. For this species then, and for others exhibiting both sex- and morphological phase-changes, the size-advantage model also explains the adaptive significance of phase-change (Rogers, 1998).

On sex- and/or phase-change, individual IP *T. bifasciatum* cease reproduction and enter a protracted nonreproductive period before resuming reproduction as TP males. As noted above, these individuals are said to have changed sex early (Hoffman et al., 1985; Iwasa, 1991). What is striking is that in this species, the nonreproductive period is generally months longer than what is required for behavioral and physiological sex- and phase-changes (Warner and Swearer, 1991). The size-advantage model predicts a transition from a low reproductive rate to a high reproductive rate, and thus, this suspension in reproduction requires an explanation.

One possibility is that this strategy may be favored by natural selection when trade-offs between life-history components result in an increase in reproductive expectations in the future sufficient to compensate for the costs of zero reproduction in the present (Hoffman et al., 1985; Iwasa, 1991). For example, a small decrease in reproductive effort resulting in a large increase in survival will be favored via the increase in reproductive value through expected reproduction in the future (Williams, 1966).

There are, however, theoretical and empirical reasons to question this explanation as it applies to the bluehead system. Rogers and Sargent (2001) note that the life-history models of early sex change by Hoffman et al. (1985) and Iwasa (1991) are assumption-bound and that the trade-off between current and future reproduction is unlikely to drive reproductive effort to zero. Specifically, in the first model, Hoffman et al. (1985) explicitly consider only two reproductive states: on and off. In this case, when a decrease in reproductive effort is predicted, it can only be a decrease to zero. Iwasa's (1991) more complex analytical model permits a continuous distribution of reproductive allocation. However, an implicit assumption in this model similarly restricts the potential optima to fully on or fully off (Rogers and Sargent, 2001). Rogers and Sargent show that when the residual reproductive value increases with size at a rate outpacing any increase in current reproductive potential, perhaps a common occurrence in protogynous sex changers, the optimal allocation of reproductive effort is predicted to decline. However, unless the relationship between reproductive output and reproductive effort is fundamentally changed, this decline is never predicted to go to zero.

If the nonreproductive period exists as a result of a shift in

allocation from current to future reproduction, then life-history components correlated with future reproduction (e.g., growth and survival rates) are predicted to increase when reproduction ceases. In agreement with this prediction, Warner (1984) found that growth rates of newly sex-changed, but not yet territorial, TP male *T. bifasciatum* were approximately 50% higher than those of like-sized IP males and females (reproductive IP growth rate $g = 0.048$ mm/day; nonreproductive TPs growth rate $g = 0.074$ mm/day) (Warner, 1984: Table 9). Although this is a substantial increase, Warner (1984) also shows that mortality rates among TP males are roughly two times higher than those of males and females in the IP (reproductive IP per capita daily death rate $q = 0.0032$; nonreproductive TP $q = 0.0062$; Warner, 1984: Table 9). Phase change in *T. bifasciatum* occurs at approximately 75 mm standard length, and territory acquisition at perhaps 95 mm. Application of these rates to determine the probability of a fish reaching a size large enough to hold a mating territory ($p = [1 - q]^{(95-75)/g}$) reveals that an individual remaining a reproductive IP female has a substantially higher likelihood of reaching 95 mm than does an early-changing competitor ($p_{IP} = 0.263$; $p_{TP} = 0.186$). That is, rather than providing the predicted benefit to future reproduction as suggested by the trade-off models, the early changer strategy appears to impose a fitness cost. Other estimates of growth and survival rates for this species (Rogers L, unpublished data) differ in degree from those of Warner (1984), but confirm the low survival probabilities of early-changing, nonreproductive TPs relative to reproductive IPs.

An alternative to the trade-off explanation for early sex change is that early-changed TPs have an increased likelihood of acquiring a harem or a mating territory when one becomes available (Aldenhoven, 1986; Hoffman et al., 1985; Rogers, 1998). Here, the advantage to early sex change is simply being the right sex at the right time. This alternative was noted but not examined in detail by Hoffman et al. (1985), but it is the focus of Aldenhoven's (1986) study on the angelfish *Centropyge bicolor*. Although the fit between Aldenhoven's model and her empirical field data is imperfect, her novel treatment of the size-advantage model emphasizes the probabilistic nature of sex-change timing inherent in many systems, and thus, her interpretation differs from previous theoretical treatments of sex change (see Hoffman et al., 1985; Leigh et al., 1976; Warner et al., 1975). Below, I develop a simple model building on Aldenhoven's perspective to consider the effects of uncertainty on the optimal timing of the shift from the initial to the terminal sex.

The probabilistic size-advantage model

The size-advantage model predicts that sex change will be favored when the functions describing the instantaneous size- or age-specific reproductive rates for males and females cross, holding all other components of the life history equal between the sexes. In this circumstance, one sex always experiences a reproductive rate advantage over the other, except at the point at which these functions intersect. At equilibrium, this intersection is the predicted size at sex change (Leigh et al., 1976; Warner, 1975; Warner et al., 1975). The age- or size-specific reproductive rate for the initial and second sexes can be represented simply as

$$\text{reproductive rate}_i(x) = f_i(x), \quad \text{and} \quad (1A)$$

$$\text{reproductive rate}_s(x) = f_s(x), \quad (1B)$$

where x is size (or age). Under the assumptions of the size-advantage model, $f_s(x)$ has a higher slope than does $f_i(x)$.

Given this, these functions will intersect, and the optimal size at sex change is at x^* satisfying

$$f_i(x^*) = f_s(x^*). \quad (2)$$

Although the size-advantage model has been successfully applied to understand the adaptive significance of sex change for 30 years, some aspects of this model have been criticized as being overly simplistic (see Hoffman et al., 1985; Rogers and Sargent, 2001; Shapiro, 1989; St. Mary, 1997; for response to Shapiro, see Warner, 1988, 1989). One simplification that has not attracted attention previously is that the functions describing the sex- and size-specific reproductive rates are effectively assumed to be realized rates, when in fact they are expected rates. That is, the function $f_i(x)$ in Equation 1A can be decomposed into the product of two component functions: $R_{ipot}(x)$, describing the size-specific potential reproductive rate, and $R_{iprob}(x)$, describing size-specific probability of realizing this potential. Similarly, decomposing Equation 1B and assigning females as the initial sex and males as the second sex (protogyny) to make this example more biologically realistic gives

$$\text{reproductive rate}_f(x) = R_{fprob}(x)R_{fpot}(x), \quad \text{and} \quad (3A)$$

$$\text{reproductive rate}_m(x) = R_{mprob}(x)R_{mpot}(x). \quad (3B)$$

Given Equation 3A, if females are mate-limiting (i.e., female fertility does not increase as a function of the number of mates, and all females are likely to find mates), the distinction between expected and realized rate is immaterial because the realized reproductive rate of individual females will be essentially the same as the expected rate. In such cases, for females the function $R_{fprob}(x)$, describing the probability of mating, is close to one at all sizes, and variance in female fertility is determined almost entirely by variance in the size-specific capacity to produce eggs, $R_{fpot}(x)$.

On the other hand, if males are mate-limited, male fertility is determined primarily by the size-specific probability of mating, $R_{mprob}(x)$ and to a much smaller extent by the size-specific ability to produce sperm, $R_{mpot}(x)$. For males then, the distinction between expected and realized rates is critical, as there is enormous variance in realized reproduction between territory-holding (reproductive) males and nonterritorial (nonreproductive) ones, even if they are the same size, owing to the uncertainty of securing a mating territory.

This probabilistic interpretation does not alter the fundamental logic of the size-advantage model, but it does yield an alternative to the life-history trade-off explanation for early sex change (see Hoffman et al., 1985; Iwasa, 1991). As in Equation 2, the predicted size at sex change (the intersection of the male and female reproductive rate functions) is at size x^* , satisfying

$$R_{fprob}(x^*)R_{fpot}(x^*) = R_{mprob}(x^*)R_{mpot}(x^*). \quad (4)$$

Rearranging this equation gives

$$R_{fprob}(x^*)/R_{mprob}(x^*) = R_{mpot}(x^*)/R_{fpot}(x^*). \quad (5)$$

If, for simplicity, we assume that all females find mates (i.e., $R_{fprob}[x] = 1$), Equation 5 shows that an IP female is predicted to change sex when she reaches the size at which her probability of successful reproduction as a male equals the ratio of the female to male potential reproductive rates. As sex change always proceeds from the sex having the lower reproductive rate to the sex having the higher reproductive rate, and given that we are assuming protogyny, it must be true that

$$R_{fpot}(x^*) < R_{mpot}(x^*), \quad (6)$$

and therefore

$$R_{mprob}(x^*) < 1. \quad (7)$$

Sex change is expected occur at a size at which successful reproduction in the second sex is not assured, and in any such population, there will always be some proportion of sex-changed, but nonreproductive, individuals.

A lottery analogy illustrates this point. Imagine a lottery that costs one unit to play and pays 10 units to the lucky winner. This cost/payoff relationship remains constant through time; however, the odds of winning increase over time, such that a small (or young) individual has a very low chance of winning, whereas a large (or old) individual has a relatively high chance of winning. During the early part of a player's life, when the probability of winning the lottery is less than the ratio of the cost-to-potential benefit (1:10), playing is a losing game. Later in life, however, when the probability of winning becomes more than 0.1, the lottery becomes a winning game, at which point it pays to play the odds. The key is that despite the fact that playing is a winning game, each individual is still much more likely to lose than to win, and we should always expect to find some number of losers (e.g., early changers) in the population.

In *T. bifasciatum*, small IP individuals may be either male or female, whereas large TP individuals are always male. IP males and females have a high probability of realizing a relatively low daily reproductive rate. TP males have very high potential reproductive rates; however, only those TPs that control mating territories are in a position to realize this potential. As IPs of either sex grow over their lifetimes, they eventually reach some critical size at which sex- and/or phase-change occurs. Rewriting Equation 5 to find the optimal size at phase change, x^* , in *T. bifasciatum* gives

$$R_{IPprob}(x^*)/R_{TPprob}(x^*) = R_{TPpot}(x^*)/R_{IPpot}(x^*). \quad (8)$$

If we assume that IP males and females mate every day, $R_{IPprob}(x) = 1$, phase change is predicted to occur at the size at which the probability of mating in the TP equals the ratio of the size-specific reproductive rate in the IP to that in the TP. Because the potential reproductive rate as a TP is always greater than the potential as an IP, $R_{TPpot}(x) > R_{IPpot}(x)$, all populations are inevitably expected to contain some fraction of "apparently early" changers. In *T. bifasciatum*, this could be a very strong effect, as empirical estimates for a territorial TP male are on the order of 20 to 30 matings per day (Warner and Schultz, 1992).

Conclusions

I develop an interpretation of the size-advantage model of sex change explicitly incorporating environmental uncertainty. This interpretation predicts that in uncertain environments the presence of early sex changers is inevitable, as individuals are selected to play the odds. More generally, this model formalizes an explanation for a class of seemingly maladaptive phenotypes.

Odds-playing in this way is distinctly different from the concept of bet-hedging. Bet-hedging is defined as a trade-off between expected fitness and the variance in fitness (Seger and Brockman, 1987). At the level of the individual, bet-hedging leads to a reduction in expected fitness in exchange for a reduction in the variance in fitness. Individuals adopting a bet-hedging strategy maximize geometric mean fitness across generations exhibiting temporal variation. An odds-

playing strategy, on the other hand, leads to a maximization of expected fitness at the level of the genotype, but at the cost of increased variance in fitness among individuals of a given genotype. This effect occurs within a generation in environments exhibiting spatial variation, and, as Seger and Brockman (1987) note, such variation does not lead to bet-hedging.

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REFERENCES

- Aldenhoven JM, 1986. Different reproductive strategies in a sex-changing coral reef fish *Centropyge bicolor* (Pomacanthidae). *Aust J Mar Fresh Res* 37:353–360.
- Charnov EL, 1982. *The theory of sex allocation*. Princeton, New Jersey: Princeton University Press.
- Ghiselin MT, 1969. The evolution of hermaphroditism among animals. *Q Rev Biol* 44:189–208.
- Hoffman SG, Schildauer MP, Warner RR, 1985. The costs of changing sex and the ontogeny of males under contest competition for mates. *Evolution* 39:915–927.
- Iwasa Y, 1991. Sex-change evolution and cost of reproduction. *Behav Ecol* 2:56–68.
- Leigh EG, Charnov EL, Warner RR, 1976. Sex ratio, sex-change, and natural selection. *Proc Natl Acad Sci USA* 73:3656–3660.
- Rogers L, 1998. *The schedule of reproductive effort and the timing of phase change in the bluehead wrasse, Thalassoma bifasciatum* (PhD dissertation). Lexington: University of Kentucky.
- Rogers L, Sargent RC, 2001. A dynamic model of size-dependent reproductive effort in a sequential hermaphrodite: a counterexample to Williams' conjecture. *Am Nat* 158:543–552.
- Seger J, Brockman HJ, 1987. What is bet-hedging? In: *Oxford surveys in evolutionary biology* (Harvey PH, Partridge L, eds). Oxford: Oxford University Press; 182–211.
- Shapiro DY, 1989. Inapplicability of the size-advantage model to coral reef fishes. *Trends Ecol Evol* 4:272.
- St. Mary CM, 1997. Sequential patterns of sex allocation in simultaneous hermaphrodites: do we need models that specifically incorporate this complexity? *Am Nat* 150:73–97.
- Warner RR, 1975. The adaptive significance of sequential hermaphroditism in animals. *Am Nat* 109:61–82.
- Warner RR, 1984. Deferred reproduction as a response to sexual selection in a coral reef fish: a test of the life historical consequences. *Evolution* 38:148–162.
- Warner RR, 1988. Sex-change in fishes: hypotheses, evidence, and objections. *Env Biol Fish* 22:81–90.
- Warner RR, 1989. Reply to Shapiro. *Trends Ecol Evol* 4:272–273.
- Warner RR, 1991. The use of phenotypic plasticity in coral reef fishes as tests of theory in evolutionary ecology. In: *The ecology of fishes on coral reefs* (Sale PF, ed). San Diego, California: Academic Press; 387–398.
- Warner RR, Robertson DR, 1978. Sexual patterns in the labroid fishes of the western Caribbean, I: the wrasses (Labridae). *Smithson Contrib Zool* 254:1–27.
- Warner RR, Robertson DR, Leigh EG, 1975. Sex-change and sexual selection. *Science (Wash DC)* 190:633–638.
- Warner RR, Schultz ET, 1992. Sexual selection and male characteristics in the bluehead wrasse, *Thalassoma bifasciatum*: mating site acquisition, mating site defense, and female choice. *Evolution* 46:1421–1442.
- Warner RR, Swearer SE, 1991. Social control of sex change in the bluehead wrasse, *Thalassoma bifasciatum* (Pisces: Labridae). *Biol Bull* 181:199–204.
- Williams GC, 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *Am Nat* 100:687–690.