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SHORT NOTE

Alternative Life-Histories in Protogynous Fishes: A General Evolutionary Theory

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ABSTRACT: Populations of many 'protogynous' fishes actually consist of 2 life-history pathways. Along one path, an individual is a male for its entire life; along the other, an individual is a female first, a male second. This paper develops a general evolutionary theory predicting the stable proportions of each type in a population – that is the Evolutionarily Stable Strategy (ESS).

Protogyny, sex reversal from female to male, is widely distributed in fish (review in Warner, 1978; Charnov, 1982). It is particularly common in parrotfish and wrasses (families Scaridae and Labridae). The life-history of these often includes 2 color phases, a duller i n i t i a l p h a s e followed by a brighter t e r m i n a l p h a s e, although some species are monochromatic. Many species (Robertson and Choat, 1974; Robertson and Warner, 1978; Warner and Robertson, 1978; Warner and Hoffman, 1980) also show 2 alternative life-history pathways coexisting in a single breeding population. A schematic representation of this is shown in Fig. 1, with special reference to wrasses of the genus *Thalassoma*. Individuals may enter initial phase as either males or females. For example, the figure shows *P* proportion of a cohort entering the male pathway. At some time later in life, not necessarily the same along each pathway, an individual enters terminal phase. Such individuals are males, and in contrast to initial phase fish, often have very different color, reproductive anatomy, and behavior patterns. Thus individuals who were female in initial phase reverse their sex to enter terminal phase (in addition to the other changes). However, the initial phase males simply alter color, anatomy and behavior, since they are already males.

This case of alternative life-histories is one of the most spectacular known for vertebrates (Gross and Charnov, 1980; review: Rubenstein, 1980); a quite comparable situation exists for some protandrous shrimp (Charnov, 1979, 1981, 1982; Charnov et al., 1978). It allows us to test one particular form of

evolutionary theory. The 2 pathways are thought to coexist because of frequency dependent natural selection. A wide variety of autosomal population genetic models predict that the proportion of individuals going down each pathway will be adjusted (in equilibrium or at ESS) such that the reproductive gains per individual are equalized for the 2 pathways (e.g. Gross and Charnov, 1980). This paper proposes a general ESS model, which theoretically links *P* to some other life history characteristics.

For the 2 pathways shown in Fig. 1 (with reference to *Thalassoma* spp.), Warner and Hoffman (1980) showed the ESS *P* to follow a particularly simple form. Their derivation assumed: (1) mortality, growth and change to terminal phase was the same on average for all initial phase individuals; (2) females mated once each day, and there was no tendency for larger or smaller females to mate with terminal as opposed to initial phase males; (3) the life history during terminal phase was on average equivalent for the 2 pathways; (4) that the population was stationary (unchanging in size with
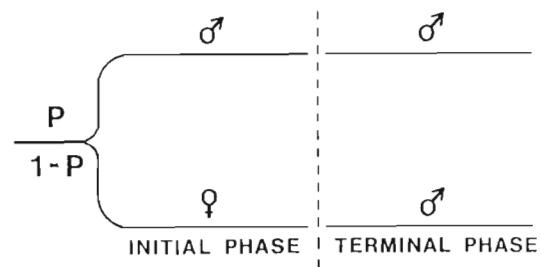

Fig. 1. *Thalassoma* spp. Alternative life-history pathways in wrasse of the genus *Thalassoma*. A certain proportion of the cohort *(P)* first mature as males, the rest *(1−P)* mature as females. These are i n i t i a l p h a s e fish. Later in life the males change color becoming t e r m i n a l p h a s e males. They then defend territories and pair-spawn with females. Later in life initial phase females change b o t h sex and color to become terminal phase males. Initial phase males (often) group spawn with some females. The ESS *P* equalizes the reproductive gains of the 2 pathways

a stable age distribution). Their result was very simple; in ESS, P was related to 2 population parameters. Define:

$T^{\bullet}$ = average number of females who mate each day with each terminal phase male.

$S^{\bullet}$ = proportion of the population in terminal phase. The Warner-Hoffman result was that

$$P = 1/2 \left[1 - \frac{T^{\bullet} \cdot S^{\bullet}}{(1 - T^{\bullet})} \right] \tag{1}$$

For the 2 species of the genus *Thalassoma* they studied, $T^{\bullet} \cdot S^{\bullet} < .1$, so that Equation (1) is almost equivalent to

$$P \sim 1/2 \, (1 - T^{\bullet} \cdot S^{\bullet}) \tag{2}$$

The testing of this relation (Eq. 2) for these 2 species is in Warner and Hoffman (1980) and Charnov (1982). Charnov (1982) showed that Equation 1 is equivalent to

$$P = \frac{h}{1 + h} \quad \left(\text{or} \ \frac{P}{1 - P} = h \right) \tag{3}$$

where h = proportion of the entire female population who mate with the initial phase males. This relation also relaxed the assumption that females mated once each day – indeed, in many laborid species females probably mate less often than once each day.

Warner (pers. comm., cited in Charnov, 1982) had noted, however, that some locations with *Thalassoma* had initial phase male, b u t that these males did not breed. Charnov (1982) suggested that this type of initial phase male could nonetheless be in ESS, provided that the initial phase non-breeding male more than doubled its chances of reaching terminal phase. That is, the nonbreeding individual might survive better and/or grow faster, contrasted to an initial phase female. According to Charnov (1982), if such a nonbreeder male has a chance α of reaching terminal phase, compared to a chance of 1 for an initial phase female (i.e... he is α times more likely to reach terminal phase), a stationary population has an ESS P where

$$P/(1 - P) = 1 - 2/\alpha \ (\alpha \geq 2) \tag{4}$$

Now, Equation (3) assumes the 2 life-history pathways to be equivalent in growth and mortality while allowing the initial phase males access to h proportion of the females. Eq. (4) allows the 2 pathways to differ in growth and mortality, but assumes that no females are available to mate with initial phase males. Clearly, the 2 key variables are h and α, and what we would like to do is to combine them into one ESS theory. I have done this for one general situation and report here the answer This ESS P was derived by introducing into a stationary population a mutant gene whose bearer alters its own P, α, or the proportion of the h females it

mates with. We then look for population values for P and α such that the mutant is always selected against. Since this method of analysis is detailed in Charnov (1982), I will not present the algebra here, but will simply discuss the final result. If h and α are assumed to take fixed values (or to be a function of each other) or if a rare mutant who alters its α to $\hat{\alpha}$ (e.g. expends more energy in reproduction) does not really alter the population wide h (the mutant ($\hat{\alpha}$) initial phase male may well garner for itself a greater fraction of the females who are available to a l l the initial phase males, but overall h of the females go to the little males), then the ESS $P/(1 - P)$ is the positive root of the following quadratic equation. Let $A = P/(1 - P)$; the equation is

$$\alpha A^2 - A(\alpha + h - 2) - h = 0 \tag{5}$$

If $\alpha = 1$, $A = h$; if $h = 0$, $A = 1 - 2/\alpha$ (these are Equations 3 and 4).

In Fig. 2, I have graphed $P/(1 - P)$ versus h for 4 α values. Somewhat surprisingly, for α between .5 and 1.5 (which seem like large deviations in the male compared to the female pathway), the rule $P/(1 - P) \sim h$ is still very close to that theoretically predicted.
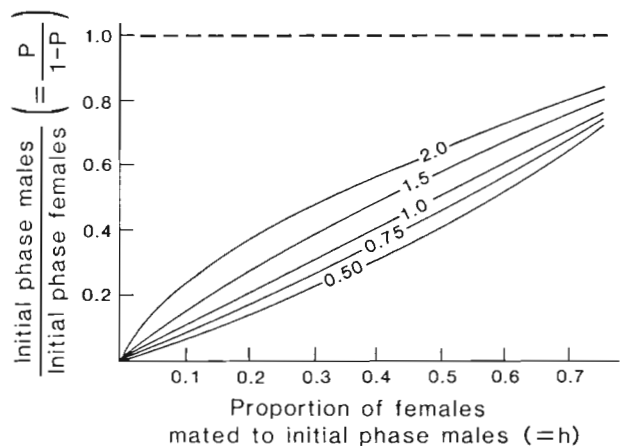

Fig. 2. The ESS $P/(1 - P)$ as a function of h, the proportion of the females who mate with initial phase males, and α, the relative chances of an initial phase male (compared to a female) making it to terminal phase. For α between .5 and 1.5, the relation $P/(1 - P) \sim h$ is a good approximation

Charnov (1982) discussed several data sets for labroid fishes (work of Warner, Robertson, Hoffman, Choat as cited above), and concluded that P was related to h as predicted (Eq. 3), at least qualitatively. While there are no published data on α, such field data may be possible . . in which case we can test the more general theory as given in Equation (5).

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