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EVOLUTION OF THE BREEDING SEX RATIO UNDER PARTIAL SEX CHANGE

ERIC L. CHARNOV
Department of Biology, University of Utah, Salt Lake City, UT 84112

One of R. A. Fisher's (1930) major insights on evolution of the sex ratio was that differential sex-specific mortality after the period of parental care would not affect the favored primary sex ratio. Many explicit population-genetic models support this conclusion (e.g., Leigh, 1970; Shaw and Mohler, 1953; Karlin and Lessard, 1986). The meaning of this is quite straightforward: the adult or breeding sex ratio is not itself a target of natural selection; it is simply the ratio that results from selection on the primary sex ratio (usually for ½) combined with the prevailing sex-specific mortality and maturation schedules. This lack of direct natural selection on the breeding sex ratio is perhaps nearly universal for typical dioecious species. Interestingly, this result is not true for sex-reversing organisms. While the usual sex-allocation problem is here taken to be natural selection acting on the age or size at sex transformation (Leigh et al., 1976; Warner, 1988*a*, 1988*b*; Charnov, 1982*a*), alteration of that age also changes the breeding sex ratio. It is a fair statement that, under sex reversal, natural selection acts directly on the breeding sex ratio (Charnov, 1982*a*; Charnov and Bull, 1989).

This paper deals with evolution of the adult sex ratio in partially sex-changing species. Consider protogyny in which an individual reproduces first as a female, then changes sex to reproduce for the rest of its life as a male. Upon closer examination, many protogynous fish species have been found to have populations that consist of sex changers and pure males (Warner and Robertson, 1978; Robertson and Warner, 1978; Choat and Robertson, 1975). The typical life history is illustrated in Figure 1. The young fish may be either male or female; the older ones are male. The initial phase may often have different coloration from the terminal phase; initial-phase males usually use different reproductive tactics than terminal-phase males (Warner and Hoffman, 1980). Charnov (1982*a*), building on the pioneering work of Warner and Hoffman (1980), showed that the ESS proportion of males among the initial-phase fish (*P*) could be written as:

$$P = \frac{h}{1 + h} \qquad (1)$$

where *h* is the proportion of the females who mate with initial-phase males. While the original derivation of (1) assumed no sex differences during the initial phase in growth, mortality, or age at change to terminal phase, later work showed that the result was fairly robust to violations of these assumptions, at least for *h* not near 1 (Charnov, 1982*b*). Let *T* be the proportion of the breeding population in the terminal phase and let *r* be the proportion of males among the breeders (the adult sex ratio). Then, *r* is of course

$$r = T + (1 - T)P;$$

or, from (1), we have

$$r = \frac{h + T}{1 + h}. \qquad (2)$$

If *h* and *T* can take on any values from 0 to 1, then virtually all sex ratios are possible. However, there is one further constraint that limits combinations of *h* and *T*. Protogynous sex reversal is only stable if males gain substantial reproductive ability with age (or size) (Warner, 1988*a*, 1988*b*). At the minimum each terminal-phase male must mate with more females per unit time does each initial-phase male. If the breeding population is of size *N*, this restriction is that
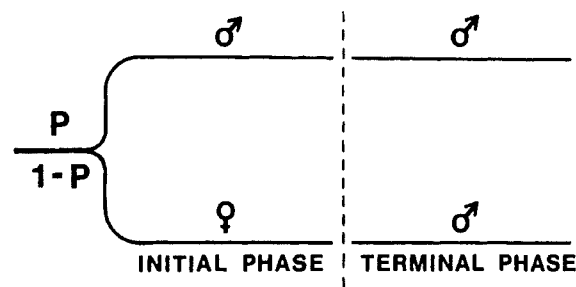

FIG. 1. Many labroid fishes have populations that consist of a mixture of protogynous sex changers and pure males. The fish often come in two color forms, initial phase (IP) and terminal phase (TP). IP fish may be male or female, while all TP fish are male. *P* is the proportion of the IP fish who are male.
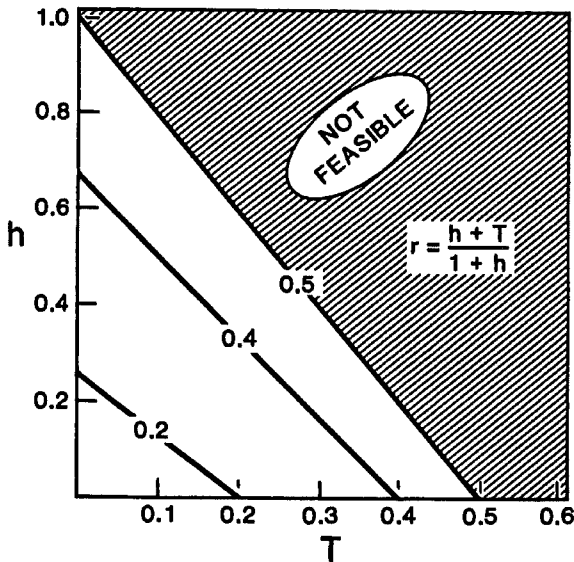
FIG. 2. The ESS breeding sex ratio (r = proportion males) is predicted to be female-biased, or $r < \frac{1}{2}$. T is the proportion of the breeding population in terminal phase, while h is the proportion of the females who mate with initial-phase males. Some combinations of h and T are predicted not to occur (the "not feasible" region), because protogyny is itself unstable, at least according to sex-allocation theory. It is for this reason that r is predicted to be less than $\frac{1}{2}$.

$$\frac{(1 - T)(1 - P)(1 - h)N}{TN} > \frac{(1 - T)(1 - P)hN}{(1 - T)PN} \quad (3)$$

or, using Equation (1),

$$h < 1 - 2T. \quad (3)$$

We might also view this stability condition to be the decision of a female to become a terminal-phase male; (3) also holds for this condition, since, at the ESS P, initial-phase females have the same fitness as initial-phase males (Warner and Hoffman, 1980).

In Figure 2, I show a plot of T and h in which the plane is divided into the two regions according to (3). I also graph the ESS adult sex ratio [Eq. (2)] in the feasible region. Interestingly, the boundary given by (3) is at $r = \frac{1}{2}$; that is, if we set $h = 1 - 2T$ and substitute it into (2), r equals $\frac{1}{2}$. Everyplace else in the feasible region, r is less than $\frac{1}{2}$. The theoretical prediction can be summarized as follows: in a mixed population of protogynous sex changers and pure males, the overall breeding sex ratio will favor females ($r < \frac{1}{2}$). It will also favor females in the purely protogynous species, where $h \to 0$ (see also Charnov and Bull [1989]).

Warner, Robertson, and Choat (Warner and Robertson, 1978; Robertson and Choat, 1973; Choat and Robertson, 1975; Robertson and Warner, 1978) have breeding sex-ratio data for 27 species of labroid fishes (Wrasses and Parrotfish) from Australia's Great Barrier Reef and from the western Caribbean. Nine of the species are "purely protogynous" with less than 2% males among the initial phase; the other 18 have mixed populations, with the proportion of initial-phase males ranging from about 5% to over 30%. Figure 3A shows
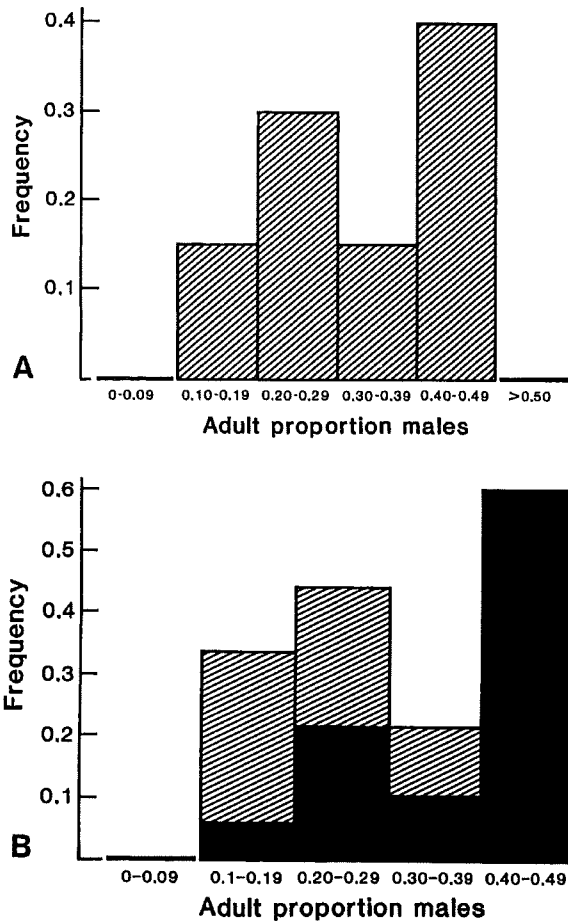

FIG. 3. A) Frequency diagram of the breeding sex ratio (r) for 27 species of labroid fishes. Nine are purely protogynous; 18 have mixed populations as in Figure 1. All have $r < \frac{1}{2}$. B) Separate frequency diagrams for the protogynous (▨) species and the species with mixed populations (■). See text for further discussion.

the breeding sex-ratio histogram for all 27 species. Clearly, all support the theoretical prediction of a female-biased sex ratio (Fig. 2). Figure 3B separates the species into those with only sex changers and those with mixed populations. The mixed-population species have the more even sex ratios, but all are female-biased. The striking part of Figure 3B is that, while about 60% of the mixed-population species have breeding sex ratios of 0.40–0.49, none goes above 0.5; it is as if 0.5 is a barrier that cannot be penetrated. This is exactly the role our ESS sex-ratio inequality assigns to $\frac{1}{2}$.

The form of evolutionary theory developed here is probably applicable to many other problems. Our goal is to divide the possible or conceivable states of the world into two kinds, those that are allowed and those that are precluded. Figure 2 shows how a combination of ESS sex-ratio theory [Eq. (2)] and the conditions for the stability of sex change itself [Expression (3)] combine to do this in the present problem. Interestingly, of the allowed feasible states, almost all occur somewhere (Fig. 3A), thus, the usefulness of our focus on the larger issue of presence versus absence, rather than the exact predictions of a numerical value in a partic-

ular case [see Warner and Hoffman (1980) for a test of
Eq. (1) in some particular cases].

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ENIGMATIC REPTILIAN SEX RATIOS

J. J. BULL
Department of Zoology, University of Texas, Austin, TX 78712

AND

E. L. CHARNOV
Department of Biology, University of Utah, Salt Lake City, UT 84112

When confronted with the academic question of sex-
ratio evolution, the untrained person typically sup-
poses that natural selection favors a female excess in
the population. However, research spanning half a cen-
tury has led sex-ratio experts to conclude that a female
excess is favored only under unusual circumstances.
An objective evaluation of sex ratios in reptiles with
environmental sex determination offers the humbling
prospect that the nonexperts are closer to the truth.
The failure of sex-ratio theory to explain reptilian sex
ratios stands in sharp contrast to its empirical success
in other groups and thus warrants special attention.

The unexplained sex-ratio phenomena in reptiles
come chiefly from species with temperature-dependent
sex determination: incubation temperature determines
whether embryos hatch as male or female in perhaps
all crocodilians, many turtles, and at least a few lizards

(Bull, 1980; Raynaud and Pieau, 1985). Two problems
arise in understanding sex-ratio evolution in these sys-
tems. First, there is no clear advantage of environ-
mental sex determination. Second, the primary sex ra-
tio of many species heavily favors females (reviewed
in Bull and Charnov [1988]). Here, we illustrate how
sex-allocation theory addresses each of these problems,
and we discuss empirical evidence in light of the rel-
evant models.

Hypotheses for Evolution of Environmental Sex Determination and a Skewed Primary Sex Ratio

Charnov and Bull (1977) proposed a model to ex-
plain the evolution of environmental sex determina-
tion which assumes that sex is determined in response
to an environmental factor differentially influencing