

Sex Change and Sexual Selection

Robert R. Warner, D. Ross Robertson, Egbert G. Leigh, Jr.



Sex Change and Sexual Selection

The reproductive biology of a labrid fish is used to illuminate a theory of sex change.

Robert R. Warner, D. Ross Robertson, Egbert G. Leigh, Jr.

Many writers have discussed sequential hermaphroditism, wherein individuals are all born of one sex and change to the other as they grow older, in terms of its advantage to the species (1). Ghiselin (2) shifted the focus by suggesting that if members of one sex increase in fertility more rapidly with age than those of the other, then natural selection will favor a genotype whose individuals are all born into the sex that suffers less from being young (the sex whose fertility increases more slowly with age) and then change to the sex that gains more from being old and large. Simulations of Warner (3) have verified Ghiselin's suggestion. The change of sex may be strictly genetically controlled, or triggered by external events such as the loss of a dominant male from a harem (4), or it may be effected by some combination of the two mechanisms.

Here we present a unified mathematical theory, in terms of selection on individuals, of the circumstances favoring sex change. We discuss the intrinsic disadvantage of changing sex, the conditions that reverse this disadvantage, and the optimum age of changing sex when one sex does gain fertility more rapidly than the other. Finally, we consider the extraordinary male dimorphism, involving small nonterritorial males and large territorial ones, that can arise when a runaway sexual selection among the members of the transformed or older sex (usually male) permits a small difference in size or age to confer a disproportionate difference in fertility. This is similar to the dimorphism between male red deer with and without antlers discussed by Gadgil (5). We believe, however, that the selective mechanism maintaining sexual dimorphism in sex-changing fish is more obvious and easier to explain.

The bluehead wrasse, *Thalassoma bifasciatum*, which lives on coral reefs throughout the western Atlantic, strikingly illustrates the type of polymorphism we wish to explain. This species has a mating

system that closely resembles that of lek-forming birds and mammals (6): each day near midday females visit a restricted area in which up to several dozen large brightly colored males hold temporary spawning territories, and choose the largest and most brightly colored of these males for mating. Sexual selection, which is extreme in such leks, results in differences in fertility among the territorial males far greater than one would expect from the differences in their sizes, and as Ghiselin predicts, we find individuals in this species that are born female and turn male when large enough to compete successfully as territory holders.

The more definite the females tend to be in their choice (that is, the greater the gain of fertility with size in the males), the larger one must be to compete successfully, so the later one should change sex. In some situations where strong sexual selection has led to a very low proportion of territorial males, there exist some individuals that are born as males, and while they are young they live, in effect, by circumventing the territorial hierarchy rather than competing in it. They do this by actively interfering in the spawning activities of territorial males. In the second part of the article, we relate our theory to the natural history of this wrasse.

Intrinsic Disadvantages of Hermaphroditism

There is likely a physiological cost to changing sex, although we have no information on its magnitude. There is also a purely genetic penalty to sex change: if death rate and the proportionate gain of fertility with age are the same in each sex, then an allele whose bearers are all born female and turn male at age T will normally be displaced by a gonochore allele whose bearers are born male and female in equal numbers and do not change sex.

The hermaphrodites can hold their own only if they change sex at just the age at which half the reproductive value of a cohort of gonochore females all born at once would have been exhausted—that is, the age at which this cohort has made exactly half of its eventual contribution to the gene pool of future generations—and this is infinitely improbable.

To show this, we consider a single locus with two alleles, A and B, in a population of sexual haploids. Assuming haploidy greatly simplifies the mathematics without affecting any conclusions of biological interest. Let $N_{Am}(t)$, $N_{Af}(t)$, $N_{Bm}(t)$, and $N_{Bf}(t)$ be the numbers of A males, A females, B males, and B females at time t . Let the offspring of matings between A and A be gonochores (which do not change sex), half of them male and half female, while the offspring of matings between B and B are all females which turn male at age T , and a quarter of the offspring of matings between A and B are male A gonochores, another quarter are female A gonochores, and the remaining half are B females which turn male at age T . Suppose that a male of any age alive at time t has a chance $\mu\Delta t$ of dying before the slightly later time $t + \Delta t$, while a female alive at time t has chance $\lambda\Delta t$ of dying before $t + \Delta t$. Finally, let an individual's fertility be e^{bx} times that of an individual of the same sex but x time units younger.

Assume that the population consists almost entirely of hermaphrodite B-bearers, whose age composition is static and whose numbers do not change with time, while the A-bearing gonochores are rare enough to have a constant logarithmic growth rate yet common enough to have attained a stable age distribution. Then the logarithmic growth rate c of the numbers of A-bearers represents the selective advantage of A over B. These assumptions permit us to find the average selective advantage of a rare gonochore allele without worrying about fluctuations in age composition and the like.

Since hermaphrodites are so common that they mate essentially only with each other, we may write

$$\begin{aligned} dN_{Bf}/dt = & -\lambda N_{Bf} + \\ & rV_{Bm}(t)N_{Bm}(t)V_{Bf}(t)N_{Bf}(t) - \\ & re^{-\lambda T}V_{Bm}(t-T)N_{Bm}(t-T)V_{Bf}(t-T)N_{Bf}(t-T) \end{aligned} \quad (1)$$

Robert Warner is an assistant professor in the Department of Biological Sciences, University of California, Santa Barbara 93106. Ross Robertson and Egbert Leigh are staff biologists at the Smithsonian Tropical Research Institute, Balboa, Canal Zone. This work was completed while Dr. Warner was a Smithsonian postdoctoral fellow and Dr. Robertson a visiting postdoctoral fellow from the Australian Commonwealth Scientific and Industrial Research Organization at the Smithsonian Tropical Research Institute.

where λ is the per capita death rate among females, $V_{Bm}(t)$ is a relative measure of the average fertility per head among B males at time t , V_{Bf} is the same for B females, the second term on the right is the number of B born per unit time at time t , and the third term on the right is the number of B females turning male per unit time at time t , which is the number of B females born T time units before times the proportion $e^{-\lambda T}$ which survive to change sex. Since we have assumed that the numbers and age composition of B are constant, we may rewrite Eq. 1 as

$$0 = dN_{Bf}/dt = -\lambda N_{Bf} + r(1 - e^{-\lambda T})V_{Bm}N_{Bm}V_{Bf}N_{Bf} \quad (2)$$

where the V 's as well as the N 's are constant. Similarly,

$$0 = dN_{Bm}/dt = -\mu N_{Bm} + re^{-\lambda T}V_{Bm}N_{Bm}V_{Bf}N_{Bf} \quad (3)$$

where μ is the male death rate: the number of B males dying just balances the number of B females changing sex.

The number of x -year-old B females in the population is the number born x years ago times the proportion $e^{-\lambda x}$ surviving to age x : since the same number of B are born each year, $e^{-\lambda x}$ measures the relative number of B females aged x . Calling e^{bx} the relative fertility of a female aged x , then

$$V_{Bf} = \frac{\int_0^T e^{bx} e^{-\lambda x} dx}{\int_0^{\infty} e^{-\lambda x} dx} \quad (4)$$

If $e^{b(T+x)} = e^{bT} e^{bx}$ is the relative fertility of a male aged $T+x$, then

$$V_{Bm} = \frac{e^{bT} \int_0^{\infty} e^{bx} e^{-\mu x} dx}{\int_0^{\infty} e^{-\mu x} dx} \quad (5)$$

Gonochores are so rare that they can mate essentially only with hermaphrodites. If matings between A males and B females produce $rV_{Am}N_{Am}V_{Bf}N_{Bf}$ offspring per unit time, of which a quarter are A males and a quarter A females (the other half being B females), and if matings between B males and A females produce $rV_{Bm}N_{Bm}V_{Af}N_{Af}$ offspring of the same genetic composition as before, then

$$dN_{Af}/dt = cN_{Af} = -\lambda N_{Af} + \frac{1}{4}r(V_{Af}N_{Af}V_{Bm}N_{Bm} + V_{Am}N_{Am}V_{Bf}N_{Bf}) \quad (6)$$

$$dN_{Am}/dt = cN_{Am} = -\mu N_{Am} + \frac{1}{4}r(V_{Af}N_{Af}V_{Bm}N_{Bm} + V_{Am}N_{Am}V_{Bf}N_{Bf}) \quad (7)$$

Both V_{Am} and V_{Af} are constant because the age composition of the A's is unchanging. Since e^{-cx} times as many A females were born x time units ago as

now, and since a proportion $e^{-\lambda x}$ of these have died, there are $e^{-(\lambda+c)x}$ times as many x -year-old as newborn females in the population, so

$$V_{Af} = \frac{\int_0^{\infty} e^{bx} e^{-(\lambda+c)x} dx}{\int_0^{\infty} e^{-(\lambda+c)x} dx} \quad (8)$$

To find V_{Am} , substitute μ for λ in Eq. 8.

To calculate the selective advantage c of A over B, notice first that Eqs. 6 and 7 imply $(\lambda + c)N_{Af} = (\mu + c)N_{Am}$, or $N_{Am} = (\lambda + c)N_{Af}/(\mu + c)$. Substituting for N_{Am} in Eq. 6 and rearranging, we write

$$\frac{d}{dt} \log N_{Af} = c = -\lambda + \frac{1}{4}r \left[V_{Af}V_{Bm}N_{Bm} + \left(\frac{\lambda + c}{\mu + c} \right) V_{Am}V_{Bf}N_{Bf} \right] \quad (9)$$

Eq. 2 implies $\lambda = r(1 - e^{-\lambda T})V_{Bf}V_{Bm}N_{Bm}$ while Eq. 3 implies $\mu = re^{-\lambda T}V_{Bm}V_{Bf}N_{Bf}$. Substituting for $V_{Bm}N_{Bm}$ and $V_{Bf}N_{Bf}$ in Eq. 9, we may write

$$\frac{d}{dt} \log N_{Af} = c = -\lambda + \frac{\lambda}{4(1 - e^{-\lambda T})} \frac{V_{Af}}{V_{Bf}} + \left(\frac{\lambda + c}{\mu + c} \right) \frac{\mu}{4e^{-\lambda T}} \frac{V_{Am}}{V_{Bm}} \quad (10)$$

One solves this equation by successive approximations. Find the first approximation for $d \log N_{Af}/dt$ by setting $c = 0$ on the right side of Eq. 10, then plug this first approximation for c in on the right to find a second, and repeat the process until successive approximations no longer differ sensibly from each other. However, it is not our business here to pass through this vale of tears: the first approximation to $d \log N_{Af}/dt$ tells us the direction of selection, which is all we need to know in this article.

Were $c = 0$, V_{Af}/V_{Bf} would be $(1 - e^{-\lambda T})/(1 - e^{-(b-\lambda)T})$, and V_{Am}/V_{Bm} would be e^{-bT} . Substituting for these ratios in Eq. 10, we find $d \log N_{Af}/dt > 0$ and A favored over B if

$$-\lambda + \frac{\lambda}{4[1 - e^{-(b-\lambda)T}]} + \frac{\lambda}{4e^{-(b-\lambda)T}} > 0$$

This inequality may be rearranged as

$$\frac{\lambda[1 - 2e^{-(b-\lambda)T}]^2}{4e^{-(b-\lambda)T}[1 - e^{-(b-\lambda)T}]} > 0 \quad (11)$$

Gonochores are favored over hermaphrodites unless $e^{-(b-\lambda)T} = 1/2$, which happens if hermaphrodites turn male at just the age where half the reproductive value of a cohort of equal-aged females would be exhausted.

More complex models occasionally admit circumstances where hermaphrodites are favored over gonochores even though each sex gains equally in fertility

with age, but in general a genetic penalty such as we have described occurs when T is genetically fixed.

Uses of Hermaphroditism

Suppose now that the relative fertility of a female aged x is e^{bx} , while that of a male aged x is $e^{b'x}$, where $b' > b$. Will a sex-change allele replace the gonochores?

Several workers (7) have shown that if male and female births cost parents the same amount, gonochores should bear equal numbers of each sex, regardless of differences between the sexes either in death rate or in the increase of fertility with age. We accordingly assume that matings between gonochores produce half males and half females.

Suppose first that the gonochore allele A prevails in the population, so that matings with hermaphrodites contribute negligibly to gonochore numbers, and suppose that gonochore numbers are constant. Then

$$0 = dN_{Af}/dt = -\lambda N_{Af} + \frac{1}{2}rV_{Am}N_{Am}V_{Af}N_{Af} \quad (12)$$

$$0 = dN_{Am}/dt = -\mu N_{Am} + \frac{1}{2}rV_{Am}N_{Am}V_{Af}N_{Af} \quad (13)$$

where

$$V_{Af} = \frac{\int_0^{\infty} e^{bx} e^{-\lambda x} dx}{\int_0^{\infty} e^{-\lambda x} dx} \quad (14)$$

and V_{Am} is defined analogously. By contrast, B-bearers are rare enough to have a constant logarithmic growth rate c but common enough to have attained a stable age distribution, making V_{Bm} and V_{Bf} constant. As B's here are born essentially only from matings between A and B we may write, recalling that N_{Am} is constant, $N_{Bf}(t - T) = e^{-cT}N_{Bf}(t)$, and so forth,

$$dN_{Bm}/dt = cN_{Bm} = -\mu N_{Bm} + \frac{1}{2}re^{-\lambda T}(V_{Am}N_{Am}V_{Bf}N_{Bf}e^{-cT} + V_{Af}N_{Af}V_{Bm}N_{Bm}e^{-cT}) \quad (15)$$

$$dN_{Bf}/dt = cN_{Bf} = -\lambda N_{Bf} + \frac{1}{2}r(1 - e^{-(\lambda+c)T})(V_{Am}N_{Am}V_{Bf}N_{Bf} + V_{Af}N_{Af}V_{Bm}N_{Bm}) \quad (16)$$

Notice that $2(\lambda + c)N_{Bf}/r(1 - e^{-(\lambda+c)T}) = 2(\mu + c)N_{Bm}/re^{-(\lambda+c)T} = V_{Am}N_{Am}V_{Bf}N_{Bf} + V_{Af}N_{Af}V_{Bm}N_{Bm}$, so that

$$N_{Bf} = \left(\frac{\mu + c}{\lambda + c} \right) \frac{1 - e^{-(\lambda+c)T}}{e^{-(\lambda+c)T}} N_{Bm} \quad (17)$$

Substituting for N_{Bf} in Eq. 15, using Eqs. 12 and 13 to eliminate N_{Am} and N_{Af} from Eq. 15, and setting $c = 0$ on the right to find whether $d \log N_{Bm}/dt > 0$, we find B is favored if

$$-\mu + \mu \frac{V_{Bm}e^{-\lambda T}}{V_{Am}} + \mu \frac{V_{Bf}(1 - e^{-\lambda T})}{V_{Af}} > 0 \quad (18)$$

Substituting in for V_{Bm}/V_{Am} and V_{Bf}/V_{Af} , we find B is favored if

$$-\mu + \mu e^{(b'-\lambda)T} + \mu(1 - e^{(b-\lambda)T}) > 0 \quad (19)$$

If $b' > b$, B is favored no matter what the age of sex change, as Warner (3) discovered from his simulations. When B is rare, the skewing of sex ratio it introduces matters hardly at all, and it is selected solely through the enhanced average fertility accruing to a hermaphrodite strategy under these conditions. As B spreads, however, selection on the age of sex change becomes more important, so we turn to this topic next.

The Proper Age to Change Sex

To find the optimum age for changing sex, we ask when selection will favor a rare allele A whose members change sex at age $T - \Delta T$, in a static population composed primarily of B-bearers changing sex at age T . That age for which a slight change ΔT in the age of sex change is selectively neutral is the best age to change sex.

We speak of the age of sex change as if it were genetically fixed. However, in a constant environment such as we have been assuming, an animal that changes sex in response to external influences should do so at the same age as an animal that changes sex at a genetically fixed stage of development.

Suppose that the fertilization and death rates of male and female hermaphrodites are the same as before. If we recall that N_{Bm} and N_{Bf} are constant, while $N_{Am}(t - T + \Delta T) = e^{-c(T-\Delta T)} N_{Am}(t)$, and so forth, and if we assume that ΔT and c are so small that their product is negligible, then

$$0 = dN_{Bm}/dt = -\mu N_{Bm} + re^{-\lambda T} V_{Bm} N_{Bm} V_{Bf} N_{Bf} \quad (20)$$

$$0 = dN_{Bf}/dt = -\lambda N_{Bf} + r(1 - e^{-\lambda T}) V_{Bm} N_{Bm} V_{Bf} N_{Bf} \quad (21)$$

$$dN_{Am}/dt = cN_{Am} = -\mu N_{Am} + \frac{1}{2} r e^{-\lambda(T-\Delta T)} (V_{Am} N_{Am} e^{-cT} V_{Bf} N_{Bf} + V_{Af} N_{Af} e^{-cT} V_{Bm} N_{Bm}) \quad (22)$$

Using Eqs. 20 and 21 to clear $V_{Bf} N_{Bf}$ and $V_{Bm} N_{Bm}$ from Eq. 22, setting

$$N_{Af} = \left(\frac{\mu + c}{\lambda + c} \right) \frac{N_{Am} [1 - e^{-\lambda(T-\Delta T)-cT}]}{e^{-\lambda(T-\Delta T)-cT}} \quad (23)$$

and setting $c = 0$ on the right, we find that A is favored if

$$\frac{\mu}{2} \left[\frac{e^{-\lambda(T-\Delta T)}/e^{-\lambda T}}{V_{Bm}} + \frac{\mu}{2} \left[\frac{1 - e^{-\lambda(T-\Delta T)}}{1 - e^{-\lambda T}} \right] \frac{V_{Af}}{V_{Bf}} - \mu > 0 \quad (24)$$

Since $V_{Af} = [1 - e^{(b-\lambda)(T-\Delta T)}]/[1 - e^{-\lambda(T-\Delta T)}]$, $V_{Bf} = [1 - e^{(b-\lambda)T}]/[1 - e^{-\lambda T}]$, and $V_{Am}/V_{Bm} = e^{-b'\Delta T}$, A is accordingly favored if

$$\frac{\mu}{2} \frac{e^{(\lambda-b')\Delta T} + \frac{\mu}{2} \left[\frac{1 - e^{(b-\lambda)(T-\Delta T)}}{1 - e^{(b-\lambda)T}} \right] - \mu > 0 \quad (25)$$

Setting $e^{(b'-\lambda)\Delta T} = 1 + (b' - \lambda)\Delta T$ and $e^{(b-\lambda)(T-\Delta T)} = e^{(b-\lambda)T}(1 - (b - \lambda)\Delta T)$, and dividing through by $\frac{1}{2}\mu\Delta T$, we find that A and B are in equipoise, and the age of sex change accordingly optimum, when

$$\lambda - b' + \frac{(b - \lambda)e^{(b-\lambda)T}}{1 - e^{(b-\lambda)T}} = 0 \quad (26)$$

that is, when

$$1 - \frac{e^{(b-\lambda)T}}{1 - e^{(b-\lambda)T}} = \frac{b' - b}{\lambda - b} \quad (27)$$

Notice that $(b' - b)/(\lambda - b)$ cannot attain to or exceed 1: in particular, $b' < \lambda$ (8). The greater $b' - b$ —that is, the stronger the gain in fertility with age of males relative to females—the smaller $e^{(b-\lambda)T}$ should be, the later one should change sex, and thus the fewer males there should be.

A sex-change allele whose bearers turn male at the optimum age can exclude any gonochore mutant whose bearers are as fertile as hermaphrodites of the same age and sex. To see this, let A be a rare gonochore allele whose carriers bear male and female offspring in the ratio $1 - k : 1 + k$, in a stable population of hermaphrodites changing sex at the optimum age T . Then

$$0 = dN_{Bf}/dt = -\lambda N_{Bf} + r(1 - e^{-\lambda T}) V_{Bm} N_{Bm} V_{Bf} N_{Bf} \quad (28)$$

$$0 = dN_{Bm}/dt = -\mu N_{Bm} + re^{-\lambda T} V_{Bm} N_{Bm} V_{Bf} N_{Bf} \quad (29)$$

$$dN_{Am}/dt = cN_{Am} = -\mu N_{Am} + \frac{1}{4} r(1 - k)(V_{Am} N_{Am} V_{Bf} N_{Bf} + V_{Af} N_{Af} V_{Bm} N_{Bm}) \quad (30)$$

Clearing $V_{Bm} N_{Bm}$ and $V_{Bf} N_{Bf}$ from Eq. 30 with the aid of Eqs. 28 and 29, setting $N_{Af} = (1 + k)(\mu + c)N_{Am}/(\lambda + c)(1 - k)$, and setting $c = 0$ on the right, we find $d \log N_{Am}/dt > 0$ if

$$-\mu + \frac{\mu}{4} \left[\left(\frac{1 - k}{e^{-\lambda T}} \right) \frac{V_{Am}}{V_{Bm}} + \left(\frac{1 + k}{1 - e^{-\lambda T}} \right) \frac{V_{Af}}{V_{Bf}} \right] > 0 \quad (31)$$

Since $V_{Am}/V_{Bm} = 1/e^{b'T}$ and $V_{Af} V_{Bf} = [1 - e^{-\lambda T}]/[1 - e^{(b-\lambda)T}]$, we may rewrite this inequality as

$$-\mu + \frac{\mu}{4} \left[\frac{1 - k}{e^{(b'-\lambda)T}} + \frac{1 + k}{1 - e^{(b-\lambda)T}} \right] > 0 \quad (32)$$

If the gonochores bear only females, so $k = 1$, gonochores are favored only if $2[1 - e^{(b-\lambda)T}] < 1$. If $b' > b$, and if the

hermaphrodites change sex at the optimum age, the gonochores are never favored (see Eq. 27). If the gonochores bear only males, so $k = -1$, gonochores are favored only if $2e^{(b'-\lambda)T} < 1$. By Eq. 27, $e^{(b-\lambda)T} = (\lambda - b')/(2\lambda - b - b') = (1 - s)/(2 - s)$, where $s = (b' - b)/(\lambda - b)$. Setting $2e^{(b'-\lambda)T} = 2e^{(b-\lambda)T(1-s)}$, we find gonochores are favored when

$$f(s) = 2 \left[\frac{1 - s}{2 - s} \right]^{(1-s)} < 1 \quad (33)$$

For $s = 0$, $f(s) = 1$; for $0 < s \leq 1$, $df/ds > 0$, so $f(s) > 1$ for $s > 0$. Gonochores bearing all males are accordingly also selected against. If gonochores bearing only females and those bearing only males are both selected against, gonochores bearing the two sexes in any intermediate ratio will be as well.

Penalty of Excess Selfishness

We have found that, in populations of sex-changers, the larger $(b' - b)/(\lambda - b)$, the smaller the proportion of males. In some populations the proportion of territorial males is so small that there is opportunity for, even a premium on, finding another way of being male which reduces the penalty of youth and small size. What conditions must these "alternative males" satisfy to become established in a population?

Consider a static population of sexual haploids with two alleles: a prevalent allele B whose bearers change sex at the optimum age T' , and a very rare allele A whose bearers are all male. Assume that B females and A males younger than T' have the same per capita death rate λ . Assume that an x -year-old female is e^{bx} times as fertile as a newborn female, and that before the age T' at which females turn male an x -year-old A male is e^{bx} times as fertile as a newborn A male, while at age T' the A males turn into territorial males identical in fertility and death rate to B males the same age. We refer to A and B males as primary and secondary males because the A's were born male and the B's were not, and we refer to males younger than and older than T' as initial phase and terminal phase males, respectively.

If initial phase A males fertilize as many zygotes per head as B females the same age, the fitness of A and B are identical, for their other life table parameters—death rate, age of transformation, and fertility in the terminal phase—are the same for both genotypes. If initial phase A males fertilize more zygotes per head than B females, then A will spread. However, as A spreads, the number of females per male declines, diminishing male fertility per head relative

Table 1. Proportions of initial phase males and primary terminal phase males in samples from large (more than 1000 individuals) and small (less than 100 individuals) populations of *Thalassoma bifasciatum*. Samples were collected by lift nets [pictured in Roede (12)], in the morning before reproductive activity began, to ensure a random sample. Initial phase males and females were separated by visual inspection of the gonads, and primary and secondary males were distinguished histologically (16). Abbreviation: *N*, sample size.

Population size	Initial color phase			Terminal color phase		
	Populations sampled	<i>N</i>	Male (%)	Populations sampled	<i>N</i>	Primary male (%)
Large	10	690	22.9	8	124	20.9
Small	14	167	1.7	18	69	4.2

to female. If terminal phase males retain an advantage in fertility over initial phase males, A will spread until initial phase A males no longer fertilize more zygotes per head than B females, at which point a balanced male dimorphism obtains. Here, initial phase males cannot outnumber the females, for they must be as fertile per head as the females.

The smaller the proportion of terminal phase males in the population, the longer a female may have to wait to spawn with its preferred male, and the more opportunity there will be for initial phase males to find matings. Other circumstances making it easier for initial phase males to mate and enhancing their fertility per head will facilitate A's spread. Notice that the stronger the increase of fertility with age in the terminal phase males, the smaller will be the proportion of terminal phase males in the population, and the less fertile initial phase males need be relative to terminal phase males in order for a rare allele A to spread.

Field Observations

The bluehead wrasse has been much investigated in the past (9-12). We have been studying this wrasse on a series of reefs in the San Blas Islands, off the Caribbean coast of Panamá.

We may distinguish two adult color phases for this species. Smaller individuals are quite variable in color: they are usually striped yellow and black or barred with gray-green, but can change quite rapidly from one pattern to the other. These "initial phase" individuals are of both sexes. Larger individuals have a blue head separated from the green body by two prominent black bars. These "terminal phase" individuals are all males.

Terminal phase males maintain reproductive territories and "pair-spawn": that is, they mate as individuals, each with one female at a time. Initial phase males are nonterritorial, submissive toward terminal phase males, rarely aggressive toward each other, and normally spawn in a group with

a single female. This dichotomy between pair and group spawning was first noted by Randall and Randall (13). Fertilization is external: eggs and sperm are ejected at the apex of an upward rush that terminates about a meter above the substrate. Both fertilized eggs and larvae are planktonic.

Males originate in two ways (14, 15). Primary males were born male and occur in all sizes of both color phases. Secondary males were born female and have changed sex. They are almost all in the terminal phase, the few secondary males in the initial coloration being found in the upper end of that phase's size range (16).

In the San Blas Islands these wrasses are found on two main types of reef: small patch reefs, with populations of less than a hundred individuals, and large fringing reefs, with hundreds or thousands of individuals. We believe, and the test of the theory assumes, that the great majority of these wrasses live on the large reefs, so to explain the major features of sex change and male dimorphism we will discuss spawning behavior on such reefs. Our assumption is critical to the argument. Theory assumes that growth and death rates are the same for females and initial phase males. On small reefs and most large reefs there is no evidence for differences in mortality (the percentages of individuals in the initial and terminal color phases which are primary males are nearly equal; see Table 1) or growth (9, 17) between adult females and initial phase males in this species. On the largest reef we sampled, however, initial phase males appeared to die faster than females (17). Primary males do appear to mature earlier, grow faster, or change phase sooner than females in some related species of sex-changing fishes (18).

On a typical San Blas fringing reef, as in other Caribbean areas (10), spawning occurs daily throughout the year, for a few hours around midday. At this time, most of the sexually active fish gather at a specific site on the reef. There the larger bluehead males set up temporary spawning territories along the outer rim of the reef while the smaller blueheads and initial

phase males gather just inshore, the latter often massing in the hundreds. Mating areas are found on the downcurrent sides of reefs (17). They are probably chosen as spawning sites because there is a greater chance that fertilized eggs released there will be swept off the reef and away from reef-based planktivores. The largest blueheads are the most strongly territorial individuals and vigorously defend their territories against the constant intrusions of smaller males of both color phases. They are more successful than smaller blueheads in their territorial defense and can generally cope with all but initial phase males intruding en masse.

Females that are ready to spawn come to the breeding area, where they attempt to mate with the largest terminal phase males. To do so, however, they must run the gauntlet of the smaller terminal phase males and the massed initial phase males. The females will often delay mating if the largest males are preoccupied rather than mate with the smaller territorial males (10, 17). This selection means that a small advantage in size can have a disproportionately strong effect on a terminal male's mating success. Large terminal phase males spawn more than 40 times a day and small ones less than twice a day (Table 2), while ripe females, by contrast, spawn only once a day (19): the fertility of the females, which is presumably proportional to the weight of their gonads, increases only slightly more rapidly than the weight of the fish (Fig. 1). The relative speed with which the fertility of terminal phase males increases with size explains why these fish change sex in the first place.

The preference of the females for large blueheads in specific territories, however, provides smaller terminal phase males and the initial phase males with a chance to tamper with females waiting to mate with the male of their choice. Individual initial phase males often turn this circumstance to account by rushing into a large terminal phase male's territory to join a pair just as they are shedding gametes into the water (which we call "streaking"). They may also unobtrusively follow a female into a bluehead's territory and attempt, by tactile stimulation, to initiate a spawning rush with the female as she rises to the actively courting territory owner ("sneaking"). Normally, however, initial phase males mate as a group with an individual female after pursuing her and subjecting her to repeated tactile stimulation (see Table 2). Initial phase males intercept these females either en route to the reef edge or within a bluehead territory. The visual stimulation provided by the nearby courting blueheads may aid in effecting a group spawning (17).

Notice that external fertilization makes sneaking, streaking, and group spawning possible. A dominant male must vigorously defend his territory and the female within it to prevent her eggs from being contaminated by other males' sperm.

Our explanation of the presence of primary males assumes that fertility increases more slowly with age in initial phase than in terminal phase males. Because initial phase males are not generally aggressive toward each other, their relative fertility may be measured by gonad weight, which overall increases at about the same rate as in females (Fig. 1). Moreover, we require that they be about as fertile per head as the females: initial phase males gain the equivalent of about one pair spawning a day (Table 2), the same as the normal female's daily spawning rate.

A proper test of theory, however, depends on comparing different populations. The theory assumes a population closed to immigration or emigration, in a constant environment. In fact, different reef populations are not truly distinct as they are settled from the same pool of pelagic larvae. This implies that the parents of a fish on a particular reef mostly lived on other reefs, and the frequency of primary males on a particular reef presumably represents the average of selection on many reefs.

In fact, the age of sex change and the proportion of initial phase males could perfectly well be tailored to local conditions on individual reefs. Fish of this species can control the age at which they change sex: if one removes all the terminal phase males from a reef, the next largest fish will change coloration, and if they are female they will change sex as well (17). Moreover, primary males make up less than 2 percent of the individuals on small reefs, compared to more than 20 percent on large ones (Table 1). It seems fantastic to assume that very young primary males all die prematurely on small reefs: we must presume that these young fish avoid small reefs or emigrate as juveniles.

How does comparison of *Thalassoma* populations on different reefs bear on our theory? On large reefs the hierarchy of reproductive success among terminal phase males is much more inequitable than on small reefs. The largest terminal phase males on large reefs sometimes mate more than 100 times a day, but small reefs do not have enough females to support such a high spawning rate: a territorial male on a small reef thus has a much lower fertility relative to females than an equivalent-sized male on a large reef. Theory would predict that terminal phase males are relatively rarer in large populations than small and, if there is an upper limit to the number of

spawnings a terminal male can manage in a day, that initial phase males are rarer on small reefs than on large. The first point is easily confirmed by surveys of the populations on large and small reefs: terminal males make up 10 to 25 percent of the population when it is small, but less than 1 percent when it is large. The second point was noted in the last paragraph.

How do data from other species of fish bear on our theory? Warner (3) has noted that many protogynous species (those born female and turning male) spawn pairwise, giving an opportunity for female choice and sexual selection. In the cleaner wrasse, *Labroides dimidiatus*, the social system is quite rigidly organized: each male main-

tains a harem of not more than ten females (4), and the males mate very rarely outside the harem (20). Thus the fertility differential between males and females is low relative to that seen in the bluehead wrasse, and the species has no primary males because it is at once so much more difficult and so much less profitable to "cheat" in so rigid a society (21). Finally, we might expect that among the protogynous species which have dense populations and lek-type mating systems there would be pronounced mating hierarchies and favorable conditions for initial phase males, whereas in the rarer species fertility differentials should be lower and conditions for initial phase males less favorable and more dependent

Table 2. Mean daily spawning frequencies of *Thalassoma bifasciatum* males on a large reef. Values for terminal phase males are from a series of paired observations of large [greater than 105 mm standard length (S.L.)] and adjacent small (less than 90 mm S.L.) individuals made over the same spawning period. Values for initial phase males are from observations of 15 different tagged individuals (mean S.L. = 68 mm). Pair spawning equivalents were computed as follows: streaking individuals were scored 0.5 pair spawning. Each spawning group was classified as small (1 to 5 participants), medium (6 to 10), or large (11 to 15), and individuals were given the equivalent of 0.2, 0.1, or 0.066 pair spawning for participation in a small, medium, or large group, respectively. The group spawning total was then reduced by half, because only half of group spawnings include a discharge of eggs (78 of 155 observed). Contributions from each spawning mode were then tallied for each individual.

Individuals	Sample size	Pair spawnings	Pair spawnings with streakers	Group spawnings	Total equivalent in pair spawnings
Terminal phase males					
Large	20	43.9 ± 7.0*	1.3 ± 0.9	0.0	43.2 ± 6.8
Small	20	1.7 ± 0.9	0.7 ± 0.4	0.6 ± 0.8	1.5 ± 0.9
Initial phase males	21	0.2 ± 0.2	0.1 ± 0.1	17.1 ± 4.0	1.1 ± 0.2

*95 percent confidence limits of the mean.

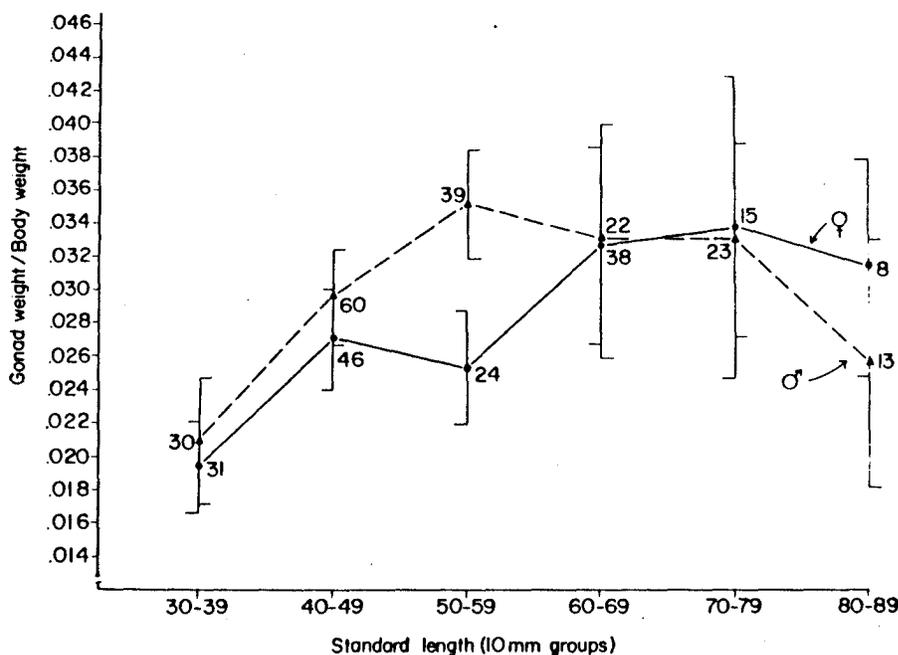


Fig. 1. Mean proportion of body weight devoted to gonad in successive length classes of initial phase males and females of *Thalassoma bifasciatum*. Also shown are sample sizes and the 95 percent confidence intervals of the mean (bracketed lines).

on social systems (21). In surveys of the protogynous wrasses (22) and parrotfish (23), we have found a positive correlation between the relative abundance of a species and the frequency of initial phase males therein.

Our mathematics suggests that animals should change sex if one sex gains in fertility much more rapidly with age than the other. However, many animals, especially mammals such as deer, sheep, and goats, do not change sex even though older males in these species monopolize a disproportionate share of matings (24). Why do not more animals change sex?

The costs of changing the reproductive anatomy of animals which practice internal fertilization, and whose females are viviparous or bear fairly large eggs, may be enormous. Sex determination in mammals and birds may be too rigid to permit sex change. Moreover, many higher vertebrates may need experience as well as size to fight successfully for mates. A large animal which has just turned male may be at a hopeless disadvantage relative to his more experienced fellows, despite his size.

References and Notes

1. C. L. Smith, *J. Theor. Biol.* 17, 76 (1965); in *Intersexuality in the Animal Kingdom*, R. Reinboth, Ed. (Springer, New York, 1975), pp. 295-310; G. V. Nikolski, *Ecology of Fishes* (Academic Press, London, 1963); M. A. Moc, *Fla. Dept. Nat. Resour. Mar. Res. Lab. Prof. Pap. Ser. No. 10* (1969).
2. M. T. Ghiselin, *Q. Rev. Biol.* 44, 189 (1969).
3. R. R. Warner, *Am. Nat.* 109, 61 (1975).
4. D. R. Robertson, *Science* 177, 1007 (1972).
5. M. Gadgil, *Am. Nat.* 106, 574 (1972).
6. For example, see A. J. Hogan-Warburg, *Ardea* 54, 109 (1966); R. L. Patterson, *The Sage Grouse of Wyoming* (Wyoming Game and Fish Commission, Cheyenne, 1952); H. K. Buechner, *Science* 133, 698 (1961).
7. For example, see R. A. Fisher, *The Genetical Theory of Natural Selection* (Dover, New York, 1958); E. L. Charnov, *Evolution* 29, 366 (1975).
8. We have assumed a stable population. If $b' > \lambda$, then the increase in fertility of the survivors of a cohort more than compensates the loss from death in the aggregate fertility of the cohort, which contradicts the assumption of the population's constancy.
9. H. A. Feddern, *Bull. Mar. Sci.* 15, 896 (1965).
10. R. Reinboth, *Helgol. Wiss. Meeresunters.* 24, 174 (1973).
11. L. M. Stoll, *Zoologica (N.Y.)* 40, 125 (1955); R. Reinboth, *Gen. Comp. Endocrinol. Suppl.* 3, 565 (1972).
12. M. J. Roede, *Stud. Fauna Curacao Other Caribb. Isl. No. 138* (1972).
13. J. E. Randall and H. A. Randall, *Zoologica (N.Y.)* 48, 49 (1963).
14. R. Reinboth, *Mem. Soc. Endocrinol.* 18, 515 (1970).
15. ———, *Gen. Comp. Endocrinol. Abstr.* 9, abstr. 146 (1967).
16. For example, we found only four secondary males, all in the largest length categories, in a size-stratified sample of 64 initial phase males collected from a single area. Primary and secondary males were distinguished histologically in all samples, using the criteria of Reinboth (14).
17. D. R. Robertson, unpublished results.
18. For example, the striped parrotfish, *Scarus croicensis*, shows accelerated growth of primary males relative to females (R. R. Warner and I. F. Downs, in preparation). Early maturation of parrotfish primary males has been reported by H. Choat and D. R. Robertson, in *Intersexuality in the Animal Kingdom*, R. Reinboth, Ed. (Springer, New York, 1975), pp. 263-283.
19. We followed 15 females (40 to 85 mm standard length) throughout a day's spawning period. Each invariably spawned, and spawned only once.
20. They did so in 2.6 percent of 400 spawnings observed.
21. D. R. Robertson and H. Choat, *Proceedings of the Second International Symposium on Coral Reefs* (Great Barrier Reef Committee, Brisbane, Australia, 1974), vol. 1, pp. 217-225.
22. R. R. Warner and D. R. Robertson, in preparation.
23. D. R. Robertson and R. R. Warner, in preparation.
24. For example, among red deer [F. F. Darling, *A Herd of Red Deer: A Study in Animal Behavior* (Oxford Univ. Press, London, 1937), mountain sheep [V. Geist, *Mountain Sheep: A Study in Behavior and Evolution* (Univ. of Chicago Press, Chicago, 1971)], and other sheep and goats [W. M. Schaffer and C. A. Reed, *Fieldiana Zool.* 61, 1 (1972)] males wait several years longer than females to reproduce because they cannot win the necessary mating combats any earlier.
25. We are most grateful for the use of the facilities of the Smithsonian Tropical Research Institute, and in particular for the use of a research vessel in the San Blas Islands. We are also very grateful to I. F. Downs and E. A. Fletcher for expert assistance in the field and laboratory, and to R. D. Alexander, S. Levings, G. H. Orians, and G. J. Vermeij for their extraordinarily helpful remarks and advice.