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Sex Ratio: Adaptive Response to Population Fluctuations in Pandalid Shrimp

Abstract. *Pandalus jordani is a protandrous (sequential) hermaphrodite. Populations show large year-to-year variation in age composition. In response to this variation, individuals alter the age at which they change sex. This response is predicted by a genetic model that assumes that an individual shrimp maximizes its genetic contribution to the next generation.*

In this report we consider the problem of how natural selection operates on an organism's ability to either choose its sex or to alter the sex ratio among its progeny in response to environmental influences [environmental sex determination (ESD)]. Trivers and Willard (*1*) and Chewyreuv (*2*) were among the first to realize that some environmental conditions favor a female's overproducing sons or daughters. In the Trivers-Willard model, the reproductive success (RS) of a son or a daughter is assumed to be closely related to the physiological condition of the mother. Applied to mammals, their model further assumes (i) both sons and daughters benefit in terms of RS when reared by a mother in good physiological condition, although (ii) a son benefits more than a daughter. They then concluded that natural selection favors females in good condition to overproduce sons and those in poorer condition to overproduce daughters. Some data from mammals may support this prediction (*1*). The key concept is that one sex gains more than the other (in terms of RS) when reared by a female in good condition.

This concept has recently been generalized to include sex expression in hermaphrodites and in dioecious species (with labile sex) in which an individual may become a male or a female depending upon the environment in which it finds itself (*3*). Some environmental conditions favor the RS of males, some that of females. Much evidence supports the prediction that hermaphrodites alter the allocation of resources to either male or female function depending on environmental conditions (*3*); that evidence has been interpreted in terms of why one sex benefits relatively more in a particular environment.

We have developed a genetic model for ESD in a dioecious species. The model makes some precise predictions, which we have tested with a protandrous hermaphrodite. (The "dioecy" assumption proves to be unimportant.)

Suppose that, because of spatial variation in food supply, members of a species (with ESD) find themselves at the time of breeding divided into big and small individuals. Sex is not yet determined. The questions of interest are (i) what fraction of the big individuals should reproduce as males? and (ii) what fraction of the small individuals should reproduce as females? In order to answer these, we must specify the consequences, in terms of individual RS, of being a male or a female of a given size.

Let *P* equal the proportion of breeders that are small. Further, let an individual which is big and reproducing as a female have an egg count of W_2 relative to a small individual as a female. Big individuals reproducing as males will be given a fertility of W_1 relative to a small individual as a male.

Consider a very large population (of size *N*) with the characteristics that the proportion r_1 of the small individuals reproduce as males, while the proportion r_2 of the big individuals are males. If we define fitness to be the probability that an individual passes its genes to a zygote formed during the current breeding season (*4–7*), the fitness of a small individual (W_s), who reproduces as a male with some other probability ($\hat{r}_1$, where $\hat{r}_1 \neq r_1$), may be written as:

$$W_s = \frac{1}{N} \left[\frac{\hat{r}_1}{Pr_1 + r_2 W_1(1 - P)} + \frac{1 - \hat{r}_1}{P(1 - r_1) + W_2(1 - P)(1 - r_2)} \right] \quad (1)$$

$$W_s = \frac{1}{N} \left(\frac{\hat{r}_1}{M} + \frac{1 - \hat{r}_1}{F} \right)$$

The fitness of a big individual (W_b) who alters the probability (with which it reproduces as a male) to $\hat{r}_2$ (again $\hat{r}_2 \neq r_2$) is similarly defined:

$$W_b = \frac{1}{N} \left(\frac{\hat{r}_2 W_1}{M} + \frac{W_2(1 - \hat{r}_2)}{F} \right) \quad (2)$$

If the situation is to be evolutionarily stable, it must be that an individual cannot increase its own fitness by altering the probability with which it becomes a male (or a female) away from the respective population values (*6*) (that is, W_s and W_b do not increase as $\hat{r}_1$ and $\hat{r}_2$ are altered from r_1 and r_2). The game now becomes to find r_1 and r_2 which satisfy this condition. The r_1 and r_2 we seek are those which maximize the product ($M \times F$). Although a formal proof is possible (*8*), we indicate here an intuitive justification for this result.

First, differentiate Eqs. 1 and 2 with respect to $\hat{r}_1$ and $\hat{r}_2$, respectively. These have the form:

$$\partial W_s/\partial \hat{r}_1 \propto \frac{\partial H}{\partial r_1} \quad (3)$$

where $H = \ln M + \ln F$, and

$$\partial W_b/\partial \hat{r}_2 \propto \frac{\partial H}{\partial r_2} \quad (4)$$

As an example, consider Eq. 3. If *H* is maximized by setting $r_1 = 1$, then $\partial H/\partial r_1 \geq 0$, which implies that $\partial W_s/\partial \hat{r}_1 \geq 0$. An individual can do no better than also setting $\hat{r}_1 = 1$. The same holds if $r_1 = 0$ maximizes *H*; here $\hat{r}_1$ should be set equal to zero to maximize W_s. If r_1 maximizes *H* by being set equal to some value between 0 and 1 (call it r_1^*), $\partial H/\partial r_1 = 0$. But then $\partial W_s/\partial \hat{r}_1 = 0$,

Table 1. Statistical analysis of Oregon data (*14*). Correlation coefficients were either the Pearson product moment coefficient (*r*) or the Spearman rank coefficient (r_s). Abbreviation: N.S., not significant.

Relation	Sample size	Regression	Correlation	P
		Area 82–84		
First breeders (female)	8	$y = .62 - .54x$	$r = -.75$	<.05
			$r_s = -.72$	<.05
Older breeders (male)	13	$y = .31 - .20x$	$r = -.84$	<.01
	13		$r_s = -.78$	<.01
		Area 86		
First breeders (female)	8*	$y = .57 - .29x$	$r = -.96$	<.01
	9†	$y = .44 - .16x$	$r = -.75$	<.05
	8*		$r_s = -.64$	<.05
Older breeders (male)	7	$y = .4 - .51x$	$r = -.73$	N.S.
	7		$r = -.38$	N.S.

*Fit without the point *x* = 3.4, *y* = .14. †Fit with the point *x* = 3.4, *y* = .14.
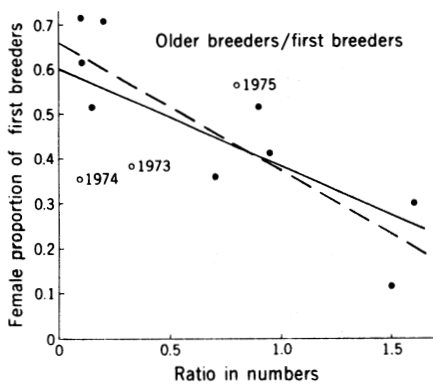
Fig. 1. *Pandalus jordani* in northern California for 12 years. Lines are the least-squares regression with (solid line) and without (dashed line) the years 1973 through 1975.

and selection is indifferent to whether an individual is a male or a female (so long as the group as a whole achieves $r_1{}^*$). A similar argument may be given for r_2.

The maximization of $M \times F$ (provided $W_2 > W_1$) follows these rules:

$$1 - r_1 \begin{cases} = \dfrac{1}{2}\left[1 - W_2\!\left(\dfrac{1-P}{P}\right)\right] & \text{if } W_2 > \dfrac{1-P}{P} \\ = 0 & \text{if } W_2 < \dfrac{1-P}{P} \end{cases} \quad (5)$$

and

$$r_2 \begin{cases} = \dfrac{1}{2}\left[1 - \dfrac{1}{W_1}\left(\dfrac{P}{1-P}\right)\right] & \text{if } W_1 > \dfrac{P}{1-P} \\ = 0 & \text{if } W_1 < \dfrac{P}{1-P} \end{cases} \quad (6)$$

This solution has the characteristics that (i) sex ratio within a size class depends on the frequency distribution of size classes, but (ii) more than 50 percent of the small shrimp should be males, while more than 50 percent of the big shrimp should be females, because females gain more RS by being big than males do (that is, $W_2 > W_1$). This corresponds to the Trivers-Willard RS assumption for mammals.

To test these predictions, we have used data from the shrimp *Pandalus jordani*, the major commercial shrimp off the northwest coast of the United States. It is a protandrous hermaphrodite (changes from male to female) that breeds once a year, in the fall. Most populations are short-lived, with at most three breeding age classes (9). The egg count of a shrimp reproducing as a female is positively related to body size (10), which increases with age. Because of large year-to-year variations in survival of the immature shrimp, the fraction of the population made up of shrimp breeding for the first time (small shrimp) varies greatly from year to year. Because most of the older breeders are second breed-

ers, we treat the problem as if two size classes are present. Provided that growth and death rates from the age of first breeding to the age of second breeding are not sex-specific (that they do not depend upon whether a shrimp breeding for the first time acts as a male or a female), natural selection should act on individual's choice of sex so that it maximizes its contribution to the zygotes formed in the current breeding season. The problem is then the same as the ESD problem just outlined; W_1 and W_2 are the relative fertilities of older shrimp, acting as males and females, respectively, and P is the fraction of the breeding population made up of first breeders. Being a sequential hermaphrodite makes no difference because the theory predicts that fewer than half of the smaller shrimp (first breeders) should be females and more than half of the bigger (older) shrimp should be females. Thus, the theory requires only that when the first breeders become 1 year older, more of them change to females.

For three populations of *P. jordani*, we estimated the following for each of several years: (i) the fraction of breeders that were breeding for the first time (age 1.5 years), (ii) the fraction of first breeders that were females, and (iii) the fraction of older breeders that were males. Two data sources reflected the differences in the data available from
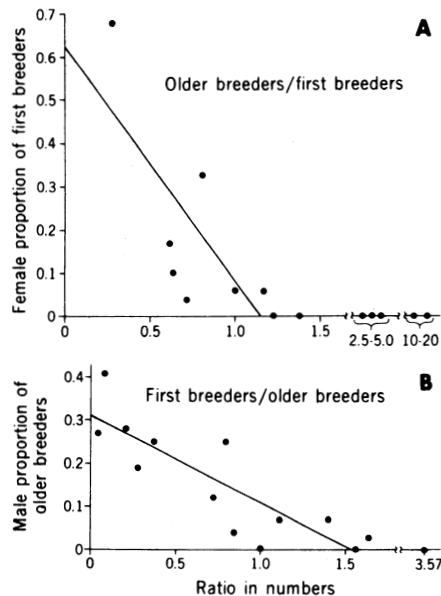
Fig. 2. *Pandalus jordani* in Oregon [fishing areas 82–84 (14)] for 14 years. (A) First breeders. (B) Older breeders.
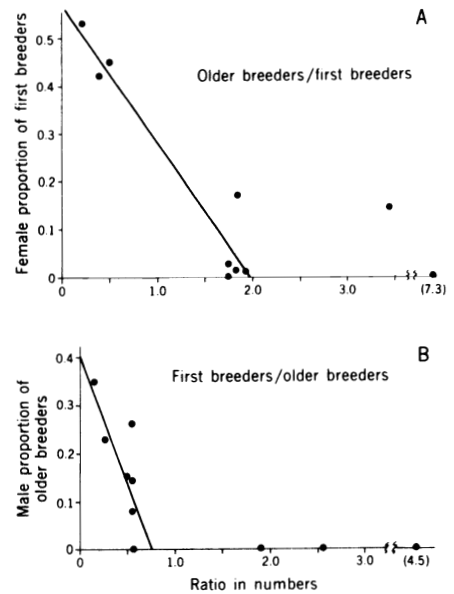
Fig. 3. *Pandalus jordani* in Oregon [fishing area 86 (14)] for 10 years. (A) First breeders. (B) Older breeders.

California and Oregon. For California, we judged the best data that from the fall research cruises of the California Department of Fish and Game. An extensive sampling program, designed specifically to estimate shrimp life history variables and abundance, has been carried out since 1964. We used estimates derived from those data from 1964 through 1975 (there was no cruise in 1976). Since the fishery may have suffered from overexploitation in the early 1970's, we did the analysis both with and without the years 1973 through 1975. For Oregon, data were mostly derived from commercial fishery samples (11) (except for a few years when the Oregon Department of Fish and Wildlife research data were available). All data refer to the fall breeding population (for Oregon, September or later; for California, the dates of the fall research cruise). We separated year classes by examining frequency distributions of shrimp length, which were fairly distinct in these populations (9, 11). There are two consistent sources of bias in this analysis. (i) Shrimp fishing gear tends to select larger shrimp (9). (ii) Shrimp at the age of first breeding that act as females are slightly larger than same-aged shrimp that reproduce as males. Likewise, older breeders reproducing as males tend to be smaller than those breeding as females (9, 11). These sources of bias imply that (i) estimates of the ratio $(1 - P)/P$ will be inflated, reflecting the extent to which the respective size groups are caught (thus their representation in the samples), and (ii) estimates of r_1 and r_2 should be smaller than the true values, reflecting the dif-

ferent probabilities within an age class of being caught.

However, these biases should not alter the general shape of the predicted relations. The hypothesis has three parts. (i) If the proportion of first breeders acting as females (*y* variable) is plotted against the ratio (in numbers) of older to first-breeders (*x* variable), we expect a negative relation for small *x* values and no relation for large *x* values. (ii) If the proportion of older breeders acting as males is plotted against the ratio of first to older breeders, we expect the same shape of relation as given in (i). (iii) We expect to find some big males and some small females only if both of the relations given above have some *y* values at zero. These three predictions are a qualitative description of Eqs. 5 and 6.

For California, the proportion of first breeders acting as females is negatively correlated with the ratio of older breeders to first breeders (Fig. 1). Least-squares regression gives the fit $y = .60 - .20x$ ($r = .67$, $N = 12$, $P < .05$). However, recent years (1973 through 1975) show a relation different from the rest of the data. If only data before 1972 are used, the regression is considerably improved ($y = .68 - .3x$, $r = .87$, $N = 9$, $P < .05$).

Since the usual assumptions of regression and correlation are probably violated in these data, we also calculated a Spearman rank correlation coefficient (r_s). With all the data, $r_s = .51$, which just reaches the .05 significance level ($N = 12$). Again, recalculating r_s without the years 1973 through 1975 greatly improves the fit ($r_s = .85$, $N = 9$, $P < .01$). The theory also predicts that no older breeding shrimp should be males; none were found.

The two Oregon populations differ from the California one in that both show years in which some older individuals reproduced as males. The data support our hypothesis (Figs. 2 and 3) (Table 1). All but one regression (for points in the positive region) are significant, and, for these, the rank correlation is also significant.

Several other systems may be used to further test the model developed here. The situation discussed by Trivers and Willard (*1*) is one such case. If *P* is the fraction of the mothers in poor condition, W_1 the relative fitness of a son of a mother in good condition, and W_2 the relative fitness of a daughter of a mother in good condition, the same sex-ratio rules apply. The same rules may also apply to some solitary wasps and bees (*2, 12*) and to various orchids (*13*). Some orchids are

sexually labile, with individuals found in the bright sunlight mostly reproducing as females and those in the shade as males. Other organisms with ESD may be treated similarly.

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5-Thio-D-Glucose Selectively Potentiates Hyperthermic Killing of Hypoxic Tumor Cells

Abstract. *To investigate the mechanisms by which heat affects cancer cells, we used 5-thio-D-glucose, an inhibitor of glycolysis in HeLa S-3 cells, under aerobic and hypoxic conditions at temperatures ranging from 37° to 43°C. Drug alone or heat alone killed a minimum number of cells under aerobic or hypoxic conditions. Exposure to drug and hyperthermia selectively increased the number of cells killed under hypoxic conditions at temperatures as low as 40.5°C but had little effect on cells incubated under aerobic conditions. These results suggest that the glycolytic pathway is a primary site of hyperthermic damage leading to cell death.*

It has been claimed repeatedly for more than a century that hyperthermia (temperatures above 40°C) can have a selective lethal effect on cancer cells. However, only sporadic attempts have been made to use these observations clinically, partly because of a poor understanding of the mechanism of enhanced thermal sensitivity of tumor cells, and partly because of the difficulty of selectively heating a chosen tumor volume at depth. Recently, more conclusive evidence of the action of heat on cancer cells both in vitro and in vivo has generated a renewed interest in this subject (*1*).

In cell culture studies (*1*), numerous cellular factors involved in the thermal response of tumor and normal cells have been identified. Thermal sensitivity is strongly dependent on such factors as cellular growth states, cell cycle phases, nutritional status, ambient oxygen concentration, and intra- and extracellular

pH (*2*). Of importance to clinical cancer therapy is the finding that hypoxic cells are sensitive to heat. Indeed, several laboratories reported hypoxic cells were far more sensitive to heat than cells cultured under aerobic conditions, though caution must be exercised in interpreting these data because the experimental induction of hypoxia is invariably associated with changes in the nutritional status of cultured cells, for example, the glucose concentration and extra- and intracellular acidity. When tumor cells are cultured at 42° to 43°C, their respiratory activity, including anaerobic glycolysis, is significantly reduced (*3*). In contrast, in normal cells cultured at the same temperature the respiratory activity is not as severely affected. The importance of anaerobic glycolysis in the pathogenesis of the cancer cell was discussed by Warburg (*4*). His original observation was that when both normal and malignant tissue slices were incubated in a medium containing