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NOTES AND COMMENTS

ADAPTIVE VARIATION IN ENVIRONMENTAL SEX DETERMINATION
IN A NEMATODE

Through environmental sex determination (ESD), offspring become male or female in response to an environmental factor or factors during development. Examples are known to occur in fish (Conover and Heins 1987), reptiles (Bull 1980), nematodes (Petersen 1972), and shrimp (Adams et al. 1987) (general ESD review in Adams et al. 1987). Current theory for the evolution of ESD suggests that it is favored over genotypic sex determination when the environment is patchy with respect to developmental opportunities and the patches have a gender-dependent influence on fitness (Charnov and Bull 1977, 1989*a,b*; Bull 1981, 1983; Bull and Charnov 1989). If, for example, large body size has a greater effect on the reproductive success of females than of males, members of a population that enter an environment allowing the attainment of larger size should become female, whereas individuals that encounter poor growing conditions would make the best of a bad situation by becoming male (Charnov and Bull 1977; Conover and Heins 1987). The patchiness may be spatial (Charnov and Bull 1977) or temporal (e.g., seasonality; Werren and Charnov 1978; Adams et al. 1987; Conover and Heins 1987; Naylor et al. 1988). The papers cited above discuss in much detail the evidence bearing on the Charnov-Bull (1977) model for the evolution of ESD; suffice it to say that in most cases there is little evidence for or against the model. However, it is also clear that the formalism has proved a useful heuristic device; that is, it has suggested what measurements to make and what they might mean (for reptiles with ESD, see Bull and Charnov 1989).

Here we provide the first evidence of adaptive variation in the expression of ESD in a spatially patchy environment. A nematode parasite of mosquito larvae shows ESD with respect to growth opportunities for immatures. Within a population, hosts that allow larger growth produce mostly females; the converse, males. However, in populations with better overall growth opportunities (i.e., the emerging worms are larger on the average), the worm size at the shift from male to female is itself larger. This between-population adjustment of the threshold size is as predicted by adaptive-sex-ratio theory.

Although ESD was first reported for nematodes by Christie (1929) in studies of a mermithid parasite of grasshoppers, the most extensive work in this group was done by Petersen (1972, 1977; Petersen et al. 1968) with parasites of mosquitoes.

Infective-stage juveniles of these mermithids actively search for and penetrate an individual host larva. Development to adult size proceeds in the host, which is killed when the worms emerge; after one more molt, they become free-living adults. Since adult mermithids do not feed, all reproductive resources are acquired during parasitic development. Some host environments allow more growth, others less; adult worm size (and presumably the amount of reproductive resources) is closely tied to the developmental environment (Petersen et al. 1968; Petersen 1972, 1977). Several ingenious experiments have demonstrated conclusively that these parasites exhibit ESD (Petersen et al. 1968; Petersen 1972, 1977); indeed, ESD seems to characterize the entire family Mermithidae, having been found in every species so far examined (Poinar 1979). Petersen showed that sex expression is closely related to the attainable adult size, with small worms becoming male. Host size, host nutrition level, and parasitic load all affect worm growth opportunities and thus sex expression.

Petersen's work strongly suggests that, within a breeding population, there exists a size threshold for sex development below which an individual becomes a male. Such a threshold for sex development is predicted by adaptive-sex-ratio theory (Charnov 1979, 1982; Bull 1981, 1983). To show this, define $f(x)$ as the proportion of the breeders of size x ; $W_1(x)$, the relative male fertility of an individual of size x ; and $W_2(x)$, the relative female fertility of a size- x individual. Provided that W_2/W_1 increases with increasing x (i.e., females gain more reproductive ability with size than do males), all small worms should be male, all large ones female. The threshold (τ) is the value that maximizes the following product relation:

$$\text{maximize } \left[\int_0^{\tau} f(x) W_1(x) dx \right] \left[\int_{\tau}^{\infty} f(x) W_2(x) dx \right], \quad (1)$$

where τ should be responsive to the population-wide growth opportunities as they set the distribution $f(x)$. Figure 1 shows the expected shift in τ from a poor-growth to a good-growth environment. For reasons discussed in detail elsewhere (Charnov 1982; Bull 1983), data on the sex-ratio changeover with size would rarely show the abrupt threshold (τ) that the most simple theory (eq. 1) would predict; a more gradual shift is expected, and here we may take τ to be the size at which equal numbers of males and females develop (i.e., a 1:1 sex ratio).

Equation (1) may also be used to make two other predictions for the between-population comparison illustrated in figure 1. Both $W_1(x)$ and $W_2(x)$ are scaled within a sex; thus, W_1 indicates how much better reproductively a male of size $x + \delta$ is relative to a size- x male (ditto for females and W_2). The "within-sex" fitness curves ($W_i(x)$) are discussed in much detail elsewhere (e.g., Bull 1981; Charnov et al. 1981; Charnov 1982, 1984; Charnov and Bull 1989a,b). If we simply agree that the two curves will cross at τ , then there exists (from eq. 1) a simple formula giving the population-wide primary sex ratio in equilibrium (Charnov 1982, 1986; Frank and Swingland 1988; Charnov and Bull 1989a,b):

$$\text{males/females} = \bar{W}_2/\bar{W}_1, \quad (2)$$

where an overbar refers to the simple average taken over the size distribution for each sex. Provided that both males and females gain reproductive ability with

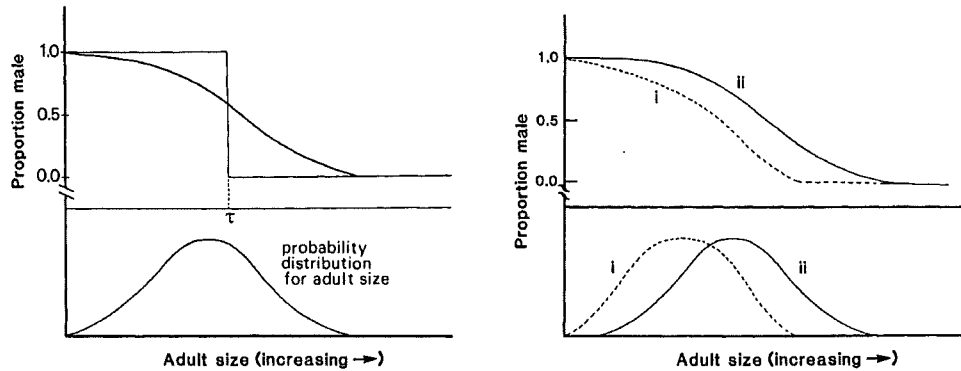


FIG. 1.—Sex ratio as a function of adult size. *Left*, Provided that females gain more fitness by being larger than males gain (i.e., $W_2(x)/W_1(x)$ increases with x), the sex ratio is predicted (eq. 1) to be female-biased among large individuals, male-biased among smaller ones. At a threshold size τ , a changeover occurs; however, actual field data would show a more gradual sex-ratio shift, and here we define τ to be the size at a sex ratio of 1:1. *Right*, If the adult size distribution differs among breeding populations, τ is predicted to also differ. Locations with mostly large individuals (*ii*) should show a larger τ when compared with locations with smaller individuals (*i*). Indeed, the entire curve showing the sex ratio as a function of adult size should shift with the adult size distribution.

increasing size (W_1 and W_2 both increase with x), the population-wide primary sex ratio will favor males since \bar{W}_2 will always be greater than \bar{W}_1 . If we shift the overall size distribution, as illustrated in the right-hand view of figure 1, we will change both \bar{W}_2 and \bar{W}_1 in the same direction. This means that the overall primary sex ratio (eq. 2) will tend to be approximately a constant across the environments. We have made some theoretical calculations with various W_1 and W_2 curves (both increasing) allied to changing $f(x)$ curves, and this approximate constancy holds generally, in the sense that the proportion of males rarely varies by more than about 10% from a central value. This male-biased sex ratio should hold for the nematodes discussed here, for the following reasons. Female fecundity increases with increasing body size; thus, W_2 increases with x . W_1 should increase or be flat with x because if it decreases, individuals under “good growth conditions” could always become more-fit males by simply not growing very big; food limitation may force small size, but food excess cannot be said to force large size.

We studied the nematode *Romanomermis nielsenii* (Tsai and Grundmann 1969) in southwestern Wyoming (two populations) and three other populations of *Romanomermis* that parasitize snowpool mosquitoes in Yellowstone National Park, Wyoming. (Methods are discussed in the figure legends and detailed in Blackmore 1989.) This is the same genus as studied by Petersen, and it clearly exhibits ESD (Blackmore 1989). Among the different breeding populations studied, the hosts varied widely in size distribution and parasitic load. The size distributions of emerged adult worms varied accordingly; small adult worms emerged from small and/or crowded hosts (Blackmore 1989). The host species and parasitic loads for the study locations are discussed in detail elsewhere (Blackmore 1989); here we summarize that variation by looking at its end product, the size distributions for the adult worms. As indicated in figure 3A, mean adult length varied from nearly 8 mm to almost 14 mm; among populations, the larger

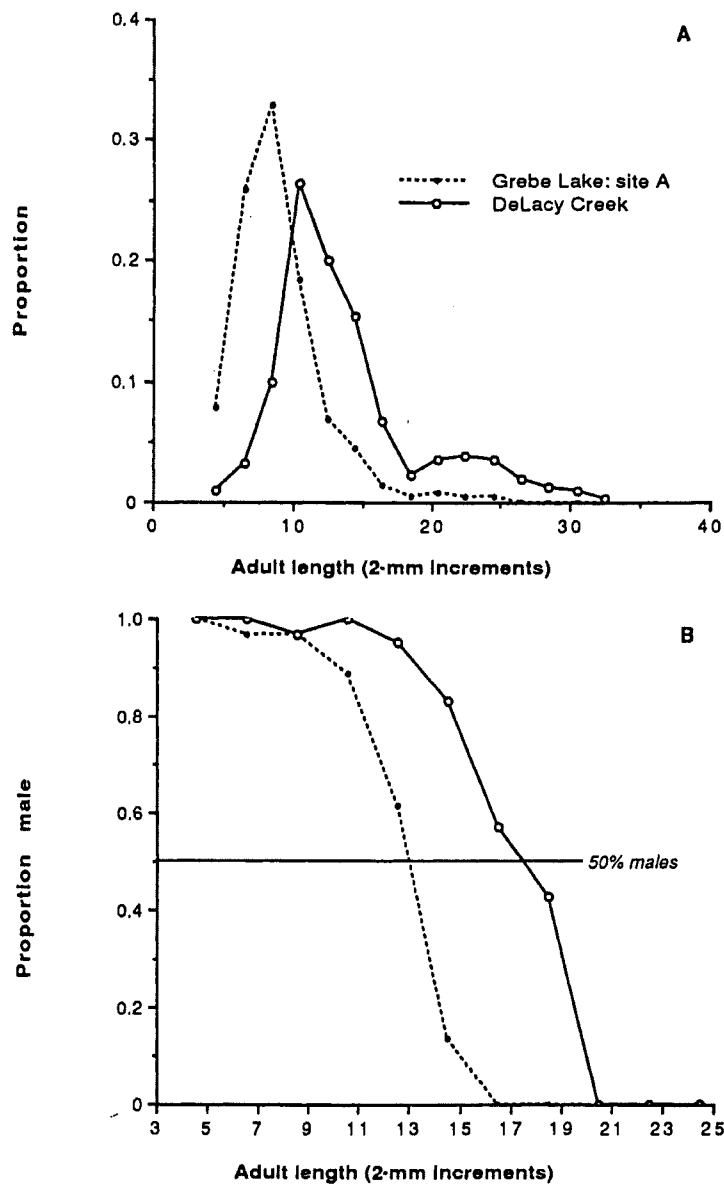


FIG. 2.—A, Distribution of adult size in two populations of *Romanomermis*. Although these particular populations are only 30 km apart, differences in composition of the host communities and worm burden per host at these localities result in quite different size distributions of adult nematodes. B, Within each population, the sex ratio shifts from all male to all female as size increases; however, the curve of sex ratio versus adult size is itself shifted upward in the population with mostly larger worms. We also indicate the size at which the sex ratio is 1:1 ($= \tau$). Interpopulation size differences result in different τ . For methods, see figure 3.

worms were over three times the average mass of the smaller. Figure 2A shows the complete size distributions at two localities. As indicated in figure 2B, the size threshold (τ = size when 50% of the individuals are male) shifted in response to the altered adult size distribution; the larger the worms, the larger the size threshold τ . Indeed, for the two populations, the curves of sex ratio versus adult size (fig. 2B) are quite different; as theoretically expected, the location with generally larger worms has the right-shifted sex-ratio curve. The kind of data shown for two populations in figure 2 also exist for the other three locations; they have exactly the same form as that shown in figure 2. Summarizing the position of the size distribution with the mean adult size (\bar{x}) for our five study locations, figure 3A shows a highly significant positive relation between τ and \bar{x} . Although there are only five data points, the correlation is significant at the 0.01 level (Snedecor and Cochran 1967). At emergence, nearly 80% of the individuals in the population are male (ranging from 0.89 to 0.70); this level may decrease with increasing \bar{x} (fig. 3B). The correlation of -0.78 is not significant with only five data points, but the effect may still be real. The sex ratio varies $\pm 12\%$ from its central value of 0.80; this amount of sex-ratio variation is at the outer limits of what we earlier termed "sex-ratio constancy." Thus, although the male-biased prediction is clearly upheld, the sex-ratio constancy is equivocal. More-precise predictions about the sex ratio must await determination of the W_1 and W_2 relations.

Two other species with ESD (fish, Conover and Heins 1987; shrimp, Naylor et al. 1988, Bulnheim 1967), both of which show temporal (seasonal) patchiness in sex expression, may also show adaptive shifts in the threshold response. For the fish, the environmental factor is developmental temperature (a seasonal indicator), and the adaptive shift relates to the sex expression at a particular temperature. The between-population variation is latitudinal along the eastern coast of North America. Photoperiod is the cue for the shrimp, and present data suggest latitudinal variation in the threshold photoperiod. In both cases, the seasonality imposes differential growth opportunities, which translate into gender-specific fitness effects. Thus, the patchiness in these two cases is *temporal* (seasonality), as opposed to *spatial*, as in the nematode. The nematode is the first example of adaptive variation in gender expression related to altered variation in spatial, as opposed to temporal, patchiness.

Although the adaptive significance of ESD remains enigmatic in groups such as reptiles (Bull 1980, 1983; Bull and Charnov 1989), the data reported here (combined with the studies of the fish [Conover and Heins 1987] and crustaceans [Naylor et al. 1988]) strongly support adaptive-sex-ratio theory. Indeed, because sex-ratio evolution is an example of frequency-dependent natural selection, these studies are among the few and the best in demonstrating this elusive phenomenon (Endler 1986).

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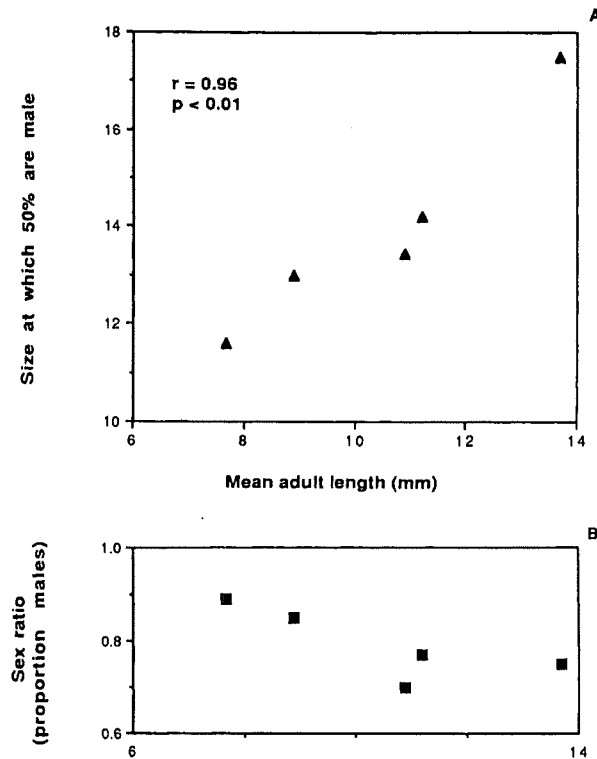


FIG. 3.—Effects of population size distribution on the sex ratio of *Romanomermis*. Mean length of adult nematodes is used as an indicator of the position of the size distribution for each of five populations studied. *A*, The size at which the sex ratio shifts from male-biased to female-biased (τ) correlates positively with the position of the population size distribution. The significance level is 0.01, even with only five points. *B*, Population sex ratio may show a decline with mean adult size, but it is always quite male-biased. See the text for further discussion.

The data shown are based on measurements of 150, 147, 489, 245, and 314 individuals obtained from five sites in western Wyoming. Infected mosquito larvae collected from vernal pools at these sites were individually reared in the laboratory until post-parasitic mermithids emerged. Emerged worms were transferred into vials containing coarse sand and deionized water and kept at 10°C until they completed development. After the final molt the adult worms were killed by heat (65°C), sexed, and measured. Parasitic load did not affect the probability of mortality among lab rearings; sex-differential mortality is thus unlikely to be a factor in the resulting population sex ratios.

The curves of figure 2 and the τ 's of figure 3 were estimated as follows. In order to have adequate sample sizes for sex ratio and frequency estimation within a size class, we averaged over successive, nonoverlapping 2-mm intervals. Thus, each sex ratio in figure 2B is for the interval ± 1 mm from the indicated adult length. τ was the size at which 50% of the individuals were male after data points were connected with straight lines, as shown in figure 2B.

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