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### ON ESTIMATING THE PRIMARY SEX RATIO FROM INCOMPLETE DATA

In sampling offspring sex ratios, one is usually faced with the problem that sex cannot be identified until long after conception, by which time the sex ratio may have changed because of differential mortality. The question then arises, Can the primary sex ratio be estimated from data on older offspring? Mayr (1939) asserted,

in effect, that the primary sex ratio of birds can be estimated from the sex ratio of those broods in which all the young survive until they can be sexed. This idea has persisted in the literature and misguided a number of later authors (e.g., Williams 1940; Kessel 1957; Pinkowski 1977; Myers 1978; and since this note was prepared Newton and Marquiss 1979), even though it is patently false, since if differential mortality exists then the sample of broods that escape mortality will be biased in favor of the sex with greater survivorship.

Suppose that (1) each zygote has probability  $p$  of being male and probability  $1 - p$  of being female; (2) there is a specific age at which the sex of all offspring can be identified, and all offspring that die before this age are of unknown sex; and (3) a zygote's probability of dying before being old enough to sex is  $\theta$  or  $k\theta$  for males or females, respectively. Then, in clutches originally of size  $N$ , the distribution at sexing age of males,  $M$ , females,  $F$ , and unsexed (dead) offspring,  $U = N - M - F$ , is

$$P(M, F, U) = \frac{N!}{M!F!U!} [p(1 - \theta)]^M [(1 - p)(1 - k\theta)]^F [p\theta + (1 - p)k\theta]^U.$$

This distribution has been found to give an approximate fit to the observed sex distribution in a population of red-winged blackbirds, *Agelaius phoeniceus* (Fiala 1979).

It follows that in the subsample comprising those broods in which a particular number,  $M + F$ , of offspring are sexed, the distribution of males and females is

$$\begin{aligned} P(M, F, U | M + F, U) &= \frac{P(M, F, U)}{P(M + F, U)} \\ &= \frac{\frac{N!}{(M + F)!U!} [p(1 - \theta) + (1 - p)(1 - k\theta)]^{M+F} [p\theta + (1 - p)k\theta]^U}{\frac{N!}{M!F!U!} [p(1 - \theta)]^M [(1 - p)(1 - k\theta)]^F [p\theta + (1 - p)k\theta]^U} \\ &= \frac{(M + F)!}{M!F!} \hat{p}^M (1 - \hat{p})^F, \end{aligned}$$

where

$$\hat{p} = \frac{p(1 - \theta)}{p(1 - \theta) + (1 - p)(1 - k\theta)}$$

is the expected sex ratio at the age of sex identification. This sex distribution is binomial with parameters  $\hat{N} = M + F$  and  $\hat{p}$ , and is independent of  $U$ . Therefore, even with presexing mortality, the expected sex ratio at the time of sexing is the same in all broods, complete or partial. To estimate the primary sex ratio,  $p$ , one would have to solve

$$p = \frac{\hat{p}(1 - k\theta)}{1 - \theta + \hat{p}\theta(1 - k)}.$$

However, this requires knowledge of the mortality rates,  $\theta$  and  $k\theta$ , which in turn requires knowledge of both  $p$  and  $\hat{p}$ . Therefore, the sex ratio sampled at one age cannot be used to estimate the sex ratio at any other age.

Failure to appreciate this has sometimes led authors to nonparsimonious conclusions. For example, Myers (1978), while correctly emphasizing the importance of avoiding "confusion between selection on sex ratio adjustment and differential mortality" (p. 387), presents an analysis of data on red-winged blackbirds that suffers from exactly this confusion. The blackbirds to which Myers refers were not sexed until they reached an age of 8–10 days, the end of the nestling period (Holcomb and Twiest 1970), and since their primary sex ratios were estimated according to Mayr's method (using only 70 of 110 fledglings), Myers' statement that "differential mortality between the sexes did not contribute to the sex ratio determination" is unjustified.

The apparent variation in sex ratio with brood size at fledging in the data cited by Myers shows that either assumption 1 or assumption 3 of the trinomial distribution is not true across clutch sizes. Either the probability of being male or the sex differential in the probabilities of dying unsexed must have varied with clutch size, but it cannot be determined which. The data are consistent with either the hypothesis of a clutch-size-dependent adjustment of the primary sex ratio, without differential mortality, or the hypothesis of proportionally higher male mortality in larger broods, with a constant (possibly 50%) primary sex ratio. As recognized by Myers, knowledge of the primary sex ratio is required to separate these hypotheses. I wish to emphasize that the primary sex ratio must be correctly estimated, i.e., it must be sampled before the ages at which differential mortality may occur (cf. Howe 1977).

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