

COMMENTARIES

An adaptive explanation for male-biased sex ratios in overwintering monarch butterflies

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Frey & Leong (1993) recently published the results of a study where they had investigated the sex ratio in a population of overwintering monarch butterflies, *Danaus plexippus*, roosting in trees at a California site. They had marked over 6000 butterflies in a manner which permitted them to distinguish males from females at roosting height using binoculars. This allowed them to rule out the possibility that males and females roost at different heights, which could result in artificially biased sex ratios in mark–release–recapture studies. The results of Frey & Leong's unique study clearly demonstrate that there is a male bias in sex ratio (about 60% males) at this overwintering site in early winter (January–February). It is generally very difficult to rule out all possible causes of artificially biased sex ratios in field studies, and for this reason the type of data presented by Frey & Leong (1993) is a welcome complement to controlled rearings (e.g. Wiklund et al. 1992). In this communication, we accept Frey & Leong's empirical result, but suggest an adaptive alternative explanation for the bias in sex ratio.

Following Brussard & Ehrlich (1970), Frey & Leong proposed several hypotheses that could explain the male-biased secondary sex ratios often observed in butterflies: (1) male-biased primary sex ratios, (2) differential mortality during pre-adult stages, (3) lags in emergence times of females relative to males (protandry) resulting in sample bias and (4) differences in 'catchability' due to sex-related differences in behaviour. Because adult sex ratios of 1:1 have been reported for monarch butterflies, Frey & Leong ruled out hypotheses (1) and (2). As the sampling was done among overwintering butterflies, they also ruled out hypothesis (3). Finally, their own results led them to rule out hypothesis (4). This left them with the

tentative explanation that there is female-biased mortality among adult monarch butterflies along the migration routes to the overwintering sites. No evidence or proposed explanation was given for this pattern of biased mortality.

It should be added that sexual differences in mortality at the overwintering sites (males are eaten preferentially by predators; Brower & Calvert 1985; Glendinning 1993), or in the duration of overwintering, or both, are also likely to affect sex ratios in overwintering populations of monarchs, and sex ratios do seem to change over time during overwintering (Van Hook 1993). The results of Frey & Leong (1993) cannot be explained by these factors because they involve a male rather than a female bias, and because sampling was done during the first months of overwintering. There may be sampling problems other than those tested by Frey & Leong. For instance, Brower & Calvert (1985) found different sex ratios on branches versus trunks of trees. However, there are other indications that sex ratios of reproductively inactive monarchs may be truly male-biased in autumn and early winter, at the overwintering sites or in the transient colonies along the migration routes, even though a more equal or female-biased sex ratio may rapidly develop over time (James 1993; Van Hook 1993). Similar patterns can be seen in related species in Australia, where the male bias in some cases seems to persist during the whole of winter (Scheermyer 1993).

An alternative explanation for male-biased sex ratios in winter is selection for protandry resulting in males having a greater propensity to enter diapause development, and accordingly being overrepresented among overwintering individuals (Wiklund et al. 1992). This hypothesis is related to hypothesis (3) above, but very different from it.

Protandry, here defined as the phenomenon that males start to emerge as sexually mature individuals before females (not to be confused with sequential protandry within individuals), is very general in seasonal populations of butterflies and other insects. Protandry probably results from sexual selection on males to maximize the expected number of matings (Darwin 1871; Wiklund & Fagerström 1977; Nylin et al. 1993). Evolutionary stable strategy models show that males should start to emerge before females, but also cease to emerge before females (Bulmer 1983; Iwasa et al. 1983; Parker & Courtney 1983). Theoretically, the male eclosion curve should be abruptly truncated before female emergence has ceased (Iwasa et al. 1983).

In temperate areas many insect populations show partial voltinism, in which some individuals of the penultimate generation develop directly to produce the final generation, whereas others enter diapause development and postpone emergence as sexually mature adults until next season. The propensity to diapause or develop directly is determined by environmental signals, especially the photoperiod experienced during the developmental stages that precede the potentially diapausing stage (Tauber et al. 1986). Wiklund et al. (1992) suggested that juvenile males should be more prone to enter diapause development late in the season (and postpone sexual maturation) than juvenile females because otherwise males would fail to emerge early relative to females and be penalized in terms of fewer mating opportunities. By postponing sexual maturation, males can instead achieve an early emergence next season by simply terminating diapause earlier than females. A resulting prediction was that (at conditions critical for the choice between developmental pathways) there should be a female-biased sex ratio among directly developing individuals and a male-biased sex ratio among diapausing individuals. This prediction was corroborated by laboratory rearings of several species of butterflies: *Pieris napi*, *Pararge aegeria* and *Polygonia c-album* (Wiklund et al. 1992). Another prediction, that males should enter diapause earlier in the season, was corroborated by laboratory and outdoor rearings of *P. napi* and *P. rapae* (Wiklund et al. 1992).

One of these species, *P. c-album*, is of special interest in the present context because, like the monarch, it overwinters in the adult stage in a

reproductive diapause (Nylin 1989, 1992). The fact that this species displays strongly and consistently male-biased sex ratios among diapausing individuals in laboratory rearings of mixed diapause/direct broods with close to zero mortality (Nylin 1992; Wiklund et al. 1992) therefore indicates that attention should be given to the possibility that the same pattern occurs in the monarch and could be given the same theoretical explanation.

It remains to be seen whether our alternative explanation is applicable to the monarch butterfly, because to our knowledge the basic data needed to conclusively demonstrate this (e.g. sex ratios in mixed diapause/direct broods) are not yet available. One reason for this may be the fact that diapause regulation, and especially sexual differences in such regulation, is difficult to study in species with adult reproductive diapause. In contrast to *P. c-album*, the monarch lacks seasonal morphs that can be used to indicate whether an adult is in reproductive diapause (Nylin 1989, 1992), which necessitates dissections of the reproductive tracts. Quantitative measures such as weight of reproductive organs have to be used, and such measures may not be directly comparable between the sexes. Using this method, Herman (1981) concluded that the adult reproductive diapause is more intense and of longer duration in female monarchs. This should not be confused with a sexual difference in the propensity to enter diapause, where information is scarce.

One piece of evidence that may fit our hypothesis comes from the results of Lessman & Herman (1983). They investigated the titres of juvenile hormone in the haemolymph of adult monarchs, wild-caught at monthly intervals over the year in Minnesota (May–September) and California (October–March). High titres of juvenile hormone and extensive development of the reproductive tracts were found during summer (June–July) in both sexes, whereas both indicators of sexual maturation scored low for both sexes in winter (November–January). More variation was found in autumn (August–October) where an anomaly (unexplained by Lessman & Herman) was found: in August, males showed very low titres of juvenile hormone. This was followed by an abrupt increase to almost summer levels in September and then a more gradual decrease towards low winter levels. In contrast, females displayed a

steady decrease from summer to winter. This sexual difference could reflect the pattern predicted by our hypothesis (Wiklund et al. 1992), that is, that diapause in males should be induced earlier in the season.

Lessman & Herman (1983) observed that mating precipitously declines in September (following the August decline in male juvenile hormone), when migration begins, but peaks again in October (following the new peak in male juvenile hormone). Possibly, this late peak represents a partial final generation of sexually mature individuals, at a time when diapausing individuals (with a majority of males) could already be migrating away from Lessman & Herman's Minnesota study site. The results of Lessman & Herman (1983) also suggest that females may be more reproductively active than males during a part of early autumn, which could result in higher female mortality. This would support both Frey & Leong's (1993) and our explanation (Wiklund et al. 1992).

Another observation of interest is the fact that male monarchs terminate diapause earlier than females at the overwintering sites, where mating takes place (Herman 1981; Lessman & Herman 1983). In other words, protandry can be realized by late males that choose to postpone sexual maturation until next season, in agreement with our theory.

The main result of Frey & Leong (1993), that is, the male bias among overwintering monarchs, is exactly the type of field data needed to test our theory (Wiklund et al. 1992). We do not expect a male-biased sex ratio to be found in all overwintering populations of insects, since, as discussed above, there are many other sources of variation. We do predict that overwintering populations, if they are recruited from populations with partial voltinism, should be at least initially male-biased. Our theory, and the explanation for the male bias given by Frey & Leong, are not mutually exclusive but rather operate on different levels. Our theory is an ultimate, adaptive, explanation following directly from evolutionary stable strategy models of optimal behaviour of the sexes, and complementing proximate explanations such as female-biased adult mortality.

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