

“Sex Ratio” Meiotic Drive in *Drosophila testacea*

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ABSTRACT

We document the occurrence of “sex ratio” meiotic drive in natural populations of *Drosophila testacea*. “Sex ratio” males sire >95% female offspring. Genetic analysis reveals that this effect is due to a meiotically driven X chromosome, as in other species of *Drosophila* in which “sex ratio” has been found. In contrast to other drosophilids, the “sex ratio” and standard chromosomes of *D. testacea* do not differ in gene arrangement, implying that the effect may be due to a single genetic factor in this species. In all likelihood, the “sex ratio” condition has evolved independently in *D. testacea* and in the *Drosophila obscura* species group, as the loci responsible for the effect occur on different chromosomal elements. An important ecological consequence of “sex ratio” is that natural populations of *D. testacea* exhibit a strong female bias. Because *D. testacea* mates, oviposits, and feeds as adults and larvae on mushrooms, this species provides an excellent opportunity to study the selective factors in nature that prevent “sex ratio” chromosomes from increasing to fixation and causing the extinction of the species.

MEIOTICALLY driven sex chromosomes not only violate Mendelian rules of segregation, but because of their influence on the relative proportions of males and females in a population, they can affect rates of population growth, the intensity of sexual selection, and effective population sizes. Furthermore, unrestrained meiotic drive of either the X or the Y can quickly result in failure to produce any individuals of one sex, thus leading to the extinction of a population or species (HAMILTON 1967).

WU and HAMMER (1990) argue on conceptual grounds that X chromosomes should be meiotically driven much more commonly than autosomal loci, because such distortion results from suppression of recombination between a locus causing meiotic drive on one chromosome and a target heterochromatic region on another chromosome whose transmission is thereby suppressed. With no recombination between the X and Y chromosomes and the extensive heterochromatization of the Y, there may be many opportunities for such interaction. If this hypothesis is correct, sex ratio meiotic drive may turn out to be more than a mere evolutionary curiosity, representing a perpetual threat to the persistence of a species.

Sex ratio meiotic drive is best known in a number of species of *Drosophila*. Male carriers of a driven X chromosome, designated SR for “sex ratio,” transmit only X-bearing sperm and thus sire only daughters. Such chromosomes were first discovered in several members of the *Drosophila obscura* species group, including *Drosophila affinis* (MORGAN, BRIDGES and STURTEVANT 1925), *D. obscura* (GERSHENSON 1928), *Drosophila pseudoobscura*, *Drosophila persimilis*, *Drosophila athabasca* and *Drosophila azteca* (STURTEVANT

and DOBZHANSKY 1936) and *Drosophila subobscura* (JUNGEN 1967). They have also been found outside the obscura group in *Drosophila paramelanica* (STALKER 1961) and *Drosophila mediopunctata* (DE CARVALHO, PEIXOTO and KLACZKO 1989).

Previous efforts to understand the selective factors that prevent spread of SR chromosomes have focused on *D. pseudoobscura* (e.g., WALLACE 1948; ANDERSON 1968; POLICANSKY 1974, 1979; BECKENBACH 1978, 1983; CURTSINGER and FELDMAN 1980; WU 1983a,b). Unfortunately, because the ecology of this species is poorly known, most studies on the fitness effects of SR have been limited to laboratory populations, and there is no assurance that selective differences (or similarities) found in the lab will apply to individuals in natural populations. As BECKENBACH (1983, p. 647) concludes, “If we wish to discover how SR is maintained in nature, nature is where we should look.” None of the other *Drosophila* species in which “sex ratio” has been discovered is obviously superior to *D. pseudoobscura* for ecological study in the wild.

Here we report the occurrence of “sex ratio” in *Drosophila testacea*, a species eminently suitable for field studies of differential fitness. This Holarctic species is common in temperate and boreal forests, where all stages of its life center around fleshy mushrooms. Adults feed, mate and oviposit on these fungi, which also serve as larval food. Among the ecological factors already known to have important effects on their populations are larval competition for food (GRIMALDI and JAENIKE 1984) and parasitism by nematodes (J. JAENIKE, unpublished results).

As we will show, “sex ratio” in *D. testacea* is unique among known cases in *Drosophila* in that it is not

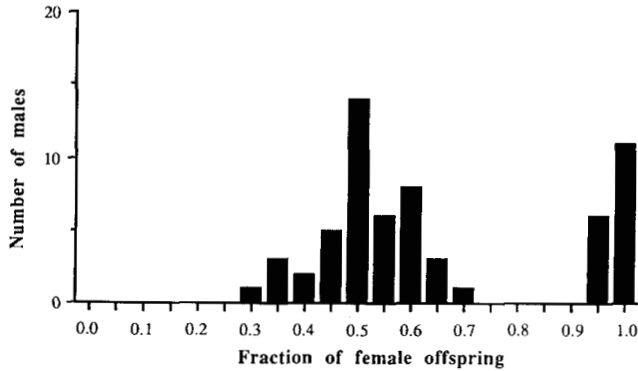


FIGURE 1.—Offspring sex ratios of male *D. testacea*, which were captured as adults at Mendon Ponds Park, New York, in June 1990. Each male was mated to a single female and the sex of all progeny was determined. Only families in which at least 20 offspring were produced are included.

associated with chromosomal inversions. This suggests that the “sex ratio” effect may be produced by a single locus in this species, thus making it a good candidate for molecular genetic analysis of the phenomenon. It also implies that the meiotic drive locus, rather than an entire inversion, is the unit of selection in natural populations. Finally, we present evidence that the “sex ratio” factor does affect population-level sex ratios.

MATERIALS AND METHODS

Characterization of “sex ratio”: “Sex ratio” was initially detected in *D. testacea* by the occurrence of all-female progeny in crosses between wild-caught males and virgin females in studies of female mate choice (JAENIKE 1988). Initial crosses of individual males to females of several different strains revealed that “sex ratio” is clearly a property of the male and not the female of a cross. To characterize the expression of “sex ratio,” males known to be genetically “sex ratio” (*SR*) or standard (*ST*) were mated to *ST/ST* females and offspring sex ratios determined.

The possibility of meiotic drive in heterozygous females was tested in *SR/ST* females, which were produced by crossing *SR* males to *ST/ST* females. The genotypes of the sons of 29 of these heterozygous females were determined by crossing them to virgin *ST/ST* females and scoring their progeny for distorted sex ratios.

The fertility of the occasionally produced sons of *SR* males was tested in *D. testacea* by crossing them to *ST/ST* females in the laboratory and scoring for the presence of viable offspring.

Occurrence of “sex ratio” in natural populations: Flies were collected from natural populations by sweeping over naturally occurring mushrooms or commercial *Agaricus bisporus* that had been set out as bait. Such collections have been made in New York, Maine, Pennsylvania, North Carolina, West Virginia and Virginia, representing a major fraction of *D. testacea*'s range in eastern North America. In our general survey work, males are scored if they sire at least 20 offspring. Males producing $\geq 90\%$ female offspring are classified as “sex ratio” (Figure 1).

Temporal fluctuations in the frequency of “sex ratio” were monitored at two sites—Mendon Ponds Park, Monroe County, New York, and Loyalsockville, Lycoming County, Pennsylvania. Collections made at regular intervals consisted of an average of over 200 wild-caught males, which

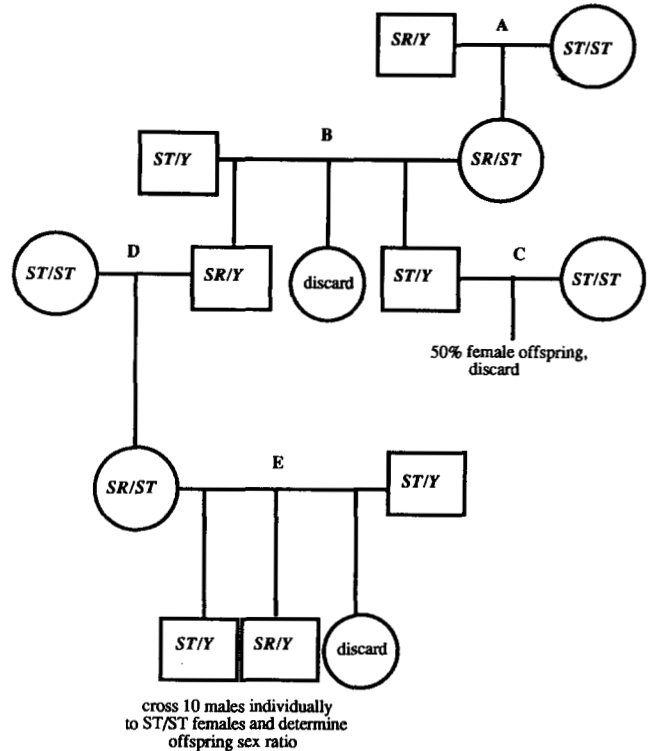


FIGURE 2.—Crossing scheme for determination of inheritance of “sex ratio.” Genotypes illustrated assume that “sex ratio” is X-linked.

were mated to laboratory reared virgin females.

Inheritance of “sex ratio”: The following mating scheme was carried out to distinguish among the X chromosome, the Y, the autosomes, and cytoplasmic inheritance as causes of the “sex ratio” effect (Figure 2). “Sex ratio” males from natural populations were crossed to females of a non-sex ratio laboratory strain (*ST/ST*). The *SR/ST* offspring (all females) from such crosses were mated to *ST* males, and the resulting sons were crossed to *ST/ST* females. Only families yielding all-female progeny from this last cross were tested further. Females from such families were crossed to *ST* males, and 10 male offspring from each female were mated to *ST/ST* females in order to determine whether these males expressed “sex ratio.” The mode of inheritance of five independently derived “sex ratio” factors from two natural populations (Maine and North Carolina) was determined in this fashion. All matings consisted of one male and two virgin females.

Cytological analysis: Polytenes chromosomes were examined to determine if *SR* is associated with inversions, as it is in other species of *Drosophila*. Salivary glands were dissected in saline solution from third instar larvae that had been raised in uncrowded conditions at 18°. They were fixed in 45% acetic acid for one minute and stained with 2% lacto-acetic orcein. The glands were placed in a pool of orcein inside an outline of wax on a slide and covered with a coverslip. Because chromosomes of *D. testacea* are prone to ectopic pairing, separation of them without breaking was achieved by gently tapping the coverslip.

The X chromosome, which is a rod in *D. testacea* (PATERSON and STONE 1952), was distinguished from the autosomes in male larvae by its narrower width and lighter staining. Female larvae heterozygous for the *SR* and *ST* chromosomes were produced by mating *SR* males to *ST/ST* females. The X was identified in females on the basis of puffing and banding patterns seen in males.

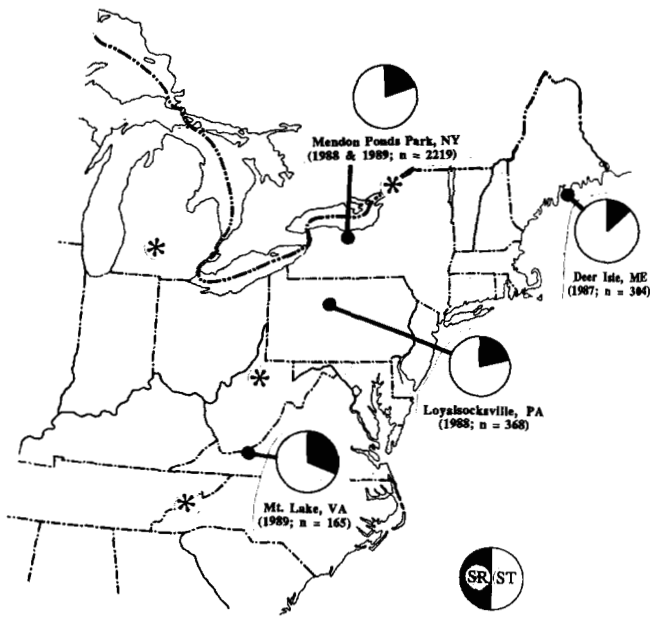


FIGURE 3.—Frequency of "sex ratio" males in natural populations of *D. testacea*. Asterisks denote localities where "sex ratio" has been found among small samples of flies.

Population-level consequences of "sex ratio": The frequency of "sex ratio" was determined among males of *D. testacea* captured from Mendon Ponds Park, Monroe County, New York, in 1986 and Mt. Lake Biological Station, Giles County, Virginia, in 1989. Simultaneously, estimates of the population-level sex ratios were determined by sexing flies that emerged from naturally occurring mushrooms.

RESULTS

Characterization of "sex ratio": Offspring of males known to be genetically "sex ratio" are 98.5% female ($n = 826$), whereas genetically standard males produce 48.9% female offspring ($n = 1,253$). Females known to be heterozygous for "sex ratio" (*i.e.*, *SR/ST*) produced 48% "sex ratio" sons among 265 male offspring tested. Thus, there is no evidence of meiotic drive in females.

In other species of *Drosophila*, the occasional sons of "sex ratio" males are sterile (PEACOCK, MILKOS and GOODCHILD 1975). Of 68 sons of "sex ratio" fathers tested, not one produced viable offspring when mated to laboratory females. Thus, the few male offspring produced by "sex ratio" males are sterile.

Occurrence in natural populations: Every population sampled has been found to harbor "sex ratio" at frequencies generally around 20% (Figure 3). At the Mendon Ponds Park and Loyalsocksville sites, the frequency of "sex ratio" fluctuated somewhat, ranging from 15% to 30% (Figure 4). The only statistically significant change in month to month frequency of "sex ratio" is between the June and July 1988 samples at the Mendon site. At the Mendon site, the frequency of *SR* declined from spring until August suggesting that it may undergo frequency variation on a seasonal basis.

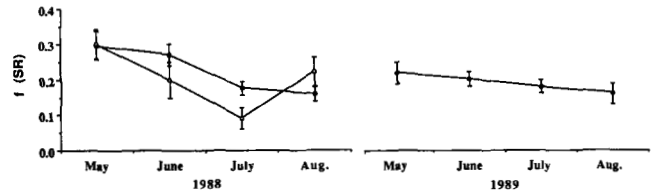


FIGURE 4.—Temporal variation in the frequency (\pm standard error) of "sex ratio" males of *D. testacea* at Mendon Ponds Park, New York (●) and Loyalsocksville, Pennsylvania (○).

Inheritance of "sex ratio": Cross A (Figure 2) of *SR* males to *ST/ST* females yielded only daughters which, when crossed to *ST* males (cross B), produced some sons exhibiting the "sex ratio" trait (cross D) and some that had normal offspring sex ratios (cross C). The expression of "sex ratio" in this generation rules out the possibility of Y-linked inheritance, as the "sex ratio" males in cross D carry a Y chromosome from the standard stock. The passage of the "sex ratio" factors through females of a non-sex ratio stock eliminates the possibility of cytoplasmic inheritance.

The occurrence of the "sex ratio" males from cross E eliminates the possibility that an autosomal recessive is the basis for this trait. If "sex ratio" is due to an autosomal recessive allele (*a*), cross E would yield only AA and Aa sons, none of which would be classified as "sex ratio."

If "sex ratio" is due to an autosomal dominant, then one-half of the type E crosses would be expected to yield only standard males, the other half both "sex ratio" and standard males. In fact, all families produced both "sex ratio" and standard males in cross E; the overall fraction of males resulting from E crosses that were "sex ratio" was 48%, as expected if "sex ratio" is X linked. Thus, the gene or genes responsible for the "sex ratio" trait are carried on the X chromosome, with meiotic drive expressed only in male carriers.

Cytological analysis: The X chromosome was identified in male larvae. The terminal 10% is characterized by a lightly staining tip, followed proximally by a constriction with three bands, a puff containing two lightly staining bands, three regularly spaced dark bands, and a second constriction.

In three female larvae heterozygous for *ST* and *SR* and in which the entire X was visible, no evidence of inversions was seen over the length of the X chromosome (Figure 5). The chromosome illustrated has a small region of asynapsis, proving that it is a diploid and thus a female, not one of the rare male offspring produced from "sex ratio" males.

Population-level effects of "sex ratio": A significant excess of females of *D. testacea* is found among emergent adults bred from naturally occurring mushrooms (Table 1). It is notable that the Mt. Lake population, in which the frequency of *SR* is greater, produced a significantly greater proportion of females



FIGURE 5.—Polytene X chromosome of a female *SR/ST* larva. The white arrow marks the chromocenter, and the black arrow marks a region of asynapsis. Note that in the region of asynapsis, the banding patterns show that the two chromosomes are homosequential.

TABLE 1

Frequencies of females and *SR* males in natural populations of *Drosophila*

| Species | Mendon (1986) | | Mt. Lake (1989) | |
|--------------------|-------------------------|-------------|-----------------|---------------|
| | f (<i>SR</i>) | f (females) | f (<i>SR</i>) | f (females) |
| <i>D. testacea</i> | 0.23 (180) ^a | 0.60* (465) | 0.31 (165) | 0.67* (1,189) |
| <i>D. putrida</i> | | 0.48 (476) | | 0.53 (358) |
| <i>D. falleni</i> | | 0.51 (680) | | 0.47 (4,130) |
| <i>D. recens</i> | | | | 0.53 (329) |

^a Sample size in parentheses.

* Significant excess of females ($P < 0.001$).

than the Mendon population ($\chi^2 = 8.14$; $P < 0.005$).

The excess of female *D. testacea* can be contrasted with the relative numbers of males and females of other species of *Drosophila* emerging from the same mushrooms and in which there is no evidence of the “sex ratio” trait. In *Drosophila recens*, *Drosophila falleni* and *Drosophila putrida*, the proportion of females was not significantly greater than 50%.

DISCUSSION

The expression of “sex ratio” in *D. testacea* is similar in several respects to that seen in other species of *Drosophila*. It is characterized by extreme meiotic drive of the X chromosome in males, resulting in the production of virtually all-female progeny. As in other drosophilids, the occasional male offspring of “sex ratio” males are invariably sterile. These sons are probably XO, resulting from nondisjunction in the “sex ratio” fathers, as in *D. pseudoobscura* (HENAHAN and COBBS 1983). If so, this would support the notion that meiotic drive results from the selective failure of Y-bearing spermatids to differentiate into functional sperm (PEACOCK, MIKLOS and GOODCHILD 1975; POLICANSKY and ELLISON 1970.).

Although the X chromosome is responsible for “sex ratio” in all species of *Drosophila* in which this effect has been found, the particular genetic element responsible varies among species. In *D. pseudoobscura* and *D. persimilis*, “sex ratio” is associated with inver-

sions on the right arm of the X chromosome (STURTEVANT and DOBZHANSKY 1936), which is homologous to the left arm of the third chromosome in *D. melanogaster* (PATTERSON and STONE 1952, Table 27). As a member of the subgenus *Drosophila*, the X of *D. testacea* is in all likelihood homologous to the X of *D. melanogaster* (PATTERSON and STONE 1952). Thus, there may be different genetic bases to the “sex ratio” phenomenon.

While the initial discoveries of “sex ratio” were limited to species of the *D. obscura* group of the subgenus *Sophophora*, our discovery of “sex ratio” in *D. testacea* brings to three the number of different species groups in the subgenus *Drosophila* in which it has been found. (We also have evidence for its existence in a fourth species group in this subgenus—*Drosophila quinaria* of the *quinaria* species group. However, we have not yet carried out genetic analyses to see if “sex ratio” is due to the X chromosome). The great evolutionary distance between these subgenera—THROCKMORTON (1975) suggests that they split in the Oligocene—and the absence of “sex ratio” in other species groups in the subgenus *Sophophora* suggest that the “sex ratio” trait has arisen independently several times in *Drosophila*. The supposition that the genetic basis for “sex ratio” differs between species in the *Sophophora* and *Drosophila* subgenera further supports this hypothesis.

In all other species of *Drosophila* in which “sex ratio” has been described, it is associated with one or more inversions on the X chromosome (Table 2). In *D. testacea*, females heterozygous for *SR* and *ST* show no evidence of any inversions over the length of their X chromosomes. WU and BECKENBACH (1983) have argued that the association of “sex ratio” with inversions is the result of tying together genes on the X that serve to counteract the effect of evolved suppressors of “sex ratio” meiotic drive. Thus, association with inversions probably means that “sex ratio” is evolutionarily old. Conversely, the lack of inversions seen in *D. testacea* suggests that “sex ratio” has arisen relatively recently in this species. Our failure to find any evidence of “sex ratio” in *D. putrida*, the only other member of the *testacea* species group, also supports a relatively recent origin of “sex ratio” in *D. testacea*.

The “sex ratio” polymorphism presumably results from a balance between meiotic drive favoring *SR* and natural selection against carriers of *SR*. In species in which “sex ratio” loci are tied up within inversions, it is not possible to determine if the reduced fitness of *SR*-carrying flies is due to the “sex ratio” loci or to linked alleles. In *D. testacea* “sex ratio” is not associated with inversions, suggesting that any reduced fitness of *SR*-carriers might be a pleiotropic effect of the meiotic drive locus. The lack of inversions associated with “sex

TABLE 2
"Sex ratio" X chromosomes in the genus *Drosophila*

| Subgenus | Species | No. of inversions associated with SR | Reference |
|-------------------|----------------------|--------------------------------------|---|
| Sophophora | <i>obscura</i> | ? | GERSHENSON (1928) |
| | <i>pseudoobscura</i> | 3 | STURTEVANT and DOBZHANSKY (1936) |
| | <i>persimilis</i> | 1 | STURTEVANT and DOBZHANSKY (1936) |
| | <i>subobscura</i> | 5 | JUNGEN (1967) |
| | <i>affinis</i> | 1 | STURTEVANT and DOBZHANSKY (1936) |
| | <i>athabasca</i> | 5 | MILLER (1971) |
| | <i>azteca</i> | 3 | DOBZHANSKY and SOCOLOV (1939) |
| <i>Drosophila</i> | <i>paramelanica</i> | 4 | STALKER (1961) |
| | <i>mediopunctata</i> | 1 | DE CARVALHO, PEIXOTO and KLACZKO (1989) |
| | <i>testacea</i> | 0 | This study |

ratio" in this species makes it unlikely that polymorphism for this trait is maintained by associative overdominance in females, a theoretical possibility in other species (EDWARDS 1961). Since single locus heterosis is apparently very rare, some form of frequency-dependent selection may be responsible for the "sex ratio" polymorphism in *D. testacea*. In addition, we note that if "sex ratio" in this species is due to the action of a single locus, as one might conclude from its lack of association with inversions, this species could be particularly suitable for molecular genetic analyses of meiotic drive.

Every population of *D. testacea* that we have surveyed in eastern North America is polymorphic for "sex ratio," with most populations having a frequency of SR of about 20% among males. Although there is modest temporal variation in its frequency at the Mendon Ponds and Loyalsockville sites (Figure 4), we observe no obvious geographical variation in its frequency. The ubiquitous occurrence of SR and the lack of noticeable geographic variation in its frequency means either that there is a great deal of gene flow among *D. testacea* populations or that "sex ratio" frequencies are subject to strong balancing selection within populations. "Sex ratio" cannot be considered a selectively neutral trait: in the absence of selection against carriers of SR, its frequency is expected to increase very rapidly—about 3–5% per generation from its current frequencies in the range of 15% to 30%.

Two observations show that SR has a significant effect on population-level sex ratios in nature (Table 1). (1) The fraction of female *D. testacea* emerging from mushrooms is significantly greater than 0.5. In contrast, *D. putrida*, *D. falleni* and *D. recens*, which are not polymorphic for "sex ratio," yielded approximately equal numbers of males and females from field-collected mushrooms. (2) For two populations of *D. testacea* we have data on both SR frequencies among wild-caught males and sex ratio of flies emerging from mushrooms. In the population with a higher fre-

quency of SR there is a significantly greater excess of emergent females. In fact, the 1989 Mountain Lake population of *D. testacea* exhibited a 2:1 ratio of females to males among emergent adults. The frequencies of females are not significantly different from expected value of $(p/2 + 0.5)$, where p is the frequency of SR, and assuming there is no selection against SR-carriers. However, this does not imply that there is no selection against these individuals, as similar female frequencies could be produced if "sex ratio" males suffer both reduced fertility and larval viability.

BRYANT, BECKENBACH and COBBS (1982) have attempted to relate the "sex ratio" polymorphism to population-level sex ratios in *D. pseudoobscura*, using the numbers of adult males and females captured at orange and grapefruit baits. However, baits may be more attractive to individuals of one sex than the other (e.g., JAENIKE 1986; HOFFMANN 1988), thus biasing estimates of population-level sex ratio. This is perhaps the reason that in most of the collections made by BRYANT, BECKENBACH and COBBS (1982), females constituted well under 50% of the captured flies. Our estimates of population sex ratios were based on flies bred directly from natural breeding sites and are thus not compromised by differences between males and females in their responses to bait types, time of collection, weather, etc.

Strongly female-biased sex ratios could have a number of important ecological effects on these populations. If there are enough males to fertilize all of the eggs produced by females, such populations should have a greater potential rate of population growth. With all else equal, a population that is 67% female should have a reproductive rate about one-third greater than one that is 50% female. With interspecific scramble competition for larval food resources, female-biased populations of *D. testacea* may fare better, as they are capable of laying relatively more eggs on the mushrooms competed for. Thus, the greater reproductive potential of such populations could result

in greater equilibrium numbers. With two females for every adult male in a population, the intensity of sexual selection may be comparatively less than in other drosophilids with population-level sex ratios closer to 50:50. Finally, if the frequency of "sex ratio" were to increase unchecked for even a few generations, the fraction of males in a population might become so low as to render a population particularly susceptible to extinction via demographic stochasticity (WALLACE 1968; GILPIN and SOULE 1986).

The possibility of extinction resulting from unbribed increase of a meiotically driven X chromosome raises the question of what selective factors prevent the spread of such chromosomes. Because *D. testacea* spends its life around mushrooms, the relative fitness of different genotypes can be studied at all life stages in the wild. As a result, it should be possible to determine how selection against carriers of a particular chromosome prevents the extinction of this species.

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