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Variation in Population Sex Ratio and Mating Success of Asexual Lineages of *Alsophila pometaria* (Lepidoptera: Geometridae)

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Abstract

Populations of *Alsophila pometaria* (Harris) are largely gynogenetic and composed of asexual females that must mate with a conspecific male to reproduce. Within this asexual contingent, there are a variety of electrophoretically defined multilocus genotypes. In this study we found that populations differ in sex ratio. We also found that there is an indication of differential mating success among asexual genotypes in a population of *A. pometaria.*

Gynogenesis is an unusual form of reproduction in which asexual females must mate before reproducing, but males make no genetic contribution to the offspring. Gynogenetic females of *Alsophila pometaria* (Harris), the fall cankerworm, pass on their genotype intact to progeny yet must mate with a conspecific male to reproduce (Mitter and Futuyma 1977). Electrophoretic surveys and breeding studies have shown that there are a variety of asexual genotypes (clones) within populations of this species (Mitter et al. 1979, Harshman 1982). Sexual reproduction is also present and sexual females are assumed to be the source of males upon which gynogenetic females depend (Mitter et al. 1979, Harshman 1982). The population sex ratio of the fall cankerworm is female-biased (Porter and Alden 1924, Balch 1938, Mitter et al. 1979), reflecting the preponderance of asexual reproduction.

In this study we have surveyed local populations for variation in sex ratio. Male abundance is a critical parameter in gynogenetic populations (Kiester et al. 1981), particularly

so where sex ratios are extreme and many females go unmated. We also studied whether or not there was differential mating success among the asexual lineages found in populations of the fall cankerworm. Gynogenetic species may often be composed of a variety of asexual genotypes (Vrijenhoek 1979, Mitter et al. 1979), and where males are in short supply, mating success could be an important component of fitness of asexual lineages.

Materials and Methods

Population Sex Ratio
On Long Island, New York, eggs of the univoltine fall cankerworm hatch in late April and early May. Larvae are polyphagous and usually found feeding on the foliage of deciduous tress. Pupation occurs in the soil, where there is an obligate summer diapause. In the last week of May 1981, late-instar larvae were collected from seven sites by striking vegetation over a beating net. Samples were brought into the laboratory and larvae were fed oak leaves (*Quercus coccinea* and *Quercus velutina*) until they were ready to pupate (usually within a week). There was little mortality in the laboratory and prepupae were placed in a mixture of sterilized sand and potting soil. After 2 months the subterranean cocoons were unearthed and pupae extracted. Male and female pupae could be distinguished by differences in body shape, genital pore position, and wing development. It is difficult to devise an unbiased sampling procedure for adults because the females are wingless and the males fly. Consequently, it seems likely that our method of determining population sex ratio from collections of larvae is more accurate than counting or trapping adults in the field.

   All the collection sites were on Long Island (fig. 1). The north shore of the island generally has mesic habitat dominated by species of the red oak group (subgenus Erythrobalanus) and red maple (*Acer rubrum*). This includes the Graduate Biology and Ashley Schiff sites, which are on the Stony Brook campus of the State University of New York, and the Village Wood site, which is located several kilometers away in the village of Stony Brook. Belmont State Park and Southern State Parkway are near the southern shore of the middle of Long Island. The Belmont State Park site is mesic and characterized by trees of the red oak group and red maple. The Southern State Parkway site is drier and dominated by white oak (*Quercus alba*) and scrub oak (*Q. ilicifolia*). The remaining two locations are in the sandy outwash plain that makes up much of the southeastern portion of the island. One of these locations, Route 27, is almost entirely composed of scrub oak and stunted pitch pine (*Pinus rigida*). The other, called Low Planes, is similar but has several additional oak species.
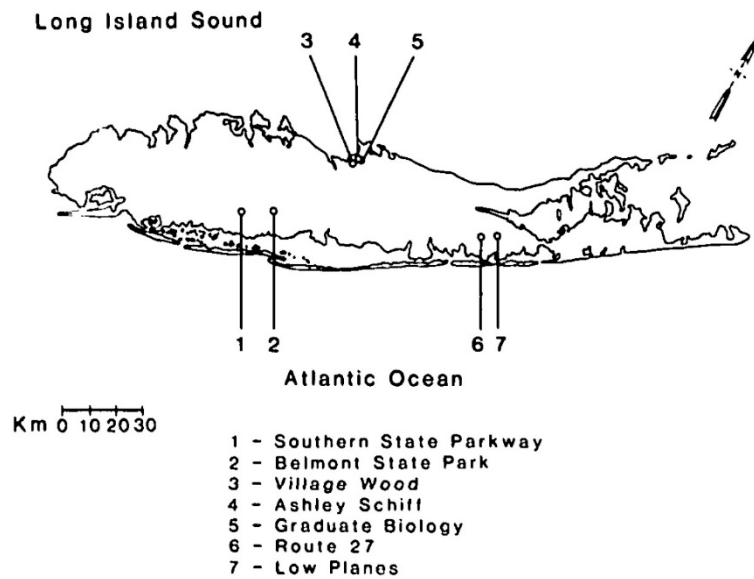
Figure 1. *Alsophila pometaria* collection sites on Long Island, New York.

Mating Success

Adults of the fall cankerworm emerge on Long Island in the late fall or early winter. Females are wingless and may be found on tree trunks, apparently releasing pheromone to attract males flying in the vicinity. Mating may last for several hours, and immediately after it is terminated females climb into the canopy to deposit their eggs. Mating success, in the context of this investigation, refers to female attainment of copulation.

In 1980, moths were collected in the Ashley Schiff site. Most were taken from 7:00 p.m. until 11:00 p.m. on the evening of 1 December. The first week in December was the mating window for adults of that generation because there were few other periods with temperatures high enough for males to fly. Many females with eggs were found on tree trunks throughout the early winter, and they presumably went unmated. On 1 December unmated and mating moths were collected at the same time. Each mating pair was transferred with soft forceps into a cardboard container. The offspring of most of these females were electrophoretically tested to determine the maternal mode of reproduction. It was possible to determine which females had not mated because they were not climbing upward and were usually in a characteristic posture they presumably assume to release pheromones. Where possible, the nearest unmated female on the same tree as a mating pair and an unmated female from the nearest tree were also collected. This pattern of sampling was employed to look for differences between mated and unmated females on a relatively fine spatial scale. All females were frozen and analyzed by electrophoresis, using the techniques of Mitter et al. (1979) and modifications of Futuyma et al. (1981). In this manner, a four-locus genotype was determined for each individual.

Results

Population Sex Ratio

The locations in table 1 are arranged in increasing order of male proportion, and it is clear that males made up a small percentage of these populations. It also appears that the sex ratio can vary over relatively short distances. For instance, collections from the three sites on the north shore varied in male proportion from 0.015 to 0.057, and Low Planes had a higher frequency of males than nearby Route 27. On the other hand, the two sites from the mid-island south shore (locations 1 and 2) had a similar proportion of males. A test of independence shows that there was overall heterogeneity among sites in population sex ratio ($G = 17.940$, $P < 0.01$). However, none of the pairwise comparisons between populations were significant when unplanned a posteriori tests were conducted using a conservative α obtained by dividing the standard significance level by the number of possible pairwise tests.

Table 1. Male proportion in Long Island sites

Location	Male proportion	n
Route 27	0.011	87
Village Wood	0.015	227
Ashley Schiff	0.029	103
Graduate Biology	0.057	210
Belmont State Park	0.063	756
Southern State Parkway	0.066	411
Low Planes	0.067	750

Mating Success

The multilocus genotype of 70% of all females collected from the Ashley Schiff population matched that of previously identified clones (Harshman 1982). In addition, an electrophoretic progeny analysis of 90 of the mated females collected on 1 December 1980 revealed that only one was sexual (Harshman and Futuyma 1985). Therefore, it seems reasonable to assume that almost all the unmated females collected in the Ashley Schiff site were asexual.

Table 2 shows the genotypes categorized on the basis of abundance. The letter portion of the designation of five common genotypes is from Mitter et al. (1979) and Futuyma et al. (1981), and the corresponding number from Harshman (1982). Clones 1(C), 2(B), 8(Y), 26(A), and 48(Z) each made up at least 5% of the total number of females collected. The "infrequent" group was made up of a few genotypes that made up between 1 and 5% of the sample. The "uncommon" genotypes were mostly unique in the sample and made up less than 1% of the total.

Table 2. Female mating success in the Ashley Schiff population of *Alsophila pometaria*

Genotype group	% Mated	No. of females
8(Y)	52.5	40
2(B)	47.5	34
26(A)	40.0	20
48(Z)	28.6	28
1(C)	16.7	18
Infrequent	52.9	17
Uncommon	33.3	45

The percentage of females that were mated ranged from 52.9% for the "infrequent" group to 16.7% for clone 1(C). A statistical analysis was conducted to determine if there was a significant difference between genotype groups in the frequency of mating and non-mating females. The results of a test of independence are marginal (G = 11.428, P = 0.08) but suggest the presence of an overall difference in mating success among asexual genotypes.

Discussion

Gynogenesis is found sporadically in animal taxa. In the insects a ptinid beetle (Moore et al. 1956), delphacid leafhopper (Drosopoulos 1976), psychid moth (Narbel-Hofstetter 1955, 1963), and the fall cankerworm are known to be gynogenetic. Factors such as male preference for sexual females must be in operation for coexistence between gynogens and bisexuals because of the reproductive advantage the asexual contingent enjoys (Moore 1976, Kiester et al. 1981). We were not able to determine if males prefer sexual females because the latter were rare in the Ashley Schiff site. However, allele frequencies from Ashley Schiff males can be used to determine the frequency that any sexual genotype will appear in the population. These calculations reveal that even the most likely sexual genotype will be classified as uncommon (Harshman 1982). In the present study there is no evidence that uncommon female genotypes have a mating advantage (see table 2). Thus, there is no evidence for frequency-dependent mating success, which would favor sexual lineages and promote the coexistence of sexual and asexual reproduction.

We have found that populations of *A. pometaria* are highly female-biased. There is geographic variation in sex ratio, and in some populations males are rare. Thus, it is likely that females often go unmated and asexual lineages compete for limited male reproductive function. In the Ashley Schiff population there was evidence for differential mating success among asexual lineages of A. *pometaria*. Females of clone 1(C) were particularly unsuccessful in obtaining a mating. It has been observed that larvae of this genotype are more likely to undergo density-dependent melanization than are larvae of other common clones (Futuyma et al. 1981). Melanization results in faster larval development and lower adult weight (Schneider 1979, Futuyma et al. 1981), and smaller females were less likely to obtain a mating in a preliminary laboratory experiment (Harshman 1982). Thus, a propensity to melanize may have resulted in lower mating success for clone 1(C). Similarly, attributes of

other asexual genotypes, such as relative time of adult eclosion (Mitter et al. 1979), may affect mating success in populations of the fall cankerworm.

Note

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