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Survivorship and Growth of Sexually and Asexually Derived Larvae of *Alsophila pometaria* (Lepidoptera: Geometridae)

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SURVIVORSHIP AND GROWTH OF SEXUALLY AND ASEXUALLY DERIVED LARVAE OF *ALSOPHILA POMETARIA* (LEPIDOPTERA: GEOMETRIDAE)

A substantial body of theory is devoted to understanding the relative advantages of sexual and asexual reproduction. It is generally understood that asexual forms potentially have a higher rate of reproduction because they save the cost of producing males. The microevolutionary consequences of sexual and asexual reproduction are less clear. Sexual reproduction generates abundant genotypic diversity which may be adaptively advantageous (Williams 1975; Maynard Smith 1978). Asexual reproduction may perpetuate combinations of genes that are coadapted (Templeton 1979), heterotic (Suomalainen et al. 1976; White 1979), or specialized (Vrijenhoek 1979, 1984). Thus, it is possible that the fitness of a sexual population may be lower than an asexual, in part, because recombination tends to break up especially favorable genotypes (Williams 1975; Hebert 1978). If it is generally observed that asexual reproduction has an immediate adaptive as well as a reproductive advantage, then it is difficult to see how sexual reproduction can be maintained by short-term advantages (Williams 1975).

A comparison of closely related sexual and asexual forms is a promising avenue of research to evaluate experimentally the consequences of both modes of reproduction (Maynard Smith 1978). In this study, geometrid moth larvae (*Alsophila pometaria*) derived from both kinds of reproduction were reared on different host plants. The goal was to assess larval viability and growth in an ecologically relevant context and thus partially characterize the fitness of sexual and asexual reproduction.

Biological Background

Alsophila pometaria, the sole Nearctic member of its genus (Inoue 1943), is a species of moth whose unusual mode of reproduction has been studied extensively with electrophoretic markers. Most females are gynogenetic and require a mating with a conspecific male in order to reproduce. Gynogenetic females of the fall cankerworm transmit the maternal genotype intact to their progeny (Mitter and Futuyma 1977). A variety of electrophoretically defined multilocus genotypes (clones) are found in asexual populations, and it has been established that there is a coexisting sexual population (Mitter et al. 1979). Electrophoretic surveys have revealed that the same alleles are present at similar frequencies in the sexual and asexual populations (Mitter et al. 1979; Harshman 1982).

The species is univoltine. Eggs are laid on trees mostly in early winter and hatch about the time of budbreak in the spring. There can be extensive dispersal of hatchling larvae by ballooning on silk threads (Futuyma et al. 1981). This larval

dispersal commonly may result in movement among different host trees (Futuyma et al. 1981). The larvae feed on the foliage of numerous deciduous tree species until early June when they drop to the ground and pupate. The correspondence between the maturation schedule of the larvae and that of the foliage on which they feed is critical because, like the European winter moth *Operophtera brumata* (Feeny 1970), they are unable to complete growth on excessively mature foliage.

Identification of Reproductive Mode

Larvae for these experiments were obtained from egg masses found on trees or directly from mating adults collected in the field. The collection sites were wood-lots dominated by oak (*Quercus* spp.) and red maple (*Acer rubrum*) near the Stony Brook campus of the State University of New York, which is located on the northern shore of Long Island. A number of eggs from each egg mass were set aside at room temperature for early hatching and subsequent electrophoretic analysis. The remainder were left outside for the winter in 1-dram glass vials to be used in experiments after larvae hatched in the spring.

It is not possible to determine the reproductive mode of adult females from their external morphology. Thus, it is our procedure to electrophorese a number of sibs from an egg mass to determine directly the mode of reproduction of the mother. First-instar larvae that hatched in the lab were homogenized in 12–14 μl of the grinding buffer used by Mitter et al. (1979). After electrophoresis, we stained for two of the polymorphic enzymes employed for adults (PGM and PGI). Usually, 10 larvae were run from each egg mass. Sexual reproduction was detected by observing recombination of electrophoretic markers among larval sibs (Harshman 1982). Larvae of specific asexual lineages were isolated from females whose multilocus genotype corresponded to that of an established clone (Mitter et al. 1979; Futuyma et al. 1981).

Growth in a Controlled Environment

In the spring of 1980, larvae from a sexually derived sibship (HL75) were compared to two asexual lineages. One lineage was the widespread and abundant asexual genotype 2(B), which is associated with oak in the field and is apparently an oak specialist (Mitter et al. 1979). The second was asexual genotype 48(Z), which is abundant in mixed oak-and-maple stands. Mitter et al. (1979) suggested that this genotype may be more generalized in its feeding habits than the oak- or maple-associated clones. Larvae of the maple-specialist genotype, 26(A), were not available for this experiment.

Larvae were reared entirely on either oak or red maple leaves obtained from the field. All larvae reared on oak were exposed to a mixture of two species (*Quercus coccinea* and *Q. velutina*). Hatchling larvae from each sibship employed in this study were split evenly between oak and maple foliage. The experiment was conducted with approximately 10 larvae per 5-liter cardboard container. Food was

replenished every other day in the form of fresh sprigs of foliage, with the twigs
inserted into flasks of water. The containers were placed in an environmental
chamber adjusted for 18 h of light at 24° C and 6 h of darkness at 16° C. Larval
survivorship was not recorded in the experiment because a major source of
mortality was uncontrolled desiccation of first-instar larvae. After 3 wk to 1 mo of
growth, prepupal larvae left the foliage and began burrowing. When an individual
reached this stage its weight was recorded. Prepupal weight is correlated with
fecundity in the fall cankerworm (Schneider 1979), and generally pre-image weight
is highly correlated with fecundity in insects (Engelmann 1970). Body size is not
necessarily a primary determinant of fitness, but it is correlated with fecundity,
which is a component of fitness.

Survivorship and Growth of Larvae in the Field

In the spring of 1981 an experiment was conducted to evaluate the survivorship
and growth of sexually and asexually derived larvae. The tested genetic groups
consisted of a sexual sibship (VW118), the oak-specialist [2(B)] and maple-
specialist [26(A)] genotypes, and two clones that are uncommon on Long Island.

The site of the study was a woodlot on the Stony Brook campus in which five
oak trees (*Quercus coccinea*) and five red maple trees were selected as host
plants. Soon after budbreak, larvae that had just hatched were placed on foliage
enclosed by fine mesh bags as described by Futuyma et al. (1981). Each host tree
supported at least two bags with three larvae from each genetic group.

After approximately 1 mo of growth, when larvae began to reach the prepupal
stage, all rearing bags were brought in from the field, and larval survivorship was
recorded. Larvae that had not attained the prepupal stage were raised for a few
days in the laboratory on vegetation similar to that available to them in the field.
All prepupal larvae were allowed to pupate in a mixture of sterilized sand and
potting soil. After 2 mo, pupae were removed from their subterranean cocoons
and sexed. They were then lyophilized and the dry weight of each individual was
determined.

Several aspects of these studies deserve comment. First, they are not designed
to quantify total fitness. Moore (1976), in a comparison of the gynogenetic fish
Poeciliopsis monacha-occidentalis with a related bisexual species, describes
three aspects of fitness. One is the twofold reproductive advantage accruing to
asexual reproduction, another is mating success, and the third is "primary
fitness," which includes fecundity and survival. In the present study on *Alsophila
pometaria*, we are concerned with measures that are analogous to "primary
fitness." A second point is that the size of our studies was limited by the scarcity
of sexual reproduction. In one survey only 2 sexual females were found in 117
progeny-tested females collected from populations near Stony Brook (Harshman
1982). Thus, our experiments were constrained in sample size and the number of
treatments employed. Finally, it was observed that the egg masses used in this
study had no egg parasites, and larvae derived from both modes of reproduction
appeared to be free of disease.

TABLE 1

PREPUPAL WET WEIGHT OF LARVAE REARED IN A CONTROLLED ENVIRONMENT

	ON OAK			ON MAPLE		
GENETIC GROUP	$\overline{Y}$(mg)	N	s^2	$\overline{Y}$(mg)	N	s^2
Sexual sibship	54.88	17	92.485	50.06	17	75.184
Asexual genotype 2(B)	55.16	57	51.564	27.92	51	56.554
Asexual genotype 48(Z)	49.88	24	56.984	27.44	25	24.340

NOTE.—Interaction (genetic group × plant): $\chi^2 = 40.7$, $P < 0.001$.

RESULTS

Growth in a Controlled Environment

Table 1 presents the average weight, variance, and sample size for larvae reared in the laboratory. The larvae cannot be sexed and consequently both males and females from the sexual sibship were weighed, which may have inflated the variance of samples. Wilson's nonparametric multi-way method (Wilson 1956) was used to analyze the data. There was a significant interaction between genetic group and host plant, which was present because red maple was an inferior host for the asexual genotypes but not for the sexual sibship. There was no evidence that genotype 48(Z) was more generalized in resource utilization than the oak-specialist genotype.

The length of the larval period was recorded in the course of the experiment. On red maple, the average larval periods were 27.0 days (sexuals), 27.3 days [2(B)], and 28.1 days [48(Z)]. On oak, the larvae matured faster: the averages were 18.2 days (sexuals), 20.6 days [2(B)], and 21.8 days [48(Z)]. There were no significant differences between genetic groups in the rate of development, and it is clear that larger larval size is not a function of an extended feeding period.

Survivorship and Growth of Larvae in the Field

Table 2 shows the proportion of larvae that survived in field cages. The average survivorship across plants was 50% for the sexually produced progeny and ranged from 29% to 39% for the asexual genetic groups. The data were evaluated using log-linear models (Sokal and Rohlf 1981), which revealed no significant three-factor interaction. The lack of independence between variables (table 2) indicated that larval mortality differed among host plants and genetic groups. Red maple was again an inferior host, and as demonstrated by Futuyma et al. (1981), the oak-specialist genotype 2(B) has poor viability on red maple.

The average dry weights of pupae are shown in table 3. Data were available only for oak-reared larvae because of high mortality on maple. Only females were weighed from the sexual sibship to make the data as comparable as possible. Nevertheless, the sexual sibship was significantly more variable than the pooled

TABLE 2

PROPORTION OF LARVAE SURVIVING IN FIELD CAGES

	ON OAK		ON MAPLE	
GENETIC GROUP	Survival Rate	N	Survival Rate	N
Sexual sibship	.80	30	.20	30
Asexual genotype 2(B)	.55	60	.03	60
Asexual genotype 26(A)	.64	45	.13	45
Uncommon asexual genotypes	.62	45	.13	45

NOTE.—Overall interaction (genetic group × plant × mortality): $G = 2.183$, NS; independence of mortality and host plant: $G = 118.585$, $P < 0.001$; independence of genotype and mortality: $G = 12.893$, $P < 0.05$.

TABLE 3

DRY WEIGHT OF FEMALE PUPAE DERIVED FROM LARVAE REARED ON OAK

GENETIC GROUP	$\bar{Y}$(mg)	N	s^2
Sexual sibship	12.68	10	34.388
Asexual genotype 2(B)	11.44	10	9.860
Asexual genotype 26(A)	8.37	19	5.138
Uncommon asexual genotypes	7.63	11	13.943

NOTE.—Kruskal-Wallis test for heterogeneity among ranked locations: $H = 19.840$, $P < 0.01$.

asexual genotypes ($F = 3.28$, $P < 0.05$), which indicates that considerable phenotypic variation is produced by sexual reproduction. A Kruskal-Wallis test shows that there is significant heterogeneity among ranked locations of genetic groups. In part, this heterogeneity exists because the top 3 larvae, and 6 of the 10 heaviest larvae, were from the sexual sibship.

DISCUSSION

A number of studies have compared sexual and asexual reproduction in closely related animals. Numerous factors have been considered, including competition (Wilbur 1971; Cuellar 1979); fertility and fecundity (Uzzell 1964; Thibault 1975; Lamb and Wiley 1979; White and Contreras 1979; Schall 1981); tolerance to stress (Lindroth 1954; Danzig 1959; Bulger and Schultz 1979); and colonization (Wright and Lowe 1968; Jaenike and Selander 1979). In general, it is difficult to know if differences between related taxa are due to mode of reproduction alone instead of other genetic attributes. For example, a comparison of asexual forms of *Poeciliopsis* (Schultz 1977) with bisexual progenitors is complicated by hybridization and polyploidy. This does not seem to be a problem in *Alsophila pometaria*, for which both sexual and asexual populations are quite similar in genetic constitution.

Apparently populations of *A. pometaria* are not composed of exceptionally fit asexual genotypes. There are a number of factors that could act to reduce the relative fitness of gynogenetic lineages. For instance, it is possible that the gynogenetic lineages carry numerous deleterious mutations (Muller 1964; Maynard Smith 1978). Another possibility, suggested by the distribution of pupal weight in our field experiment, is that sexual reproduction produces especially fit ephemeral genotypes (Williams 1975). There is no indication that, on their optimum host, the specialized asexual genotypes are more fit than a sample from the sexual population. Moreover, there is a preliminary suggestion that the sexuals may have a broader niche than the asexual genotypes. This observation warrants further investigation, especially in view of the argument that a battery of asexual genotypes may have greater niche breadth than a freely recombining sexual population (Roughgarden 1972). In summary, this study on *A. pometaria* has produced no evidence that asexual reproduction has an adaptive advantage.

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