

Original papers

Facultative sex ratio shifts by a herbivorous insect in response to variation in host plant quality

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Received April 28, 1992 / Accepted in revised form July 13, 1992

Summary. We tested predictions of sex allocation theory with a series of field experiments on sex allocation in an herbivorous, haplodiploid, sawfly, *Euura lasiolepis*. Our experiments demonstrated the following points. 1) Adult females allocated progeny sex in response to plant growth. 2) Population sex ratios varied in response to plant quality, being male-biased where plant growth was slow and female-biased where plant growth was rapid. 3) Family sex ratios varied in response to plant quality, being male-biased on slow-growing plants and female-biased on rapidly-growing plants. 4) Female fitness increased more rapidly as the result of developing on more rapidly-growing plants than male mass. We conclude from these results that there are unequal returns on investment in male and female progeny. This results in facultatively biased sawfly sex ratios as an adaptive response to variation in plant quality.

Key words: *Euura lasiolepis* – Sawfly – Willow – Sex ratio – Plant quality hypothesis

A great deal of research has focused on sex allocation in parasitic, entomophagous wasps in response to various host attributes including host size (Clausen 1939; Charnov 1982; King 1987), and the level of local mate competition (Werren 1986). Hymenoptera determine egg sex during oviposition either by fertilizing it to produce a female or laying an unfertilized egg to produce a male. Sawflies are hymenopterous herbivores that also have the potential to control progeny sex in response to variation in host attributes (Flanders 1956). Sawflies have been widely reported to have significantly skewed sex ratios, but there has been little investigation as to causes of variation in sex allocation in this group. Craig and Mopper (1992) in a review of sex ratios in 43 sawfly species found that 39 had female-biased sex ratio and only 4 had male-biased sex ratios. Only Mopper and Whitham

(1992) have provided evidence that the primary sex ratio was biased and that sex ratio bias was not due to secondary mortality alone. They found that sex ratio varied in response to variation in host plant quality. In none of the studies has the adaptive significance of sex ratio variation been explained fully.

We investigated sex ratio variation in relation to host plant quality in the tenthrinid sawfly, *Euura lasiolepis*, which forms galls on the arroyo willow *Salix lasiolepis*. *Euura* life history was described by Price and Craig (1984). Sawflies are synovigenic producing one egg in each of its 12 ovarioles per day. In northern Arizona the sawfly oviposits into petioles of rapidly-growing willow shoots in late May and early June in northern Arizona. A gall is induced in the internode and the larva develops, feeds, and pupates in the gall, emerging the following spring. The host plant is a highly variable resource for larval development, and there is wide variation in oviposition site quality for larval survival both within a willow clone and among willow clones (Craig et al. 1989). The probability of survival increases with shoot length from less than 40% on the shortest shoots to 85% on the longest shoots (Craig et al. 1989). *Euura* on willow clones that have rapidly-growing shoots have higher survival rates than those on plants with slow-growing shoots. Larval survival is lower on plants that are water-stressed and slow-growing than on well-watered plants with rapidly-growing shoots (Preszler and Price 1988; Craig et al. 1990).

Euura oviposition preference is highly responsive to variation in host plant quality (Craig et al. 1989). Female *Euura* prefer ovipositing on rapidly-growing shoots where larval survival is highest, and refrain from ovipositing if suitable resources are unavailable (Craig et al. 1989, 1990), but the threshold of shoot length acceptable for oviposition is flexible and sawflies will attack shorter shoots when longer shoots are not available. There is competition for scarce oviposition sites on long shoots (Craig et al. 1990). We hypothesize that control of sex ratio could provide the sawfly with further ability to respond adaptively to host plant variation.

Sex ratio variation and plant quality

Fisher (1930) showed that in sexual, outbreeding populations, parental investment in male and female offspring should be equal. He argued that mutations leading to skewed sex allocation will be selected against because if there is an excess of one sex, the rare sex will be at a selective advantage. For example, if the offspring sex ratio was female-biased then each male would on average mate with more than one female and parents producing males would leave more grandchildren than those producing females. For many organisms the result of this frequency-dependent selection described by Fisher is an equal ratio of males and females. However, there are many species, including many sawflies, where sex ratios depart from 1:1 and numerous hypotheses have been advanced to explain this bias.

A critical assumption of the Fisher model is that the reproductive return on investment in both males and females is linear and equal (Frank 1987, 1990). In other words, any additional allocation to either sex, when the population allocation to the sexes is equal, will result in the same increase in fitness for the parents. If there is a differential return on producing males and females in a particular situation or environment then biased sex allocation by individual females is expected (Bull 1981; Charnov 1982; Frank 1987, 1990). Variation in the quality of the resource on which larvae develop can have a differential impact on the fitness of males and females leading to biased sex allocation.

The host size hypothesis, developed for parasitoids, is an example of how variation in resource quality can lead to unequal returns on investment in the sexes resulting in skewed sex ratios. In many parasitoids a female lays a single egg in each host. The quantity of resources available to a developing parasitoid larva depends on the size of the host. Therefore parental investment in an offspring is proportional to the host size chosen by an ovipositing female (Charnov 1982). The host size hypothesis (Charnov 1982) predicts parasitoids should allocate male and female eggs to different sized hosts based on the relative benefit each sex gains from increased host size. Both sexes may benefit from being in a large host, but if the degree of benefit is unequal, the sex that benefits most from a large host should be preferentially placed in large hosts. A hypothetical example is illustrated in Fig. 1. Both male and female mass is positively correlated with host size. Male fitness increases with increasing host size up to the minimum host size required for normal development. Developing in hosts larger than the minimum does not increase male fitness because physical competition for mates is absent and size is not related to mating success. As a result, larger males do not receive higher fitness from developing in a larger host, and the return on investment rapidly asymptotes. Female fitness increases linearly with host size because bigger females have higher fecundity. In this case males should be laid in small hosts and females in large hosts. The different returns on increased investment in males and females can result in male- or female-biased family sex ratios. For example, a female encountering a series

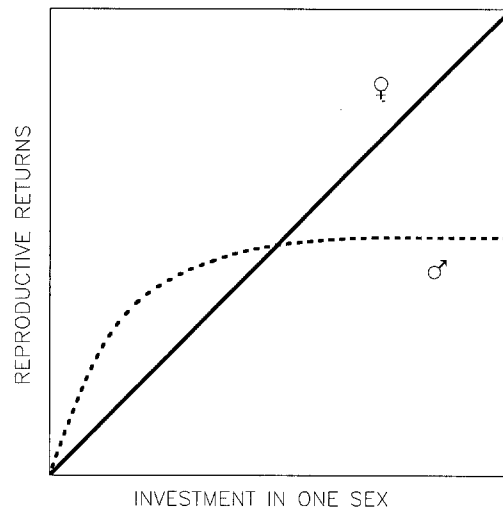


Fig. 1. A hypothetical example of returns on investment in male and female offspring. The example illustrates how a non-linear return on investment in males can select for changes in allocation of investment to the sexes. At high levels of investment the production of females is favored

of large hosts would produce a female-biased family sex ratio.

Contrary to the usual assumption of equal population sex allocation, if there are nonlinear returns on investment, the population sex allocation is expected to depart from 50:50. The mathematics of this idea were developed by Bull (1981), and Frank (1987, 1990) and these papers should be consulted for a detailed explanation of this prediction. The expected sex ratio depends on the shape of the return functions on male and female investments and the frequency distribution of resources available to each individual.

The following hypothetical situation illustrates how unequal returns on male and female investment and the distribution of the amount of resources each individual encounters can lead to unequal population sex allocation. First, assume there is a population where female fitness increases with host quality but male fitness does not. Second, assume that 100 male progeny and 100 female progeny have been oviposited. Females then encounter a superior quality resource where the return on investment is $1/N$ for males and $2/N$ for females. N is the number of males and females in the population. The return on investment will be 0.01 for males and 0.02 for females resulting in strong selection for investment in females. The result will be a female-biased population sex ratio. When there are 200 female progeny and 100 male progeny then the return on additional investment will be equal. As a result the stable population sex allocation is 1 male to 2 females.

Predictions about sex allocation in the *Euura* system

The plant quality hypothesis is that plant growth differentially affects the fitness of male and female *Euura*, and that individual females will allocate egg sex to max-

imize their fitness. We predict that both male and female *Euura* will increase in size when developing in rapidly-growing willow shoots, but that larger females will realize greater fitness from increased fecundity than larger males will realize in increased mating success. The relationship is the same as the hypothetical one in Fig. 1. To maximize fitness, male eggs should be allocated to slowly-growing plants and female eggs to rapidly-growing plants. The allocation of males and females to willow shoots growing at different rates will result in biased sex ratios, both at the family and population level. The plant quality hypothesis generated the following predictions that we tested in this study.

Prediction 1. The sawfly population sex ratio will vary from 1:1 as plant quality varies. Frank's (1987) model predicts that organisms with sequential periods of investment, one offspring per investment period, and differential returns on investment in males and females will have skewed population sex ratios. The population sex ratio will vary as the distribution of the amount of resources available to each individual changes. For *Euura* the distribution of shoot lengths available for oviposition changes (Craig et al. 1989) as the mean growth rate of the willow changes. As a result, we predicted that the population sex ratio of *Euura* should vary among populations encountering willows growing at different rates.

Prediction 2. Females ovipositing on rapidly-growing willows will produce female-biased family sex ratios and females ovipositing on slowly-growing willows will produce male-biased family sex ratios. *Euura* utilizing this allocation pattern will obtain the highest fitness levels if the return on the investment in males is higher at low plant growth rates and the return on females is higher on rapid plant growth rates (as hypothesized in Fig. 1).

Prediction 3. Female fitness will increase more rapidly with plant growth than male fitness. The host plant quality hypothesis predicts that population and family sex ratios will be biased only if there are differential returns on producing males and females. Previous studies have indicated that female fecundity increases with mass (Craig et al. 1990) but that male mating success does not (Price and Craig 1984). We test the hypothesis in this study that both male and female sawfly mass increases with increasing plant growth. If both sexes increase their mass as plant growth increases, then female fitness would have been demonstrated to increase more rapidly with plant growth than male fitness.

Prediction 4. Males from all-male clutches will have greater mass than males from mixed clutches. We hypothesize that mated females allocate female eggs to oviposition sites where larval growth is high and male eggs to sites where larval growth is low. We also hypothesize that unmated females will allocate their eggs to sites where larval growth is high, not having the option of producing female eggs, male eggs will be allocated to

high growth sites. As a result of these allocation decisions, males in all-male clutches will have greater mass.

Methods and materials

Population sex ratio studies

Field surveys. To test prediction 1 that population sex allocation will vary in response to variation in plant growth, we measured sawfly population sex ratios in the field and in an experiment. We collected galls for rearing sawflies from wild willows at three sites differing in water availability on the property of the Museum of Northern Arizona 5 km N of Flagstaff, Arizona. Willow clone designations reflect long-term use and are provided so that direct comparisons can be made to other publications in this series. Willows at the MH site were near or in the McMillan House Spring. We collected galls in 1984 from willow clones MH 1–5, 12 and in 1985 galls from clones MH 1–12, 16, 17, 27, 28. Willows in this site had variable access to water and had a wide range of mean shoot lengths and gall densities (Craig et al. 1986; Craig unpublished data). Gall density, of individual clones and overall, at the MH site was relatively stable among years (Craig et al. 1988; Craig unpublished data). Galls at the CS site were collected from clones growing at Coyote Spring (CS 1,2) where water availability was consistently high throughout the year. The two willows at this site had vigorous shoot growth and high, stable gall densities (Craig et al. 1988; Price et al. 1990). Galls at the MNA and NP sites were collected from clones growing along Schultz Creek, an intermittent stream that is dry most of the year, (MNA 1–7, NP 8, 9). Water availability is highly variable among years and gall density and shoot growth vary widely among years (Price and Clancy 1986; Craig et al. 1988).

In 1984, we measured the relationship between shoot growth and sawfly mass. In May, at the end of the oviposition period, a random sample of 100 shoots was measured on each willow clone. To determine sawfly sex ratio, we collected galls from the field in early May after pupation was initiated and reared insects in shell vials and petri dishes kept in high humidity conditions. To determine sawfly mass in 1984, we oven-dried adults and weighed them on a Cahn electrobalance.

High host quality experiment. To determine the population sex ratio when willow growth was extremely vigorous we grew potted plants under optimal plant growth conditions and exposed them to natural attack. Ten cuttings of each of 15 willow clones in 18.9 L pots were exposed to sawfly attack in their second year of growth by placing them close to wild willows CS-1 and CS-2 in 1986. The potted plants were watered daily and fertilized every two weeks. The galls were collected and insects reared the following spring.

Family sex ratio studies

The lifetime-sex ratio experiment. The lifetime-sex ratio experiment determined the family sex ratios of females confined on different quality resources to test prediction 2. Differences in plant growth were created with water treatments. Thirty willow cuttings of each of two genotypes HS-1 and HS-2 (collected from Schultz Creek near Flagstaff High school) were made in 1984 and grown in 3.8 L pots. We watered cuttings daily and fertilized them with Peter's Professional Fertilizer (20–20–20, P–N–K) every 3 weeks. We transplanted the cuttings to 18.9 L pots on 5 May 1985. All plants were watered and fertilized that day. Each plant was placed in a wire cage 91.5 cm high and covered with bags of mycetophilid fly netting on 5 May. We randomly assigned willows to one of three treatments with 20 replicates each initiated on 19 May: mated-high-water, unmated-high-water, and mated-low-water. A planned unmated-low-water treatment had to be eliminated because of the loss of a

large number of potted willow replicates during transplantation of cuttings to pots. Mated-low-water treatment plants were not watered between 5 May and 19 May, after 19 May they were watered daily and fertilized every three weeks. On 19 May one virgin female and one male sawfly were placed in each low-water cage and observed to mate. Mated-high-water and unmated-high-water treatment plants were watered daily and fertilized every three weeks throughout the experiment. The mated-high-water treatment plants had one virgin female and one male sawfly placed in each cage on 19 May and observed to mate. The unmated-high-water treatment cage had one virgin female sawfly placed in each cage on 19 May.

The following spring we collected all the galls and the insects reared from them using the same techniques described in the field survey. The reduced N numbers in some of the analyses resulted from the lack of emergence from galls on some replicates and the exclusion of plants which were accidentally not watered and wilted, influencing sawfly survival. Adult offspring from the unmated-high-water experiments and the mated-high-water experiments were dried in a drying oven and weighed using a Cahn electrobalance. The mass of these sawflies was compared to those that had developed on wild clones in the field survey.

We measured primary sex ratios by first determining the mortality rates of males and females in identical host plants and used this information to calculate the sex ratios of mixed broods of offspring prior to mortality. In haplodiploid organisms this can be done by comparing the mortality of the offspring of unmated females, which will be all male, with the offspring of mated females (Sandlan 1979; King 1988). We used the method developed by Wellings et al. (1986) to calculate the primary sex ratio by comparing the survival of the offspring of mated and unmated females. The primary sex ratio (P_i) of the mated-high-water treatment was calculated by comparing the survivorship to the unmated-high-water treatment using the formula $P_i = M_i / (T_i * S_{mi})$ (Wellings et al. 1986), where T_i = the total number of hosts parasitized, M_i = the number of male survivors from the mated females, and S_{mi} = survival probability of males of unmated females. In order to do this calculation we first had to calculate S_{mi} using the formula, $S_{mi} = U_i / T_{ui}$ where S_{mi} = survival of males from mated females, U_i = survival of unmated males, T_{ui} = total hosts parasitized.

We could not use the "unmated female technique" to measure differential mortality on the low-water-mated treatment; we used the "mortality minimization technique" used by Mopper and Whitham (1992). Preszler and Price (1988) have demonstrated that there is almost no mortality during the egg stage even under extreme plant water-stress conditions. So by equalizing the watering rates in all treatments as soon as oviposition began we minimized the differences between plants at the stage where mortality was likely to occur. Thus the final sex ratios were good estimates of the primary sex ratio in this experiment.

Renewed-resources experiment. The renewed-resources experiment examined family sex ratios when sawflies were placed on exclusively high-quality or low-quality resources. This contrasted with the resources available in the lifetime-sex ratio experiment; while the high-water treatments of the lifetime-sex ratio experiment had high mean shoot growth and the low-water treatment had low mean shoot growth, there was variation among shoot lengths within each plant. We hypothesized that we might not detect a strongly biased sex ratio in the lifetime-sex ratio experiment if females in the high-water treatment exhausted all the oviposition sites on rapidly-growing shoots and oviposited on more slowly-growing shoots. Similarly if a female in the lifetime low-water treatment only oviposited in a few shoots she might have used the few available more vigorously growing shoots. By offering individual females more high quality or low quality oviposition sites daily than a female could utilize, we provided a control for this potential effect.

Eighty, three-year-old cuttings of the clone HS-1 were randomly divided into low-water and high-water treatments. Cuttings were treated as described in the lifetime-sex ratio experiment. Low- and high-water treatments were conducted as described in the lifetime-sex ratio experiment. We placed on male and one virgin female

sawfly in small nylon mesh bags which enclosed ten shoots selected as being all rapidly-growing or slow-growing and left for 24 h, in 20 high-water replicates and 22 low-water replicates. We observed the male and female sawfly till they mated. Each shoot has 2–3 oviposition sites available each day, so there were 20–30 oviposition sites in each bag. Since a female can produce 12 eggs per day, oviposition sites would not be exhausted during a single day. We then moved the sawflies to a new branch on a randomly selected cutting of the same treatment on each of four subsequent days. The same plants, but not the same shoots, were used for two or three different sawflies. Experiments were initiated between 20 May and 5 June 1986. We reared insects from galls (as described earlier) the following spring and the results from all four days for each sawfly were pooled. A few females did not survive for all four days and so the data from these replicates are from less than four days.

Statistical analysis

We calculated a goodness-of-fit test to a binomial distribution using the normal approximation that is recommended for large sample sizes (Zar 1984) to determine if the population sex ratios departed from equality. In the lifetime-sex ratio and renewed-resources experiments where the offspring of individual females were counted, we calculated the proportion of males in each sample and compared treatments with a two-sample t -test. The proportion data were arc-sin-square root transformed before analysis.

Results

Prediction 1. Population sex ratio and resource quality

The *Euura* population sex ratio varied in response to variation in willow growth, supporting prediction 1. Sawfly sex ratio at the dry MNA site, where willow growth was slow, was significantly skewed toward males in 1984, but not in 1987 (Table 1). Precipitation in the December–May period (data from U.S. Weather Bureau Flagstaff), which determines run-off in the stream, was below normal in 1984 (15.79 cm, normal = 27.56 cm) and near normal (25.79 cm) in 1987. Sawfly sex ratio did not significantly differ from 1:1 at the MH site in either 1984 or 1985 (Table 1). The MH site has a moderate, constant water availability and variable willow growth. The sawfly sex ratio at the uniformly wet CS site, where willow growth is rapid, was non-significantly skewed toward females in 1984, and significantly skewed toward females

Table 1. Summary of population sex ratios. Column 4 reports the P values of goodness of fit to the binomial distribution

Study	% Male	Total Males	Total Females	Binomial Probability
Field:				
1984 MNA Clones	60.04	77	54	<0.01
1987 MNA Clones	50.00	146	146	>0.05
1984 CS Clones	44.38	75	94	>0.05
1987 CS Clones	38.61	161	256	<0.001
1984 MH Clones	48.00	127	117	>0.05
1985 MH Clones	50.46	914	897	>0.05
Experiment:				
High-Quality-Host	35.19	1656	2162	<0.001

in 1987 (Table 1). The well-watered, high-host-quality experiment produced very vigorously growing plants and a highly female-biased population sex ratio (Table 1). Overall, as plants received more water and their shoots grew faster, the sawfly population sex ratio became more female-biased.

Prediction 2. Family sex ratio variation and plant quality

Family sex ratios varied in response to plant growth: they were female-biased on plants with rapid shoot growth and male-biased on plants with slow shoot growth in both the experiments measuring family sex ratios. Primary sawfly family sex ratios differed significantly between treatments with different mean shoot size in the lifetime-sex ratio experiment. The treatments produced different shoot lengths at the time of oviposition (low-water treatment $\bar{x} \pm \text{SE} = 52.76 \pm 3.90$ mm, high-water treatments = 86.89 ± 5.02 cm). The mean proportion of male offspring per family was significantly higher on the low-water treatment than on the high-water treatment in agreement with prediction 2 (Fig. 2).

Primary sex ratios were biased and differential mortality of the sexes had little impact on the emergence sex ratio. In the lifetime-sex ratio experiment, we calculated

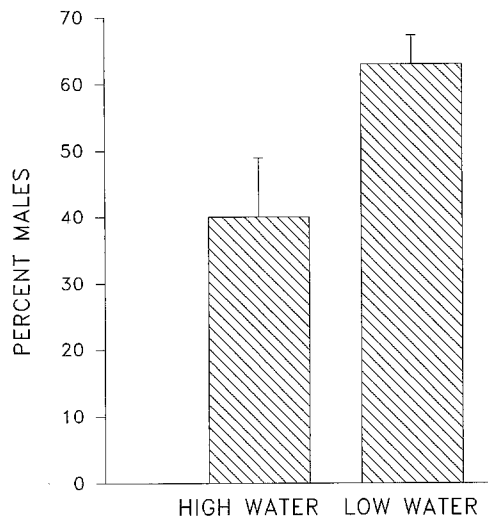


Fig. 2. The percent of males (± 1 SE) in the high and low water treatments in the lifetime-sex ratio experiment. The mean proportion of males differed significantly between treatments (two-sample t -test $t = 2.22$, $P < 0.038$, $df = 33$). Data were arc-sin square root transformed before analysis

the primary sex ratio (using the method of Wellings et al. 1986) of the high-water-mated treatment to be 0.357 male. The skewed primary sex ratio indicated that the difference in sex ratios between treatments was due to facultative allocation of females to vigorously growing plants.

The male-biased sex ratio on the mated low-water treatment was also probably due to a bias in the primary sex ratio and not differential mortality of the sexes in the lifetime-sex ratio experiment. Table 2 shows that sawfly numbers were reduced on the low-water treatment compared to the high-water treatments. Data from this study and that by Preszler and Price (1988) indicate that this was due to egg retention by females and not mortality. One cause of reduced sawfly numbers was a reduction in oviposition attempts: females left fewer oviposition scars on plants in the low-water treatment. A second cause of reduced numbers in the low-water treatment was a failure to oviposit after the ovipositor was inserted in the plant. Compared to the high-water-mated treatment 23% fewer of the scars in the low-water treatment resulted in gall formation (Table 2). Preszler and Price (1988) conducted similar water treatment experiments on potted willows at the same time and location as this experiment. In treatments similar to ours, they found that the proportion of scars without eggs was 30% higher in a low-water treatment than in a high-water treatment. So it is likely that the reduction in gall formation in our study was also due to increased egg retention in the low-water experiment. It is unlikely that extensive mortality in the low-water treatment created the male bias. Preszler and Price (1988) also found almost no mortality in the egg stage. In our experiment, water stress had been relieved in the low-water treatment before larval eclosion when significant mortality occurs on low-water plants (Preszler and Price 1988). The proportion of larvae surviving from gall formation to emergence did not differ among treatments (ANOVA $F_{2,50} = 0.42$, $P > 0.05$) indicating that there was no differential mortality among treatments during the later stages of larval development. We conclude that while we have not directly measured the impact of secondary mortality on the sex ratio in the low-water treatment, mortality was probably so low that it did not significantly alter the primary sex ratio.

Euura family sex ratios differed significantly between treatments with different plant growth rates in the renewed-resources experiment. The treatments produced different shoot lengths at the time of oviposition (High-water treatment $\bar{x} \pm \text{SE} = 85.47 \pm 2.08$ mm; Low-water treatment = 53.07 ± 1.72 mm). The mean proportion of

Table 2. The mean numbers ($\pm \text{SE}$) of oviposition scars, galls and emerging adults in each treatment of the lifetime-sex ratio experiment. Also shown are the percent changing from each stage to the next stage

Water And Mating Treatment	Mean No. Oviposition Scars	Percent Scars Resulting In Galls	Mean No. Galls	Percent Galls Resulting in <i>Euura</i>	Mean No. <i>Euura</i>
Low-Mated	36.00 ± 6.55	51.16	18.59 ± 3.59	45.80	8.53 ± 2.09
High-Mated	53.60 ± 4.78	74.34	39.85 ± 4.61	47.55	18.95 ± 3.29
High-Unmated	54.19 ± 6.98	69.88	37.87 ± 4.88	56.66	21.44 ± 4.43

males was significantly higher on low-water plants than on high-water plants (Fig. 3). Comparison of Fig. 2 and Fig. 3 shows that sex ratios were very similar in the high- and low-water treatments whether the sawflies were given new resources daily or continued to oviposit on the same plant. This indicates sex allocation in the lifetime-sex ratio experiment was not influenced by a shortage of oviposition sites of a particular quality.

Prediction 3. Female and male fitness and plant growth

A comparison of the mass of sawflies reared from the slower-growing plants in the field and those from the more rapidly-growing plants in the high-water treatment of the lifetime-sex ratio experiment shows that sawfly size increased with increasing plant growth. Shoot length of the plants at the time of oviposition was greater in the lifetime-sex ratio experiment ($\bar{x} \pm SE = 86.89 \pm 5.22$ mm) than in the field survey ($\bar{x} \pm SE = 51.55 \pm 6.88$ mm). Both female and male mass was significantly higher in the lifetime-sex ratio experiment than in the field (Fig. 4). Sawflies in the field were only 77% of the mass of those in the lifetime-sex ratio experiment.

Prediction 4. Male mass in mixed and all-male clutches

We supported prediction 4 that eggs in all-male clutches grew into larger adults than males in mixed clutches. Male offspring from unmated females weighed significantly more than the male offspring of mated females on high-water plants in lifetime-sex ratio experiment (Unmated treatment $\bar{x} \pm SE = 0.97 \pm 0.034$, mated treatment = 0.85 ± 0.032 , ANOVA $F_{1,31} = 6.57$, $P < 0.025$). Female offspring from the mated-high-water treatment were much larger than the male offspring (Fig. 4).

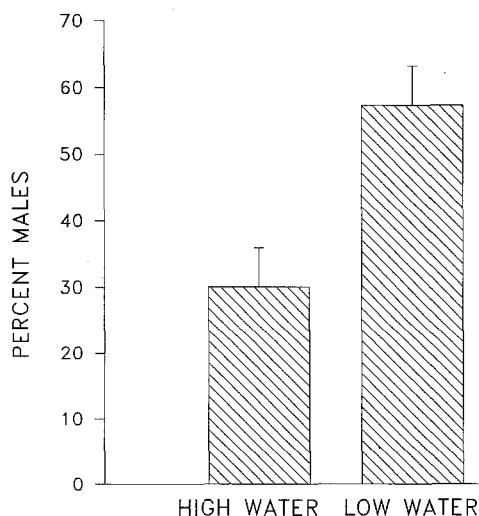


Fig. 3. The percent of males (± 1 SE) in the high and low water treatments in the renewed-resources experiment. The mean proportion of males differed significantly between treatments (two sample t -test $t = 3.32$, $P < 0.002$, $df = 40$). Data were arc-sin square root transformed before analysis

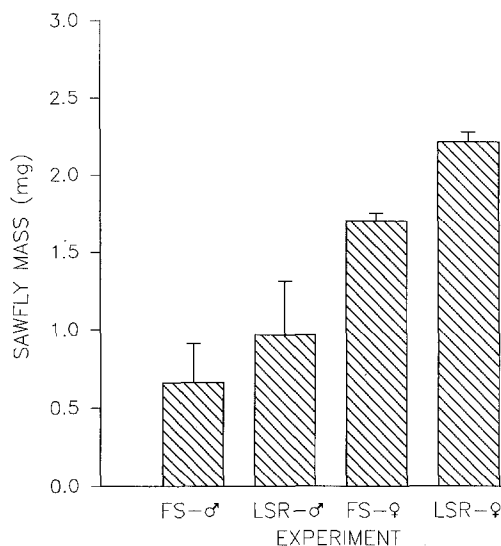


Fig. 4. The mass of male and female sawflies in the field survey (FS), where plants were growing slowly, and the lifetime-sex ratio experiment (LSR) high-water treatment, where plants were growing rapidly. Male mass was significantly greater in the LSR high-water treatment than in the FS (two-sample t -test, $t = 7.25$, $P < 0.001$, $df = 22$). Female mass was significantly greater in the LSR experiment than in the FS (two sample t -test, $t = 5.3$, $P < 0.001$, $df = 87$)

Discussion

Euura sex ratios varied in response to host plant quality, as measured by plant growth rate. *Euura* consistently had female-biased sex ratios on vigorously growing plants and male-biased sex ratios on less vigorously growing plants. Sex ratio variation was due to differences in primary sex ratios and not secondary mortality. All of the predictions of the plant quality hypothesis were supported: 1) Population sex ratios varied as plant growth varied. 2) Family sex ratios varied in response to plant growth. 3) Female fitness increased more rapidly with plant growth than male fitness. 4) Males in all-male clutches had greater mass than males in mixed clutches.

Prediction 1. Population sex ratios and resource quality

In agreement with prediction 1 the population sex allocation changed as the distribution of the resources changed. Because they received different amounts of water, the willows in the field and in the experiment presented sawfly populations with very different sets of resources for oviposition. Increasing the water a willow receives not only increases the mean shoot length but also the shape of the distribution of shoot lengths available (Craig et al. 1989). A relationship was seen between the amount of water the willows received and the sawfly population sex allocation. The poorest quality resources were found in dry years at the MNA site where shoot growth was low, and they had even or male-biased sex ratios. Plant growth was highly variable at the MH site (see Craig et al. 1986 and 1989) and the population sex ratio was near equality. The most vigorously growing

field plants were at the CS site where the sex ratio was significantly female-biased. The most vigorous plants were in the high-host-quality experiment where the population sex ratio was highly female-biased.

While the general prediction of variation in sex ratios was supported, we cannot determine why we obtained the specific population sex ratios we did. Predicting sex ratios using the model of Frank (1987) requires knowledge of the shape of the return functions for male and female investment. We have indications that the return functions for investment in males and females differ and that they may be similar to those hypothesized in Fig. 1 (see prediction 3 discussion). However, we have not been able to precisely quantify the return on investment for males and females over a range of investments. Frank's model also requires that the distribution of the amount of resources available to each individual be measured. Measuring the distribution of shoot lengths actually encountered by individual ovipositing females in the field is an extremely difficult task which has not been attempted.

Prediction 2. Family sex ratios variation and plant quality

In both the lifetime-sex ratio experiment and the renewed-resources experiment we found female-biased sex ratios on vigorously growing plants and male-biased sex ratios on slow-growing plants in agreement with prediction 2. Because female fitness increased more rapidly than male fitness with increasing plant growth (prediction 3) this pattern of sex allocation would be adaptive for individual females. The lifetime-sex ratio experiment showed that primary sex ratios were skewed, and that differential mortality was unimportant in producing biased sex ratios. We calculated that the primary sex ratio on the high-water treatment of the lifetime-sex ratio experiment was skewed toward females, and was little altered by secondary mortality. The "mortality minimization" technique used to compare the high-water-mated and low-water-mated treatments resulted in a less precise measure of the impact of secondary mortality, but it gave a strong indication that differential mortality alone did not produce the male-biased sex ratio in the low-water treatment. Differential mortality could account for some of the sex ratio bias, but the lifetime-sex ratio experiment showed that it was not likely to be the only or most important factor. We conclude that facultative sex allocation decisions were made by females in response to host plant growth.

Prediction 3. Female and male fitness and plant growth

A combination of the results presented here and from previous studies supports prediction 3 that female fitness increased more rapidly with increasing shoot growth than male fitness. We demonstrated that both male and female mass increased with increasing plant growth,

previous studies have indicated that female fitness increases with increasing mass but male fitness does not. Craig et al. (1989) found that female size was related to fecundity; in two out of three years the relationship was significant (1984 $y = 10.31 + 4.13x$, $r^2 = 19.0\%$, $P < 0.05$, $n = 30$; 1985 $y = 26.4 + 2.22x$, $r^2 = 0.3\%$, $P > 0.05$, $n = 58$; 1986 $y = 1.88 + 6.74x$, $r^2 = 23.8\%$, $P < 0.05$, $n = 99$). These correlations are low compared to other weight-fecundity correlations found in protoovigenic sawflies, with all eggs present at emergence, where adults or pupae were dissected and the eggs counted (Carne 1969, Hard and Toger-son 1975, Zhang and Wagner 1991, Mopper and Whitham 1992). Because *Euura* are synovigenic, the correlations in Craig et al. (1989) were obtained by actually counting the number of eggs oviposited during the lifetime of a female in outdoor cages. Exposing sawflies to the environment creates more "noise" that lowers the correlation between weight and fecundity. We believe that obtaining any significant correlation under these conditions indicates a biologically important relationship.

We did not directly test the effect of male size on fitness. However, *Euura* behavior suggests that size is not critical to male mating success. There is no physical competition for access to females, although females possibly exert some choice of mates (Price and Craig 1984). Virgin females, when released in the field or in large cages with many males, generally mate with the first male encountered (Craig personal observation). A better measure of the characteristics that determine male fitness would aid in testing hypotheses about sex allocation. However, such measurements are difficult to take, and have rarely been done in tests on sex allocation hypotheses in hymenopterans.

In summary, we tentatively conclude that female fitness increases more rapidly with increasing plant growth than male fitness. Large females that developed on rapidly-growing shoots had greater fitness than large males that developed on rapidly-growing shoots. It would therefore be adaptive, as predicted by the plant quality hypothesis, for ovipositing females to allocate males to slow-growing plants and females to rapidly-growing plants.

Prediction 4. Male mass in mixed and all-male clutches

Male mass was significantly larger on plants where unmated females oviposited only male eggs than on plants where females oviposited both male and female eggs. We hypothesize that the difference in mass could be explained if, once having chosen similar shoots for oviposition, an unmated female oviposited male eggs in sites that a mated female would allocate to female eggs. Females weigh more than males and may need higher quality sites to complete development. Males developing in these superior "female sites" accumulated mass faster than developing in lower quality "male sites". These results provide additional support to the hypothesis that male and female eggs are allocated to different quality sites by ovipositing females.

Alternative hypotheses on sex ratio variation

Numerous alternative hypotheses have been developed to explain biased sex ratios in sawflies (Craig and Mopper 1992). We have examined the following hypotheses in the *Euura* system (Craig, Price, and Itami, unpublished data): 1) Biased sex ratios were due to a predominance of sib-mating. 2) Biased sex ratios were due to a differential costs of producing males and females. 3) Failure of females to mate biases sex ratios. 4) Sex ratios vary in response to willow genotype. We found no support for these alternative hypotheses, although the possibility that these factors may influence sex ratio under some circumstances cannot be ruled out.

The adaptive nature of sex ratio manipulation

Facultative shifts of sex ratio in response to resource quality variation has been found in a range of organisms. The adaptive nature of these shifts has been established for several hymenopteran parasitoids (King 1987). Much less work has been done on the causes of facultative sex ratios shifts in herbivores. In an experiment, Young et al. (1986) found a small but significant difference in the primary sex ratio of an herbivorous mite, with a higher proportion of females found on poor quality leaves than on good quality leaves. They suggested that it is adaptive to produce females when dispersal is obligatory in order to colonize new resources. Crespi (1988) found that the thrips, *Elaphothrips tuberculatus*, produced all male offspring when it was found in fungal patches where offspring growth was high, and produced all female offspring in poorer patches. He concluded that this was adaptive because male reproductive success was positively correlated with size. The primary sex ratio of a di-prionid sawfly, *Neodiprion edulicolis* has been demonstrated to vary in response to host plant quality but the adaptive nature of sex ratio variation has not been established (Mopper and Whitham 1992). Our study is the first to demonstrate an adaptive cause for sex ratio variation in an herbivorous insect. Further studies are needed to establish why female-biased sex ratios are so common in sawflies. Comparison of sex ratio variation in a wide range of organisms is needed to understand the adaptive reasons for the variation of offspring sex ratio in relation to resource quality.

Conclusion

Euura lasiolepis has previously been shown to have a very fine-tuned ability to respond to host plant variation (Craig et al. 1986, 1988, 1989, 1990). A strong relationship exists between preference for oviposition sites and offspring performance in these oviposition sites. This study demonstrates a second level of discrimination: once an oviposition site is selected, the female determines the sex of the egg to be oviposited based on host plant quality. This study provides support for the plant quality hypothesis as an adaptive explanation for sex ratio variation in an herbivorous insect.

Acknowledgements. We thank L. Hall and M.J.C. Kearsley for help in weighing sawflies. We thank S. How, S. Mopper, B.K. Sullivan, C. Tobin, S. Zvirgzdins for commenting on a draft of the manuscript. We are grateful for permission from the Museum of Northern Arizona to establish study areas on museum property. Staff and resources provided by the R.M. Bilby Research Center are gratefully acknowledged. Financial support was provided through grants from the National Science Foundation (BSR-8314594, BSR-8705302, BSR-8715090) and Northern Arizona University.

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