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EVOLUTION OF SEX ALLOCATION IN THE GENUS *TETRANEURA* (APHIDIDAE: PEMPHIGINAE)

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Abstract

Sexuparae (autumnal migrants) of the Pemphiginae produce sexual males and females at once, and the sexuals mature without food intake. Hence, sex ratio and the size of sexuals are completely determined by the mothers (sexuparae). This study examined variation in sex ratio among species of *Tetraneura* and its allied genera. The relative size of sexuals to sexuparae (mothers) varied greatly among species. In species with relatively small sexuals, each sexupara produced both males and females; the number of males was constant and the number of females tended to increase in larger sexuparae. Sex allocation in these species can be explained by Yamaguchi (1985)'s model. In contrast, in species with relatively large sexuals, a considerable fraction of sexuparae produced sexual females alone. Rearing experiments in *T. sp. O* showed that sexuparae from one clone produced sexual females only, while those from other clones produced both males and females. In species with relatively large sexuals, the relative investment in both sexes was highly female-biased. Local mate competition has been assumed to be responsible for female-biased sex allocation. However, this comparative study suggests that sex allocation is also affected by the relative size of sexuals. The size of sexual females is highly correlated with that of first instar fundatrices (gall makers). Therefore, it is suggested that advantage of larger size in fundatrices, for example in fighting, has led to larger body size in sexual females and more highly female-biased sex allocation.

Introduction

Sexuparae (autumnal migrants) of the Pemphiginae deposit sexual males and females at once on the trunk of the primary host, and the sexuals mature after four molts without taking food. Therefore, sexuals of the Pemphiginae obtain all resources for their development and reproduction from their mothers (sexuparae). Sex ratio and the size of males and sexual females are thus determined by how sexuparae allocate their resources to their sons and

daughters. This characteristic of Pemphigin sexuparae makes it easy to quantify their investment in both sexes (Yamaguchi, 1985).

It is hypothesized that sex ratio is affected by the population structure of an aphid species; if a breeding population is composed of the offspring of a few sexuparae and if the sons of these sexuparae search for mates in the isolated small patch, local mate competition among the sons is inevitable, leading to the evolution of female-biased sex ratio (Yamaguchi, 1985; Foster and Benton, 1992; Moran, 1993). Yamaguchi (1985) documented female-biased sex ratio and a constant number of males per sexupara in *Prociphilus oriens* (Pemphiginae), and postulated local mate competition to explain this tendency. In contrast, if sons can move from patch to patch for mates while daughters remain in the natal patch, the daughters of a sexupara may compete for local resources, for example, for the nutrition of a single shoot. This situation could lead to the evolution of male-biased sex ratio (Moran, 1993). In spite of the development of theoretical studies, very few empirical studies have been accumulated on the sex ratios of aphids. For an understanding of the evolution of sex ratio in aphids, it is needed to examine variation in this trait throughout a phylogeny of aphids and to determine the association between sex-ratio characteristics and environmental conditions. This study examines variation in sex ratio among species of *Tetraneura* and its allied genera (Pemphiginae), basically gall makers on trees of Ulmaceae.

Materials and Methods

Sexuparae of nine species of *Tetraneura* and its allied genera were collected on the primary host plants in Bibai, northern Japan in mid October, and used for the survey of sex ratios. For each species, the relationship between the size of sexuparae and that of sexual males and females was examined based on 4 to 10 sexuparae. Each sexupara's abdomen was dissected, and all embryos (mature males and females) were mounted on a slide using Hoyer medium, together with the sexupara. The slide-mounted specimens were kept at 65 °C for a few days. Each sexual's image was then video-captured and processed by a computer. The area of the images was measured with NIH Image (ver.1.62f) and recorded in a unit of pixel.

For each of the 61 mounted sexuparae belonging to the nine species, four characters were selected from wings and hind legs and their size was measured with an eyepiece micrometer installed in a binocular. To quantify the general size of each sexupara, a principal component analysis was applied, and the scores on the first axis (PC1) were calculated for those sexuparae as an index of body size. The relationship between the body size of sexuparae (measured by PC1) and their sexual offspring (measured by embryos' area) was analyzed for the nine species

by a simple regression after the area of sexuals was ln-transformed.

Based on the result of the interspecific comparison of sexual size, five species, *Tetraneura sorini*, *T. triangula*, *T. radiculicola*, *T. sp. O* and *Paracolopha morrisoni*, were selected. The numbers of male and female embryos each sexupara contained in its abdomen were counted by dissection. For each species, the mean maternal investment in males and females was estimated by multiplying the mean number of male and female embryos per sexupara by their mean area.

To examine how sexuparae of a single species control their investment in males and females depending on different nutritional conditions, several clones of *T. sp. O* were reared separately in pots on their secondary host *Setaria glauca* from early summer to autumn, and sexuparae emerging in autumn were collected for each clone. The relationship between the size of the sexuparae and their sex allocation was compared among clones.

Results

Principal component analysis applied to the 61 sexuparae belonging to 9 species showed that the first axis accounted for 92.5% of the total variation, suggesting that PC 1 scores are a good index of body size. The relative size of sexual females compared to sexuparae varied greatly among species, and the regression of sexual size on sexupara size (PC 1 scores) was not significant ($df=7$, $t=1.63$, $P=0.14$). Four species belonging to the subgenus *Tetraneurella*, *T. sorini*, *T. fusiformis*, *T. nigriabdominalis* and *T. sp. O*, had relatively large sexuals. In contrast, *T. triangula*, whose sexuparae are largest in size, had relatively small sexuals (Table 1). The relative size of males to sexuparae had a similar tendency to that of sexual females.

The area of sexual females was two to three times that of males (Table 1), while the relative number of males to females varied greatly among species. Sexuparae of *T. sorini* that contained relatively largest sexuals produced more females than males, whereas sexuparae of *T. triangula* that contained relatively smallest sexuals produced 1.7 times as many males as females. Sex allocation estimated from maternal investment was female-biased in all species, but there was a tendency for species with relatively larger sexuals to have more intensely female-biased sex allocation (Table 1). In particular in *T. sorini*, maternal investment in females was 3.62 times that in males, and the relative female size to male size was the largest.

In all the species but *T. triangula*, there were two types of sexuparae; sexuparae producing both males and females and sexuparae producing sexual females alone. *T. triangula* contained only the first type of sexuparae, while *T. sorini* contained a high proportion of female-producing

Table 1. Relative size of sexual males and females, their mean numbers per sexupara and sex allocation in *Tetraneura* and *Paracolopha*

Species	N ¹⁾	Relative sexual size ²⁾	Male size ³⁾	Female size ^{3), 4)}	% sexuparae with females alone	No. males ⁵⁾	No. females ⁵⁾	Allocation to females ⁶⁾
<i>T. sorini</i>	107	0.70	939.2	2830.9 (3.01)	48.6	2.22 4.33	2.67 1.93	3.62 1.34
<i>T. sp. O</i>	202	0.36	535.0	1362.1 (2.55)	23.3	3.58 4.67	3.03 2.77	2.16 1.51
<i>T. radicola</i>	50	0.08	503.1	1254.7 (2.49)	10.0	4.72 5.24	4.16 4.00	2.20 1.90
<i>T. triangula</i>	55	-0.39	488.8	1284.4 (2.63)	0.0	- 10.14	- 5.91	- 1.53
<i>P. morrisoni</i>	71	-0.69	283.0	574.2 (2.03)	1.4	5.28 5.36	3.55 3.54	1.36 1.34

1) No. of sexuparae examined, 2) residuals in the regression of sexual female size on sexupara size, 3) represented by no. of pixels, 4) ratio of sexual female size to male size (in parenthesis), 5) mean no. of males or females per sexupara (upper, including female-producing sexuparae; lower, excluding female-producing sexuparae), 6) ratio of maternal investment in females to that in males (upper, including female-producing sexuparae; lower, excluding female-producing sexuparae).

Table 2. Sex allocation of 10 clones of *Tetraneura* sp. O. Allocation to females indicates the ratio of maternal investment in females to that in males

Clone no.	No. sexuparae examined	Allocation to females	% sexuparae with females alone
1	50	0.49	6.0
6	41	0.90	4.9
8	50	0.66	0.0
10	50	0.65	2.0
11	53	-	100.0
13	50	0.85	4.0
16	19	0.62	0.0
17	50	0.62	2.0
23	55	0.52	1.8
32	32	0.69	15.6

sexuparae (Table 1). The fraction of female-producing sexuparae tended to increase in species with relatively larger sexuals. A highly female-biased sex allocation in *T. sorini* and *T. sp. O*

was due to the abundance of these sexuparae. In sexuparae producing males, the number of males was constant and generally equal to 6 in all the species but *T. triangula*, in which a peak male number was 12.

Clonal rearing in *T. sp. O* indicated that the distinction between the two types of sexuparae has a genetic basis. Of the 10 clones reared, one clone yielded female-producing sexuparae alone, but most of sexuparae from the remaining clones produced both males and females (Table 2). In these clones, sex allocation was male-biased. The number of males per sexupara was constant with 91% of the sexuparae containing 5 or 6 males, while the number of females increased with increasing body size of sexuparae (regression analysis, $df=202$, $t=21.1$, $P<0.001$).

Discussion

There were great differences in numerical sex ratio and sex allocation among species. *Paracolopha morrisoni* and *Tetraneura triangula*, both of which produce relatively small sexuals, exhibited an approximately 1:1 sex allocation. Other species produced high proportions of female-producing sexuparae, which contributed to female-biased sex allocation. This result could result from local mate competition. However, evidences for local mate competition in the field are lacking. In autumn, a number of *Tetraneura* sexuparae migrate to elm trees simultaneously, and on the trunk they form a large aggregate, in which the resultant sexuals mate randomly. It is likely that *Tetraneura* species are outbreeding, because forced mating among sexuals from the same sexupara (i.e., selfing) results in a high level of inbreeding depression (Akimoto, unpublished). *T. sorini*, with highly female-biased sex allocation, is a very common species in the locality, and many sexuparae aggregate on an elm trunk. Therefore, it is difficult to suppose inbreeding and intense local mate competition.

Another hypothesis for female-biased sex allocation could be that natural selection that has favored large-sized sexuals has also led to female-biased sex allocation. Interspecific comparison showed that the relative size of sexuals is associated with relative investment in sexual females and with the proportion of female-producing sexuparae. In *T. sorini* it is reported that the first instar fundatrices often compete with one another for incipient galls (Akimoto and Yamaguchi, 1997). It is most likely that large-sized fundatrices are advantageous in fighting. Because the size of first instar fundatrices is highly correlated with that of sexual females in the Pemphiginae, selection for larger size in fundatrices may have led to large sexual females and large sexual dimorphism.

Mathematical models on the sex allocation of aphids implicitly assume that with an

increasing maternal investment in daughters, returns to the mother increase linearly. In contrast, returns from maternal investment in sons are assumed to increase rapidly and then level off as the investment increases, because of competition among sons for mates (e.g., Yamaguchi, 1985). This asymmetry in returns could lead to the evolution of female-biased sex allocation and a constant number of males (for the explanation of constant males, a more realistic model is proposed by Kindlmann and Dixon (1989)). However, in situations where fundatrices fight with one another, an increase in maternal investment in each sexual female may result in an accelerated increase in the returns to the mother. Larger allocation to each sexual female can be accomplished by decreasing the number of females per sexupara. Furthermore, it is hypothesized that the sexuparae that allocate part of the resources to be invested in males to each female could gain more returns, resulting in more female-biased sex allocation. A similar discussion is found on the evolution of sex allocation in plants (Lloyd, 1984). However, female-biased sex allocation in *T. sorini* and *T. sp. O* was mainly due to the high proportions of female-producing sexuparae. Results of rearing of *T. sp. O* clones suggest that differences in sex expression among sexuparae are mainly genetic, with clones producing males+females coexisting with clones producing only females. At present, it remains to be explained why polymorphism, not continuous variation is maintained in the sex expression of these species.

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