

WHY ARE APHID GALLS SO RARE?

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ABSTRACT: Galls of facultatively host-alternating aphid species are usually rare, while those of obligatorily host-alternating aphid species are not. The reason is explained by the bad-gene hypothesis: the facultatively host-alternating species lose in the arms race with their primary host owing to the "introgression" of those genes which have hardly passed or undergone selection for gall-forming ability on the primary host in recent years. Combined with Yamaguchi's ESS sex ratio theory, the bad-gene hypothesis predicts a constant number of males for each sexupara in an obligatorily host-alternating species, but large variation in a facultatively host-alternating species. The number of males contained in each sexupara was counted for nine species. The results tend to support this prediction.

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1. Introduction

The title of this paper may not be accurate, because galls of some aphid species are quite common. For instance, one will find many galls of Kaltenbachiella japonica and Tetraneura spp. on the Japanese elm, Ulmus davidiana var. japonica, on the campus of Hokkaido University in Sapporo, northern Japan. Galls of Pemphigus spyrothecae are numerous on the Lombardy poplar, Populus nigra var. italica, throughout central Europe. It was difficult for us to find Lombardy poplars free of its galls during our short stays in Wien, Salzburg and Budapest. Galls of Ceratovacuna nekoashi can also easily be found on the snowbell Styrax japonica in the vicinity of Tokyo.

These aphid species have either non-host-alternating life cycles (Kaltenbachiella japonica: Akimoto 1985b; Pemphigus spyrothecae: Lampel 1968), or obligatorily host-alternating cycles (Tetraneura spp. in Sapporo: Akimoto 1990, personal communication; Ceratovacuna nekoashi: our observation). They are in the minority among gall-forming aphids, or among aphids of the subfamilies Pemphiginae and Hormaphidinae (sensu Moran 1988). There are many gall-forming species having facultatively host-alternating life cycles, and galls of these species are usually uncommon. Before giving examples, we will explain the difference between obligate and facultative host alternation in gall-forming aphids.

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2. Obligate and Facultative Host Alternation

Host-alternating aphid species migrate between two different kinds of plants, the primary and secondary hosts. The primary host is defined as the plant on which sexual reproduction takes place, and it is usually a woody plant such as Ulmus, Zelkova, Populus and Styrax. Galls are usually formed on the primary host. The secondary host is defined as the plant on which only asexual reproduction occurs. Secondary hostplants are usually herbs, and sometimes trees, of various plant families.

Secondary hostplants are essential to both obligatorily and facultatively host-alternating species. Neither can survive without migrating to their secondary hosts. Primary hostplants are also essential to obligatorily host-alternating species (Fig. 1A), but not to facultatively host-alternating species (Fig. 1B). Aphids of the latter species can propagate themselves by parthenogenesis throughout the year, or can hibernate during winter, on the secondary hostplants. This distinction is important for the hypothesis presented later [1].

A facultatively host-alternating species may consist of various clones, as shown for Myzus persicae (Blackman 1971; see also Blackman 1974, 1981, Hughes 1989) and as suggested for Pemphigus betae (Moran & Whitham 1988): some clones may be obligatorily host-alternating, and some may be facultatively host-alternating and produce sexuparae in various proportions.

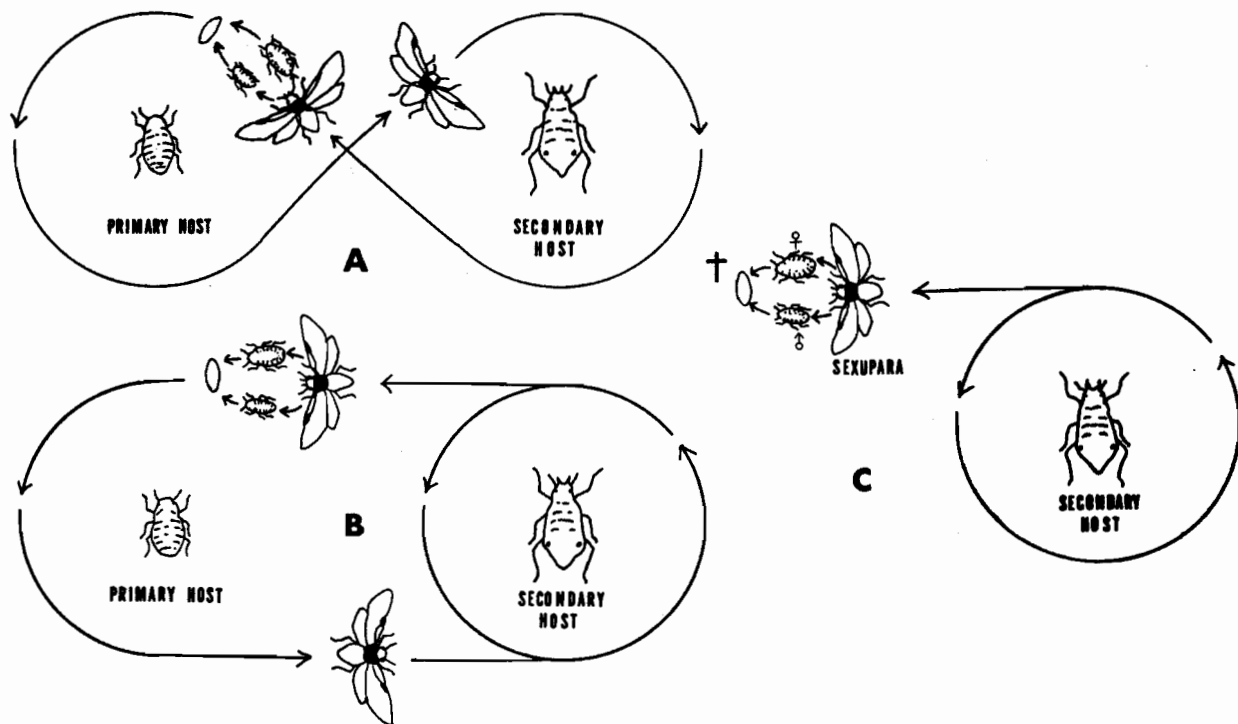


Fig. 1. Three types of aphid life cycles: A, obligate host alternation; B, facultative host alternation; C, anholocycly on the secondary host. Cerataphidines are drawn in the figure.

3. Examples of Rare Aphid Galls

Galls of facultatively host-alternating species are usually uncommon. As researchers on soldier-producing aphid species, we have searched the keyaki, Zelkova serrata, (Ulmaceae) for galls of Colophina over ten years. There are three species of Colophina in Japan: C. clematis, C. arma and C. clematicola, whose secondary hosts are Clematis apiifolia (Aoki 1977a), C. stans (Aoki 1977b) and C. terniflora (Kurosu & Aoki 1988), respectively. All three species facultatively migrate to Zelkova serrata, their primary host; they form galls on its leaves (Aoki 1980, our observation).

Galls of C. clematis are the commonest of the three. We have found a number of galls (>10) on several trees of Z. serrata in and around Nishinasuno, Tochigi Pref., Japan. Nevertheless, we know only two records elsewhere in Japan. Until Aoki's (1980) finding, no aphidologists had recorded its galls from Japan. [Okamoto and Takahashi (1927) recorded its galls from Korea, and we (unpublished) found some galls in Taiwan.]

Galls of Colophina arma are rarer than those of C. clematis. As far as we know, there are only two records. Aoki (1980) found a few galls of this species at Todai, Nagano Pref., Japan, in 1978. Later, S. Akimoto (personal communication) found additional galls at the same locality.

Galls of Colophina clematicola are the rarest. We (unpublished) attached eggs of C. clematicola to a bonsai keyaki, and obtained a few galls of C. clematicola formed on its leaves. However, no gall has yet been found in the field.

Zelkova serrata is one of the commonest trees in Honshu, Shikoku and Kyushu, three main islands of Japan. So their rarity is not due to host rarity.

One might point out that there are rare phytophagous animals feeding on common plants. Collectors of cerambycid beetles in Japan agree that Xylotrechus villioni is rare, although its larvae are known to feed on firs. A fritillary, Fabriciana nerippe, whose larval food is various violets, has recently become one of the rarest butterflies in Japan. One could add many others to this list.

However, despite the rarity of their galls on Zelkova serrata, colonies of the three Colophina species are not rare on their secondary hosts, Clematis spp. Colonies of Colophina clematis on Clematis apiifolia can easily be found, for instance, at Takao-san, Tokyo, in the autumn. Colonies of Colophina arma are common on Clematis stans in the autumn at the riversides between Bamba and Fudakake, Tanzawa, Kanagawa Pref., Japan, and at Todai. One can also easily find colonies of Colophina clematicola around the campus of Rissho University, Kumagaya, Saitama Pref. There are many keyaki trees at the localities mentioned above, and again no galls have yet been found there except at Todai. Curiously enough, all the three species produce many alate sexuparae (i.e. those alates that migrate to the primary host where they produce sexuales) on the secondary hosts in the autumn.

4. The Bad-Gene Hypothesis

Then, why are galls of facultatively host-alternating aphid species so rare?

We think that these aphid species lose in the "arms race" (Dawkins & Krebs 1979, Seger & Hamilton 1988; see also Van Valen 1973) with their primary hostplants. Gall formation is a complicated process, and presumably is even difficult for an aphid fundatrix (a fundatrix is defined as a sexually produced aphid; she usually hatches from an overwintered egg, and usually only her generation can form galls). The occurrence of gall usurpation among conspecific fundatrices (e.g. in Epipemphigus niisimae: Aoki & Makino 1982; Ceratovacuna nekoashi: Kurosu & Aoki 1990) suggests that this is the case [2]. To form a gall, a fundatrix must stimulate an appropriate part of the hostplant at an appropriate time (Dunn 1960, Dixon 1973); she can use only her stylets and saliva as tools and chemicals. It is likely that there has been, and still is, an arms race between a gall-forming aphid species and its host tree. A host tree species often includes individuals which are resistant to attack by gall-forming aphids (Rohfritsch 1981, 1988, Stoetzel & Tedders 1981, Wool 1984, Moran & Whitham 1988, Akimoto 1990), and even individual trees may acquire resistant parts through somatic mutations (Whitham 1981, Whitham & Slobodchikoff 1981, Whitham et al. 1984, Gill & Halverson 1984). Whitham (1989) has recently found that galls of Pemphigus betae are formed more abundantly on hybrid cottonwoods (crosses between the native host of this aphid and a non-host cottonwood) than on its native host cottonwood (Populus angustifolia)[3]. His finding strongly supports the idea that host tree species have developed defensive mechanisms against gall-forming aphids. (On breakdown of a coadapted genome owing to hybridization, see Shields 1982.)

Why, then, do facultatively host-alternating aphid species lose in the arms race, despite the fact that the life-cycle time of an aphid species (usually one year [4]) is much shorter than the generation time of the host tree (more than several years)?

In a host-alternating aphid species, alate sexuparae migrate from the secondary host to the primary host (usually in the autumn for temperate species). The sexuparae carry genes from the secondary host to the primary host. In an obligatorily host-alternating species, all these genes passed selection for gall-forming ability on the primary host in the last gall-forming season (usually in the last spring). In a facultatively host-alternating species, on the other hand, genes carried by sexuparae did not necessarily pass or undergo selection for gall-forming ability on the primary host in the last year (or even may have passed or undergone no selection for past few years), because part of genes can persist in aphids on the secondary host throughout the year without going back to the primary host (Fig. 1B). Note that, in both Pemphiginae and Hormaphidinae, aphids produced on the primary host (fundatrices in the present context) are quite different in morphology, and no doubt also in behavior, from those produced on the secondary host with the same genotype (Mordvilko 1928, Moran 1988). It has been suggested (e.g. by Akimoto 1985a) that different sets of genes code for the

different phenotypes. (Of course, this does not deny the existence of genes which affect more than one phenotype.) If this is the case, a set of genes coding for a phenotype on the primary host is not directly exposed to selection on the secondary host, and in a facultatively host-alternating species the genes coding for the phenotype on the primary host will accumulate deleterious mutations during the stay on the secondary host, just as "pseudogenes" have been doing so (see Kimura 1983, Nei 1987). Muller's ratchet (Maynard Smith 1978, 1988, Bell 1982) may also help accumulate mutations which are not only deleterious to the phenotype on the primary host but also slightly deleterious to phenotypes on the secondary host. Sexuparae of a facultatively host-alternating species therefore bring not only "good" genes (which have frequently passed selection for gall-forming ability on the primary host) but also "bad" genes (which have hardly [5] passed or undergone selection on the primary host in recent years) to the primary host, on which they are mixed together. Because of the "introgression" of these bad genes, a facultatively host-alternating aphid species often loses the arms race with the host plant [6,7].

5. How to Test the Hypothesis

The bad-gene hypothesis is testable in at least one way. Without the "introgression" of bad genes, most fundatrices of a facultatively host-alternating species could use the best available phenotype in the fight against the host tree. The same will be true for sexuparae gathering on the primary host. Consider a sex-ratio game played by them. In an obligatorily host-alternating species, an optimal or evolutionarily stable strategy will be retained. However, in a facultatively host-alternating species, this need not be true. A clone which can persist on the secondary host throughout the year may continue to produce sexuparae which lay their offspring (sexual females and males) in a non-ESS proportion. This, in turn, will affect the strategies of obligatorily host-alternating clones of the facultatively host-alternating species. The bad-gene hypothesis therefore predicts that we will find an ESS sex ratio in an obligatorily host-alternating species [8], but not in a facultatively host-alternating species.

6. Yamaguchi's Sex Ratio Theory

Yamaguchi's (1985) sex-ratio model is useful for our purpose. Her model is more inclusive than Hamilton's (1967) well-known model of local mate competition. In Hamilton's model, the mating site is divided into many small patches; copulation takes place randomly between members in a patch, and the copulated females disperse and mix well with copulated females from other patches. When the number of mothers that produce offspring in each patch is n , the ESS sex ratio for each mother is $(n - 1)/2n$.

The assumptions are the same for Yamaguchi's model except one. In her model, the n mothers do not necessarily produce the same quantity of offspring; some mothers may be larger than

others and may produce more offspring. Let the quantity of the i th mother's resources devoted to her offspring be R_i , and suppose, for simplicity, that there are not extremely small mothers. Then the ESS sex ratio (s^*) for the i th mother will be

$$s^*_i = \{(n - 1)/2n\}(\bar{R}/R_i),$$

where $\bar{R} = (R_1 + R_2 + \dots + R_n)/n$.

Hence, only mothers with the mean R (i.e. $R_i = \bar{R}$) will adopt Hamilton's ESS sex ratio; larger mothers adopt more female-biased sex ratios, while smaller mothers adopt more male-biased sex ratios. A useful prediction from Yamaguchi's model is that all mothers invest equally in males irrespective of their size, provided, again, that there are not extremely small mothers. This is because

$$s^*_i R_i = \{(n - 1)/2n\}\bar{R} = \text{Constant}.$$

If we can neglect differences in size among males at birth, the prediction will be that each mother produces a constant number of males [9].

As Yamaguchi (1985) presents sex ratio data for a host-alternating pemphigine, Prociphilus oriens, to support her theory, her model is well applicable to host-alternating aphid species of the Pemphiginae and the Hormaphidinae (see also Hales et al. 1989), whose sexuparae fly from secondary hostplants to primary hostplants and there produce sexual females and males. Descendants of copulated females, though not their direct offspring, disperse to secondary hostplants prior to the next mating season.

7. Prediction

Since we have found no remarkable difference in the size of males within a species, we predict that sexuparae of an obligatorily host-alternating aphid species have a constant number of males, while those of a facultatively host-alternating species do not have a constant number of males. There are also "anholocyclic" species on the secondary hosts. Anholocyclic species (Fig. 1C) lack their primary hosts; aphids live on the secondary hosts throughout the year without sexual reproduction as in facultatively host-alternating species. Some anholocyclic species lost sexuparae completely, but others still produce sexuparae constantly or only at times (Mordvilko 1935, Lampel 1968, Blackman 1981)[10]. We can also predict that these sexuparae do not have a constant number of males because of no selection for the sex ratio. In the following we will see whether these predictions are true.

8. Materials and Methods

Sexuparae of the following nine host-alternating or anholocyclic species were collected from their secondary hostplants: Colophina clematis, C. arma, C. clematicola, Kaltenbachiella elsholtriae, Ceratovacuna nekoashi, C. lanigera,

Table 1. Collection data of sexuparae of nine aphid species.

Species	Secondary host	No. of sexuparae	Locality*	Date
<u>Colophina clematis</u>	<u>Clematis</u>	31	Niiza**	14-19 x 1987
	<u>apiifolia</u>	100	Niiza**	26 x 1988
		14	Takao	11 x 1980
		20	Saku	30 ix 1976
<u>C. arma</u>	<u>C. stans</u>	100	Tanzawa	20 x 1987
		50	Tanzawa	17 x 1981
		12	Sado	? x 1981
<u>C. clematicola</u>	<u>C. terniflora</u>	9	Kumagaya	17 x 1987
<u>Kaltenbachiella elsholtriae</u>	<u>Elsholtzia ciliata</u>	26	Sapporo	22 ix 1981
<u>Ceratovacuna nekoashi</u>	<u>Microstegium vimineum</u>	114	Kumagaya	18 x 1986
<u>C. lanigera</u>	Sugarcane	304	Fuchu	1-18 xi 1985
<u>Astegopteryx bambucifoliae</u>	<u>Bambusa</u> sp.	59	Sun Moon Lake (Taiwan)	26 ii - 1 iii 1988
<u>Pseudoregma alexanderi</u>	<u>Dendrocalamus latiflorus</u>	60	Sun Moon Lake (Taiwan)	27 ii - 1 iii 1988
<u>P. panicola</u>	<u>Oplismenus undulatifolius</u>	130	Fuchu	17 x -
				26 xi 1987

* Localities are in Japan unless otherwise indicated.

** Ancestors of these aphids were collected at Hachioji on October 3, 1987, and were transferred to a planted Clematis apiifolia at Niiza.

Astegopteryx bambucifoliae, Pseudoregma alexanderi and P. panicola. Their collection data are summarized in Table 1. The first four species belong to the Eriosomatini (Pemphiginae), and the others to the Cerataphidini (Hormaphidinae). Sexuparae were deposited in 80% alcohol immediately after collection to avoid larviposition. They were later dissected under a dissecting microscope, and the numbers of male and female embryos were counted for each sexupara. For all the species examined, discrimination between sexes was easy because female embryos were much larger than male embryos. Extremely small embryos, which were found in a small number of sexuparae and could not be sexed, were regarded as aborted embryos and were not included in the counts.

9. Results and Discussion

Except for Colophina clematicola, the frequency distribution

Table 2. Actual or supposed primary host, the degree of rarity of galls, the type of life cycle, and the coefficient of variation of the numbers of males, for nine aphid species.

Species	Locality	Primary host	Gall	Life cycle	CV of nos. males**
<u>Colophina clematis</u>	Japan	<u>Zelkova serrata</u>	less common	FHA	20.16 (56.42)
<u>Colophina arma</u>	Japan	<u>Zelkova serrata</u>	rare	FHA	46.99 (46.40)
<u>Colophina clematicola</u>	Japan	<u>Zelkova serrata</u>	unfound outside	FHA	?
<u>Kaltenbachiella elsholtriae</u>	Japan	?	?	OHA	4.68 (30.67)
<u>Ceratovacuna nekoashi</u>	Japan	<u>Styrax japonica</u>	common	OHA	8.43 (26.12)
<u>Ceratovacuna lanigera</u>	Japan	absent*	absent	AH	81.96 (23.01)
<u>Astegopteryx bambucifoliae</u>	Taiwan	<u>Styrax suberifolia</u>	common	FHA	14.66 (17.63)
<u>Pseudoregma alexanderi</u>	Taiwan	absent?*	absent?	AH?	8.92 (25.79)
<u>Pseudoregma panicola</u>	Japan	absent*	absent	AH	30.94 (25.81)

Abbreviations: OHA: obligate host alternation; FHA: facultative host alternation; AH: anholocycly.

*Their primary hosts, if they exist elsewhere, presumably belong to the genus Styrax.

**The CV of the numbers of females is in parentheses.

of the numbers of males for each species is shown in Fig. 2. The numbers of males for C. clematicola were 1, 2, 3, 4, 4, 4, 5, 6 and 9. For each species Table 2 summarizes the actual or supposed primary host, the degree of rarity of the galls, the type of life cycle, and the coefficient of variation (CV) of the numbers of male embryos. For comparison, the CV of the numbers of female embryos is also shown in parentheses. The degree of rarity is admittedly subjective, but we believe that it is not far-fetched.

The numbers of males for three species, Ceratovacuna nekoashi, Kaltenbachiella elsholtriae and Pseudoregma alexanderi, fit well with the prediction from Yamaguchi's model that each sexupara produces a constant number of males (CV < 10)[11]. (On the other hand, the CV of the numbers of females is more than 25 for these three species.) As already mentioned in Section 1,

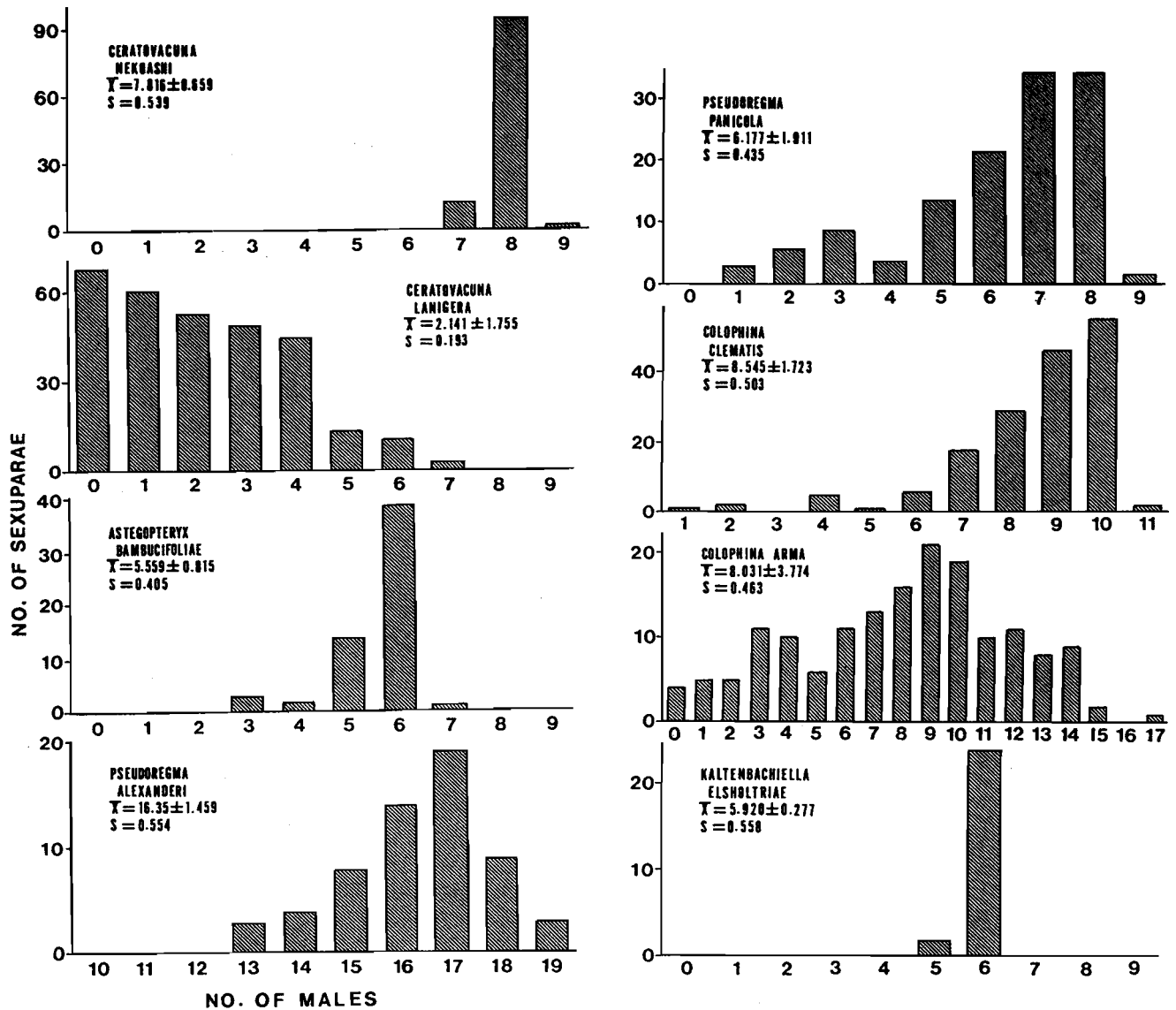


Fig. 2. Frequency distribution of the number of males contained in a sexupara for eight aphid species. \bar{X} is the mean number of males in a sexupara (\pm SD). $S = (\text{total no. of males})/(\text{total no. of males and females})$.

galls of *C. nekoashi* are common, and it migrates obligatorily between the hosts (since its secondary host *Microstegium vimineum* is an annual grass), hence its constant male number supports the bad-gene hypothesis. Although the primary host of *Kaltenbachiella elsholtziae* has not yet been found (Akimoto 1985b, personal communication), it should have an obligatorily host-alternating life cycle because its secondary host *Elsholtzia ciliata* is also an annual. We predict, then, that galls of this species (if it is a gall-inducer like its congeners) will be abundantly found. The case of *Pseudoregma alexanderi* may be more

problematic. Aoki et al. (1981) supposed that this species does not have any primary host in Taiwan, because Dendrocalamus latiflorus, its secondary host, is not native to Taiwan (Suzuki 1978). If their supposition is true, the aphid might have recently been introduced from a place where P. alexanderi has an obligatorily host-alternating life cycle.

There are other species producing a constant number of males. Prociphilus oriens, whose sex ratio was studied by Yamaguchi (1985) in her seminal paper, migrates between Fraxinus mandshurica and roots of Abies sachalinensis. She later mentioned that, except extremely small ones, most sexuparae of P. oriens produce four males (Yamaguchi 1987). Although this species is not a true gall-inducer (it forms so-called "pseudogalls"), it is worth noting that it has an obligatorily host-alternating life cycle according to Kôno (1976). Tetraneura spp. have obligatorily host-alternating life cycles in Sapporo, and their sex ratios also fit with the prediction that the number of males is constant (S. Akimoto, personal communication).

In contrast, the numbers of males for four species, Colophina clematis, C. arma, Ceratovacuna lanigera and Pseudoregma panicola, show wide variation (CV > 20). Although the sample size is small, the numbers of males for Colophina clematicola also seem to show high variance. As mentioned before, the three Colophina species have facultatively host-alternating life cycles and their galls are rare, hence the results well support the bad-gene hypothesis. Ceratovacuna lanigera (Kurosu & Aoki 1986) and Pseudoregma panicola (Aoki 1982) are no doubt anholocyclic, at least in the localities where the present materials were collected [12].

The numbers of males for Astegopteryx bambucifoliae show intermediate variation (CV = 14.66). Galls of this species are common on Styrax suberifolia in Taiwan (Takahashi 1939; our observation), but it has a facultatively host-alternating life cycle. According to Takahashi (1923), however, only a small number of aphids remain on bamboos during summer without returning to the primary host. We were also able to find only a small number of aphids of this species on bamboos in July of 1986 and 1990 in and around Puli, central Taiwan [13]. The effect of bad genes upon the optimal sex ratio may therefore be small in this case.

10. Concluding Remarks

The results thus do tend to support the bad-gene hypothesis. Although one might think that cyclic parthenogenesis is an ideal way of life, it often leads to the collapse of its sexual phase in the long run when the organism can live on without sexual reproduction.

11. Notes

[1] There are some host-alternating species which use their primary hosts obligatorily but use their secondary hosts facultatively (Mackenzie & Dixon 1990, Moran 1990). Such species do not appear in this paper.

[2] A vicious cycle of gall usurpation and failure in gall formation might even arise, because, if a fundatrix who failed in forming her gall succeeds in usurping the gall of another fundatrix (who succeeded in forming her gall), a set of genes that failed to pass the selection for gall-forming ability, instead of a set of genes that passed it, will be passed to the next fundatrix generation.

[3] The most preferred hostplants may actually be complex backcrosses between the F_1 hybrids and Populus angustifolia (Paige et al. 1990).

[4] Aphids have several generations a year, but usually only the fundatrix generation can form galls. Therefore the selection for gall formation occurs once a year.

[5] Of course, there are "bad" genes which are not bad enough to always be eliminated on the primary host.

[6] Lynch and Gabriel (1983; see also Lynch 1984) propose a similar idea in a different context. When normally obligate parthenogens engage in sex (rarely with their sexual ancestors), many genes previously hidden in the parthenogens are released. The release of hidden genetic variance may lead to the rapid and radical evolution of their descendants. We stress a negative aspect of such release in this paper.

[7] There may be another obstacle to the spread of "good" genes for gall formation. In a facultatively host-alternating species, aphids of facultatively host-alternating or anholocyclic clones already exist on some of its secondary hostplants when alate aphids come from the primary host. So, if intraspecific competition is intense on the secondary host, clones that passed selection for gall formation will not produce as many sexuparae as those of an obligatorily host-alternating species could.

[8] The same is also true for non-host-alternating species provided that there is an ESS sex ratio. However, since breeding structures of these species seem highly complicated, we do not treat their sex ratios in this paper.

[9] As n becomes large, the mean sex ratio approaches $1/2$. However, each mother still produces a constant number of males provided that the number of patches (N) is sufficiently large. If $N = 1$, then the ESS sex ratio for each mother will be $1/2$.

[10] For example, Paraprociophilus baicalensis on Alnus sp. in Siberia has been producing functionless sexuparae since its presumed primary hosts, maples of the section Saccharina, which now exist only in North America, became extinct there (Mordvilko 1935). Colopha kansugei on Carex sp. in Japan is another example if Akimoto (1985b) is right. How these anholocyclic species can retain sexuparae remains to be explained. S. Akimoto once told us that sexuparae of these species may play a role in avoiding overcrowding on the secondary hostplants. We are not sure how serious he was, but his hypothesis is possible because kin selection may operate to retain such altruistic suicides.

[11] According to Yamaguchi's model, when there are extremely small sexuparae, these sexuparae should produce only males. The number of males produced by each extremely small sexupara is smaller than or equal to that produced by a normal sexupara. The presence of extremely small sexuparae may therefore increase the variance of the numbers of males. However, this effect, if any,

is small for the species treated in this paper, because only one sexupara of Ceratovacuna nekoashi and four sexuparae of Colophina clematis contained males only. When these daughterless sexuparae are excluded, the CV of the numbers of males is 8.36 for Ceratovacuna nekoashi and 20.32 for Colophina clematis.

[12] The sex ratio of Myzus persicae studied by Hales et al. (1989) is male-biased, and therefore does not agree with the prediction from Yamaguchi's (1985) sex ratio theory or Fisher's (1930). Since M. persicae is a facultatively host-alternating species (Blackman 1974), the disagreement might be due to bad-gene effects.

[13] Unlike those of temperate species, sexuparae of this species appear in spring. Migration from the primary to secondary hosts occurs from August to November (Kurosu & Aoki, in press).

12. Acknowledgments

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13. Glossary

Anholocycly: A life cycle without sexual reproduction, but with or without functionless sexuparae. An anholocycle can readily be derived from a facultatively host-alternating cycle when the primary host is lost.

Facultative host alternation: Host alternation in which the use of the primary host is not obligate.

Fundatrix: A sexually produced aphid. With a few exceptions, only the fundatrix generation can form galls.

Obligate host alternation: Host alternation in which the use of the primary host is obligate.

Primary host: A hostplant on which sexual reproduction (as well as parthenogenetic reproduction) occurs.

Secondary host: A hostplant on which only parthenogenetic reproduction occurs.

Sexupara: An aphid producing sexuales, which are sexually reproducing females and males. In the Pemphiginae and Hormaphidinae, sexuparae are almost always winged. In host-alternating species, they are produced on the secondary host and fly to the primary host.

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