DISTRIBUTIONAL AND ECOLOGICAL DIFFERENTIATION BETWEEN ASEXUAL GYNOGENETIC PLANTHOPPERS AND RELATED SEXUAL SPECIES OF THE GENUS *MUELLERIANELLA* (HOMOPTERA, DELPHACIDAE)

C. J. H. Booij and J. A. Guldemond

Department of Entomology, Agricultural University, Wageningen, The Netherlands

One of the most intriguing questions in evolutionary biology is why most organisms reproduce sexually and not parthenogenetically. Although parthenogenetic forms potentially have a great reproductive advantage over sexual species, they rarely displace their sexual relatives completely. Apparently sex and recombination give the sexual species some advantage which compensates for the reproductive disadvantage.

Although most authors agree that parthenogenetic forms are doomed to extinction sooner or later by lack of evolutionary potential, it is still a matter of debate whether sexuality has also short term advantages which compensate for the lower reproductive rate (Williams, 1975; Maynard Smith, 1978). Since theoretical models developed by population geneticists do not give an adequate answer to this question, it seems important to collect evidence from field populations of related asexual and sexual forms. The question in that case could be what the outcome is of competition between the two forms, and which ecological conditions favor asexual or sexual reproduction.

In most asexual-sexual complexes the asexual forms have replaced related sexual species from part of their ecological or geographical range and do not compete any longer (Suomalainen, 1950; Glesener and Tilman, 1978). The situation is quite different, however, in gynogenetic and hybridogenetic forms, which reproduce parthenogenetically but depend on sperm of their sexual relatives. In such forms the geographic distribution of the asexuals is closely linked to that of the sexual species, and they are forced to compete at least for sperm, but probably also for food, space and other resources.

If competitive relations in such complexes are only determined by the difference in reproductive capacity of the two forms, the mixed population would be highly unstable. Because of the twofold reproductive advantage of parthenogenesis, the frequency of asexual females in mixed asexual-sexual populations should tend to increase rapidly from generation to generation. Finally, the sexual population will go extinct when, by sampling error, only asexual females are inseminated by the few remaining males. Without sperm resource, the demise of the asexual population follows in the next generation.

These problems have been studied in mixed populations of sperm-dependent asexual forms and related sexual fish species of *Poeciliopsis* (Moore et al., 1970; McKay, 1971; Moore and McKay, 1971; Schultz, 1971; Moore, 1975, 1976; Thibault, 1978) and in salamanders of the genus *Ambystoma* (Uzzell, 1964; Wilbur, 1971). The frequency of asexual forms in the populations was found to differ considerably between localities, but at most sites it remained stable from year to year. Apparently there are mechanisms which stabilize the mixed populations and allow the two forms to coexist.

In the asexual-sexual fish populations the frequency of asexual females is stabilized, because the tendency of males to discriminate against asexual females in-

creases when the asexuals become more frequent. The level at which the asexual frequency is balanced depends on the mating behavior of the males and on differences in primary fitness between sexual and asexual females (Moore, 1976). These primary fitness differences include differences in fecundity and mortality and are related to environmental factors. Thus, by comparing the asexual frequencies of populations in different environments, it is possible to study the ecological conditions which are favorable for sexual or asexual reproduction, respectively.

Recently an asexual-sexual complex comparable to those in *Poeciliopsis* and *Ambystoma* was discovered by Drosopoulos (1976, 1977) in the planthopper genus *Muellerianella* (Delphacidae). The asexual forms of this genus are triploid and reproduce by gynogenesis. Sperm may be supplied by males of *M. fairmairei, M. brevipennis,* or *M. extrusa.* In the field the asexual females are usually associated with *M. fairmairei* because they live on the same hostplant and have similar life histories (Booij, 1982). At some localities the asexuals occur syntopically with *M. brevipennis,* but since they are confined to different hostplants, there is no competition for food, space or oviposition sites. In this situation the asexual females only steal some copulations with *M. brevipennis* males.

Mixed populations of *M. fairmairei* and the asexual forms are mainly found in moist to wet grasslands, where the hostplant, *Holcus lanatus,* grows together with *Juncus effusus,* in which the hibernating eggs are laid. In one such population Drosopoulos (1977) found that the frequency of asexual females was remarkably stable, and he suggested that the two forms may have different ecological requirements which enable them to coexist.

We have studied the occurrence of asexuals in 62 mixed *Muellerianella* populations throughout Europe and found that the sexual and asexual forms are adapted to different geographic regions and ecological conditions.

MATERIAL AND METHODS

Samples of mixed *Muellerianella* populations were taken at 35 sites throughout Europe (Fig. 1) and at 27 sites in the Netherlands (Fig. 2). At each site notes were made about general habitat type, vegetation structure and composition, soil-type, soilwater level, and land use.

To determine the frequency of asexual females in the populations, larvae, adults, or *Juncus* stems with diapausing eggs were collected from samples regularly spaced over the site. Eggs and larvae were reared to adulthood in the laboratory. The asexual frequency (Moore, 1976) is defined here as the ratio of asexual females to *M. fairmairei* females + asexual females.

To discriminate between asexual triploid females and diploid sexual *M. fairmairei* females, which are morphologically indistinguishable, chromosome preparations were made of ovarian eggs of freshly killed animals.

Experiments to study reproductive capacity of females and mating capacity of males were all made in the laboratory at 20 C and long-day conditions (LD 18:6). In one experiment total egg-production per female was determined by placing single fertilized females in tubes containing suitable stems of *Holcus lanatus.* Every second day fresh stems were offered and the eggs laid were counted. In another experiment the adult progeny per female was determined from single mated females kept in cages with *Holcus* for four weeks. To determine mating capacity of *M. fairmairei* males, single males were kept in cages with 25 or 50 asexual females for one or two weeks, respectively. Insemination of females was checked by examining the spermatheca for the presence of mobile sperm.

RESULTS

Stability of Asexual Frequencies in Mixed Muellerianella Populations

The primary source of instability of mixed populations of sperm-dependent asexual forms and sexual species is the twofold reproductive advantage of asex-

TABLE 1. Reproductive capacity of asexual (gynogenetic) *Muellerianella* females and sexual *M. fairmairei* females in laboratory experiments. Mean values and standard deviations are given for egg production (x) or adult offspring per female (xx).

Origin of females		Reproduction	
		M. fairmairei ♀♀	Gynogenetic ♀♀
Nevers (France)	x	175 ± 108 (N = 23)	217 ± 112 (N = 15)
Bitola (Yugoslavia)	xx	266 ± 12 (N= 3)	265 ± 39 (N = 3)
Leersum (Netherlands)	xx	164 ± 76 (N = 5)	296 ± 53 (N = 5)

ual females, which is only realized if both female types have equal chances to be inseminated and if they produce the same number of eggs.

For *Muellerianella* females, Drosopoulos (1977) suggested that in the laboratory asexual females produce more eggs than the sexual *M. fairmairei* females. Our experiments also showed that the asexual females on average can produce as many as, or even more offspring than, *M. fairmairei* females (Table 1). The apparent differences between populations are not significant. Egg-fertility and larval survival are high and about equal in both female types (Drosopoulos, 1977).

Thus, when sperm is not limited and mortality rates are the same, the twofold reproductive advantage of the asexuals can be realized. As might be expected, the asexual females rapidly outcompete the sexual *M. fairmairei* in mixed laboratory populations (Drosopoulos, 1977).

With regard to discriminative mating behavior of males as a stabilizing factor in asexual-sexual populations, the situation in *Muellerianella* is different from that in poeciliid fishes (Moore, 1976) and in salamanders of the genus *Ambystoma* (Uzzell, 1964), where males discriminate against asexual females. *Muellerianella* males, however, are not very selective in courting and mating females. As a rule it is the female that discriminates between males. *Muellerianella fairmairei* males readily court asexual females and preliminary experiments (Guldemond, unpubl. data) indicate that males do not significantly prefer sexual females. The low selectivity of *M. fairmairei* males is partly

compensated by their ability to inseminate about 15 females a week (Table 2). In the laboratory at 20 C males live for about two months. Assuming that they survive on average for two weeks in the field, they may inseminate as many as 30 females. This means that even in a mixed population with an asexual frequency of .97, sufficient males are present to inseminate all females. It should be realized, however, that in the field the mean distance between animals is greater than in the laboratory cages.

Even if males do not discriminate at all, sexual females could have better chances to be inseminated than asexuals if the asexuals and sexuals are more or less segregated in the field. Such a segregation may arise because the eggs are laid in clusters and the larvae move only over very small distances. Most adults are brachypterous and not very mobile either. Some degree of spatial isolation between asexuals and sexuals may also arise if the two forms prefer different microhabitats.

In one population with an asexual frequency of .78 (Leersum, The Netherlands) we found that 14 out of 55 mature females (25%) were not inseminated even though the population was at the end of its generation. Of 12 sexual *M. fairmairei* females 11 (92%) were inseminated, whereas of the 43 asexual females only 30 (70%) were inseminated. Although the difference is not significant (Fisher's exact probability test, *P* = .12), there is a good indication that the sexual females have better insemination chances.

The stability of asexual frequencies in

TABLE 2. Capacity of *M. fairmairei* males to inseminate receptive asexual females in laboratory cages.

No. of ♀♀ offered/♂	Period	No. of ♀♀ inseminated
25	1 week	15, 15, 14 resp.
50	2 weeks	35, 30, 27, 35 resp.

TABLE 3. Year to year changes in the asexual frequency of *Muellerianella* populations at five sites in the Netherlands.

Site	Sample date	Sample size	Asexual frequency
17 Leersum	7.vii.78	100	.72
	3.vii.79	23	.74
	30.ix.81	55	.78
11 Rhenen	10.xii.78	120	.90
	14.xii.79	123	.75
21 Geldrop I	2.x.77	44	.43
	18.vii.78	18	.44
25 Geldrop II	18.vii.78	49	.20
	18.vii.79	35	.14
27 Renesse	18.vii.77	40	.00
	19.x.78	29	.12

several of the populations studied indicates that the success of the asexual females must be limited in some way. For the mixed Dutch population at Leersum (site 33) Drosopoulos (1977) reported that the sex-ratio in suction samples changed only little from year to year (1973: .30, 1974: .36, 1975: .37), which points to a constant asexual frequency. Direct estimates of asexual frequencies at Leersum and at other sites also suggest little change in most populations (Table 3). Although changes occur, there is no indication for a general increase. We are aware of the fact that at several of our sample sites the asexual frequency may not have been at equilibrium, especially at newly invaded sites, or at places where conditions rapidly change.

Asexual Frequencies in Muellerianella *Populations from Different Parts of Europe—Geographic Trends*

Booij (1981) showed that the asexual forms of *Muellerianella* are widespread in a great part of Europe and that the distribution approximately coincides with the area of sympatry between the sexual species *M. fairmairei* and *M. brevipennis.*

Here we will analyze the pattern of asexual frequencies of 62 populations from different regions in Europe. The results of these investigations are presented in Figure 1 and Table 4. Due to varying sample sizes the estimated asexual frequencies are not equally accurate for each population, but some obvious conclusions may be drawn. The asexual forms seem to be absent in populations from the southernmost part of the range of *M. fairmairei.* There is a significant trend for the asexual frequencies to increase with latitude and altitude. The asexual frequency may reach 1.00 (defined in relation to *M. fairmairei*) in the northeastern borderline populations in Denmark and the submontane areas of W. Germany and Belgium (sites 3–6 and 44–52). Here the asexual females are associated with the more northern species *M. brevipennis,* which lives on another hostplant (see also introduction). High asexual frequencies are found in the region where *M. fairmairei* is at its northeastern distribution limit, which coincides approximately with the 0 C isotherm in January. At these sites the growing season is relatively short and only one generation per year can be completed (Booij, 1982). The opposite conditions are found in the Mediterranean region where the asexuals are absent (Portugal, Spain and Greece). Here the winter temperatures are much higher and the growing season is much longer. *Muellerianella fairmairei* often completes three or more generations per year in these regions.

At the remaining sites of W. Europe usually two generations are completed. Of this category the highest asexual frequencies are found in Ireland. Since the climate of this country is mild but very wet, we suggest that wetness favors the asexual forms. In this context it should
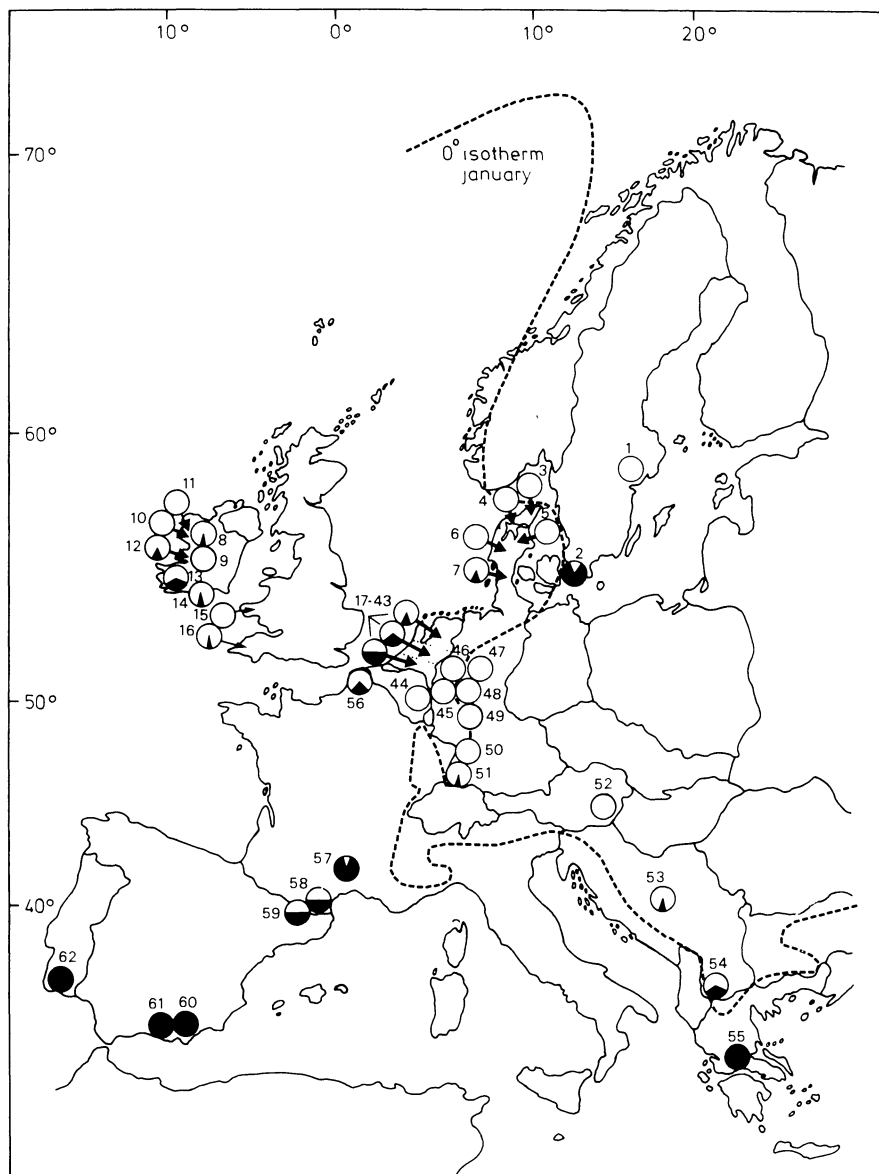
FIG. 1. Frequency of triploid gynogenetic *Muellerianella* forms in mixed populations with the sexual species *M. fairmairei,* in different parts of Europe. At sites 3–6, 44, 45, 47–49 and 52 the asexuals are associated with *M. brevipennis.* White: gynogenetic females, black: *M. fairmairei* females.

be mentioned that a great excess of fe-
males in *M. fairmairei* populations has
been observed at the Azores (Remane,
pers. comm.). These islands are situated
at the same latitude as the Mediterranean
site of *M. fairmairei,* but there is a much

more atlantic climate. It is also striking
that the lowest asexual frequency in Ire-
land was found in a population near
Glengarriff. This place is well known for
its extremely mild climate. It is the only
known Irish site were probably three gen-

TABLE 4. Asexual frequencies in mixed populations of *M. fairmairei* and triploid gynogenetic forms in various parts of Europe. Estimations of asexual frequencies are based on cytogenetic examination of the females, except for sites 16, 58 and 59 where the sex-ratio was used. Sites where the asexual females are associated with *M. brevipennis* are marked with an asterisk. e: sample of eggs, l: sample of larvae, a: sample of adults.

Site		Altitude (m)	Sample date	Sample size	Asexual frequency
1 Alunda	Sweden	25	15.ix.77	7 (e)	1.00
2 Krankesjön	Sweden	50	22.viii.77	50 (e)	.20
3 Fröstrup	Denmark	25	1.viii.79	24 (l, a)	1.00*
4 Rödhus	Denmark	25	1.viii.79	16 (a)	1.00*
5 Rebild	Denmark	75	31.vii.79	44 (l, a)	1.00*
6 Varde	Denmark	25	1.viii.79	26 (l)	1.00*
7 Aabenraa	Denmark	25	29.vii.79	42 (a)	.79
8 Knock/Castlerea	Ireland	100	27.xi.77	49 (e)	.98
9 Derrywode	Ireland	100	28.ix.78	15 (e)	1.00
10 Recess	Ireland	50	29.ix.78	7 (e)	1.00
11 Letterfrack	Ireland	25	29.ix.78	13 (e)	1.00
12 Lissycasey	Ireland	100	30.ix.78	24 (e)	.79
13 Glengarriff	Ireland	25	2.x.78	40 l, a)	.68
14 Dungarvan	Ireland	0	3.x.78	37 (e)	.91
15 St. Davids	Wales (UK)	50	26.ix.78	38 (e)	1.00
16 Portreath Cornwall	England (UK)	?	21.vii.70	—	.94
17 N. Netherlands	(10 sites)	0	1978/1979	268 (e, l, a)	.94
: C. Netherlands	(7 sites)	0	1978/1979	656 (e, l, a)	.64
43 S. Netherlands	(10 sites)	0	1978/1979	445 (e, l, a)	.46
44 Francorchamps	Belgium	500	31.vii.78	70 (l, a)	1.00*
45 Sourbrodt	Belgium	600	31.vii.78	25 (l, a)	1.00*
46 Dülmen	W. Germany	100	5.vii.79	45 (l, a)	1.00
47 Blankenrode	W. Germany	400	5.ix.79	10 (a)	1.00*
48 Brilon	W. Germany	300	4.ix.79	9 (a)	1.00*
49 Laasphe	W. Germany	600	28.viii.79	4 (a)	1.00*
50 Emmendingen	W. Germany	350	29.ix.79	14 (a)	1.00
51 Steinen	W. Germany	350	29.ix.79	20 (a)	.95
52 Graz	Austria	300	3.vi.79	25 (l)	1.00*
53 Zvornik	Yugoslavia	300	1.vi.79	45 (l)	.87
54 Bitola	Yugoslavia	600	26.v.79	12 (l)	.58
55 Skaloula	Greece	550	2.iv.80	10 (l, a)	.00
56 Cap Gris Nez	France	0	29.xi.79	24 (l, a)	.79
57 Privas	France	650	23.x.79	15 (l, a)	.13
58 Lavalle	France	300	vi-75/vi-77	—	.50
59 Sant Julia	Andorra	1,000	vi-75/vi-77	—	.50
60 Orgiva	Spain	450	22.iii.78	7 (l)	.00
61 Capifeira	Spain	1,600	24.iii.78	22 (e)	.00
62 Monchique	Portugal	300	25.iv.80	10 (l, a)	.00

erations are completed instead of two (Booij, 1982). We suggest that the frequencies of asexuals increase with wetness of climate and decrease with the length of the growing season.

It should be kept in mind that deviations from the observed trends may be found due to microclimatic or other ecological conditions at particular sites. Moreover, several geographic regions are insufficiently explored. Additional data are necessary to test the validity of the supposed trends.

Asexual Frequencies in Muellerianella Populations from the Netherlands— Ecological Trends

In the Netherlands asexual frequencies were determined in 27 mixed populations of gynogenetic forms and *M. fairmairei*, from different parts of the Netherlands and from a wide variety of

habitats. All sites were situated at alti-
tudes below 50 m.

The results of the investigations are
given in Figure 2 and Table 6. Because
suitable habitats for *M. fairmairei* and
the asexual forms are not very common
and only present in certain parts of the
Netherlands, sample sites could not be
selected at random or regularly spaced.
Some of our data are based on rather
small samples, which reduces the accu-
racy of the estimated asexual frequencies.
Despite these limitations, it was ob-
served that the average asexual frequency
increases slightly but significantly from
the southwestern to the northeastern parts
of the Netherlands (Spearman rank cor-
relation, $r_s = .66$, $N = 27$, $P < .001$).
Simple regression coefficients were cal-
culated of the asexual frequencies with
12 climatic variables concerning tem-
peratures and humidity (data obtained
from the Dutch climatic atlas, K.N.M.I.,
1972). Asexual frequencies appeared to
be significantly related to six of these
variables. Because the climatic variables
were correlated with each other, the data
were analysed by multiple regression
analysis, for which initially six climatic
variables were chosen of which the three
best were included in the final calcula-
tions (Table 5). Because the distribution
of the asexual frequencies was highly
skewed towards high frequencies, an arc-
sin transformation was applied before
analysis.

A substantial part of the variation in
asexual frequencies can be explained by
three climatic factors. The asexual fre-
quency tends to be high where the
number of days with snowcover is high,
spring-temperatures are low, or where
precipitation during the growing season
is high (see Fig. 3). The best prediction
can be made when the first two variables
are taken into account. Also variables two
and three together do rather well. These
results agree with the European trends
that asexual frequencies tend to be high
where winters are severe, the growing
season is short or where humidity is high.
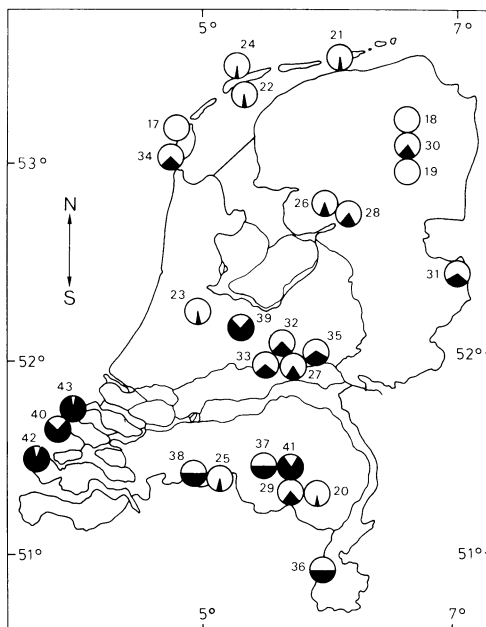Regional climatic differences only

FIG. 2. Frequency of triploid gynogenetic *Muel-
lerianella* females in mixed populations with the
sexual species *M. fairmairei* in the Netherlands.
White: gynogenetic females, black: *M. fairmairei*
females.

partly explain the variation in asexual
frequencies among sites. The remaining
variation may be due to differences in
microclimate, vegetation structure and
other ecological features of the habitat.
Since the range of variation between
asexual frequencies at Dutch sites is al-
most as wide as the variation in the whole
of Europe, these local factors must be
very important.

From Table 6 it is evident that at all
sites which are mown once a year, asex-
ual frequencies are high. At sites which
are only extensively grazed or which are
not used for agricultural purposes, asex-
ual frequencies tend to be lower. Fur-
thermore, the asexuals are more abun-
dant at ecotone situations like trenches
and sharp transitions between wet and
dry (sites 18, 20, 22, 25 and 35). The
asexuals seem also to be favored by wet
and very wet conditions, whereas the sex-
ual form is more abundant at sites which
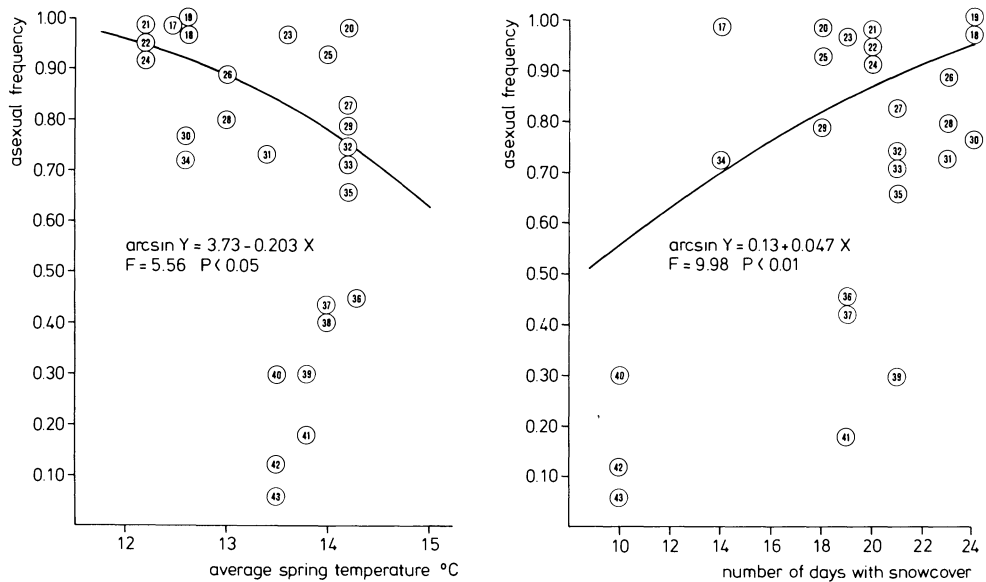are relatively drier.

FIG. 3.   Correlations of the asexual frequency in Dutch asexual-sexual *Muellerianella* populations with two regional climatic factors. The figures refer to site numbers.

The relation of asexual frequency with regional climate, land use and wetness of the habitat was recognized from the samples taken in 1978. At the new sites, sampled in 1979, predictions for the asexual frequency, based on regional climate and habitat features, were made before the population was actually sampled. As Table 7 shows, the predictions were pretty good. Therefore it seems justified for the moment to state that the gynogenetic *Muellerianella* forms are more abundant in cool, wet and disturbed (mown) habitats, whereas the sexual species, *M. fairmairei* is favored at warmer, moist and less disturbed localities.

DISCUSSION

A fundamental question in the population ecology of gynogenetic forms and the sexual species on which they depend for sperm, is what allows the two forms to coexist (Moore, 1976). When the twofold reproductive advantage of the asexuals is realized in the field, they will rapidly displace the sexual species on which they depend. The instability of such mixed populations may be reduced if the asexuals have less chance to be inseminated or if their primary fitness is much lower than that of the sexual species (Moore, 1976). By studying the competitive relations between the asexual and sexual forms we may find out what the use of sexuality is, or at least in what situations sexuality is favored.

As was shown in this paper, the fecundity of gynogenetic *Muellerianella* females is at least as high as that of the sexual *M. fairmairei* females, with which they are associated. Moreover, *M. fairmairei* males probably do not discriminate against the asexual females and may inseminate several tens of females of both forms. In this respect the planthopper complex differs essentially from comparable complexes in fishes and salamanders, where mate-discrimination is an important mechanism to stabilize mixed asexual-sexual populations (Uzzell, 1964; McKay, 1971; Moore and McKay, 1971; Wilbur, 1971; Moore, 1975, 1976). Yet the asexual frequency in mixed *Muellerianella* populations appeared to be rather stable.

At present it is not clear how the asex-

TABLE 5. Results of a multiple regression analysis of asexual frequencies in the Netherlands with three regional climatic factors. An arcsin transformation was applied to the asexual frequencies before analysis. The independent factors are X1: average number of days with snowcover, X2: average temperature during the period April, May and June (°C), X3: average precipitation in the growing season (May–October) in mm. Significance levels: * < .05, ** < .01, *** < .001. SS-regr: sum of squares regression, SS-res: Residual sum of squares. b1, b2 and b3 are the regression coefficients.

	Variables included						
	X1	X2	X3	X1, X2	X1, X3	X2, X3	X1, X2, X3
Constant	.13	3.73	−1.38	2.64	−.65	1.32	1.97
b1	.047**	—	—	.044**	.038*	—	.037*
b2	—	−.20*	—	−.18*	—	−.18*	−.18*
b3	—	—	.06*	—	.002 ns	.005*	.002 ns
SS-regr	.96	.61	.59	1.46	1.02	1.08	1.49
SS-res	2.41	2.76	2.78	1.91	2.34	2.28	1.87
F-value	9.98**	5.56*	5.33*	9.17***	5.22**	5.72**	6.13**

ual frequency in *Muellerianella* populations is stabilized. Field data indicate that sexual females are somewhat more easily inseminated than asexual females if the asexual frequency is high. We suggest that this might be due to a different microdistribution of asexuals and sexuals in the field, males being on average closer to sexual than to asexual females.

In order to reach a balance between asexuals and sexuals, a reduction in the insemination of asexuals by 50% is needed, compensating for the twofold reproductive advantage. We think that such a reduction is only possible at asexual frequencies at least above .75. Since at many places the frequency is much lower, the reproductive success of asexuals must be reduced by other factors there. It seems likely that at those places the primary fitness of asexual females is much lower than that of sexual females due to ecological factors. Consequently the asexual frequency at a given locality may be considered as an indication for the relative fitness differences between asexuals and sexuals at that site (Moore, 1976).

As was shown the asexual frequency in mixed *Muellerianella* populations varies geographically and depends on ecological conditions. This suggests that the two forms are adapted to different environments and different geographic regions. Many authors (e.g., Suomalainen, 1950; Wright and Lowe, 1968; Moore,

1976; Glesener and Tilman, 1978) have provided evidence that asexual forms in general are favored at high altitudes and latitudes and in "weedy" habitats. Asexual forms often have features of "*r*-strategists," and may not be able to displace the more "*K*-selected" sexual species from more stable, biologically complex environments (Glesener and Tilman, 1978).

It might be argued that the ecogeographic trends outlined above do not hold for gynogenetic and hybridogenetic forms, because these can only occur together with the sexual species on which they depend for sperm (Cuellar, 1977). The distribution of gynogenetic and sexual forms of *Muellerianella*, however, are in general agreement with the ecogeographic trends of parthenogenesis.

Gynogenetic *Muellerianella* forms are absent from the southernmost part of the range of the sexual species *M. fairmairei* and the asexual frequencies increase with latitude. Thus there is good evidence for geographic replacement and adaptive differences between asexuals and sexuals. One may argue that this pattern can also be explained by a historical diffusion process starting from the region where the asexual forms arose. Though this cannot be excluded for certain, it seems unlikely. Due to the twofold reproductive advantage the asexuals would increase rapidly once established in a population. Without adaptive differences, asexual fre-

TABLE 6. Asexual frequencies of mixed populations of *M. fairmairei* and triploid gynogenetic forms in the Netherlands. For each sample, sample date, sample size, asexual frequency and notes on the habitat are given. The samples are arranged in order of decreasing asexual frequency. e: sample of diapausing eggs, l: sample of larvae, a: sample of adults, w: wet, vw: very wet, m: moist, fl: fluctuating groundwater, gr: extensively grazed, mw: mown once a year.

Site	Sample date	Sample size	Asexual fre- quency	Habitat	Land use	Soil- mois- ture
17 Texel I N-Holland	3.xi.78	8 (e)	1.00	dune valley with marshy grassland	?	w
18 Z. Laren Drenthe	2.x.77	10 (e)	1.00	sharp transition heath— sedge swamp	?	fl
19 Drenthse Aa I Drenthe	19.ix.78	29 (a)	1.00	unfertilized wet meadow	mw	vw
20 Weert II Noord-Brabant	21.xi.78	43 (e)	.98	deep trench along roadside	mw	fl
21 Schiermonnikoog Friesland	11.xi.78	35 (a)	.97	sheltered car-track	mw	m
22 Terschelling II Friesland	10.ix.79	40 (l)	.97	deep trench along sandy road	mw	fl
23 Langeraar Z-Holland	17.xi.78	29 (a)	.97	fertilized meadow bordering on a lake	mw	w
24 Terschelling I Friesland	10.ix.79	40 (l)	.95	sharp transition dune—dune lake	—	fl
25 Baarle Nassau Noord-Brabant	5.x.79	14 (a)	.93	deep trench along sandy road	mw	fl
26 Wolvega I Friesland	26.ix.79	28 (l, a)	.89	hay-pasture surrounded by water and carr	gr/mw	w
27 Rhenen Utrecht	10.xii.78 14.vii.79	120 (e) 123 (a)	.83	flush with fen-like vegetation	gr/mw	vw
28 Wolvega II Friesland	26.ix.79	35 (a)	.80	unfertilized wet meadow	mw	w
29 Weert I Noord-Brabant	21.ix.78	33 (e)	.79	gradual transition pasture —fen	gr	w
30 Drenthse Aa II Drenthe	19.ix.78	22 (a)	.77	unfertilized wet meadow	mw	vw
31 Denekamp Overijssel	15.ix.78	106 (a)	.73	unfertilized wet meadow	mw	w
32 Veenendaal Utrecht	8.xi.78	37 (a)	.73	unfertilized wet meadow	mw	w
33 Leersum Utrecht	7.vii.78 3.vii.79	100 (a) 23 (a)	.73	very extensively grazed pasture	gr	m
34 Texel II N-Holland	3.xi.78	21 (e)	.72	car-track	?	?
35 Renkum Gelderland	12.x.78	44 (a)	.66	trench between pasture and meadow	mw	fl
36 Elsloo Limburg	9.x.79	40 (a)	.45	flush with fen-like	—	vw
37 Geldrop Noord-Brabant	2.x.77 18.vii.78	44 (e) 18 (a)	.43	car-track	?	m
38 Ulecoten Noord-Brabant	5.x.79	22 (a)	.41	neglected clearing	—	w
39 Kortenhoef Utrecht	13.ix.78	74 (a, l)	.30	fenlike grassland	gr	w
40 Burgh-Haamstede Zeeland	17.xii.77 19.x.78	6 (e) 47 (l, a)	.30	poor pasture grazed by sheep	gr	m

TABLE 6. Continued.

Site	Sample date	Sample size	Asexual fre-quency	Habitat	Land use	Soil-mois-ture
41 Geldrop II	18.vii.78	49 (a)	.18	mesotrophic carr	—	m
Noord-Brabant	18.vii.79	35 (a)				
42 Vrouwenpolder	18.xii.77	25 (e)	.12	pasture	gr	m
Zeeland						
43 Renesse	18.xii.77	40 (e)	.06	pasture	gr	w
Zeeland	19.x.78	29 (a)				

quencies should be zero or very high, or, when intermediate, be unstable, irrespective of their location. Since this is not the case, we don't think the patterns stem from a historical process, although it is possible that the asexuals have not reached the southernmost *Muellerianella* populations yet.

It seems likely that the present distribution of the gynogenetic forms is correlated with their origin. According to Drosopoulos (1977, 1978), they probably arose through hybridization between the originally southeuropean species *M. fairmairei* and the more northern species *M. brevipennis* (see also Booij, 1981, 1982). The restriction of the gynogenetic forms to the area of sympatry between the parental species, and high asexual frequencies in regions where both species occur syntopically support the hybrid origin hypothesis. Asexual forms are usually most successful in ecological conditions which are intermediate between those of the parental species (Uzzell and Darevsky, 1975; Moore, 1976; Thibault, 1978).

At a more regional scale (The Netherlands) we found that the asexual frequencies are weakly correlated to climatic factors, the trends being consistent with those found for the whole of Western Europe. However, local ecological conditions like microclimate, vegetation structure and land use seem to affect the asexual frequency more strongly. High asexual frequencies were often found in meadows, trenches and ecotones between wet and dry. In extensively grazed pastures and unmanaged grassy places, the sexual species is usually dominating.

Abiotic and biotic features which characterize these two habitat categories may have significant effects on the reproduction and survival of the animals. Meadows are usually wet in spring which keeps temperature relatively low during the first months of the growing season. The meadows in which *Muellerianella* occurs are mown only once in late summer. Mowing has a sudden and severe effect on the vegetation structure, the microclimate, and the insects themselves (Morris, 1981). Because mowing prevents tussock formation, meadows are structurally rather homogeneous and microclimatic differentiation is rather poor (Larsson, 1976). Also trenches and ditch-sites are usually mown once a year. At these places and at ecotones between dry and wet, groundwater levels often fluctuate throughout the year. It should be noted that mowing and fluctuating groundwater may not only affect primary fitness of the animals directly, but may also disturb the spatial population structure. Since a clustered population structure is thought to be important to reduce the insemination chances of the asexual females, disturbance of this structure may favor the asexuals by increasing their insemination chances.

In extensively grazed pastures, the oviposition plant of both forms, *Juncus effusus,* forms tussocks which are little affected by cattle. In and around these tussocks, *Holcus lanatus* grows optimally. Such a vegetation offers a wide variety of microniches to the planthoppers. Moreover, the vegetation structure is relatively stable throughout the year. In

TABLE 7. Predicted and observed asexual frequencies of samples taken in mixed asexual-sexual *Muellerianella* populations in 1979. Predictions were based on ecogeographic trends found in samples taken in 1978 at other sites.

Site	Asexual frequency	
	Predicted	Observed
6 Terschelling II	.90	.95
8 Terschelling I	.90	.97
9 Baarle Nassau	.70	.93
10 Wolvega I	.70	.89
12 Wolvega II	.90	.80
20 Elsloo	.40	.45
22 Ulicoten	.40	.41

spring the microclimate of pastures is usually less wet and warmer than that of meadows. Also in more natural habitats there is a wide variety of microniches and there are no sudden changes as in meadows or trenches.

All these considerations justify the conclusion that the asexuals are better adapted to environments that are wet and cold in spring, that are poorly structured, and in which abiotic factors suddenly change during the season. The sexual species is more successful at places where abiotic factors are more stable, which are warmer and drier in spring, and where the vegetation structure offers a lot of variation.

These conclusions agree well with the idea of Glesener and Tilman (1978), who suggest that asexual organisms tend to occur in "physically controlled" environments which are poorly structured and where "biological uncertainty" is low. Sexuality, however, seems to be favored in abiotically more stable environments which are complex and "biologically unpredictable."

SUMMARY

The occurrence of asexual gynogenetic planthoppers in association with the related sexual species *Muellerianella fairmairei* was studied in 62 populations in Western Europe. It was found that the frequency of asexual females in mixed populations tends to increase with alti-

tude and latitude and is related to wetness of the climate and the length of the growing season. At a local scale, cool, wet and disturbed habitats like meadows seem to favor the asexuals, whereas the sexual species is dominating at warmer, moist and less disturbed habitats such as pastures.

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Corresponding Editor: D. J. Futuyma