POPULATION STUDIES OF SUPERNUMERARY CHROMOSOMES IN A MEALY BUG^{1,2}

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THE supernumerary chromosomes of the mealy bug, *Pseudococcus obscurus* Essig are able to increase in number from generation to generation because of an accumulation mechanism operative at spermatogenesis (NUR 1962b). Spermatogenesis leads to the production of two functional sperm and two non-functional products and the supernumeraries segregate preferentially into the functional products. While the females transmit the reduced number of supernumeraries, the males pass on an unreduced number except for occasional loss. The intriguing questions arose as to whether natural populations of this species are in equilibrium with regard to the number of supernumeraries and, if so, how this equilibrium is maintained.

Supernumeraries of many plant species as well as a few animal species are known to possess accumulation mechanisms (MÜNTZING 1958). ÖSTERGREN (1945, 1947) was the first to suggest that in those species in which supernumeraries possess accumulation mechanisms, their maintenance would not depend solely on the advantage that they might confer to the carrier species, but that the supernumeraries might have an independent, parasitic existence. They would struggle for their own existence and in so doing might even be harmful to the individuals or the species carrying them.

ÖSTERGREN's ideas received support from MÜNTZING (1961), who gave evidence that the supernumeraries of *Secale cereale* are maintained by an accumulation mechanism despite their harmfulness to the individual. Likewise, KIMURA and KAYANO (1961) proved that supernumeraries, regardless of the number present, reduced the fitness of individual plants of *Lilium callosum* but continued in existence because of preferential segregation at megasporogenesis.

WHITE (1954) and DARLINGTON (1956) have contended that supernumeraries are always beneficial either to the population or, if not too many present, to the individual. According to WHITE, the supernumeraries are sometimes of ancient origin and would have otherwise long since disappeared, while DARLINGTON

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believed that they may have been beneficial to the species as a whole by conferring additional variability.

The present report is concerned with population studies of *Pseudococcus obscurus* which were undertaken in order to determine the role of the supernumeraries in population dynamics. Because of the limitations of the material, the requisite parameters for determining selective differentials of the supernumerary classes, rate of development, fecundity, and viability, could not be obtained from the wild populations. Included in the investigation, however, were the possible relationships of the supernumeraries to mating behavior, size, host plant, and geographical distribution.

MATERIALS AND METHODS

For sampling the various populations, third instar or adult females were fixed in Bradley-Carnoy, 4 chloroform:3 absolute alcohol:1 glacial acetic acid, and stored in 70 percent alcohol in the refrigerator. Prior to study, the females were stained in bulk in a modified-Mayer's hydrochloric-carminc (GRAY 1954; SNOW, unpublished). Each female was placed on a slide in a drop of Hoyers' mounting medium, the two hind legs were removed and placed at the edge of the drop, the reproductive system was dissected out and a cover slip added.

Before squashing, the hind tibiae of the adult females were measured at 150X with an ocular micrometer scaled to ten microns, and estimated to the nearest micron. Although somewhat crude, the measurements were always made before cytological analysis and were therefore without bias in this regard. Following the measurements, the material was squashed, the karyotype determined and the reproductive tract of the adult females examined for sperm bundles. The number of supernumeraries was determined from nurse cells, egg-sheath cells, oocytes, oogonial divisions, or from cells of the Malpighian tubules and related cells (for details see NUR 1962b). For laboratory experiments, mealy bugs from population 1 were grown on potatoes (*Solanum tuberosum*) as described by NELSON-REES (1960).

Until recently, *P. obscurus* has been confused with the very similar *P. maritimus* (Ehrhorn). Females from population 1 were kindly identified as *Pseudococcus obscurus* Essig by Mr. HOWARD L. MCKENZIE, Department of Entomology, University of California, Davis. The other populations were identified by crossing them with population 1, or by utilizing morphological criteria suggested by Mr. H. L. MCKENZIE. Females from populations 17 and 18 were collected by Mr. D. BERRY, County Extension Agent, Medford, Oregon, who also drew my attention to the availability of population 19. Material from population 12 was made available by Mr. GLENN L. FINNEY, University of California Experiment Station, Albany. The author is grateful to these men for their help and cooperation.

OBSERVATIONS

Samples were obtained from populations living under quite divergent conditions. The populations from the wild came from the coastal area at Berkeley

and vicinity, and from less temperate regions in the Sacramento Valley (Fairfield, Davis, and Marysville). The populations were collected from a variety of host plants which were always trees and evergreen shrubs. Population 15 was collected in a greenhouse of the University of California Botanical Garden, where the temperature was kept at about 26°C and the humidity close to 100 percent. Populations 12 and 20 were experimental populations raised under laboratory conditions. Population 12 was established several years ago by MR. G. L. FINNEY from individuals collected in the Berkeley area and was maintained at a constant temperature of about 26°C. Population 20 was started from a cross between a male with two supernumeraries and a female with none, both from population 1. It was maintained at a mean temperature of about 22.5°C for over a year before the first sample (20a) was taken. All the other populations were wild populations which were growing outdoors.

Life cycle, fertilization and supernumeraries: Under laboratory conditions at a temperature of about 22.5°C, the generation time (from egg to egg) is 60–70 days. At 18°C it is about twice as long, and below 15°C development stops. The populations in the Sacramento Valley apparently hibernate in the winter, and it is estimated that they complete two generations a year. In Berkeley, females in all stages of development could be found throughout the year and here the species probably completes two to three generations a year. In all the samples from the Sacramento Valley, 73–100 percent of adult females were found to be fertilized, regardless of the time of year (Table 1), while in Berkeley and Oakland the percent of females fertilized was high in the fall (74–90 percent) but varied greatly (2–87 percent) in the spring. In population 1 the percent of fertilized females was consistently low in the spring and early summer, and high in late summer and in the fall.

Because the females were not uniformly fertilized, it was possible to test for an association between the number of supernumeraries and the percent of fertilized females. The percent of fertilized females in the various supernumerary classes varied from one population to another, and between samples from the same population. No overall trend could be observed but in two samples from population 6 the percent of fertilized females decreased as the number of supernumeraries increased from one to four and then increased again in the class with five supernumeraries (for further details see NUR 1962a).

Supernumerary frequencies in the various populations: The supernumeraries of *P. obscurus* and their behavior in males and females from population 1 were described earlier (NUR 1962b). Cytologically, the supernumeraries from the other populations were similar to those of population 1, except for population 15 from Berkeley and 18 from Fairfield, whose supernumeraries were probably slightly smaller.

Supernumeraries were found in all the populations studied but their numbers varied greatly (Table 1). The frequencies of the supernumeraries seemed to depend closely on geographic location. The frequencies were high for the collections in the coastal region, while all those for the Sacramento Valley were low.

TABLE 1

The mean number of supernumeraries, the mean tibia length and the percent of fertilized females in the various populations

Area	Popu- lation	Locality	Host plant	Date	Mean no. of sups.*	Mean tibia length (μ)	Percent females fertilized
Coastal	1a	Berkeley	<i>Taxus baccata</i>	3/23/60	1.56 $\pm$.17		
	1b	Berkeley	<i>Taxus baccata</i>	7/5/60	1.59 $\pm$.11	344 $\pm$ 3(71) [†]	30.1 (93) [†]
	1c	Berkeley	<i>Taxus baccata</i>	11/13/60	1.63 $\pm$.11	328 $\pm$ 3(63)	74.0 (77)
	1d	Berkeley	<i>Taxus baccata</i>	3/22/61	1.68 $\pm$.11	317 $\pm$ 3(87)	31.0 (87)
	1e	Berkeley	<i>Taxus baccata</i>	8/13/61	1.70 $\pm$.12	308 $\pm$ 4(49)	93.9 (49)
	1f	Berkeley	<i>Taxus baccata</i>	3/23/62	1.69 $\pm$.11	307 $\pm$ 3(83)	37.3 (83)
	2	Berkeley	<i>Buxus sempervirens</i>	4/2/60	1.21 $\pm$.09		
	5	Berkeley	<i>Taxus baccata</i>	7/5/60	1.89 $\pm$.12	309 $\pm$ 5(45)	2.0 (99)
	6a	Berkeley	<i>Buxus sempervirens</i>	6/8/60	1.75 $\pm$.12		86.5 (89)
	6b	Berkeley	<i>Buxus sempervirens</i>	6/21/60	2.27 $\pm$.13	333 $\pm$ 4(46)	81.1(111)
	6c	Berkeley	<i>Buxus sempervirens</i>	11/16/60	1.71 $\pm$.14	304 $\pm$ 4(37)	89.7 (58)
	7	Oakland	<i>Clematis</i> sp.	7/10/60	2.74 $\pm$.16	337 $\pm$ 4(37)	92.9 (56)
Lab. and Greenhouse	12a	Albany	potato (lab. culture)	9/12/60	2.30 $\pm$.23	313 $\pm$ 3(16)	
	12b	Albany	potato (lab. culture)	12/8/61	0.29 $\pm$.11	236 $\pm$ 3(18)	
	15	Berkeley	<i>Polypodium vitiense</i>	12/7/60	1.90 $\pm$.17	337 $\pm$ 7(15)	97.4 (39)
	20a	Berkeley	potato (lab. culture)	7/12/61	2.81 $\pm$.25	373 $\pm$ 4(19)	
Sacramento Valley	20b	Berkeley	potato (lab. culture)	4/1/62	2.64 $\pm$.28	330 $\pm$ 3(25)	
	9	Davis	<i>Myrtus communis</i>	7/27/60	0.22 $\pm$.05	298 $\pm$ 4(27)	100.0 (27)
	10a	Davis	<i>Clematis</i> sp.	8/10/60	0.21 $\pm$.06	275 $\pm$ 5(20)	94.7 (38)
	10b	Davis	<i>Clematis</i> sp.	9/7/61	0.37 $\pm$.19	274 $\pm$ 6(13)	84.6 (13)
	10c	Davis	<i>Clematis</i> sp.	5/14/62	0.33 $\pm$.12	355 $\pm$ 5(30)	73.3 (30)
	13	Davis	<i>Canna</i> sp.	8/10/60	0.92 $\pm$.08	312 $\pm$ 3(49)	83.6 (73)
	17	Marysville	Pear	5/16/61	0.05 $\pm$.05	390 $\pm$ 5(17)	100.0 (19)
	18	Fairfield	Pear	5/19/61	0.20 $\pm$.14	374 $\pm$ 10 (9)	80.0 (10)
	19	Davis	<i>Heuchera maxima</i>	9/7/61	0.01 $\pm$.01	291 $\pm$ 4(25)	73.3 (25)

* Number of observations from which means were calculated is given in Table 2.

[†] Number of observations.

The means did not overlap; those for Berkeley ranged from 1.21 to 2.74 while those from the Valley were from 0.01 to 0.92.

The distributions of the various supernumerary classes resembled a Poisson distribution; but in all populations except those with very low means the within population variance was smaller than the mean. Repeated samplings of population 1 over two years (Table 2) revealed that the population was in equilibrium and that there were no seasonal fluctuations similar to those observed, for example, in the percent of females fertilized. After combining the classes with four and five supernumeraries, a heterogeneity test of the six samples from population 1 gave a $\chi^2_{20} = 9.8$ with $P > 0.95$ so that the variability over the two-year period was even smaller than that expected by chance.

Although population 1, consisting of mealy bugs from a single tree, showed a high degree of constancy in supernumerary numbers, population 6, collected on a long hedge, did not. Two samples, 6a and 6b, collected 13 days apart and from

TABLE 2

Percentages of females with the various numbers of supernumeraries

Population	No. of supernumeraries							n	Mean no. of sups.
	0	1	2	3	4	5	6		
1a	16.3	34.9	30.2	13.9	4.7	..	..	43	1.56
1b	15.0	39.0	25.0	16.0	3.0	2.0	..	100	1.59
1c	15.8	29.7	35.7	12.9	5.9	..	..	101	1.63
1d	14.7	34.3	27.4	16.7	5.9	1.0	..	102	1.68
1e	17.0	27.0	31.0	19.0	5.0	1.0	..	100	1.70
1f	16.0	28.0	31.0	21.0	4.0	..	..	100	1.69
2	25.8	36.6	29.7	6.9	1.0	..	..	101	1.21
5	8.9	32.7	25.7	26.7	5.0	1.0	..	101	1.89
6a	14.0	36.9	22.8	15.8	7.0	3.5	..	114	1.75
6b	9.8	26.2	21.3	18.0	18.9	5.8	..	122	2.27
6c	16.2	31.1	28.4	16.2	6.8	..	1.3	74	1.71
7	6.9	17.6	21.6	23.5	14.7	10.8	4.9	102	2.74
12a	3.7	11.1	44.5	33.3	7.4	..	..	27	2.30
12b	73.1	23.1	3.8	..	..	..	..	26	0.29
15	8.5	39.0	18.6	25.4	5.1	3.4	..	59	1.90
20a	..	11.5	38.4	19.2	23.1	3.9	3.9	26	2.81
20b	8.0	16.0	12.0	40.0	16.0	8.0	..	25	2.64
9	77.6	22.4	..	..	..	..	..	85	0.22
10a	81.2	17.5	..	1.3	..	..	..	80	0.21
10b	78.9	10.5	5.3	5.3	..	..	..	19	0.37
10c	76.7	13.3	10.0	..	..	..	..	30	0.33
13	36.4	40.2	18.7	4.7	..	..	..	107	0.92
17	95.0	5.0	..	..	..	..	..	20	0.05
18	80.0	20.0	..	..	..	..	..	10	0.20
19	98.8	1.2	..	..	..	..	..	81	0.01

different places along the hedge, differed significantly in frequency of supernumeraries (Tables 1 and 2). This high degree of local differentiation could not be studied further; sample 6c was collected before 6b had been analyzed and, due to the scarcity of the insects, was made from the entire hedge. Sample 6c resembled 6a in the mean number of supernumeraries and had a much smaller mean tibia length than did 6b; it might have been collected largely from the territory of the sample 6a. Population 10 was sampled three times and although the samples were taken almost over a two-year period there were no significant differences between them.

The effect of the host on supernumerary frequencies: *P. obscurus* can be found on a great variety of plant species but in the areas studied, those hosts given in Table 1 were the preferred ones, and from these, large samples could be collected. From an examination of the frequency of supernumeraries on the various hosts, it appears that the host does not play an important role in determining supernumerary frequencies. Population 2 had the lowest supernumerary mean in Berkeley and population 6 had the second highest mean but both grew on *Buxus*.

Similarly, population 7 with a mean of 2.74 supernumeraries and population 10 with a mean of only 0.22 were both found on Clematis.

The size of the tibia: The various populations differed significantly in body size as expressed by the length of the tibia. Tibia size dropped sharply in population 1 during the first year of sampling (Table 1), but did not reveal any seasonal fluctuations. This drop in size was not accompanied by a significant change in the frequency of supernumeraries. The size change may possibly have been a response, for unknown reasons, to the sampling itself. In population 10 from the Valley, the tibiae were much longer in the spring than in two collections from the fall and similarly populations 17 and 18 which were collected in the spring had much longer tibiae than nos. 9, 13, and 19 which were collected in the summer or fall. It seems therefore that the populations from the Valley, unlike those from Berkeley, did go through seasonal fluctuations in tibia size.

In the two experimental populations (12 and 20, Table 1) a reduction in tibia size was observed, and in population 12 it was associated with a drop in the mean number of supernumeraries. In population 20 this reduction was probably the result of a change in culture methods, since 20b was raised under slightly different conditions than 20a. Population 12, on the other hand, was raised under constant temperature (26°C) and humidity, and was established several years before the first sample was taken. The drastic drop in tibia size was associated with a similar sharp drop in the number of supernumeraries. At the time of the second collection (12b), the population seemed to be on the verge of extinction; the animals were very small and developed very slowly. The mean tibia length observed, 236 microns, was considerably smaller than that of any other population studied. There was no change in the external environment which could have accounted for the drop in size so that in this case the size of the tibia probably reflected the general lack of well-being of the culture.

A comparison of the mean tibia size in the different supernumerary classes in any one sample did not reveal any strong effect of the number of supernumeraries on size. In several samples, however, there was a trend for tibia size to increase with the increase in number of supernumeraries. Many more animals were measured from population 1 than from the others and in this population a clear trend was established for the length of the tibia to increase with an increase in number of supernumeraries when all the samples were considered (NUR 1962a). The mean tibia lengths for the zero, one, two, three, and the combined four and five classes were 316.9, 318.3, 321.8, 326.1, and 327.6 microns, respectively. It appears that there was an increase of about 11 microns, or of three percent from no supernumerary to the highest class. Although the cause of the increase is unknown, it might have been due to an increase in cell size. In *Secale cereale*, MÜNTZING and AKDIK (1948) reported that the presence of supernumeraries led to an increase in cell size. In *P. obscurus* an addition of five supernumeraries would increase the bulk of the chromosomes in the nucleus by about 30 percent and this increase might be expected to enlarge the diameter of the cells by about ten percent which is sufficient to account for the increase in tibia size.

The distortional load: When supernumeraries possess an accumulation mechanism, some of the individuals with supernumeraries must be eliminated every generation to eliminate the extra chromosomes added by the accumulation mechanism. It was earlier reported (NUR 1962b) that the supernumeraries segregated preferentially into the functional sperm during spermatogenesis so that the males transmitted an almost unreduced number of supernumeraries. The females transmit a reduced number so that the expected increase per generation is about 50 percent. The results of these transmission studies (NUR 1962b) are summarized in Table 3.

Actually, in population 1 the male transmitted on the average 88 percent of his supernumeraries to the sperm, while the female transmitted about 45 percent of her supernumeraries to the egg. It follows that in the zygotes the total increase in the number of supernumeraries will be about 33 percent every generation and the number of supernumeraries will climb rapidly unless the extra supernumeraries are eliminated. This elimination of individuals with supernumeraries imposes a distortional load on the population (KIMURA and KAYANO 1961). The load can be estimated on the basis of the frequency of the supernumeraries and their rate of transmission. The rate of transmission of males with five supernumeraries was not studied so it was assumed to be similar to that of males with four supernumeraries (Table 3).

If we assume that all the supernumerary classes have equal fecundity and that the frequencies of the various classes of males are like those of the females, we can calculate the types and frequencies of the different gametes, and the frequencies of the different types of zygotes at fertilization. These frequencies are given in Table 4; it is clear that they differ from the observed frequencies. Since population 1 was in equilibrium (Table 1), the calculated frequencies must be adjusted to agree with those observed. Such an adjustment requires the different

TABLE 3

*Transmission of supernumeraries by males and females from population 1**

Cross	Inds. tested	Percent of offspring in the various supernumerary classes						No. of offspring	$k_{\dagger}$
		0	1	2	3	4	5		
Male transmission									
0 × 1	5	11.4	88.1	0.5	..	..	..	176	0.891
0 × 2	9	0.8	15.8	76.4	7.0	..	..	205	0.948
0 × 3	5	0.8	8.4	26.7	64.1	..	..	150	0.847
0 × 4	3	..	8.3	12.4	30.4	48.9	..	66	0.800
0 × 5 (assumed)		..	5.0	10.0	15.0	30.0	40.0	...	0.790
Female transmission									
1 × 0	12	66.4	33.6	..	..	..	..	242	0.336
2 × 0	12	7.7	89.0	3.3	..	..	..	244	0.478
3 × 0	15	..	60.6	39.4	..	..	..	164	0.465
4 × 0	1	..	..	100.0	..	..	..	9	0.500
5 × 0	1	..	..	66.7	33.3	..	..	12	0.467

* Condensed from NUR 1962b.

† Rate of transmission.

TABLE 4

The calculated relative viability of the various supernumerary classes in population 1

	0	1	Number of supernumeraries				
			2	3	4	5	>5
Observed frequencies	0.158	0.319	0.300	0.170	0.046	0.007	
Frequencies at fertilization	0.077	0.231	0.302	0.236	0.116	0.032	0.006
Relative viability	1.000	0.628	0.488	0.353	0.194	0.111	0.000

classes to have different viabilities. The results of such an adjustment are given in Table 4 with all the viabilities expressed in terms of the viability of the zero class. It is immediately clear from these calculations that under our assumptions all the supernumerary classes were less viable than the zero class and that viability decreased with the increase in the number of supernumeraries. From the calculated frequencies of the classes at fertilization and their respective viabilities, the distortional load in this population due to the presence of the supernumeraries was calculated to be 0.521. Thus, according to our assumptions the supernumeraries would be harmful in all doses and would reduce the fitness of the population by more than 50 percent. One way to reduce the load is for the individuals with many supernumeraries to have very low fertility and viability, since in this way many supernumeraries can be eliminated at the cost of only a few individuals. Another way is for the individuals with a few supernumeraries to have a higher fecundity than those with none but for those with more supernumeraries to have a much lower fecundity.

The load can also be reduced by positive assortative mating according to the number of supernumeraries. Mating between individuals with supernumeraries will produce individuals with even higher numbers of supernumeraries and these can be eliminated. MELANDER (1950) suggested that assortative mating based on the presence or absence of supernumeraries might take place in the turbellaria *Polycelis tenuis*. Under laboratory conditions, the supernumeraries in this species slowed down development. MELANDER suggested that in nature, individuals with supernumeraries would tend to reach maturity only at the end of the mating season, hence mating mostly with other individuals with supernumeraries. In *P. obscurus* an effect of the supernumeraries on the rate of development was not shown, but in this species positive assortative mating might also take place as a result of inbreeding. Mealy bugs are very restricted in their movements and the adult males do not live for more than a few days. Males would tend to fertilize the female adjacent to them which might be related and thus similar in their supernumerary frequencies.

DISCUSSION

The results so far reported showed large differences between the various populations with respect to the characters studied but gave only little information about the causes of these differences. The calculations of the distortional load in population 1 indicated that the supernumeraries must have a significant effect

on individuals carrying them and on the population. Yet in this population the only noticeable effect was a slight increase in tibia size with the increase in the number of supernumeraries. A preliminary comparison between females with one and those with no supernumeraries under laboratory conditions (NUR 1962a) also failed to show any significant differences. The effect of the supernumeraries became more pronounced with the increase in their number in regard to tibia size and to some extent also in their effect on the percent of fertilized females. The inability to find differences between females without and with one supernumerary might be explained by the slight effect of a single supernumerary and in the future, the effect of the supernumeraries should be studied in females with several supernumeraries as well as in males.

The differences in the mean number of supernumeraries in the coastal region and the Sacramento Valley probably resulted from different ecological conditions under which the equilibria in the number of supernumeraries were established. These ecological differences were probably reflected in the differences between the two regions in regard to the presence or absence of seasonal fluctuations in tibia size and in the percent of fertilized females in the spring.

In the Sacramento Valley populations, the great majority of females had one supernumerary or none at all. If the rates of transmission of supernumeraries in these populations are not very different from those in population 1, some of the individuals with supernumeraries must be eliminated to balance the accumulation mechanism, and these would be mostly individuals with one supernumerary. In a population like no. 19 where only one female out of 81 had supernumeraries, females with two supernumeraries are expected in a frequency of about 0.004 percent and the expected ratio of those with two to those with one is 1:300. In such a population, an increase in the number of supernumeraries of only ten percent every generation would require the reduction in fitness of at least some of the individuals with one supernumerary. Even if the individuals with two supernumeraries were completely inviable, their elimination would account for less than ten percent of the supernumeraries that must be eliminated to balance the accumulation. Thus at least in some of the populations from the Sacramento Valley the supernumeraries are probably harmful and are maintained by the accumulation mechanism. In order that individuals with supernumeraries be eliminated, they must differ in their response to natural selection from those without them, but the nature of the differences is not known.

DARLINGTON (1956) suggested that the beneficial effect of the supernumeraries might sometimes be to increase the variability of the population, rather than to increase the fitness of the individuals carrying them. In species with an accumulation mechanism, the mere increase in variability does not seem sufficient to counteract the effect of the distortional load. In those instances in which an increase in variability would be advantageous, this increase could probably be achieved by an increase in genetic variability due to the normal chromosomes. Moreover, this increase in genetic variability could later be utilized for the production of new genotypes. The variability produced by the supernumeraries, on the other hand, is due to the fact that some individuals carry supernumeraries

while others do not. Thus, the effect of the supernumeraries on variability is a nonspecific one and in this respect resembles that produced by the environment.

The high frequency of supernumeraries in the Berkeley area might be explained in one of two ways. The supernumeraries might be only slightly harmful so that their number must reach a high level before this harmful effect becomes pronounced. Alternatively, the supernumeraries might confer an advantage at least to some of the individuals carrying them. The data so far available do not allow us to discriminate between these two possibilities, but even if the supernumeraries do confer some advantage in certain doses, the high level of supernumeraries observed might still be a combination of the beneficial effect and the accumulation mechanism. It is difficult to suggest what advantage the supernumeraries might confer. However, the constancy of the number of supernumeraries over the year suggests that their effect is not restricted to a particular season.

The mean number of supernumeraries in the various populations might be grouped into those with a mean of 0.4 or less and those with 0.9 or more. The two groups differ not only in their means but also in the structure of the populations. Those with a mean of 0.4 supernumeraries or less were composed mostly of females with one supernumerary or none, while those with the high means contained an appreciable number of females with two or more supernumeraries. The lack of populations with an intermediate mean and the fact that when the mean in 12b decreased it dropped to less than 0.4 might have some bearing on the nature of the equilibrium.

The high and low levels of supernumeraries might be two levels at which the supernumeraries would tend to stabilize. Under conditions in which a single supernumerary is harmful the equilibrium might be established at the low level. When the presence of a single supernumerary is advantageous or only very slightly harmful the level of the supernumeraries would increase until a sufficient number of individuals with more than one supernumerary are present so that by their elimination an equilibrium can be established.

It was shown in Table 3 that females with one supernumerary have a much lower k value (0.34) than those with two (0.48). When females with two or more supernumeraries start to appear in the population, the mean rate of transmission increases and with it the tendency of the supernumeraries to accumulate. Thus a slight decrease in the degree to which a supernumerary is harmful might lead to a corresponding increase in the number of supernumeraries and this, in turn, would lead to an increase in the total rate of transmission. The two processes would interact, aid and abet each other so that the new level of equilibrium would be considerably higher than the original one.

SUMMARY

Spermatogenesis in the mealy bugs is a highly modified meiosis in which only the maternal set of chromosomes form functional sperm. The supernumeraries of *Pseudococcus obscurus* Essig segregate preferentially into the functional sperm,

and an accumulation mechanism is thereby created. The nature of the supernumeraries and their maintenance in populations from several localities in California were studied.

Samples from 14 populations from the areas around Berkeley and Davis were studied cytologically. In each population the frequencies of females with the various numbers of supernumeraries were recorded, as well as the size of the hind tibiae of each female and the percent of adult females which were fertilized. The number of supernumeraries per female ranged from zero to six. The mean number of supernumeraries per female varied greatly in the different populations (0.01–2.74) but remained unchanged in two populations which were sampled over two years.

Two experimental populations, grown under laboratory conditions, were also studied. In the first, the number of supernumeraries dropped sharply over a short period of time, while in the second it remained unchanged.

The number of supernumeraries in the various wild populations seemed to be related to the locality in which the population was found but not to the host plant. The size of the tibiae varied greatly but a trend was evident for tibia size to increase with the increase in the number of supernumeraries.

The nature of the equilibrium in the number of supernumeraries is discussed. Two possibilities are considered: that the supernumeraries are maintained by their accumulation mechanism, and that the supernumeraries are present because they are beneficial to the species.

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