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Predation on Drosophila melanogaster by Scutigera coleoptrata. Genetic origin of a disadvantageous behaviour

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Zoologia. — *Predation on* Drosophila melanogaster *by* Scutigera coleoptrata. *Genetic origin of a disadvantageous behaviour* (*). Nota (**) di FRANCESCO LE MOLI (***), presentata dal Socio S. RANZI.

RIASSUNTO. — Sono riferiti i risultati ottenuti sottoponendo a predazione, da parte di centopiedi *Scutigera coleoptrata*, *Drosophila melanogaster* selvatiche e maschi white ibridi, nati dall'incrocio tra femmine white e maschi selvatici. Gli esperimenti sono stati eseguiti sia in condizioni di buio che di luce parziale. Al buio non esiste predazione preferenziale per nessuno dei due tipi di drosofile saggiate, e ciò sta a dimostrare che negli ibridi white scompare l'effetto svantaggioso dell'addomesticamento di laboratorio riscontrato saggiando il comportamento delle drosofile white di ceppo puro. Alla luce le drosofile white ibride (come anche le white di ceppo puro) sono notevolmente svantaggiate rispetto a quelle di tipo selvatico, e ciò dipende dall'effetto specifico della mutazione « white » che gioca un ruolo preminente nel comportamento delle drosofile mutate.

INTRODUCTION

Although white mutants of *Drosophila melanogaster* lack the protective pigments responsible for eye colour [1], the electroretinogram (ERG) is fundamentally similar to that of wild individuals [2]. These results are in agreement with those of other research workers [3]; however, the absence of shielding pigments makes the eyes of white mutants very sensitive to light stimuli.

Since the conditions are present in white mutants for supposing an altered visual behaviour, an experimental investigation has been performed to see how far this mutant, as compared to the normal type, is at a disadvantage when subjected to predation by centipedes *Scutigera coleoptrata*.

In the research done for this purpose [4, 5] it has been shown that there is clear preferential predation on white mutants when these are offered together with wild individuals to the predators. This phenomenon, which is already apparent in the dark, increases considerably in conditions of partial light. On the other hand no difference has emerged in predation on one or other of the sexes within the strains.

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At this point in the investigation, the disadvantage to the white strain could be brought down to two fundamental parameters: subjection to different selection due to breeding conditions in the laboratory and the specific effect of the " white " mutation on behaviour. To demonstrate to what extent these two factors influence predation on white mutants, Oregon flies were used as controls, a laboratory strain phenotypically similar to the wild flies. From the second part of this research, two different responses were obtained, depending on whether the experiments were carried out in the dark or in the light. In the dark there was no preferential predation, while in the light the white *D. melanogaster* again appeared at a disadvantage; moreover, in both cases no difference was recorded in predation on one or other sex of the respective strains.

The most plausible hypothesis formulated in the face of this phenomenon, is that the absence of differential predation in the dark in Oregon flies and in white mutants, is to be attributed to the fact that both strains have undergone a sort of progressive domestication in that they have been bred in laboratory conditions. (This hypothesis is supported by the fact that in the dark wild drosophilae are less preyed upon than either Oregons or whites; they therefore have a greater possibility of escape from a predator than the laboratory strains). Preferential predation on white flies observed in the light, is to be attributed to the mutation itself, which in conditions of illumination has a determining influence on predation.

As a final trial, wild drosophilae and Oregons were submitted to predation by centipedes; a disadvantage was recorded for the laboratory strain both in dark and light conditions. At this stage it was possible to affirm that this disadvantage, when compared with the wild strain, derives from the different selective pressures due to the prolonged breeding period in the laboratory to which the Oregon strain have been subjected.

To conclude, from the experiments carried out [4] it has been possible to show that laboratory *D. melanogaster* are more easily preyed upon by *Scutigera coleoptrata* than wild drosophilae. The reason for this difference in all probability lies in the different action of the selective mechanisms in the two conditions. For white strain drosophilae, when predation takes place in the light, the specific effect of the " white " mutation is added to this cause.

In the present research, the investigation has been modified to study predation by *Scutigera coleoptrata* on F_1 hybrid white *D. melanogaster* obtained by crossing wild males and pure white females belonging to a laboratory strain. These hybrids have a chromosomic set of half white and half wild derivation. It was supposed that in these individuals the disadvantageous effects of laboratory breeding (comparable to a sort of domestication and in which in-breeding probably plays a very important part) ought to decrease considerably in conditions of predation, while the damaging effect of the mutation itself should remain the same.

Materials and Methods

Scutigera coleoptrata L. is an agile nocturnal predator on insects, particularly diptera. Its predatory activity has been described in the past [6, 7, 8] and seems to be guided according to some Authors by visual stimuli [9, 8, 10] and, according to others by a complex of chemico–tactile stimulations [11].

In a series of experiments carried out both in the light and in the dark, wild *D. melanogaster*, both males and females, were offered as prey to the centipedes together with white hybrid males, obtained from the same cross between white females and wild males. Male and female wilds were used indifferently as it had been previously observed that there is no difference in predation on the two sexes [4, 5].

The female whites were taken from strains that have by now been bred for some time in our laboratory, but which came originally from the Genetics Department of the University of Pavia. The wild drosophila on the other hand, were obtained by cross-breeding individuals collected around Parma, Mantua and Piacenza.

The *Scutigera coleoptrata* were mostly caught in the summer months from 1969 to 1971 mostly in the habitat round Parma or in the immediate neighbourhood of Chioggia.

During the experiments the centipedes were kept isolated in plexiglass containers $25 \times 19 \times 8$ cm.. The walls and the base were black, while the lid which could be slid backwards and forwards was transparent and had a hole in it in the middle for ventilation. In each container we placed a round glass dish which was 8 cm in diameter and full of fine wet sand to keep the relative internal humidity between 90 and 95 %. These humidity values were chosen in accordance with the natural needs of the centipedes, even if this did not correspond to optimal conditions for the *D. melanogaster* which prefer a drier atmosphere [12, 13]. Internal temperature varied between 20 and 25° C.

A cilindrical drum, 3 cm. in diameter and filled with feeding ground for the fruit flies, was put into each container so that the flies could feed normally. The plexiglass containers themselves were then placed on the bottom of a wooden box $100 \times 55 \times 55$ cm. In these conditions experiments could then be carried out in the dark or in the light. Darkness was obtained by simply shutting the lid of the box. Conditions of light however, were obtained by attaching a neon 8 watt light to the internal surface of the lid of the box. The light was screened by opaque moveable shields in such a way that light intensity on the bottom of the box was recorded at about 50 lux.

The experiment was divided into two sections: *i*) predation on wild *D. melanogaster* and male white hybrids in darkness; *ii*) predation on the same insects in conditions of light. Ten individuals of one type and 10 of the other were given to one centipede at the same time. The experiments, which lasted approximately 16 hours each time, were mostly performed during the night because of the natural habits of the predators.

RESULTS

After 10 experiments carried out in darkness, with an interval of 48 hours between one experiment and the next, it was shown that, of a total of 2200 drosophilae given to 11 predators, 1411 (64.1 %) were preyed on, of which 736 (52.2 %) were male white hybrids and 675 (47.8 %) were wilds (Table I). The χ^2 calculated between these two values is 2.637 and confirms the hypothesis of casuality in the predation of centipedes. The χ^2 for homogeneity was also calculated to check variability in differential predation of the individual predators. The result ($\chi^2 = 10.198$ with 10 degrees of freedom) is not significant and confirms the hypothesis of homogeneity in the predatory behaviour of the centipedes.

TABLE I

Experiments carried out in darkness.

To each *S. coleoptrata* 200 *D. melanogaster* were supplied in all to make a total of 2200 in 10 experiments. In each experiment 10 white hybrid drosophilae and 10 wild drosophilae were administered.

PREDATOR	*D. melanogaster* preyed upon		*D. melanogaster*		χ^2 for 1 : 1
	N.	%	white (*)	wild (**)	(1 d.f.)
Sc/H ♂	136	68.0	71	65	0.264
Sc/L ♂	104	52.0	50	54	0.153
Sc/M ♀	155	77.5	77	78	0.006
Sc/N ♀	136	68.0	75	61	1.441
Sc/P ♂	127	63.5	59	68	0.627
Sc/S ♀	129	64.5	60	69	0.637
Sc/W ♀	103	51.5	58	45	1.640
Sc/X ♂	159	79.5	81	78	0.056
Sc/Y ♀	114	57.0	60	54	0.315
Sc/6 ♀	106	53.0	59	47	1.358
Sc/12 ♀	142	71.0	86	56	6.338
TOTALS . . .	1411	64.1	736	675	
			$\chi^2 = 2.637$ (***)		

(*) White males born from wild males and white females.
(**) Males and females.
(***) Not significant.

χ^2 for homogeneity = 10.198 with 10 degrees of freedom. Not significant.

On the other hand, having controlled separately the variability between the totals of drosophilae preyed upon by each predator with the χ^2 one-sample-test [14], it was found that these quantities are significantly different among themselves ($\chi^2 = 30.391$ with 10 degrees of freedom, $p < 0.001$). This phenomenon is probably to be attributed to the size and the moulting period of the centipedes.

These results, obtained in darkness, enable us to claim, that there is no preferential predation for either of the two types of drosophilae sampled. Therefore both the wild drosophilae and the white hybrids behave very similarly in the presence of the predator.

All this is considerably different from what had been observed in previous experiments [4], which had also been carried out in darkness where a clear selection against the pure white mutant was recorded, whenever it was submitted together with wild individuals to predation by *Scutigera coleoptrata*. The fact that this preferential predation is no longer observable in the case in question, serves to show that these white drosophilae have gained a considerable advantage from hybridization, in that they lost for the most part the negative effects which derived from their prolonged period of breeding in the laboratory.

Repeating the same number of experiments in the light, with 12 centipedes, of a total of 2400 drosophilae introduced, 1505 were preyed upon. The total percentage of drosophilae preyed upon shifts from 64.1 % in darkness to 62,7 % in the light. The difference however between these two values is not statistically significant ($\chi^2 = 0.948$) and this serves to show that in the different experimental situations the behaviour of the predators is highly homogeneous.

Out of the 1505 *D. melanogaster* preyed upon, 864 were white hybrids and 641 were wilds (Table II). These frequencies in terms of percentages corrispond to 57.4 % and 42.6 % respectively. The corrisponding χ^2, this time, is highly significant ($\chi^2 = 33.042$, $p < 0.001$) and therefore one can claim that the general phenomenon, in the light, denotes a selection for predation towards white hybrid individuals. In this case also the differences, which have been observed in the predation of centipedes and are represented by the χ^2 1 : 1 at the side of the table, which oscillate between 0.257 and 9.000, are not significant, since the χ^2 for homogeneity is below tabular level ($\chi^2 = 4.870$ with 11 degrees of freedom). The χ^2 one-sample-test however continues to be significant ($\chi^2 = 38.348$ with 11 degrees of freedom, $p < 0.001$).

As can be seen, in the light there is a percentage increase in the white hybrid drosophilae preyed upon: in fact this goes from 52.2 % in darkness to 57.4 % in the light. This situation is even clearer if one considers the percentages of white hybrids and wilds preyed upon compared with the number of individuals of the two types introduced in the light and in darkness, (Table III). In all 1100 white hybrid drosophilae and an equal number of wilds were introduced into the plexiglass containers in darkness, while in the light the number of *D. melanogaster* introduced was 1200 in both cases. In the

TABLE II

Experiments carried out in the light.

To each *S. coleoptrata* 200 *D. melanogaster* were supplied in all to make a total of 2400 in 10 experiments. In each experiment 10 white hybrid individuals and 10 wilds were administered.

PREDATOR	*D. melanogaster* preyed upon		*D. melanogaster*		χ^2 for 1 : 1 (1 d.f.)
	N.	%	white (*)	wild (**)	
Sc/12 ♀	123	61.5	71	52	2.934
Sc/14 ♀	132	66.0	75	57	2.454
Sc/19 ♀	118	59.0	66	52	1.661
Sc/20 ♀	111	55.5	61	50	1.090
Sc/22 ♀	113	56.5	64	49	1.991
Sc/23 ♀	140	70.0	73	67	0.257
Sc/25 ♂	134	67.0	75	59	1.910
Sc/27 ♀	171	85.5	98	73	3.654
Sc/28 ♂	121	60.5	77	44	9.000
Sc/30 ♂	142	71.0	83	59	4.056
Sc/32 ♀	114	57.0	70	44	5.929
Sc/33 ♀	86	43.0	51	35	2.976
TOTALS . . .	1505	62.7	864	641	
			$\chi^2 = 33.042$ (***)		

(*) White males born from wild males and white females.
(**) Males and females.
(***) $p < 0.001$.
χ^2 for homogeneity = 4.870 with 11 degrees of freedom. Not significant.

dark the percentage of white hybrid drosophilae preyed upon, compared with the actual number introduced is 66.9 %; in the light this value is considerably increased going up to 72.0 %. The corrisponding χ^2 is significant ($\chi^2 = 6.787$, with one degree of freedom; $0.005 < p < 0.0010$). Considering the number of wilds preyed upon in comparison with the number introduced, there is a drop from 61.4 % in the dark to 53.5 % in the light. In this case too χ^2 is significant ($\chi^2 = 14.483$, with one degree of freedom; $p < 0.001$).

From all this one can deduce that white hybrid in the light are at a considerable disadvantage in comparison with the wild phenotype and that this

depends on the specific effect of the " white " mutation which plays a role of primary importance in the behaviour of mutated drosophilae.

At this point we thought it interesting to be able to compare the results of white hybrid drosophilae with those obtained in a previous research, [4], on white drosophilae of the pure strain. Considering the experiments that were carried out in darkness, of 900 white drosophilae introduced 650 were preyed upon (72.2 %); on the other hand for the white hybrids, of the 1100 drosophilae introduced, 736 (66.9 %) were preyed upon. The difference between these two percentages is significant ($\chi^2 = 6.320$, with one degree of freedom; $0.010 < p < 0.025$). In the light significance is even higher. In fact, of 800 white drosophilae introduced 84.7 % i.e. 678 individuals were preyed upon; while for the white hybrids, of a total of 1200 drosophilae introduced those preyed upon were 864 (72.0 %) ($\chi^2 = 43.475$, with one degree of freedom; $p < 0.001$).

TABLE III

Comparison between the numbers of white hybrids and wild D. melanogaster *preyed upon when introduced in darkness and in the light.*

	DARKNESS			LIGHT		
	Introduced	Preyed upon		Introduced	Preyed upon	
	N.	N.	%	N.	N.	%
Whites (*)	1100	736	66.9	1200	864	72.0
Wilds (**)	1100	675	61.4	1200	641	53.4

(*) White males born from wild males and white females.
(**) Males and females.

It can be seen therefore that whether in darkness or in the light the white drosophilae of the pure strain are more easily preyed upon by *Scutigera coleoptrata* than the white hybrids. The advantage of the hybrids can certainly be attributed to the fact that the cross with wild individuals has considerably reduced the negative effects of prolonged breeding in the laboratory with reconstitution of a general heterozygote situation.

The present results confirm the hypothesis therefore [4] that preferential predation by *Scutigera coleoptrata* on pure strain white drosophilae is to be attributed to two fundamental parameters: *i*) the effect of the different selective pressure due to breeding in captivity of the strain in question compared to the wild drosophilae (a condition which determined a sort of progressive domestication), and *ii*) the disadvantageous effect of the " white " mutation on the visual behaviour of drosophilae.

In fact in the wild x white hybrids with white eyes the genetic effects of breeding in the laboratory are annulled, although the negative influx of the absence of protective pigments responsible for eye colour is maintained.

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