Estimates of between- and within-family components of variation

Population	PI*	Culm height**		Panicle length**		Days to flowering	
		CV_b	CV_w	CV_b	CV_w	CV_b	CV_w
1	0.108	0.120	0.115	0.139	0.158	0.168	0.106
2	0.006	0.201	0.130	0.116	0.145	0.102	0.098
3	0.038	0.127	0.104	0.108	0.123	0.140	0.123
4	0.124	0.148	0.127	0.108	0.147	0.216	0.116
5	0.098	0.192	0.129	0.114	0.126	0.155	0.174
6	0.243	0.239	0.123	0.130	0.129	0.227	0.084
7	0.080	0.139	0.157	0.143	0.184	0.140	0.091
8	0.177	0.145	0.134	0.109	0.155	0.165	0.128
	Correlation coefficient (r)	0.08		0.59		−0.12	

* PI = polymorphism index based on allozyme variation at a total of 10 esterase and cathodal peroxidase loci and a locus for lemma hairiness. ** Data of Moraes[4].

progeny generation (1976). Rank orders of progeny CV_w are plotted against the rank orders in the parental generation (1975) for flowering time (figure 2). Estimates of regression coefficients were $b = 0.56 \pm 0.18$ (pop. 2) and 0.83 ± 0.14 (pop. 6). Both values of b are significant, suggesting a significant genetic determination of phenotypic plasticity in flowering time. Similar results were obtained for panicle length but regression coefficients for culm height were nonsignificant ($p > 0.10$).

Observations of greater genotype-specific plasticity in species with lower genetic variability were made earlier in 2 different genera of Gramineae: *Avena*[5,6] and *Bromus*[7], and in *Limnanthes*[8] (Limnanthaceae). In each case, a pair of congeners seemed to have alternative strategies of adaptation. Baker[3] had also provided a few such examples in weedy and nonweedy pairs of congeneric species. Both theoretical and experimental analyses of these examples in terms of natural selection for plasticity would be of considerable interest in plant evolution.

Inheritance of phenotypic plasticity is widely implied in the discussions of its evolution. It needs to be demonstrated and measured by appropriate experimental designs in quantitative genetics. Such experiments are likely to be difficult in ascertaining the control of environments, choice of characters, and interpretation of adaptive significance of nongenetic variation, but results of this study show that these are not unsurmountable problems.

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Larval necrophagy and photopigment phenocopying in *Musca domestica* (L.)[1]

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Summary. The intensity of photopigment modification in green-eyed house flies increased with increasing larval density and the relative frequency of +-type larvae. Phenocopying in these precursor deficient mutants resulted from the consumption of their dead 3rd instar +-type sibs.

The manipulation of insect photopigment expression in mutant strains by the transplantation of imaginal discs, the injection of body fluids or extracts, the feeding of pupae or adults, as well as the feeding of specific chemical precursors has been well-documented[3]. In *Drosophila* no modifications were induced by feeding or injecting photopigment deficient mutants with other mutant or +/+-larvae, and only boiled pupae containing the necessary precursors produced phenocopying[4]. While examining photopigment development in several Diptera species, Ward and Hammen[5] reported 'pink intermediates' among green-eyed house flies where the extent of modification was dependent upon the density and relative frequency of genotypes in the medium. This gn/gn-mutant accumulated tryptophan indicating a block in the first step of ommochrome synthesis: the oxidation of tryptophan to formyl-l-kynurenine. Their explanation was that the observed phenotypic variation resulted from +/+-larval excretory products contaminating the medium thereby conferring the necessary precursors to the mutants. The present observations of a gn/gn-strain[6] likewise produced offspring from hybrid and test crosses with phenotypes ranging from typical 'green' through several blends to a light red eye color. Genotypic ratios for these crosses approached the expected values when all eye

Table 1. Summary of simulated genetic crosses producing eye pigment modifications as a function of frequency and density dependence

Simulation	Initial density (+/+ : gn/gn)	Percent surviving +/+	Percent surviving gn/gn	Pigmentation index
$F_1 \times F_1$	30:10 (6)	43.3	40.0	1.13
	60:20 (6)	41.9	46.7	1.38
	120:40 (6)	35.8	40.8	1.58
+/gn × gn/gn	20:20 (4)	42.5	41.3	1.00
	40:40 (5)	37.0	35.0	1.19
	80:80 (5)	43.8	44.5	1.24

Vials were established with newly eclosed +/+- and gn/gn-larvae in the expected ratios from selfed F_1 and test crosses. Number of replicates is given in parentheses.

color variants were summed. The degree of photopigment modification was similarly shown to increase with increasing larval density and frequency of phenotypically wild larvae. To examine the causes of this phenocopying, several genetic cross simulation and feeding experiments were conducted.

Materials and methods. To illustrate the relationship between increasing density and +-type frequency on the extent of phenocopying, newly eclosed +/+- and gn/gn-larvae were placed in standard food vials[7] at combined densities of 40, 80 and 160 in ratios which simulated the expected results of hybrid and test crosses. The first feeding experiment examined photopigment modification by excreted products. Medium on which a cohort of +/+-larvae matured was cleared of all living and dead larvae and subsequently used for rearing a newly eclosed cohort of gn/gn-larvae. 3 additional feeding experiments examined the photopigment modifications resulting from the consumption of dead +/+-larvae by gn/gn-larvae. 1. The effect of +/+-larval age, processing procedures, and body region were examined by placing 100 newly eclosed gn/gn-larvae in standard food vials supplemented with 400 mg (wet wt) of variously prepared +/+-larvae. 2. The duration and period of development that gn/gn-larvae were exposed to dead +/+-larvae was examined. Entire 3rd instar +/+-larvae (400 mg wet wt) were placed in a standard food vial to which 100 gn/gn-larvae of the appropriate age were added for 24, 48, or 76 h. 3. The quantity of dead 3rd instar larvae added to standard vials with 100 gn/gn-larvae was varied in a graduated series from 50 to 1200 mg. A pigmentation index (PI) was devised to describe the degree of phenocopied modification. Typical gn/gn-flies were designated class 1; a light blend, class 2; a dark blend, class 3; and the most intense effect, a light red, class 4. The PI was the sum of the proportion of individuals of each category multiplied by its class value.

Using procedures identical to those described above, the following control experiments were conducted. 1. Genetic cross simulations were repeated using commercial CSMA fly rearing medium. 2. Feeding supplement tests were conducted with dead 3rd instar gn/gn- or +/gn-larvae in place of +/+-larvae.

Results and discussion. In 8 replicates at varying densities, no variation from the normal gn eye color was observed when gn/gn-larvae were reared on +/+-conditioned medium. This result is in contrast to the suggestion by Ward and Hammen and implies an alternative route for the transmission of pigment precursors. The results of the genetic cross simulations confirm the relationship that increasing density and +-type frequency intensifies the extent of phenocopying (table 1). Approximately 60% of the developing larvae died regardless of density or genotype. An examination of the medium after 72 h showed larvae within and consuming the contents of their sibs' larval skins. Whether this was cannibalism or simply necrophagy has not been determined.

Supplements of dead +/+-larvae to the medium showed that homogenized or entire 1st or 2nd instar +/+-larvae produced no phenocopying, but additions of 3rd instar larvae showed major effects in all methods of preparations. The diluted form of homogenized larvae produced the lowest PI of 1.76; the anterior and posterior portions of bisected larvae yielded similar but higher PI's; and entire larvae produced the greatest modification (table 2).

Varying the time and duration of exposure suggested that 2nd instar gn/gn-larvae are sufficiently robust consumers for an adequate time to induce the greatest degree of photopigment modification. Resources are apparently lacking for 3rd instar larvae for sequestering the necessary precursors, but 14% of the population showed a PI of 3 or higher. The high proportion of unmodified flies in this case suggests that a limited number of gn/gn-larvae had access to the available corpses ($\simeq 12$). As expected, increasing quantities of dead +/+-larvae added to the medium resulted in a series of increasing PI-values (table 2).

Table 2. Results of 3 necrophagy feeding experiments to test eye pigment modification of gn/gn-flies when the larvae were fed on medium containing dead +/+-larvae

Experiment	+/+-Larval treatment wet wt (mg)	Instar	gn/gn exposed (h)	Pigmentation class (percentage) 4	3	2	1	Pigmentation index	Percent larvae surviving
I	$400^{f,h*}$	1	>96	-	-	-	100	1.00	56
	$400^{f,e}$	1	>96	-	-	-	100	1.00	60
	$400^{f,h}$	2	>96	-	-	-	100	1.00	52
	$400^{f,e}$	2	>96	-	-	-	100	1.00	63
	$400^{f,h}$	3	>96	-	1	74	25	1.76	52
	$400^{f,a}$	3	>96	-	17	68	16	2.01	48
	$400^{f,p}$	3	>96	-	27	40	33	1.94	43
	$400^{f,e}$	3	>96	7	19	63	11	2.22	59
II	$400^{f,e}$	3	0-24	-	-	-	100	1.00	48
	$400^{f,e}$	3	0-48	-	-	8	92	1.08	50
	$400^{f,e}$	3	0-72	-	-	13	87	1.13	48
	$400^{f,e}$	3	72-P**	5	9	13	74	1.45	44
	$400^{f,e}$	3	36-P	41	38	7	14	3.05	46
III	$50^{f,e}$	3	>96	-	-	1	99	1.01	44
	$100^{f,e}$	3	>96	-	-	29	71	1.29	47
	$200^{f,e}$	3	>96	-	5	51	45	1.60	44
	$400^{f,e}$	3	>96	7	19	63	11	2.22	59
	$600^{f,e}$	3	>96	60	30	8	2	3.48	54
	$900^{f,e}$	3	>96	89	11	-	-	3.89	47
	$1200^{f,e}$	3	>96	100	-	-	-	4.00	51

Experiment I examines the effects of +/+-larval age, method of processing, and +/+-body region; experiment II examines the period of feeding by gn/gn when dead +/+-larvae were present in the medium; and experiment III considers the effects resulting from quantitative additions of +/+-larvae to the rearing medium. 100 gn/gn-larvae, 2 ± 2 h old, were added to each vial and each treatment was replicated 3 times. * Method of +/+-larvae preparation; [f] frozen; [h] homogenized; [e] entire; [a] anterior half; [p] posterior half. ** P, The time at which the larvae leave the medium to pupate on the floor of the cage.

The use of CSMA fly rearing medium failed to elicit any eye color modification. The custard-like texture of the milk-yeast gel (which was similar to that used by Ward and Hammen) provided a matrix permitting larval necrophagy. In other control experiments, the feeding of of dead 3rd instar gn/gn-larvae to developing gn/gn-larvae produced no photopigment modification. And similarly, feeding experiments utilizing +/gn as a supplement produced results identical to those reported in the +/+ feeding tests.
Additions of 0.5 to 2.5 mg of d-l-kynurenine (Sigma) to the surface of food vials in which gn/gn-larvae were reared produced adults with increasing degrees of photopigment modification. Adults from each treatment were homogenous but the eye color produced was an increasing intensity of brown and not the yellow-green to light red pattern resulting from larval necrophagy. From visual observation, it appears that Ziegler's suggestion that the substance secreted into the medium by the +/+-larvae in Ward and Hammen's study was kynurenine was not confirmed. The reddish color suggests that the pterin and not ommochrome synthesis was affected by larval necrophagy.
We may conclude that in the photopigment development of gn/gn-house flies, the genotype, age and quantity of the sib it eats determines the extent of phenocopied modification.

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A sex pheromone from the mandibular glands in bumblebee queens

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Summary. In this paper it is shown that the mandibular glands of young bumblebee queens produce a species-specific sex pheromone. From our results it becomes obvious that the pheromone is a releaser for the mating attempts made by the conspecific males.

During the past 3 decades, several authors investigated behavioural and physiological aspects of mating in bumblebees. After Frank's[2] description of flight paths characteristic for male bumblebees, much attention was paid to this phenomenon[3]. Krüger[4] presumed that the function of the scents deposited on marking spots is to attract females. Stein[5] isolated the marking secretion from the heads of *Bombus terrestris* males and identified the active component as farnesol. Many other substances from male bumblebee glands have since been identified[6].
The role of virgin queens in bumblebee mating biology was studied by Krüger[4] and Free[6], who described the queen as rather passive. Free suggested that males might recognize queens by their size and colour pattern.
Preliminary experiments with virgin queens, either flying free or tied to a line, gave us the impression that the queen is able to communicate to the male her receptiveness. If tethered no copulation occurred. For such a signal, pheromones from the mandibular glands could be involved. In this paper we report on such a sex pheromone from the mandibular glands of bumblebee queens.
The experiments were carried out in flight rooms either at the Zoological Institute II, Würzburg (Federal Republic of Germany) or at the Laboratory of Comparative Physiology, Utrecht (Netherlands). In Würzburg we used *Bombus terrestris* males and females emerging from nests initiated in the Institute. In Utrecht we used males and queens produced in nests of *B. hypnorum*, *B. pratorum* and *B. terrestris* which were collected in the field previously and kept in confinement.
A few dozen of males were set free in a flight room. After a few days they had set out a flight path generally having only a few marking spots. These marking spots were readily detectable as they were visited frequently by the males. In the Utrecht experiments, males of more than one species were kept together. They shared most of the marking spots.
Once the flight path was established, normal young queens were introduced into the room. The behaviour of the males towards such queens was studied. To the same males we offered also:
1. Living virgin queens whose mandibular glands were extirpated.
2. Similar queens without mandibular glands but impregnated with an acetonic extract of mandibular glands of a queen of their own species.
3. Queens without mandibular glands which had been dead for at least 2 weeks. These were impregnated with acetonic extracts of mandibular glands of queens of their own species or of another species.
The extirpation was done under CO_2-narcosis; a window was made in the malar area which was closed again after removal of the mandibular gland. Operated queens were