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Effects of body pigmentation mutations on *Drosophila melanogaster* mating behavior

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The model of congenic strains of *Drosophila melanogaster* was used to investigate the peculiarities of the effect of mutations in *yellow* (*y*), *ebony* (*e*), and *black* (*b*) genes involved in biogenesis of cuticle pigments on imago mating behavior indicators. The aim of this study was to find out if the effect of the given mutations on *Drosophila* imago mating behavior depends on the general genetic background on which they are realized. To achieve this goal, pairs of congenic strains were constructed using successive saturation crosses followed by selection for the marker phenotype resulted in each of the mutant alleles introduced in homozygous condition into the genotype of either *Canton-S* or *Oregon-R* wild-type stock instead of the corresponding wild-type allele present in these stocks initially. Individuals of strains resulted were tested for mating receptivity of females and mating activity of males. Each of the indicators was evaluated as a proportion of sexually mature but virgin individuals of a particular sex copulated successfully within the first hour after placing them in a test chamber with an excess of individuals of the opposite sex. According to the data obtained and the results of their statistical analysis, it was proved that the introduction of a mutation into the genetic background of the wild-type stock is accompanied with a change in the studied characteristics of imago mating behavior. The effect depends on the mutation introduced and on the genotype of the recipient stock. Thus, males of the $y_{C\text{-}S}$ strain are characterized by increased mating activity comparatively to males of the wild-type *Canton-S* stock. These results expand the known effects of *yellow* mutation. Males of the $b_{C\text{-}S}$ and $e_{C\text{-}S}$ strains, on the contrary, are less active than the males of the wild-type *Canton-S* stock. The most pronounced effects on mating receptivity of females were fixed for *b* (an increase in the indicator when introduced into *Oregon* genetic background) and *e* (a decrease when introduced into *Canton-S* genetic background) mutations. The indicators studied under the conditions of the given experimental scheme change in direct proportion (r_S = 0,76; p < 0,05). In other words, if the strain is characterized by high mating activity of males, as a rule, a high mating receptivity of females will be also observed.

Key words: *Drosophila melanogaster, mutations yellow, ebony, and black, congenic strains, mating receptivity of females, mating activity of males.*

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Introduction

Insect pigments biogenesis is a network of genetically determined interrelated metabolic transformations. For a number of genes, mutations in which lead to a change in the pigmentation of the anatomical structures of larvae and adults, pleiotropic effects on behavioral traits have been established. Detailed studies also revealed functional links between the pigment synthesis pathway and behavior mediated by the nervous system (Hotta, Benzer, 1969; Heisenberg, 1971; Borycz et al., 2002; Richardt et al., 2002; True et al., 2005; Suh, Jackson, 2007; Zhuravlev et al., 2020).

The insect exoskeleton contains melanin, a dark pigment derived from dopamine (DA) precursors tyrosine and L-Dopa (L-3,4-dihydroxyphenylalanine) (Yamamoto, Seto, 2014). T.R. Wright showed that genes essential for melanin synthesis in cuticle also regulate DA synthesis in insect brain, the same is typical for mammalian brains (Wright, 1987), while the mechanism of genetic control of mammalian skin melanization differs (Raposo, Marks, 2007). Upon molting and eclosion, *Drosophila* epidermal cells synthesize and secrete DA. The latter is then incorporated into the cuticle and oxidized into melanin by phenoloxidases such as Laccase2. In addition, metabolites of DA such as NBAD (N-β-alanyl dopamine) and NADA (N-acetyl dopamine) are required for hardening of the cuticle (sclerotization). Genetically determined changes in cuticle pigmentation can be used in experimental models based on forward genetic approach to identify genes that regulate DA dynamics in both the cuticle and the nervous system.

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Everything above mentioned makes *Drosophila melanogaster* an excellent model species to investigate the regulation of melanin patterns (Wittkopp et al., 2002). For example, some of the enzymatic steps in the melanin synthesis pathway are well understood both genetically and biochemically (Wright, 1987). Tyrosine hydroxylase (TH; encoded by the gene *pale*) and dopa decarboxylase (DDC) convert tyrosine to dopa and dopamine, respectively, which are then processed by a system of Phenol Oxidases (POs; among others encoded by the genes *yellow*, *black and ebony*) and co-factors to form melanin.

The aim of this study is to find out if the effect of the mutations in genes *yellow, ebony, and black* on *Drosophila* imago mating behavior depends on the genetic background in which they are realized.

Materials and methods

We used *Drosophila melanogaster* stocks described below from *Drosophila* stocks collection of Genetics and Cytology Department of V.N. Karazin Kharkiv National University. This collection is an item of National Heritage of Ukraine (Order…, 2013).

Wild-type stocks used:

Canton-Special: *C-S*. Standard laboratory stock historically obtained from the natural population of Canton Valley, Ohio, USA. Selected by Bridges. Is referred to as carrying a recessive mutation of multiple thoracic and scutellar bristles, which partially overlaps the wild type but manifests sporadically in stocks partially obtained from *Canton-S*. Salivary gland cell chromosomes are known to be normal (http://flybase.org/reports/FBsn0000274.html).

Oregon-R: *OR*, *Or*. Standard laboratory stock historically derived by D.E. Lancefield from the natural population of Rosenburg, Oregon, USA. Is referred to as carrying a minor *ebony* allele. Occasional individuals have phenotypes with branching of the posterior crossvein of the wing (chromosome 2) or ladle wings (http://flybase.org/reports/FBsn0000276.html).

Stocks carrying single-gene mutations, disturbing body pigmentation:

yellow: *y*. Localization: 1–0.0. Origin (historically): spontaneous. Discoverer: E.M. Wallace. Phenotype: body color is yellow, hairs and bristles are brown with yellow dots. The veins of the wing are yellow. The bristles and mouth appendages of the larvae may have a color from yellow to brown unlike dark brown in wild type larvae. Imago can synthesize tyrosinase (http://flybase.org/reports/FBgn0004034.html).

black: *b*. Localization: 2–48.5. Origin: (historically) spontaneous. Discoverer: T.H. Morgan, 1910. Phenotype: body color of mutant individuals is black (darkens with age and at reduced developmental temperature), as well as legs and wing veins. The ability of integument to reflect light is only 40 % compared to wild-type flies. The trait is not very clearly defined in individuals just after eclosion. Heterozygotes are somewhat darker than the wild type, but lighter than homozygotes. The puparium is lighter than the wild type. Imago can synthesize tyrosinase but cannot synthesize β-alanine. Injection or food supplement with β-alanine to mutants causes a reversion to the wild phenotype (http://flybase.org/reports/FBgn0000153).

ebony: *e*. Localization: 3–71. Origin: (historically) spontaneous. Discoverer: E.M. Wallace. Phenotype: body color of homozygous mutant individuals varies from strong shining black but depends on allele. Puparia are much lighter comparatively to the wild type ones. The gene encodes for a cytoplasmic protein with beta-alanyl-dopamine synthase activity (links beta-alanine to biogenic amines like dopamine or histamine). It controls (negative regulation) the amount of free biogenic amines: dopamine (during formation of cuticle) and histamine (while visual signal transduction). It is also involved in behavioral rhythmicity (http://flybase.org/reports/FBgn0000527).

To study the effect of the loci on the components of mating behavior, saturation crosses were conducted under the directed selection for marker mutant phenotype according to the scheme below (Nikoro, Vasilyeva, 1978):

P: ♀ M × ♂ C-S (Or)	$P_{b(2-7)}$: ♀$M_{(F2)}$ × ♂ C-S (Or)	*M* refers to a mutant phenotype;
F_1: ♀ F_1 × ♂ F_1	$F_{1(Pb)}$: ♀ F_1 × ♂ F_1	*N* refers to a normal phenotype (wild type);
F_2: 3 N : 1 M	$F_{2(Pb)}$: 3 N : 1 M	F_1 – first generation hybrids;
or for X-linked locus	or for X-linked locus	F_2 – second generation offspring
F_2: 1 N : 1 M	$F_{2(Pb)}$: 1 N : 1 M	P_b – backcross

For each initial mutant stock, 7 complete saturation crosses were performed either with *C-S* stock or with *Or* stock. Thus, the stocks were aligned (uniformed) with genetic background (hereinafter: $M_{C\text{-}S}$ – the stock in which the mutation (*M*) was transferred into *C-S* wild-type genetic background; M_{Or} – the stock in which the mutation was transferred into *Or* wild-type genetic background). Finally, we obtained two sets of congenic strains.

The mating activity of males (MAM) was evaluated by the number of the latter that mated within 1 hour. To do this, females and males were placed in a test chamber (chemically clean tubes with a volume of 20 cm^3 without nutrient medium) at a ratio of 2n♀♀ : n♂♂. We recorded the proportion of males that copulated within 1 hour. Analysis of the mating receptivity of females (MRF) was carried out similarly. However, for the testing, females and males were taken at a ratio of n♀♀ : 2n♂♂. The proportion of females that copulated within 1 hour was recorded (Pole, 1979; Subocheva et al., 2003). The numbers of individuals tested are in Table 1.

Flies were reared in culture vials (height 10 cm, diameter 2.0 cm) with a standard sugar-yeast medium (volume of nutrient medium in each vial – 3 ml) at 23±1°C. During the first day after eclosion females and males were segregated. Both were kept separately in vials with temporary medium until sexual maturation (till the age of 3–5 days). Only virgin individuals were used for behavioral tests. All behavioral tests were performed without prior anesthetizing the insects, under the conditions of constant uniform illumination and temperature (20–25°C).

The effect of the locus on mating behavior was assessed by comparing the values of the corresponding indexes in the wild-type basestock and in congenic strains.

The proportions of individuals of either sex participated in copulation were fixed to evaluate mating activity of males and mating receptivity of females. The confidence limits for the proportions were calculated for these indexes. Comparison of groups was performed by analysis of variance for qualitative traits. Associations were determined using multivariate and 2×2 contingency tables, χ^2 criteria, exact two-sided Fisher criteria, as well as the criteria of evaluation of strength of linkage between the risk factor (specific mutation) and phenotype analyzed. The linkage between indexes studied was analyzed with Spearman rank correlation coefficient (r_S) (Atramentova, Utevskaya, 2006; De Muth, 2006; Plokhinsky, 1970). To perform calculations we used on-line calculators (https://medstatistic.ru/calculators/calchi.html; https://epitools.ausvet.com.au/ciproportion, https://statpages.info/ctab2x2.html).

Results and discussion

Behavior tests have shown that individuals from stocks analyzed differ in mating activity of males and mating receptivity of females (Table 1). For example, most of males of *C-S*, $y_{C\text{-}S}$ and b_{Or} stocks succeeded in performing copulation during the first hour of interaction with females. Contrary, less than 60 % of males of *Or*, $e_{C\text{-}S}$ and e_{Or} stocks appeared to be successful under the same conditions.

Table 1. Mating behavior indexes of stocks studied

Genotype		Mating activity of males				Mating receptivity of females			
Mutant allele	Genetic background	*N* (♂)	$\hat{p}$	*Lower 95 % CL*	*Upper 95 % CL*	*N* (♀)	$\hat{p}$	*Lower 95 % CL*	*Upper 95 % CL*
+; +; +	*C-S*	83	0,81	0,71	0,88	64	0,83	0,72	0,90
+; +; +	*Or*	37	0,57	0,41	0,71	55	0,36	0,25	0,50
y; +; +	*C-S*	67	0,96	0,88	0,98	71	0,66	0,55	0,76
y; +; +	*Or*	100	0,63	0,53	0,72	99	0,54	0,44	0,63
+; b; +	*C-S*	106	0,65	0,56	0,73	58	0,81	0,69	0,89
+; b; +	*Or*	94	0,79	0,69	0,86	89	0,64	0,54	0,73
+; +; e	*C-S*	123	0,53	0,44	0,61	103	0,59	0,50	0,68
+; +; e	*Or*	69	0,52	0,41	0,64	90	0,38	0,28	0,48

N – number of individuals analyzed, $\hat{p}$– proportion, CL – confidence limit (Wilson score interval), y – yellow, b – black, e – ebony, C-S – Canton-Special, Or – Oregon-R.

To evaluate the effects of factors controlled experimentally we used algorithm of analysis of variance for qualitative traits. The results are in Table 2. It was proved that all factors fixed in the

experiment had significant effect on indexes measured, the same is true for uncontrollable ones (environmental and internal fluctuations).

Table 2. Results of analysis of variance for qualitative traits

Mating activity of males				
Factor	η^2	*F*	*p* value	effect
Singe gene mutation (*y* / *b* / *e* / *none*)	0,04	9,67	<0,01	proved
Genetic background (*C-S* / *Or)*	0,01	8,98	<0,05	proved
Singe gene mutation and Genetic background	0,04	8,49	<0,01	proved
Uncontrolled	0,09	9,06	<0,01	proved
Mating receptivity of females				
Singe gene mutation (*y* / *b* / *e* / *none*)	0,03	5,85	<0,05	proved
Genetic background (*C-S* / *Or)*	0,05	36,04	<0,01	proved
Singe gene mutation and Genetic background	0,02	3,47	<0,05	proved
Uncontrolled	0,09	9,14	<0,01	proved

η^2 – effect size, F – Fisher criterion, p – probability value, y – yellow, b – black, e – ebony, C-S – Canton-Special, Or – Oregon-R.

In order to find out if there is an association between mutation-induced body pigmentation change in specific genetic background and traits studied we organized data in multivariate contingency tables and calculated χ^2 criteria (Table 3). The results obtained show that changes in pigmentation caused by mutations studied are strongly associated with changes in mating activity of *Drosophila melanogaster* males and mating receptivity of females in both *C-S* and *Or* genetic background. The conclusion about the presence of a statistical relationship between the studied factor and the result (a change in mating behavior) was made if the value of χ^2 criterion obtained exceeded the critical one at the probability value $p < 0.01$ applied for this study.

Table 3. Mutation presence association with mating behavior

Genetic background	Mating activity of males			Mating receptivity of females		
	χ^2	$\chi^2_{0,01(3)}$	effect	χ^2	$\chi^2_{0,01(3)}$	effect
C-S	43,71	11,35	proved	14,62	11,35	proved
Or	13,98	11,35	proved	16,92	11,35	proved

χ^2 – chi-square test statistic; $\chi^2_{0,01(3)}$ – critical value of the chi-square test statistic under the probability value 0,01 and degree of freedom 3; C-S – Canton-Special; Or – Oregon-R.

The next step of analysis was devoted to comparison of effects of single mutations. To do that we organized data in 2×2 contingency tables and calculated χ^2 criteria, exact two-sided Fisher criteria, as well the criteria of evaluation of strength of linkage between the risk factor (specific mutation) and the phenotype analyzed (Table 4). The obtained value of exact Fisher criteria of more than 0.05 indicated the absence of statistically significant differences. A value less than 0.05 indicated their presence.

In order to study the regularity according to which mating activity of males and mating receptivity of females are going to change, a nonparametric method was used. The Spearman rank correlation coefficient (r_S) was calculated. Correlation coefficient values were interpreted in accordance with the Chaddock scale (Hinkle et al., 2003). It was found that under the conditions of the experiment the given indexes (MAM and MRF) change in direct proportion ($r_S = 0.76$; $p < 0,05$). The latter means that stocks characterized by high level of mating activity of males also have females with high level of mating receptivity.

The molecular mechanisms of the revealed effects of the studied mutations on mating behavior of *Drosophila* imago, as well as correlated changes in the behavior of individuals of different sexes, can be partially explained in terms of the known pleiotropic effects of the products of these genes on the cuticular

hydrocarbon composition (Massey et al., 2019a), genitalia (Dobzhansky, Holz, 1943; Singh, Singh, 2016) and sex combs (Massey et al., 2019b) structure.

Table 4. Effects of single-gene mutations disturbing pigmentation on mating behavior of *Drosophila melanogaster*

Index	Mutant locus	Genetic background	χ^2 (*p*)	$F_{(exact)}$ (*p*)	*φ* (*strength*)	*C* (*strength*)	*C`* (*strength*)
Mating activity of males	*y;+;+*	*C-S*	**7,34 (0,007)**	**0,007 (<0,05)**	**0,22 (medium)**	**0,22 (medium)**	**0,31 (medium)**
		Or	0,44 (>0,05)	0,56 (>0,05)	0,06 (ns)	0,06 (ns)	0,08 (ns)
	+;b;+	*C-S*	5,64 (0,018)	- (>0,05)	0,17 (weak)	0,17 (weak)	0,24 (weak)
		Or	**6,43 (0,012)**	**0,016 (<0,05)**	**0,22 (medium)**	**0,22 (medium)**	**0,31 (medium)**
	+;+;e	*C-S*	16,73 (<0,001)	- (>0,05)	0,29 (medium)	0,27 (medium)	0,39 (medium)
		Or	0,20 (>0,05)	0,69 (>0,05)	0,04 (ns)	0,04 (ns)	0,06 (ns)
Mating receptivity of females	*y;+;+*	*C-S*	**4,84 (0,03)**	**0,032 (<0,05)**	**0,19 (weak)**	**0,19 (weak)**	**0,26 (weak)**
		Or	**4,18 (0,04)**	**0,04 (<0,05)**	**0,17 (weak)**	**0,163 (weak)**	**0,23 (weak)**
	+;b;+	*C-S*	0,07 (>0,05)	0,82 (>0,05)	0,023 (ns)	0,023 (ns)	0,033 (ns)
		Or	**10,47 (0,002)**	**0,002 (<0,05)**	**0,27 (medium)**	**0,26 (medium)**	**0,36 (medium)**
	+;+;e	*C-S*	**10,14 (0,002)**	**0,002 (<0,05)**	**0,25 (medium)**	**0,24 (medium)**	**0,34 (medium)**
		Or	0,03 (>0,05)	1,0 (>0,05)	0,014 (ns)	0,014 (ns)	0,02 (ns)

χ^2 – chi-square test statistic; $F_{(exact)}$ – exact two-sided Fisher criteria; p – probability value; φ – Phi coefficient; C – Pearson`s contingency coefficient; C` – Sakoda's adjusted Pearson's C; y – yellow, b – black, e – ebony, C-S – Canton-Special, Or – Oregon-R, ns – not significant.

Conclusions

Mutations of body pigmentation (*yellow*, *black* and *ebony*) make pleiotropic effect on *Drosophila melanogaster* mating behavior. The effect depends on the genetic background.

Among studied, the most pronounced and unexpected effect was found for *yellow* mutation in *C-S* genetic background. Introduction of mutation was accompanied with rise of mating activity of males but with reduction of mating receptivity of females comparatively to wild type parental stock.

Indexes studied (mating activity of males and mating receptivity of females) under the conditions of the experiment changed in direct proportion (r_S = 0,76; p<0,05).

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Вплив мутацій пігментації тіла на статеву поведінку *Drosophila melanogaster*

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На моделі конгенних ліній *Drosophila melanogaster* досліджували особливості впливу мутацій у генах *yellow* (*y*), *ebony* (*e*) і *black* (*b*), які задіяні у біогенезі пігментів кутикули, на статеву поведінку імаго. Метою даного дослідження було з'ясувати, чи залежить ефект даних мутацій на статеву поведінку імаго дрозофіли від загального генетичного фону, на якому вони реалізуються. Для досягнення поставленої мети були сконструйовані пари конгенних ліній, в яких шляхом послідовних насичуючих схрещувань з добором на маркерний фенотип кожен з мутантних алелів був введений у гомозиготному стані у генотип ліній дикого типу *Canton-S* або *Oregon-R* замість присутнього у цих лініях алеля дикого типу відповідного гена. У особин отриманих ліній оцінювали статеву рецептивність самок і статеву активність самців. Кожен з показників оцінювали як частку статевозрілих віргінних особин певної статі, які вступають у парування протягом першої години після внесення їх у тестерну камеру з надлишком особин протилежної статі. Згідно з отриманими даними і результатами їх статистичного аналізу доведено, що внесення мутації на генетичний фон лінії дикого типу призводить до зміни досліджених показників, які характеризують статеву поведінку імаго. Ефект залежить

як від внесеної мутації, так і від генотипу лінії-реципієнта. Так, самці лінії $y_{C\text{-}S}$ характеризуються підвищенням статевої активності в порівнянні із самцями лінії дикого типу *Canton-S*. Ці результати розширюють відомі уявлення про можливі ефекти даної мутації. Самці ліній $b_{C\text{-}S}$ і $e_{C\text{-}S}$, навпаки, менш активні, в порівнянні з самцями лінії дикого типу *Canton-S*. Найбільш виражені ефекти щодо статевої рецептивності самок відзначені з боку мутацій *b* (збільшення показника при внесенні на генетичний фон *Oregon*) і *e* (зниження при внесенні на генетичний фон *Canton-S*). Досліджені показники в умовах даної постановки експерименту змінюються прямо пропорційно (r_S = 0,76; p < 0,05). Іншими словами, при високій статевій активності самців у лінії, як правило, спостерігається і висока статева рецептивність самок.

Ключові слова: *Drosophila melanogaster, мутації yellow, ebony та black, конгенні лінії, статева рецептивність самок, статева активність самців*.

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Влияние мутаций пигментации тела на половое поведение *Drosophila melanogaster*

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На модели конгенных линий *Drosophila melanogaster* исследовали особенности влияния мутаций в генах *yellow* (*y*), *ebony* (*e*) и *black* (*b*), которые задействованы в биогенезе пигментов кутикулы, на половое поведение имаго. Целью данного исследования было выяснить, зависит ли эффект данных мутаций на половое поведение имаго дрозофилы от общего генетического фона, на котором они реализуются. Для достижения поставленной цели были сконструированы пары конгенных линий, в которых путём последовательных насыщающих скрещиваний с отбором на маркерный фенотип каждый из мутантных аллелей был введен в гомозиготном состоянии в генотип линий дикого типа *Canton-S* или *Oregon-R* вместо присутствующего в этих линиях аллеля дикого типа соответствующего гена. У особей полученных линий оценивали половую рецептивность самок и половую активность самцов. Каждый из показателей учитывали как долю половозрелых виргинных особей определённого пола, которые вступают в спаривание в течение первого часа после помещения их в тестерной камере с избытком особей противоположного пола. Согласно полученным данным и результатам их статистического анализа доказано, что внесение мутации на генетический фон линии дикого типа приводит к изменению исследованных показателей, характеризующих половое поведение имаго. Эффект зависит как от вносимой мутации, так и от генотипа линии-реципиента. Так, самцы линии $y_{C\text{-}S}$ характеризуются повышением половой активности по сравнению с самцами линии дикого типа *Canton-S*. Эти результаты расширяют известные представления о возможных эффектах данной мутации. Самцы линий $b_{C\text{-}S}$ и $e_{C\text{-}S}$, наоборот, менее активны, по сравнению с самцами линии дикого типа *Canton-S*. Наиболее выраженные эффекты в отношении половой рецептивности самок отмечены со стороны мутаций *b* (увеличение показателя при внесении на генетический фон *Oregon*) и *e* (снижение при внесении на генетический фон *Canton-S*). Исследованные показатели в условиях данной постановки эксперимента изменяются прямо пропорционально (r_S = 0,76; p < 0,05). Другими словами, при высокой половой активности самцов в линии, как правило, наблюдается и высокая половая рецептивность самок.

Ключевые слова: *Drosophila melanogaster, мутации yellow, ebony и black, конгенные линии, половая рецептивность самок, половая активность самцов*.

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