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Differential responses to artificial selection on oviposition site preferences in *Drosophila melanogaster* and *D. simulans*

Eduardo M. Soto, María I. L. Betti, Juan Hurtado and Esteban Hasson

Departamento de Ecología, Genética y Evolución, IEGEBA (CONICET-UBA), Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina

Abstract The preference–performance relationship in plant–insect interactions is a central theme in evolutionary ecology. Among many insects, eggs are vulnerable and larvae have limited mobility, making the choice of an appropriate oviposition site one of the most important decisions for a female. We investigated the evolution of oviposition preferences in *Drosophila melanogaster* Meigen and *Drosophila simulans* Sturtevant by artificially selecting for the preference for 2 natural resources, grape and quince. The main finding of our study is the differential responses of *D. melanogaster* and *D. simulans*. Although preferences evolved in the experimental populations of *D. melanogaster*, responses were not consistent with the selection regimes applied. In contrast, responses in *D. simulans* were consistent with expectations, demonstrating that this species has selectable genetic variation for the trait. Furthermore, crosses between *D. simulans* divergent lines showed that the genetic factors involved in grape preference appear to be largely recessive. In summary, our artificial selection study suggests that *D. melanogaster* and *D. simulans* possess different genetic architectures for this trait.

Key words artificial selection; behavior; *Drosophila*; genetic variation; natural resources; oviposition preference

Introduction

The study of ecological factors in speciation, particularly the role of behavioral choices, has received renewed attention in recent years (Coyne & Orr, 2004; Craig & Itami, 2008; Feder & Forbes, 2008; Gripenberg *et al.*, 2010). Oviposition preference is the tendency of females to lay eggs in a particular host when given a choice between various equally abundant resources (Jaenike, 1983; Sezer & Butlin, 1998; Sheeba *et al.*, 1998; Miller *et al.*, 2011). Resource use (or performance) is the efficiency in the exploitation of a resource, and can be evaluated by means of the analysis of life history traits (Fox, 1993; Stearns, 2000).

Correspondence: Eduardo M. Soto, Ciudad Universitaria, Pabellón II (C1428 EHA), Buenos Aires, Argentina. Tel: +54 011 4576 3348; fax +54 011 4576 3354; email: edusoto@ege.fcen.uba.ar

In many insects, eggs are vulnerable and larvae have limited mobility, thus the choice of an oviposition site is one of the most important decisions for a female (Berenbaum & Feeny, 2008). Accordingly, the ability to detect and avoid unfavorable sites is expected to be under strong natural selection, and has received intense scrutiny in studies of oviposition site preference (Thomson & Pellmyr, 1991; Bernays & Chapman, 1994).

In the context of plant–insect interactions, the preference–performance relationship is a central theme in evolutionary ecology (Thompson, 1988; Jaenike, 1990; Craig & Itami, 2008; Gripenberg *et al.*, 2010). The "mother-knows-best" hypothesis is based on the idea that females will evolve preferences for oviposition sites in which offspring fare best (Jaenike, 1978; Thompson, 1988; Mayhew, 1997; Gripenberg *et al.*, 2010). However, evidence of the expected direct relationship between preference and performance remains unclear (Rausher, 1980; Underwood, 1994; Faria & Fernandes, 2001).

Alternatively, the "feeding niche constraint" hypothesis argues that the evolution of preference–performance relationships will be determined by adaptations that allow the exploitation of a herbivore's feeding niche (Craig & Itami, 2008). A testable prediction of this hypothesis is that insects with similar feeding niches will evolve similar preference–performance relationships (Craig & Itami, 2008).

Insect females use a complex array of olfactory and gustatory cues to decide whether or not to oviposit on a given site (Markow *et al.*, 2009; Schwartz *et al.*, 2012). Also, complex olfactory and gustatory systems, with multiple sensory structures, play crucial roles in both survival and reproductive success, mediating complex behaviors such as feeding, mating, and oviposition (Hallem *et al.*, 2006; Yang *et al.*, 2008). In fruit flies, odor perception occurs via antennae, although the maxillary palps and tarsi also play important roles (reviewed in Hallem *et al.*, 2006).

Drosophila species are excellent models to investigate the evolution of host plant use because flies do most of their activities (feed, court, mate, and oviposit) on, or near, the selected host (Markow & O'Grady, 2008). The *Drosophila melanogaster* subgroup is an ensemble of 8 species whose ecological status may represent 4 steps in a gradual shift from specialization to opportunism and human commensalism (Lachaise & Silvain, 2004). The extremes of such variation are represented by ecological specialists, such as *D. erecta* Tsacas and Lachaise and *D. sechellia* Tsacas and Baechli, and cosmopolitan generalists, such as *D. melanogaster* Meigen and *Drosophila simulans* Sturtevant (Jaenike, 1983; R'Kha *et al.*, 1991). Of these 2 cosmopolitan species, *D. melanogaster* is more widely distributed than *D. simulans* (Lachaise & Silvain, 2004). Such difference in biogeographical patterns may be explained by the diversity of resources that flies have encountered in different agroecosystems during their expansion, as well as by their specific preferences and abilities to exploit them (Lachaise & Silvain, 2004). Thus, we may ask whether the association with human activities, and the concomitant shifts towards domestic substrates, have been key factors in the recent evolutionary history of these cosmopolitan species (Lachaise & Silvain, 2004).

In a previous work, we studied oviposition site preference, host acceptance and performance in grape (*Vitis vinifera* Linneo) and quince (*Cydonia oblonga* Miller), 2 different natural fruit crops that *D. melanogaster* and *D. simulans* utilize in agroecosystems in Argentina. We have shown that: (i) females of both species preferred *V. vinifera* over *C. oblonga*; (ii) *D. melanogaster* exhibited a higher preference for *V. vinifera* than its sibling; (iii) flies reared in *C. oblonga* developed faster and were more viable than in *V. vinifera*, regardless of the species (Soto *et al.*, 2011).

Here, we investigate the evolution of oviposition preferences in *D. melanogaster* and *D. simulans* by means of laboratory selection experiments for grape and quince. We also examine the correlated responses of performance traits to selection for oviposition site preference, by measuring viability and developmental time in flies raised in the 2 alternative breeding sites. Our hypotheses are: (i) that both species have selectable genetic variation for the preference for alternative oviposition sites, (ii) that both species will evolve similar responses to artificial selection, and (iii) that the evolution of alternative oviposition site preferences will prompt correlated responses in performance traits.

Materials and methods

Collection and maintenance of stocks

Experimental stocks of *D. melanogaster* and *D. simulans* were established with flies collected in the locality of Lavalle (32.5°S 68.28°W, Mendoza Province, Argentina) in March 2005. Orchards of *C. oblonga* (quince) and vineyards of *V. vinifera* (grape) are the main fruit crops in the sampling area, providing potential breeding substrates for both species. Fresh and naturally rotten materials of fruits from both plant species were also collected for the preparation of "seminatural" experimental media, as described in Soto *et al.* (2011). Flies were collected by net-sweeping on baited traps and sexed upon arrival to the laboratory. Sets of 50 isofemale lines of both species were founded by placing individual gravid females in vials containing 5 mL of Instant *Drosophila* Medium. All lines were maintained under identical conditions (25 ± 1 °C and 12 : 12 h light : dark photoperiod). In the 6th laboratory generation, for each species 35 isofemale lines were randomly selected and mixed in equal numbers to create an outbred stock. These outbred stocks were reared under standard conditions for 5 generations before starting the artificial selection protocol described below.

Artificial selection protocol

We generated 3 types of experimental populations (henceforth, selection regimes) with 2 replicates for each type (lines from hereon). The first was generated from eggs oviposited in *V. vinifera* (G) and the second from the eggs laid in *C. oblonga* (Q). The third, which may be considered a control, was originated with flies that developed from the eggs laid in *V. vinifera* and *C. oblonga* dishes, independently of the number of eggs laid in each type of resource (C).
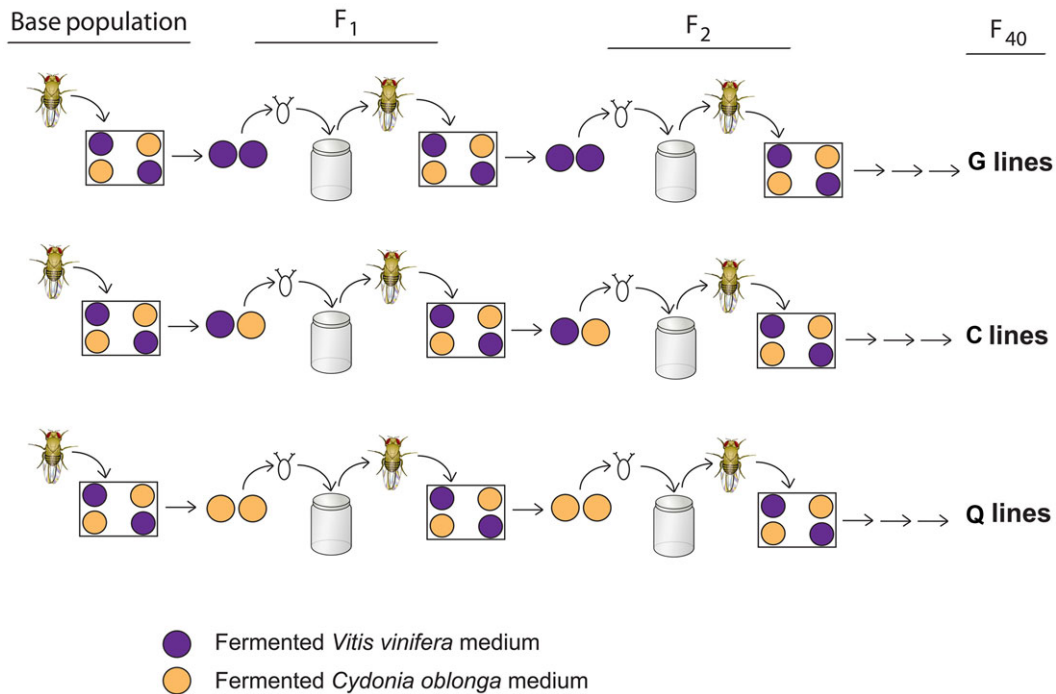
Fig. 1 Schematic representation of the artificial selection protocol used to generate the experimental populations: G selection regime (originated from the eggs oviposited in *V. vinifera*, dark/purple circles), Q selection regime (from the eggs oviposited in *Cydonia oblonga*, light/orange circles), and C selection regime (originated with flies that developed from the eggs layed in *V. vinifera* and *C. oblonga*). See text for details.

To initiate the experimental populations, batches of one hundred pairs of sexually mature flies (4–5 d old) were released in egg-collecting chambers of $20 \times 15 \times 10$ cm (4 chambers for each species). In each chamber 4 dishes containing media prepared with either fermented *V. vinifera* or *C. oblonga* were randomly distributed. The fruit media were fermented for 24 h before releasing the flies in the chambers by inoculating 1 drop of natural ferment of each fruit species collected from naturally fermenting fruits (see above). After 24 h, all dishes were removed and samples of eggs were transferred to culture vials containing 5 mL of Instant *Drosophila* Medium (Fig. 1).

Artificial selection was applied for 40 generations. Every 10 generations we measured the response to selection, except generation 10 for *D. melanogaster* which was not assessed due to logistical problems.

Traits scored

Oviposition site preference Oviposition site preference (OP) was measured by releasing batches of twenty pairs of sexually mature flies (4–5 d old) of a certain selection line in egg-collecting chambers (20 chambers

were set up for each selection line). Three dishes containing fermented *V. vinifera* and 3 containing *C. oblonga* were randomly distributed in each chamber. After 48 h dishes were removed and photographed for egg counting, using a digital camera attached to a binocular microscope. OP was estimated as the number of eggs laid on *V. vinifera* minus the number of eggs on *C. oblonga*, divided by the total number of eggs laid in the chamber (Joseph *et al.*, 2009). A mixed ANOVA design was used to analyze OP, with Selection regime (G, Q, and C), as the only fixed factor, and Line (1 and 2) nested in Selection regime.

Performance traits Larval viability (LV) and developmental time (DT) were measured in both species before starting the artificial selection protocol (Generation zero -G_0-) and at the 40th generation of artificial selection. To measure LV and DT, 100 sexually mature males and females of each species/line were released in egg-collecting chambers containing dishes with an oviposition medium prepared with a 2% agar–agar solution with the addition of commercial yeast (*Saccharomyces cerevisiae*) on its surface. Eggs were allowed to hatch and batches of 30 1st-instar larvae (previously washed with distilled
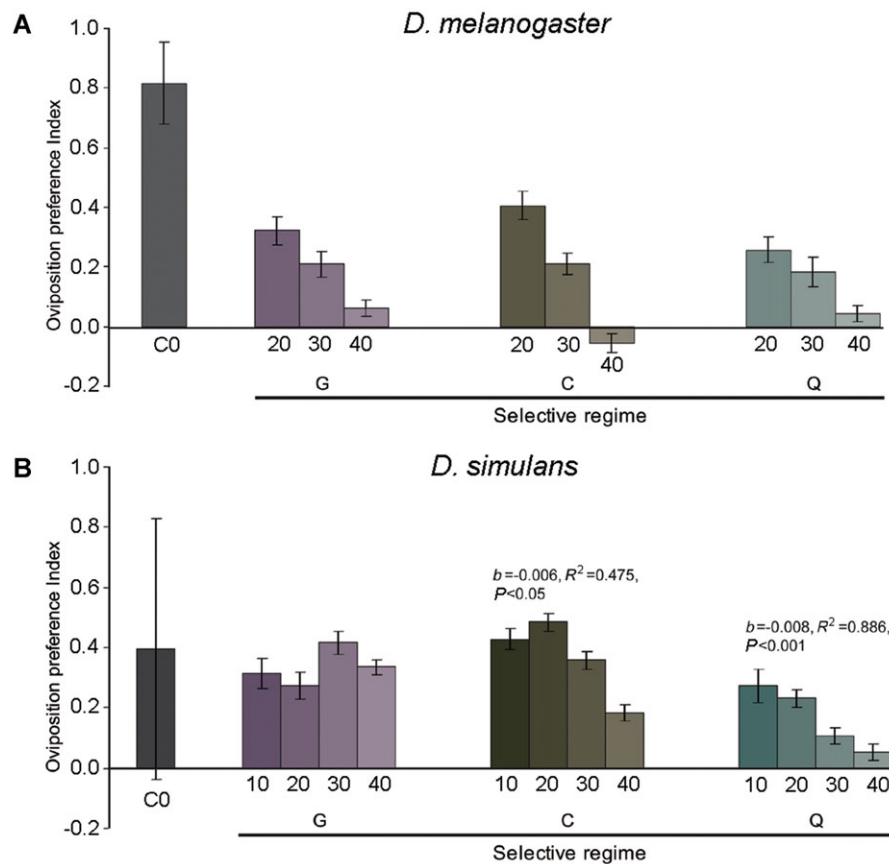
Fig. 2 Means and standard deviations (in bars) of oviposition preference index for base population (C0) and selective regimes (G, lines selected for their preference for *V. vinifera*; C, control lines; Q, lines selected for their preference for *C. oblonga*) in *Drosophila melanogaster* (A) and *D. simulans* (B) throughout the selective generations. For each selection regime we give the results of regression analyses (slope *b*, square of the correlation coefficient R^2 and *P* value of the regression). Only the results of significant regressions are given (see text for more details).

water) were transferred to culture vials containing one of the seminatural media described above (grape or quince). Ten vials were run for each combination of selection regime and resource (5 vials per selection line). Vials were incubated as described above until the emergence of adults.

LV was estimated as the proportion of adults emerged relative to the number of larvae seeded in each vial. LV data were analyzed using a mixed ANOVA with Selection regime (fixed), Resource (fixed), and Line (random) nested within Selection regime as main sources of variation. An angular transformation was applied prior to statistical analysis.

DT was measured as the time (in hours) elapsed between the transfer of 1st-instar larvae to the vials and adult emergence. For DT estimation, emerged flies were collected every 4 h until the emergence of the last fly. The same sources of variation for LV were considered in the

mixed ANOVA model used to analyze DT data, with the addition of Vial (nested within the Line by Resource interaction) set as random factor in a mixed ANOVA model. DT data were log-transformed prior to the ANOVA.

All statistical analyses were performed using a General Linear Model (GLM) implemented in the STATISTICA 7.0 software package (StatSoft, 2001).

Results

The ANOVA used to evaluate differences among treatments after 40 generations of selection showed that differences among selection regimes were not significant in *D. melanogaster* ($F_{2,3} = 0.467$, $P = 0.666$). In contrast, differences between Lines (nested in selection regime) were significant ($F_{3,114} = 13.282$, $P < 0.001$). Lines selected for grape and quince preference did not diverge from each

other throughout the experiment. However, both G and Q regimes exhibited a general departure from the initial preference for *V. vinifera* toward an OP value close to 0 (Fig. 2A). Thus, we did not further investigate these lines for performance traits.

On the contrary, *D. simulans* exhibited a clear response to selection for OP as indicated by the significant differences among selection regimes ($F_{2,3} = 22.296$, $P < 0.05$). *D. simulans* showed a significant response over the artificial selection experiment, which was evident from the 20th generation onwards (Fig. 2B). To investigate which groups (C, G, and Q lines) are responsible for the significant selection regime effect, we employed the *a posteriori* Tukey's HSD test. The application of this procedure revealed that all comparisons between lines were significant (Error: MS = 0.007, df = 112; $P < 0.001$ for the comparison between G and C; $P < 0.01$ for C–Q and $P < 0.001$ for G–Q). Grape lines maintained the initial preference for *V. vinifera* observed in G0 over the experiment (68% eggs oviposited in *V. vinifera*) and Q lines increased significantly their preference for *C. oblonga* (Fig. 2B). Control regime showed intermediate value as compared to G and Q regimes in the 30th and 40th generations. To evaluate the temporal trends, we regressed OP on time (in generations). Regression analysis revealed significant and negative trends for the preference of grape in C regime ($b = -0.006$, $R^2 = 0.475$, $r = -0.735$, $P < 0.05$) and Q regime ($b = -0.008$, $R^2 = 0.886$, $r = -0.949$, $P < 0.001$). On the contrary, the regression analysis was not significant for G regime ($b = 0.001$, $R^2 = 0.126$, $r = 0.122$, $P = 0.754$). Tests of parallelism of slopes revealed significant differences between Q versus G and Q versus C regimes (Q–G, $F_{2,23} = 4.879$, $P < 0.05$; Q–C, $F_{2,23} = 7.772$, $P < 0.01$; G–C, $F_{2,23} = 0.379$, $P = 0.688$, respectively).

In *D. simulans* OPs were also evaluated in the progeny of crosses between the most divergent selection lines (G1 and Q2). The ANOVA showed that differences among genotypes were significant ($F_{3,75} = 17.365$, $P < 0.001$). Tukey's tests revealed that the parental lines employed in these crosses maintained the differences registered in previous assays (error: MS = 0.029, df = 75; $P < 0.001$) and that hybrids OPs derived from both reciprocal crosses, were alike the Q parent and differed significantly from the G parent (error: MS = 0.029, df = 75; $P = 0.999$ for the comparison between G1Q2 and Q2; $P = 0.752$ for Q2G1 and Q2; $P < 0.001$ for G1Q2 and G1; and $P < 0.001$ for Q2G1 and G1) (Fig. 3).

In view of the responses to selection observed in *D. simulans*, we evaluated the performance of G, C, and Q regimes by measuring larval viability (LV) and developmental time (TD) in *V. vinifera* and *C. oblonga* media. The ANOVA for LV showed that the Selection regime by
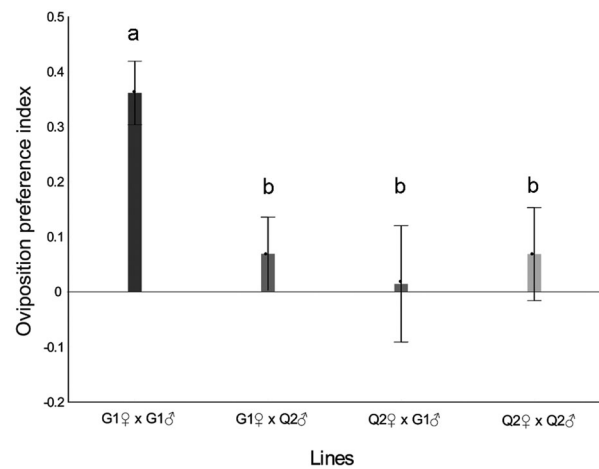

Fig. 3 Means and standard deviations (in bars) of oviposition preference index for the G1 and Q2 selective lines, and F$_1$ hybrids products of both reciprocal crosses (G1♀ × Q2♂ and Q2♀× G1♂). The results of *a posteriori* Tukey's comparisons are represented by letters.

Table 1 Analyses of variance for the larval viability and developmental time in selection regime for the oviposition site preference of *D. simulans*, in the generation 40.

Variance	Larval viability		
	df	MC	F
Selection regime (SR)	2	0.288	3.081
Resource	1	1.406	67.221[**]
SR × Resource	2	0.275	13.135[*]
Line (nested in SR)	3	0.094	4.475
Line (nested in SR) × Resource	3	0.021	0.745
Error	48	0.028	

Variance	Developmental time		
	df	MC	F
Selection regime (SR)	2	0.006	0.177
Resource	1	0.516	35.502[**]
SR × Resource	2	0.024	1.629
Line (nested in SR)	3	0.033	2.096
Line (nested in SR) × Resource	3	0.016	1.994
Vial (nested in Line × Resource)	48	0.010	4.994[***]
Error	932	0.002	

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Resource interaction was significant (Table 1) suggesting differences in the response magnitude of the selection regime to rearing in grape or quince (Fig. 4A). *A posteriori* Tukey's comparisons revealed that viability differences between flies reared in grape and quince were only
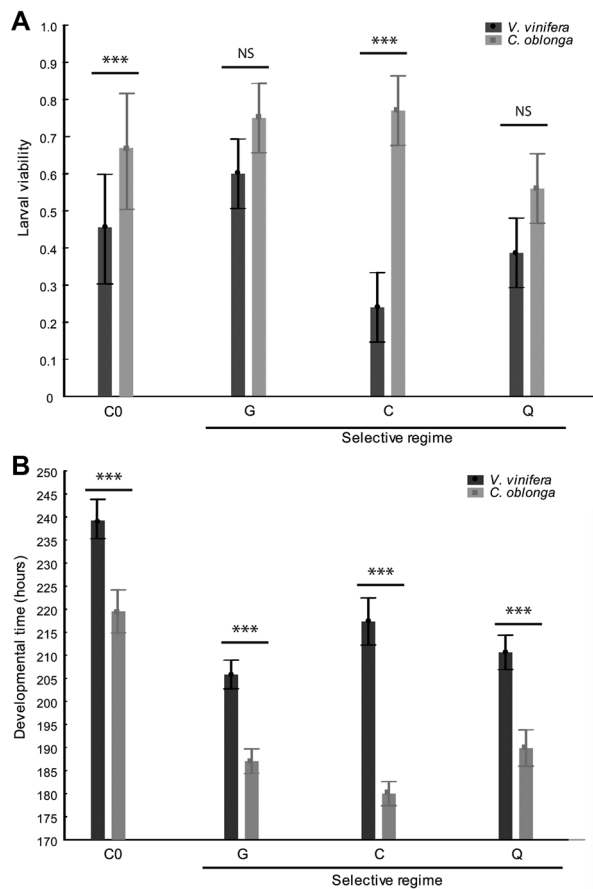
Fig. 4 Means and standard deviations (in bars) of larval viability (A) and developmental time (B) for base population (C0) and selective regimes (C, control lines; G, lines selected for their preference for *V. vinifera*; Q, lines selected for their preference for *C. oblonga*) of *D. simulans* in different breeding resources. *A posteriori* Tukey's comparisons. NS, non significant difference, ***$P < 0.001$.

significant in C lines (error: MS = 0.028, df = 48; $P < 0.001$), flies reared in *C. oblonga* had higher viability than in *V. vinifera* (Fig. 4A). Only differences between Resources were significant in the ANOVA for DT (Table 1), flies tended to develop faster in *C. oblonga* than in *V. vinifera* (Fig. 4B).

Discussion

The main finding of our work is the differential response of *D. melanogaster* and *D. simulans* to artificial selection for oviposition site preference. On one hand, *D. melanogaster* did not show a clear response to selection, since patterns of evolution for oviposition site preferences were very similar across treatments. G, Q, and C regimes exhibited an evident decline of the strong grape preference observed in the base population (OP = 0.8), reaching oviposition scores close to 0 irrespective of the selection regime. Thus, we may conclude that the evolution of OP in *D. melanogaster* is not compatible with expectations based on the artificial selection regimes applied. On the contrary, these results resemble the consequences one might expect from some kind of laboratory selection for nonchoosy flies or even with random trait evolution. Furthermore, the sustained evolution toward nonchoosiness in *D. melanogaster* lines suggest that the base population harbored standing genetic variation for the trait. These results are in agreement with a previous survey in *D. melanogaster* natural populations (including the population studied in this paper) which revealed substantial genetic variation in OP for grape and orange (Betti *et al.*, 2008, 2014). Moreover, earlier studies of oviposition site preference reported significant responses to selection when flies were offered nonnatural media as oviposition substrates: lab medium versus paper, potato-based versus sugar and killed yeast containing medium (Bird & Semionoff, 1986; R'Kha *et al.*, 1991; Miller *et al.*, 2011; Abed-Vieillard *et al.*, 2013). In addition, other studies reported significant responses to selection for other aspects of oviposition, such as gregarious behavior (Ruiz-Dubreuil & del Solar, 1986) and learning ability (Mery & Kawecki, 2002). The available evidence indicates that, in general, *D. melanogaster* populations harbor substantial variation for oviposition behavior (Bird & Semionoff, 1986; Ruiz-Dubreuil & del Solar, 1986; Mery & Kawecki, 2002; Miller *et al.*, 2011). However, we cannot rule out the absence of standing genetic variation associated with the choice between grape and quince in *D. melanogaster*.

On the other hand, it was possible to generate divergent lines for OP in *D. simulans*. Therefore, we can conclude that the natural population harbors selectable genetic variation for the trait. Patterns of response in *D. simulans* were consistent with what would be expected according to the selection regimes applied. First, oviposition preference scores in G lines did not depart from the initial preference observed in the base population, suggesting some kind of genetic constraint and/or that preference for grape may be at an evolutionary maximum in the natural population studied. In contrast, both C and, particularly, Q lines showed a consistent decrease from the initial preference for grape observed in the base population. In this vein, it may be argued that OP evolution in Q and C populations may reflect the effect of uncontrolled laboratory selection. However, it should be noted that Q and C populations differed in one important aspect, the rate of change was more evident in the populations selected for increased preference for quince (Q) than in the control (C).

We further investigated OP in the F_1 progeny of crosses between G and Q lines. The results of these experiments showed that the preference of F_1 flies was similar to the Q parent and differed from the G parent, suggesting that the alleles governing preference in the Q line are dominant relative to those in the G line. Thus, we hypothesize that the evolution of OP in Q lines may be accounted for by the accumulation of dominant alleles that were low in frequency in the base population. This explanation may also account for the lack of selection response to increased preference for grape in G lines, since the effect of the genetic factors involved in grape preference appear to be largely recessive alleles found in high frequencies in the base population. However, as noted above, preference for grape also decreased in C lines, though less markedly than in Q lines, suggesting that these lines responded, at least partially, to common selective factors. Unfortunately, we did not perform the crosses between Q and C lines to investigate whether the putatively coincident responses had a similar genetic basis. In any case, detailed and specific genetic studies are needed to unveil the genetic architecture of OP.

Habitat divergence speciation models propose that barriers to gene flow may evolve when 2 ecological races have (i) markedly different preferences for alternative resources, and (ii) some degree of assortative mating between individuals that develop in the same resource (Coyne & Orr, 2004; Feder & Forbes, 2008). In this context, and according to the "mother knows best" hypothesis, preference and performance should be correlated (Jaenike, 1978; Thompson, 1988; Mayhew, 1997; Mery & Kawecki, 2002; Yang *et al.*, 2008), however, current evidence for such relationship remains ambiguous. A reanalysis of the available data produced support for the preference–performance hypothesis when factors related to the feeding niche were taken into account (Gripenberg *et al.*, 2010). We investigated whether our results were consistent with the prediction of a preference–performance genetic correlation in *D. simulans*, by assessing developmental time and viability in G, Q, and C regimes reared in the same media used as alternative oviposition sites. The rationale of these experiments is that artificial selection for preference may have brought with a correlated response in performance traits involved in the use of alternative rearing resources (Coyne & Orr, 2004). The significant selection regime by resource interaction observed for viability may be considered, at first sight, as supporting evidence for "mother knows best" hypothesis, since it suggests a dependence on the rearing substrate. However, viability differences in quince and grape were only significant in control lines, but not in selection lines, which was our *a priori* expectation. In summary, our artificial selection study suggests different genetic architectures for oviposition site preference in *D. melanogaster* and *D. simulans*. One possible way to further investigate the behavioral differences between these closely related species may be to perform a comparative genomic study at the DNA sequence level to establish the specific rates of sequence evolution and rates of gene gain/loss involved in oviposition behavior. Also, studies at the gene expression level may help to elucidate the specific roles of chemosensory genes in the different stages of decision making during oviposition.

Acknowledgments

Disclosure

We have not conflicts of interest relevant to the subject of this work.

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