

Mating success depends on rearing substrate in cactophilic *Drosophila*

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Abstract *Drosophila buzzatii* and *D. koepferae* coexist in the arid lands of southern South America and exploit different types of cactus as breeding hosts. The former prefers to lay eggs on the rotting pads of prickly pears (genus *Opuntia*) whereas *D. koepferae* exhibits greater acceptance for columnar cacti (e.g., *Echinopsis terschekii*). Here, we demonstrate that the rearing cacti affect male mating success, flies reared in each species' preferred host exhibited enhanced mating success than those raised in secondary hosts. *Opuntia sulphurea* medium endows *D. buzzatii* males with greater mating ability while *D. koepferae* males perform better when flies develop in *Echinopsis terschekii*. These effects are not mediated through body size, even in *D. buzzatii* whose body size happens to be affected by the rearing cacti. This scenario, which is consistent with the evolution of host specialization and speciation through sensory drive, emphasizes the importance of habitat isolation in the coexistence of these cactophilic *Drosophila*.

Keywords Cactus hosts · Habitat isolation · Host specialization · Mating success · Sensory drive · Sexual selection

Introduction

A wide variety of insects exploit different types of host plants as feeding or breeding resources (Jaenike 1990). How they choose between alternative hosts remains an open debate. According to the preference-performance hypothesis (Craig and Itami 2008; Gripenberg et al. 2010), natural selection should favor females exhibiting an oviposition

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preference for resources on which larvae fare best. Despite numerous studies have shown that female preference and offspring performance appear uncoupled (e.g., Fritz et al. 2000; Faria and Fernandes 2001), a recent meta-analysis produced evidence supporting the preference-performance hypothesis when factors related to niche complexity and searching constraints were considered (Gripenberg et al. 2010). Thus, insects reared in a species' preferred host might be expected to exhibit higher mating success.

The relationship between resources and mating success has been examined in many cases including *Drosophila* fruit flies. For instance, a series of experiments in *D. melanogaster* showed that larvae reared in an enriched environment are twice as successful in acquiring mates as are males reared in standard medium (Dukas and Mooers 2003). In addition, it has been shown that mate choice, courtship success and song variation are influenced by the rearing substrate in the cactophilic *D. mojavensis* (Brazner and Etges 1993; Etges and Tripodi 2008). In this species, the host cactus where larvae develop affects adult epicuticular hydrocarbon profiles, which have been implicated as determinants of mate choice and mating success (Stennett and Etges 1997; Etges et al. 2007).

One question that arises is how larval breeding resources can influence mating success. First, nutritional deficiencies or the presence of toxic compounds may lead to suboptimal development of mating related traits in some resources. Indeed, some handicap models supported by strong empirical evidence state that the expression of secondary sexual traits depends on environmental conditions and is a fair predictor of male mating success (Rowe and Houle 1996; David et al. 2000). Second, particular larval environments may endow adults with features that make them more likely to be detected and chosen by the opposite sex. In this case, mating signals may adapt to particular environments through sensory drive. Theoretically, habitat adaptations in perception (perceptual tuning) make females (usually the "choosy" sex) more sensitive to particular smells, sound frequencies or electromagnetic wavelengths than to others (Boughman 2002). Thus, particular rearing substrates could facilitate males to exploit a preexisting female sensory bias. For instance, males that have grown up in such environments would be able to produce signals that make them more likely to be detected by females.

The cactophilic *D. buzzatii* and *D. koepferae* are sibling synmorphic species that have recently diverged in the arid lands of southern South America and coexist in vast areas of Argentina and Bolivia (Fontdevila et al. 1988; Fanara et al. 1999; Hasson et al. 2009). These species utilize different, but not mutually exclusive, microhabitats consisting of the necrotic cladodes of prickly pears of the genus *Opuntia*, which are *D. buzzatii*'s preferred egg laying site and columnar cacti of the genera *Echinopsis* and *Cereus* that provide the main breeding and feeding hosts for *D. koepferae* (Hasson et al. 1992).

How two similar species such as *D. buzzatii* and *D. koepferae* can coexist avoiding the effects of competition is a challenging question in evolutionary ecology. A possible answer to this question is that each species prefers alternative host plants to lay eggs. Such differential preference may lead to microhabitat isolation between sympatric species (Feder et al. 1994). Also, competition can be avoided if differential performance causes each species predominate over the other in a different breeding host (Feder et al. 1994). Both mechanisms, separately or combined, can shape habitat selection and influence the evolution of species by promoting host specialization and contributing to the origin of new species (Feder and Forbes 2008). Previous studies in *D. buzzatii* and *D. koepferae* revealed the paramount importance of the host plant on wing and genital morphology, viability and developmental time (Fanara et al. 1999; Soto et al. 2007, 2008a, b). Also, there is evidence that these species differ in their preferences for egg laying sites (Fanara and Hasson 2001). These evidences are consistent with the evolution of host specialization (Hasson et al.

2009). However, it remains unclear whether biological performance is maximized in each species' preferred host as the preference-performance hypothesis predicts since none of the adult traits studied so far that exhibited plastic responses associated to the rearing cactus are directly related to fitness. In this paper we investigate mating success in *D. buzzatii* and *D. koepferae* reared in two of the main natural breeding hosts: *O. sulphurea* and *E. terschekii*, that flies exploit in a vast area of the arid lands of Argentina (Hasson et al. 2009).

Materials and methods

Drosophila cultures

Experimental populations of *D. buzzatii* and *D. koepferae* were founded with flies derived from collections performed in the locality of Valle Fértil (San Juan, Argentina) in March 2006. Two outbred stocks, one for each species, were founded with the progeny of 40 wild inseminated females and maintained for five generations before the experiments. Fresh and rotting materials of *O. sulphurea* and *E. terschekii* were also collected for the preparation of two types of seminatural cactus media (see Fanara et al. 1999 for details).

Laboratory assays

Batches of first instar larvae were seeded and reared to adulthood in vials containing either *O. sulphurea* or *E. terschekii* medium. Thirty-first instar larvae were seed per vial since no density effects are expected with less than 40 larvae per vial (Fanara et al. 1999). All virgin adult flies were stored in sex-specific vials with Instant *Drosophila* Medium-culture.

To assess male sexual performance, groups consisting of one six-day-old virgin male and five six-day-old virgin females were released in a mating arena at 7 pm. We measured the number of copulations achieved by each male during a 30 min interval. We considered copulation as effective when the male mounted the female for at least 30 s since these flies often perform brief pseudocopulations that merely involve mounting. In view of the fact that *Drosophila* females play a quite passive role during courtship whereas males chase females and display an elaborate courtship behavior prior to mating (Spieth 1974), we decided to consider mating frequency (the number of copulations) as a surrogate of mating success. According to our observations, female remating is very unlikely within 30 min (data not shown), so *MMS* is expected to vary between 0 and 5. Two factors were controlled in these experiments: male rearing cactus (*MC*) and female rearing cactus (*FC*) both with two levels (*O. sulphurea* and *E. terschekii*). This experimental scheme consisting of groups of one male and five females was replicated 21 and 25 times for each factor level combination (e.g., *MC* = *O. sulphurea* and *FC* = *E. terschekii*) for *D. buzzatii* and *D. koepferae*, respectively.

Positive association between body size and mating success was reported in a wide variety of taxa (e.g., Markow and Ricker 1992; Wikelski and Romero 2003). Particularly, there is evidence that male (but not female) body size is a fair predictor of mating success in *D. buzzatii* (Santos et al. 1988; Norry et al. 1995). For this reason, after measuring *MMS*, male heads were photographed at 40× and interocular distance, which strongly correlates with several dimensions of male body size in *D. buzzatii* (Norry et al. 1995), was measured as a surrogate for male body size. Interocular distance was estimated from digital images using TPS DIG (<http://life.bio.sunysb.edu/morph/index.html>).

Statistical analysis

The outcome variable—number of copulations— which theoretically ranges from 0 to 5 cannot be thought as a binomial variable because, among other reasons, previous copulations change male physiology and behavior and thus the probability of obtaining further copulations. Thus, in our experimental conditions, mating success needs to be treated as an ordinal categorical variable. Therefore, cumulative logistic regression models were fitted to estimate the effect of male and female rearing medium on *MMS*. Let us consider the following simple model:

$$\log\left(\frac{\Pr(MMS > j|MC, FC)}{\Pr(MMS \leq j|MC, FC)}\right) = \beta_{0j} + \beta_1 MC + \beta_2 FC$$

where $j = 0, 1, \dots, 4$ denotes a threshold number for *MMS*, Pr stands for probability and *MC* (*FC*) is the male (female) rearing cactus with *MC* or *FC* = 1 if rearing medium was *O. sulphurea* and *MC* or *FC* = 0 for *E. terschekii*. This model assumes that the effect of the rearing medium on the log-odds is the same for any possible threshold j (0, 1, ..., 4). Odds ratios (OR) can be derived from the model coefficients. For example, for any given j , e^{β_1} is the OR of more than j copulations for males reared in *O. sulphurea* ($MC = 1$) versus “*E. terschekii* males” ($MC = 0$) when female rearing medium is kept constant and $OR > 1$ ($\beta_1 > 0$) indicates a greater *MMS* for “*O. sulphurea* males”.

We considered different cumulative logistic regression models. The first one (Model 1) included the three main factors (male and female rearing medium and species) and all the possible interaction terms. Since species strongly interacted with the rearing medium independent models were fitted for each species (Model 2) to facilitate interpretation of the results. An additional model including male body size as a potential explanatory variable for *MMS* was also fitted for each species (Model 3). Additionally factorial ANOVA was performed to evaluate the effect of rearing medium and species on male body size.

All statistical analyses were performed using the General Linear/Non linear Model procedures implemented in the STATISTICA 6.0 software package (<http://www.statsoft.com>).

Results

Mean numbers of copulations achieved by males in each factor level combination are shown in Fig. 1 which reflects that *MMS* was greater when both males and females grew up in each species’ preferred host. *D. buzzatii* mated more frequently when it grew up in *O. sulphurea* while *D. koepferae* was more likely to mate when it developed in *E. terschekii*. These observations were confirmed when Models 1 and 2 were fitted (Table 1). Due to the strong interaction effects between species and (male and female) rearing medium Model 2 was fitted for each species separately. Table 1 (Model 2 for *D. buzzatii*) shows that *D. buzzatii* males reared in *O. sulphurea* confronted with females reared in any medium displayed significantly greater chances of mating than “*E. terschekii* males” ($OR = 3.05$; $P < 0.01$). In addition, *D. buzzatii* males reared in any medium confronted with “*O. sulphurea* females” displayed higher chances of mating than those confronted with “*E. terschekii* females” ($OR = 2.54$; $P < 0.05$). Likewise, *D. koepferae* males reared in *E. terschekii* or confronted with “*E. terschekii* females” displayed higher chances of mating than

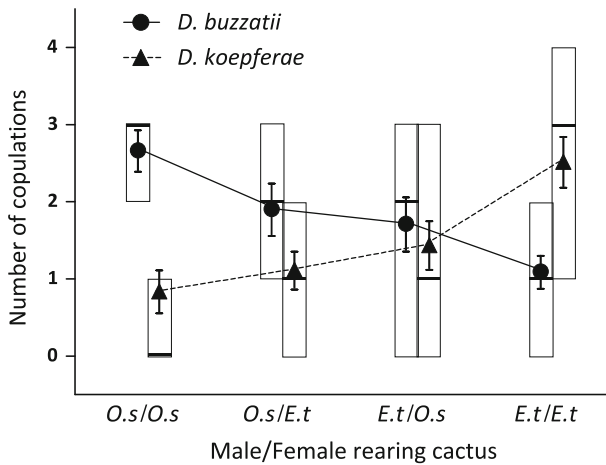


Fig. 1 Mean (\pm SE) number of copulations and 25–50–75% percentile for each combination of male and female rearing medium: *O. sulphurea* (O.s) and *E. terschekii* (E.t) based on 21 (25) observations per class in *D. buzzatii* (*D. koepferae*)

“*O. sulphurea* males” (OR = 0.30; $P < 0.01$) or those confronted with “*O. sulphurea* females” (OR = 0.38; $P < 0.05$). Similar conclusions were obtained applying a two-way ANOVA with male and female rearing media as factors (results not shown).

To study the effect of larval diet on male body size we compared interocular distance between males reared in *O. sulphurea* and *E. terschekii*. Mean \pm SE interocular distance was $402.66 \pm 4.31 \mu\text{m}$ ($404.89 \pm 3.26 \mu\text{m}$) in “*O. sulphurea* males” and $363.52 \pm 5.28 \mu\text{m}$ ($412.24 \pm 3.12 \mu\text{m}$) in “*E. terschekii* males” in *D. buzzatii* (*D. koepferae*). A two way ANOVA of male body size with factors male rearing medium and species showed a species by rearing medium interaction effect on male body size ($F_{1,180} = 34.16$; $P < 0.001$). Principal effects analysis run separately for each species revealed a significant effect of the rearing medium on *D. buzzatii* male body size ($F_{1,82} = 33.00$; $P < 0.001$). In contrast, there were no interocular distance differences between *D. koepferae* males reared in different cacti ($F_{2,98} = 2.64$; $P = 0.11$) which may reflect the great tolerance of this species to the “hostile” environment of columnar cacti.

As found in many taxa including *D. buzzatii*, male body size positively affects *MMS*. To evaluate if at least part of the effect of the rearing medium on *MMS* was mediated through body size Model 3 was fitted. Table 1 (Model 3) reveals that after controlling for male body size there is a significant male rearing medium effect on *MMS*, i.e. we can speculate that there is a direct path from rearing substrate to mating success not mediated through male body size. Model also shows that body size *per se* is a weak predictor of *MMS* in both species. Some interaction terms are not presented in model 3 since none of them was significant.

Figure 2 represents a possible causal structure for the investigated problem derived from the experimental design and the statistical analysis. The graph was drawn under the additional assumption of no common causes between male body size and *MMS* which can be supported by the controlled experimental conditions (Pearl 2000). Female rearing medium was not included in the graphs as no common causes exist between female substrate and any other variable in the graph. The relationships between male rearing

Table 1 Estimated odds ratios (OR) of achieving more than *j* copulations between each factor level evaluated in the fitted models 1, 2 and 3. OR, 95% confidence interval (CI) and *P* value are shown for each case and a goodness of fit test based on deviance is shown for each model

	Model 1		Model 2		Model 3	
	<i>D. buzzatii</i>	<i>D. koepferae</i>	<i>D. buzzatii</i>	<i>D. koepferae</i>	<i>D. buzzatii</i>	<i>D. koepferae</i>
<i>Male rearing medium (MC)</i>						
OR	0.84		3.05	0.30	>99999	0.00
(95% CI)	(0.50, 1.42)		(1.38, 6.75)	(0.14, 0.62)	(3.86, ∞)	(0.00, 0.12)
<i>P</i>	0.515		0.006	0.001	0.027	0.024
<i>Female rearing medium (FC)</i>						
OR (95% CI)	0.86 (0.51, 1.45)		2.54 (1.11, 5.34)	0.38 (0.18, 0.79)	2.50 (1.13, 5.53)	0.31 (0.14, 0.67)
<i>P</i>	0.574		0.026	0.010	0.023	0.003
<i>MC * FC</i>						
OR	0.77		0.85	0.71	–	–
(95% CI)	(0.45, 1.30)		(0.39, 1.83)	(0.34, 1.46)	–	–
<i>P</i>	0.322		0.677	0.352	–	–
<i>Male body size (MBS)</i>						
OR	–		–	–	1.01	1.00
(95% CI)	–		–	–	(0.99, 1.02)	(0.99, 1.02)
<i>P</i>	–		–	–	0.399	0.654
<i>MC * MBS</i>						
OR	–		–	–	1.01	0.98
(95% CI)	–		–	–	(1.00, 1.03)	(0.97, 1.00)
<i>P</i>	–		–	–	0.038	0.037
<i>Species (SP)</i>						
OR	1.76		–	–	–	–
(95% CI)	(1.04, 2.99)		–	–	–	–
<i>P</i>	0.035		–	–	–	–
<i>SP * MC</i>						
OR	0.31		–	–	–	–
(95% CI)	(0.18, 0.53)		–	–	–	–
<i>P</i>	0.000		–	–	–	–

Table 1 continued

	Model 1		Model 2		Model 3	
			<i>D. buzzatii</i>	<i>D. koepferae</i>	<i>D. buzzatii</i>	<i>D. koepferae</i>
<i>SP * FC</i>						
OR	0.40	—	—	—	—	—
(95% CI)	(0.24, 0.68)	—	—	—	—	—
<i>P</i>	0.001	—	—	—	—	—
<i>SP * MC * FC</i>						
OR	0.88	—	—	—	—	—
(95% CI)	(0.52, 1.48)	—	—	—	—	—
<i>P</i>	0.632	—	—	—	—	—
<i>Deviance</i>						
χ^2	572.42	263.35	263.35	257.50	301.18	297.24
DF	908	412	412	411	492	491
<i>P</i>	1.000	1.000	1.000	1.000	1.000	1.000

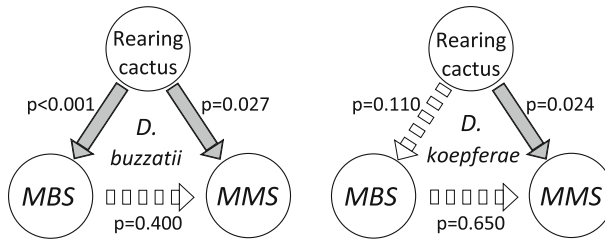


Fig. 2 Proposed causal relationships between male rearing substrate, male body size (*MBS*) and male mating success (*MMS*) for each species irrespective of the female rearing medium level. Direction of the arrows indicates direct causal effects (not mediated through any other variable in the graph). *P* values are shown for each arrow. *Discontinuous white arrows* indicate not significant relationships

medium and body size are supported by the ANOVAs with male body size as outcome while the rearing cactus-*MMS* and body size-*MMS* relationships are supported by Model 3 analysis.

Discussion

We demonstrate that males exhibit greater mating success when flies develop in the resources they prefer to exploit or have been selected to primarily use in nature. Hence, our data provide support for the preference-performance hypothesis and may be interpreted as evidence for the evolution of host specialization in these flies.

We may ask: what did evolve first: female preference or adaptation to mate in the environment provided by a particular host plant? If female oviposition preference evolved first, e.g., as a mechanism for interspecific competition avoidance, it would have involved perceptual tuning of the sensory system for the detection of specific cactus signals. In such case, sensory drive might have differentially shaped sexual signaling in each species. Adult flies would be more likely to mate if mating signals (e.g. sexual pheromones) matched the signals used for perception of the specific feeding or breeding plants (i.e., *O. sulphurea* and *E. terschekii* kairomones for *D. buzzatii* and *D. koepferae* respectively). In this sense, our results are consistent with the sensory drive hypothesis. However it remains unknown whether or how the rearing cactus alters mating signals. Alternatively, adaptation may have evolved first, thus female oviposition preference could have adaptively evolved after initial divergence as a consequence of preexisting performance differences in alternative host plants. Although, the answer to this question must await further studies, our report emphasizes the importance of habitat isolation in the coexistence of *D. buzzatii* and *D. koepferae*.

The chemical characteristics of each cactus type, which influence the composition of the microbiota associated with the decaying process, are likely to underlie the general effects of cactus hosts on flies (Fogleman and Danielson 2001; Berenbaum and Feeny 2008). Interestingly, prickly pears are nutritionally richer (have a higher content of free sugars and lipids) than columnars, while columnar cacti have a more complex chemistry including large amounts of toxic compounds like alkaloids, terpenoids and atypical fatty acids (Fogleman and Danielson 2001; Stintzing and Carle 2005).

What are the possible mechanisms through which differences between cactus hosts produce mating success variation? Cuticular hydrocarbons are known to play a major role

in fly mating (Markow and Toolson 1990; Billeter et al. 2009). For example, the larval rearing substrate is known to affect the relative amounts of epicuticular hydrocarbons that function as sex pheromones in the cactophilic *D. mojavensis* and *D. arizonae* (Markow and Toolson 1990; Eteges and Tripodi 2008). Alternatively, nutritional condition of larvae could imprint adult mating behavior affecting, for instance, the number of courtship attempts, courtship songs or female receptivity. Our analysis revealed that both the male and female rearing substrate affect *MMS* in *D. buzzatii* and *D. koepferae* suggesting an effect of the rearing substrate on male and female factors that influence *MMS*. On the male side such factors may be the capability to detect females, quantity and quality of courtship attempts or attractiveness while on the female side such factors may be receptivity or detectability. In this vein, sex pheromones as well as nutritional condition could account simultaneously for some of the male and female factors. For instance, epicuticular hydrocarbons profile may affect male attractiveness and female detectability as well as nutritional condition may determine male courtship ability and female receptivity. Nevertheless, the elucidation of the mechanisms through which the rearing substrate modulates mating success must await studies of the interplay between cuticular hydrocarbon profiles, nutritional condition and courtship behavior in *D. buzzatii* and *D. koepferae* reared in alternative cactus hosts.

Although additional studies are required, we can advance the conclusion that either the decaying plant or its associated microbiota affects fly attractiveness or modulate mating behavior. However, there appears to be no assortative mating influenced by cactus hosts since the regression interaction terms between male and female rearing medium ($MC * FC$) were not significant (Table 1, Model 2). The male rearing medium effect thus appears to be independent of the female rearing medium in both species.

We found that male body size *per se* was not a fair predictor of *MMS*. However the larval rearing medium affected interocular distance in *D. buzzatii* where “*O. sulphurea* males” were larger than “*E. terschekii* males”. In contrast, the absence of significant differences between *D. koepferae* males reared in different cacti may reflect the great tolerance of this species to the “hostile” environment of columnar cacti.

Finally, the relationship between mating ability and the breeding substrate underscores the plasticity of *MMS*. Whether these plastic responses have a genetic basis warrants further investigation as do the relationships among host plant use, sexual selection and reproductive isolation.

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