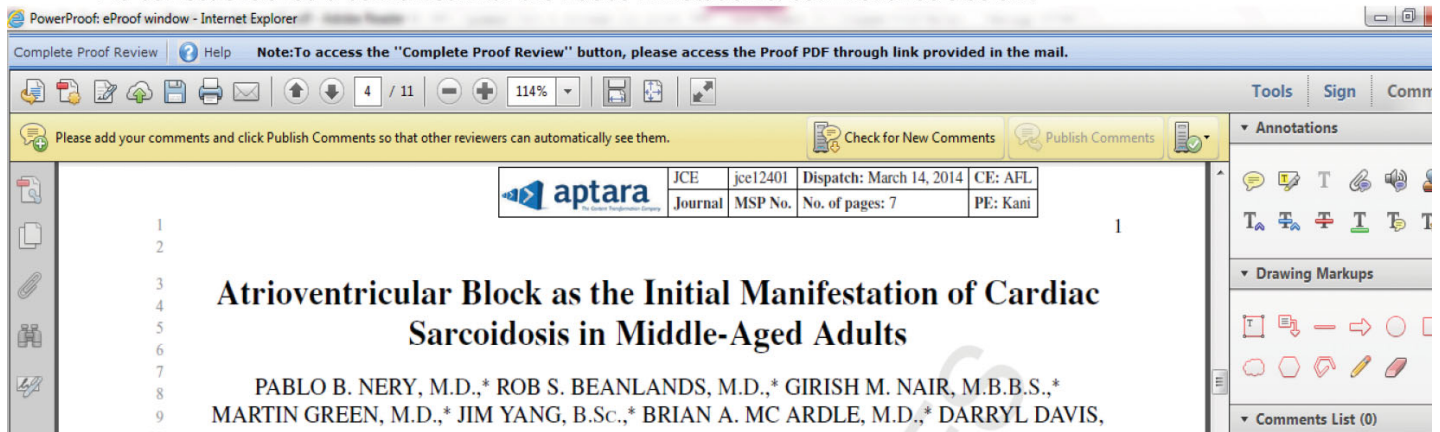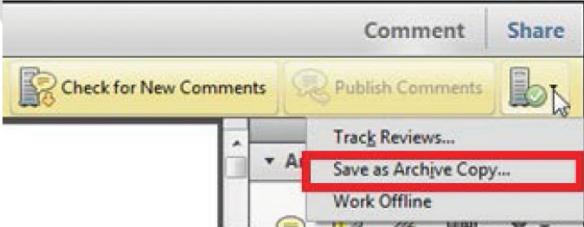# WILEY

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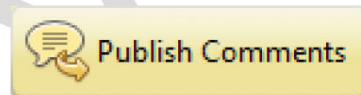
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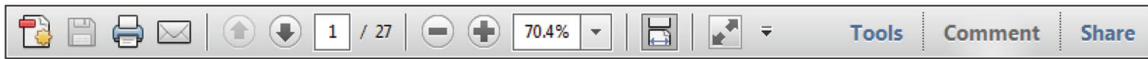
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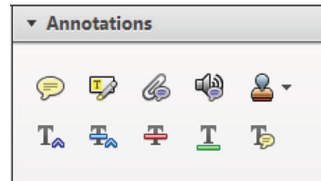
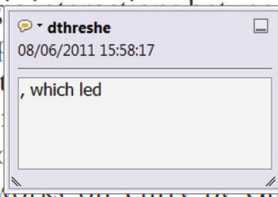### 1. Replace (Ins) Tool – for replacing text.

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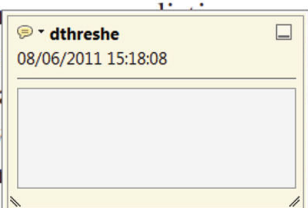
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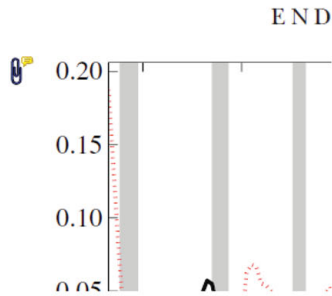**6. Add stamp Tool – for approving a proof if no corrections are required.**

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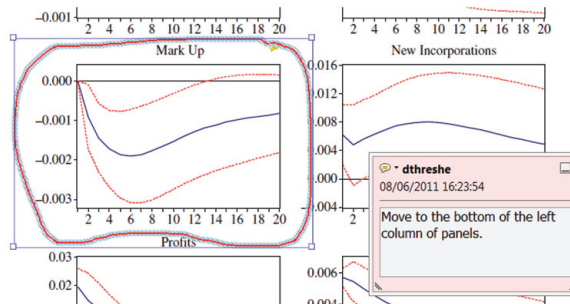
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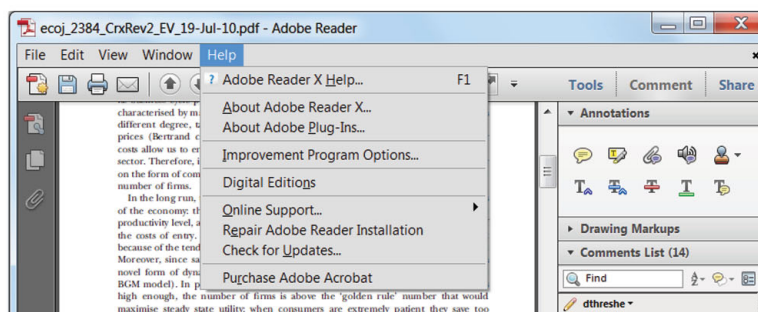
ORIGINAL ARTICLE

Phenotypic plasticity in *Drosophila* cactophilic species: the effect of competition, density, and breeding sites

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Abstract   Changes in the environmental conditions experienced by naturally occurring populations are frequently accompanied by changes in adaptive traits allowing the organism to cope with environmental unpredictability. Phenotypic plasticity is a major aspect of adaptation and it has been involved in population dynamics of interacting species. In this study, phenotypic plasticity (i.e., environmental sensitivity) of morphological adaptive traits were analyzed in the cactophilic species *Drosophila buzzatii* and *Drosophila koepferae* (Diptera: Drosophilidae) considering the effect of crowding conditions (low and high density), type of competition (intraspecific and interspecific competition) and cacti hosts (*Opuntia* and *Columnar* cacti). All traits (wing length, wing width, thorax length, wing loading and wing aspect) showed significant variation for each environmental factor considered in both *Drosophila* species. The phenotypic plasticity pattern observed for each trait was different within and between these cactophilic *Drosophila* species depending on the environmental factor analyzed suggesting that body size-related traits respond almost independently to environmental heterogeneity. The effects of ecological factors analyzed in this study are discussed in order to elucidate the causal factors investigated (type of competition, crowding conditions and alternative host) affecting the election of the breeding site and/or the range of distribution of these cactophilic species.

Key words   adaptation; body size; colonization; Drosophila cactophilic species; wing aspect; wing loading

Introduction

It has been pointed out that phenotypic plasticity represents a solution to the challenge of environmental heterogeneity by increasing the possible outcomes fitted to diverse ecological scenarios (Debat & David, 2001; Fucso & Minelli, 2010). In this sense, experimental and theoretical works have demonstrated that phenotypic plasticity plays a major role in the population dynamics of interacting species (Fanara & Hasson, 2001; Fanara *et al.*, 2004; Fordyce, 2006). Moreover, genetic variation for phenotypic plasticity (i.e., genotype by environmental interaction) has been involved in the maintenance of natural genetic variation (Carreira *et al.*, 2006; Fanara *et al.*, 2006). Therefore, understanding how different environments affect diverse genotypes is a necessary condition to address the effects of heterogeneous environments on developmental systems that allow the organism to cope with environmental unpredictability (Whitman & Ananthakrishnan, 2009; Moczek *et al.*, 2011).

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Changes in the environmental conditions experienced by naturally occurring populations are frequently accompanied by changes in life-history and morphological traits. Body size is a trait correlated with diverse fitness components such as fecundity, longevity or stress environment resistance (Kingsolver & Huey, 2008; Shingleton, 2011). In holometabolous organisms the variation in adult body size depends on growth during larval stages as well as differentiation of different structures in the pupa stage that is regulated and coordinated by different hormones (Nijhout *et al.*, 2014). Body size of *Drosophila* is determined by ensembles of multiple segregating genes (Carreira *et al.*, 2013). On the other hand, body size is strongly influenced by environmental conditions like nutrition (Kolss *et al.*, 2009), temperature (Carreira *et al.*, 2013), oxygen level (Peck & Maddrell, 2005) and larval crowding (Werenkraut *et al.*, 2008) indicating that this trait is sensitive to environmental changes (i.e., phenotypic plasticity). However, notwithstanding the adaptive importance of each body size-related trait, composite traits involving body size-related traits would be related to adult performance in natural populations. For instance, wing loading (usually expressed as the thorax length/wing length ratio) and wing aspect (estimated as wing length/wing width ratio) are 2 complex traits presumably related to flight performance (Betts & Wootton, 1988; Berwaerts *et al.*, 2002; Gibb *et al.*, 2006). Both composite traits display considerable genetic variation in natural populations and are dependent on different environmental factors (Fernandez Iriarte *et al.*, 2003; Fragata *et al.*, 2010).

Drosophila buzzatii Patterson & Wheeler and *Drosophila koepferae Fontdevila & Wasserman* are 2 cactophilic sibling species that belong to repleta group (Ruiz & Wasserman, 1993). These species have overlapping distribution ranges in arid regions of Southern South America (Fanara *et al.*, 2006) although *D. buzzatii* has successfully colonized many regions of the world determining that this species exhibits a subcosmopolitan distribution (Barker, 2013). *D. buzzatii* is largely associated with *Opuntia* cacti (prickly pears) while *D. koepferae* breeds primarily on columnar cacti of the genera *Cereus* and *Trichocereus*, even though both *Drosophila* species utilize *Opuntia* and columnar cacti as breeding hosts (Fanara *et al.*, 1999; Hasson *et al.*, 2008; Soto *et al.*, 2012). The relationship between adaptive traits and host cacti exploited by these cactophilic *Drosophila* species has been documented in diverse studies (Fanara & Hasson, 2001; Fernandez Iriarte *et al.*, 2003; Fanara *et al.*, 2006; Werenkraut *et al.*, 2008; Soto *et al.*, 2012). Further, the effect of host diversity also affects body size-related traits (Fanara *et al.*, 2004; Carreira *et al.*, 2006; Soto *et al.*, 2008) indicating that cacti heterogeneity plays an impor-

tant role in morphological plasticity in these species. Unfortunately, there is not much evidence with respect to the other environmental factors (e.g., larval density) attributable to produce phenotypic plasticity in these species (but see Werenkraut *et al.*, 2008).

Switches among alternative phenotypes as a response to environmental changes depend on the effect of environment on trait expression (the environmental induction; Gabriel *et al.*, 2005; Fitzpatrick, 2012). Thus, considering that in nature these species should be faced with different ecological scenarios, we investigated the trend in phenotypic plasticity of body size exhibited by *D. buzzatii* and *D. koepferae* when they were reared under different environments. The analysis of the norm of reaction of body size-related traits (wing size and thorax size) and 2 composite body size traits (the ratios thorax length/wing length and wing length/wing width) enables us to evaluate whether the effect of developmental plasticity varied among traits and between these cactophilic *Drosophila* species under different types of competition, larval crowding and host cacti.

Materials and methods

Flies analyzed in the present study were collected in the locality of Ruinas de Quilmes (Northwestern Argentina; see Fanara *et al.*, 1999 for further details). In this locality, *Opuntia sulphurea* and *Trichocereus terschekii* are the 2 different host cacti that serve as breeding and feeding resources. Flies were collected by means of net sweeping on fermented banana baits and sorted by sex. Isofemale lines were founded in vials containing 5 mL of lab medium (David, 1962) and identified to species by the inspection of the genitalia of male progeny (Soto *et al.*, 2007). Two **Q4** outbreed stocks were set up, 1 of each species, using 22 and 20 isofemale lines for *D. koepferae* and *D. buzzatii*, respectively. These stocks were reared in the same conditions for 3 generations in bottles containing 30 mL of lab medium and never exposed to the cacti medium. Since we are interested in evaluate the phenotypic plasticity of *D. koepferae* and *D. buzzatii* when they cope with environmental heterogeneity, we compare the response of both *Drosophila* species under the situation that one of the host cactus belongs to the population analyzed (*T. terschekii*) whereas the other resource: *Opuntia quimilo* was novel for the flies from Ruinas de Quilmes. Besides, *O. quimilo* is the most abundant host cactus of the phytogeographical Chaco province wherein *D. buzzatii* is the dominant species *Drosophila* while *D. koepferae* is at very low density (Hasson *et al.*, 1992). In order to prepare cacti medium ("seminatural" medium) rotting cladodes and fresh

material of *T. terschekii* were collected from the same
locality while *O. quimilo* was collected from the local-
ity of Río Hondo (Hasson *et al.*, 1992). Pieces of fresh
cactus were stored at –20 °C and the fermenting juice of
each cactus was maintained in the laboratory by adding
10 g of fresh cactus every 2 weeks until the onset of the
experiments.

Large quantities of first instar larvae of each *Drosophila*
species were obtained by placing batches of 100 pairs of
sexually mature flies into egg-collecting chambers. Eight
chambers were set up for each combination of *Drosophila*
(*D. buzzatii* and *D. koepferae*) and cactus species (*O. quim-
ilo* and *T. terschekii*). In each chamber, egg-laying medium
was poured into a medium size Petri dish and the ferment-
ing juice of the corresponding rotting cactus species was
spread onto the egg-laying medium surface to stimulate
oviposition. Twelve hours later, all flies were removed
from the egg-collecting chambers. Batches of first instar
larvae were collected from the egg-laying medium and
seeded in vials containing the same cactus medium used to
stimulate oviposition (Fanara *et al.*, 1999). Briefly, pieces
of *O. quimilo* or *T. terschekii* were mixed in a blender and
5 mL were poured into each glass vial and autoclaved. Af-
ter cooling, each vial was inoculated with 0.1 mL of the
corresponding fermenting juice obtained from naturally
occurring rots.

Two different types of vials were set up: single and
mixed species cultures. In single species cultures, 40 and
120 first instar larvae (low- and high-density treatment, re-
spectively; Fanara *et al.*, 1995) of each *Drosophila* species
(100% *D. koepferae* or 100% *D. buzzatii*) were seeded in
vials containing cactus media. In the case of mixed species
cultures both *Drosophila* species were initially present in
the same proportions (interspecific competition) but the
total number of larvae varied according to the density (40
or 120 larvae per vial). Thus, 20 larvae of each species
were seeded in mixed species vials at low density (40 lar-
vae per vial) and 60 larvae of each species were seeded in
mixed species vials at high density (120 larvae per vial).
For each species culture, cactus host medium and density,
5 replicated vials were started, making a total of 4 800
first instar larvae seeded in 60 vials (3 species culture × 2
cactus host × 2 densities × 5 replicates). All experiments
were conducted at 25 °C with 14 L : 10 D photoperiod.

Wing length (WL) and wing width (WW) were scored
in the right wing following Norry *et al.* (1995) while
thorax length (TL) was measured from the anterior mar-
gin of the thorax to the posterior tip of the scutellum.
All measurements were done by one of us (VW) only in
males since females of both species are morphologically
indistinguishable. All measurements were performed in
3–5 males (randomly chosen) emerged from each vial

with a Wild microscope fitted with an ocular microm-
eter. We also calculated the thorax length-wing length
ratio (TL/WL) as an estimate of wing loading (Loeschcke
et al., 1999) whereas wing aspect that was computed as
wing length-wing width ratio (WL/WW; for details of this
estimation see Gibb *et al.*, 2006).

All traits were analysed by means of ANOVAs with,
Drosophila species (*D. buzzatii* and *D. koepferae*), type of
culture (single and mixed culture), density (low and high),
and cacti (*O. quimilo* and *T. terschekii*) as fixed factors. All
ANOVAs tests were performed using the GLM procedure
and we applied the Bonferroni correction for multiple
tests.

We also evaluated a phenotypic plasticity index (PPI;
Valladares *et al.*, 2006) for all traits analysed in *D.
buzzatii* and *D. koepferae*. The PPI was calculated as:
(single species culture – mixed species culture)/single
species culture; (low density – high density)/low den-
sity; and (emerged from *O. quimilo* – emerged from *T.
terschekii*)/emerged from *O. quimilo* for type of culture,
density, and cactus host, respectively.

Results

Body size-related traits analysis

Mean for all body size-related traits are shown for each
factor analyzed in this study: type of culture, density, and
cactus host in Table 1. As usual, *D. koepferae* was bigger
than *D. buzzatii* considering all combination of body size-
related traits and environmental factors measured. The
largest size for all body size-related traits were measured
in both Drosophila species at low density (40 larvae per
vial) while the smallest size was observed at high den-
sity (120 larvae per vial). The ANOVA results indicated
(Table 2) that flies of *D. koepferae,* reared at low den-
sity and emerged from *O. quimilo* were larger than *D.
buzzatii*, reared at high density and emerged from *T. ter-
schekii* for all body size-related traits while differences
between single and mixed culture were observed only
for WL where flies showed a larger size when they were
reared in single culture. The significant interactions for
all body size-related traits where *Drosophila* participate
(Table 2) revealed that the size of both *Drosophila* species
depend on the environmental factor analyzed (type of cul-
ture, density, and cactus host). Certainly, only *D. buzzatii*
showed significant larger size for both wing measure-
ments (Tukey's test: $P < 0.05$) under single species con-
dition. Then, the not significant result observed for type
of culture when WW was the body size-related trait stud-
ied could be consequence of a compensation effect. Both

Table 1 Mean (*x*) and standard deviation (SD) of wing length (WL), wing width (WW), thorax length (TL), wing loading (TL/WL), and wing aspect (WL/WW) for *D. buzzatii* and *D. koepferae* reared under different types of culture (single or mixed species culture) at low and high density (40 and 120 larvae per vial, respectively) in vials prepared with *O. quimilo* and *T. terschekii*. Data for wing length, wing width, and thorax length are in millimeters..

Q5

	Wing length		Wing width		Thorax length		Wing loading		Wing aspect	
	x	SD	*x*	SD	*x*	SD	*x*	SD	*x*	SD
D. buzzatii										
Single culture	1.842	0.084	1.021	0.051	1.013	0.051	0.550	0.011	1.804	0.031
Mixed culture	1.774	0.084	0.994	0.049	1.034	0.060	0.565	0.012	1.786	0.028
Low density	1.867	0.048	1.038	0.028	1.047	0.023	0.561	0.014	1.799	0.031
High density	1.749	0.082	0.977	0.051	0.969	0.050	0.554	0.010	1.791	0.030
O. quimilo	1.816	0.075	1.009	0.043	1.018	0.044	0.561	0.013	1.800	0.027
T. terschekii	1.800	0.104	1.006	0.059	0.999	0.064	0.554	0.010	1.790	0.033
D. koepferae										
Single culture	1.931	0.137	1.047	0.078	1.026	0.106	0.530	0.018	1.844	0.031
Mixed culture	1.937	0.119	1.063	0.073	1.052	0.076	0.543	0.012	1.824	0.041
Low density	2.029	0.054	1.112	0.031	1.101	0.040	0.542	0.009	1.825	0.041
High density	1.839	0.106	0.998	0.062	0.977	0.088	0.530	0.019	1.843	0.032
O. quimilo	1.987	0.088	1.074	0.050	1.088	0.048	0.547	0.009	1.850	0.028
T. terschekii	1.881	0.139	1.036	0.091	0.990	0.101	0.525	0.015	1.818	0.040

Drosophila species exhibited phenotypic plasticity in flies reared under different density conditions since development at low density determines significant larger size for all body size-related traits (Tukey's test: $P < 0.05$). Finally, host cacti variation determined a different pattern compared with the previous environmental factors. In fact, only *D. koepferae* was affected when flies developed in different host cacti since flies emerged from *O. quimilo* were significantly larger than flies emerged from *T. terschekii* for TL and WL (Tukey's test: $P < 0.05$).

Wing loading and wing aspect analysis

The analysis considering composite traits TL/WL and WL/WW which are correlated with wing loading and wing aspect, respectively, revealed that most of the factors analyzed in this study showed significant effects (Table 2). For *D. koepferae*, flies reared in *O. quimilo* and under single species type of culture conditions showed higher values of wing aspect (Table 1), indicating that these factors generated longer/narrower wings compared to the smaller wing aspect values (broader wings) observed in *D. buzzatii*, flies reared in *T. terschekii* and under mixed species type of culture conditions (Table 1). Interestingly, a significant interaction involving *Drosophila* species was detected only for wing loading. The significant interaction *Drosophila* species by type of culture by density (Table 2, Fig. 1) suggests that the *Drosophila*

species are affected by different factors. Nevertheless *D. buzzatii* always shows higher wing loading values than *D. koepferae* for all combinations of factors. Furthermore, these results indicate that this composite trait varied depending on the type of culture and crowding conditions in both *Drosophila* species. Actually, *D. koepferae* exhibited a significant change between single (lower wing loading) and mixed culture only under the high-density condition (Tukey's test: $P < 0.05$; Fig. 1A) whereas in *D. buzzatii* this pattern was detected only under the low-density condition (Tukey's test: $P < 0.05$; Fig. 1A). Thus, the crowding condition affects differently the phenotypic plasticity of *D. buzzatii* and *D. koepferae* estimated through the effect of intra and/or interspecific competition. The analysis of the other significant interaction (*Drosophila* species by density by cactus host, Fig. 1B) determines that flies of *D. koepferae* reared at high-density conditions exhibited phenotypic plasticity for cactus host. The comparison between breeding sites determined a significant higher wing loading score (Tukey's test: $P < 0.05$) in flies emerged from *O. quimilo* cactus media. All the others comparisons considering the combination of *Drosophila* species and density did not show significant differences between cactus hosts.

Phenotypic plasticity index

A perspective of variation according to Phenotypic Plasticity Index (PPI) denotes that there is not a single

Table 2 Analysis of variance testing for differences in wing length (WL), wing width (WW), thorax length (TL), wing loading (TL/WL), and wing aspect (WL/WW) for both species (*D. buzzatii* and *D. koepferae*) reared in different types of culture (mixed or single species culture) at 2 different densities (40 and 120 larvae per vial) when flies were developed in separate host cacti (*O. quimilo* and *T. terschekii*). In all cases degrees of freedom are 1, 64 (within).

	Wing length		Wing width		Thorax length		Wing loading		Wing aspect	
	SS	*F*	SS	*F*	SS	*F*	SS	*F*	SS	*F*
Species (S)	341.3	147.6***	49.1	47.9***	20.3	19.5***	56.8	102.1***	16.9	34.3***
Type of culture (TC)	19.5	8.5*	0.7	0.7	1.4	1.3	24.1	43.6***	4.4	8.9*
Density (D)	511.1	221.1***	164.6	160.8***	220.4	211.6***	12.8	23.1***	0.3	0.6
Cactus (C)	79.6	34.4***	8.9	8.8*	72.9	69.9***	25.7	46.2***	5.1	10.4*
S × TC	29.5	12.8**	9.9	9.7*	7.1	6.8*†	0.1	0.2	0.1	<0.1
S × D	27.6	11.9**	14.9	14.6**	11.5	11.1*	1.3	2.3	1.9	4.0*†
S × C	44.4	19.2***	6.9	6.8*†	33.1	31.7***	9.0	16.2**	1.2	2.4
TC × D	17.1	7.4*	8.5	8.3*	5.8	5.6*†	0.1	<0.1	0.4	0.8
TC × C	51.3	22.2***	32.1	31.3***	22.3	21.4***	1.6	2.8	5.3	10.8*
D × C	67.1	29.0***	28.4	27.8***	32.3	31.0***	3.9	7.0*†	0.9	1.7
S × TC × D	0.1	<0.1	0.1	<0.1	3.6	3.1	6.5	11.7*	0.1	<0.1
S × TC × C	2.1	0.9	0.1	0.1	2.1	2.0	1.1	2.0	0.4	0.8
S × D × C	0.1	<0.1	0.3	0.3	2.1	2.0	5.5	9.8*	0.6	1.2
TC × D × C	13.6	5.9*†	5.9	5.7*†	6.3	6.1*†	0.9	1.6	0.5	1.0
S × TC × D × C	0.1	<0.1	0.1	<0.1	0.1	<0.1	0.1	0.1	0.1	<0.1
Error	2.3		1.1		1.1		0.6		0.5	

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

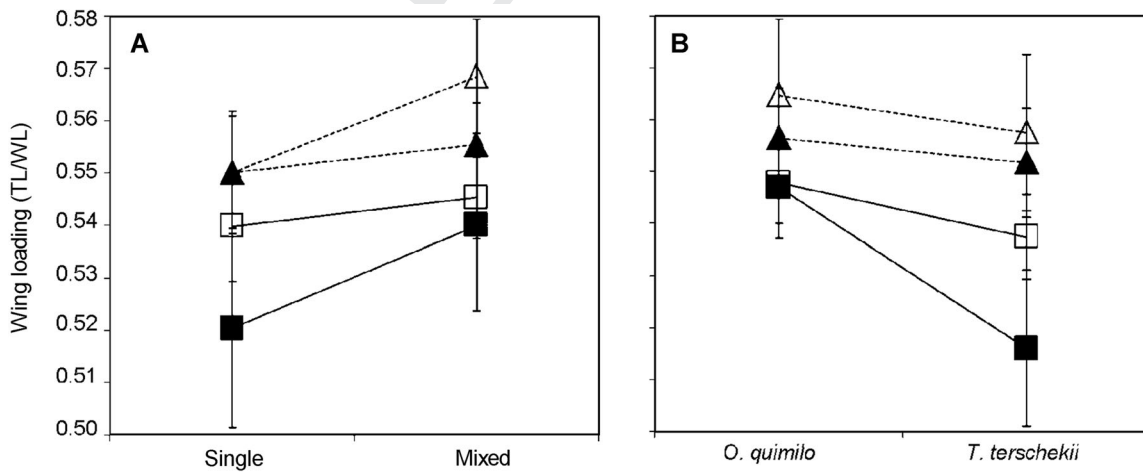†Not significant after Bonferroni correction for multiple tests.

Fig. 1 Mean and standard deviation of wing loading (thorax length/wing length) of *D. buzzatii* (triangle) and *D. koepferae* (square) for flies reared at low (open figure) and high (filled figure) density (40 and 120 larva per 5 mL of culture media) reared in: (A) under different type of culture (single and mixed culture) and (B) different host cacti (*O. quimilo* and *T. terschekii*).

pattern of phenotypic variation (Fig. 2). In fact, *D. koepferae* exhibited larger phenotypic plasticity than *D. buzzatii* for all traits analyzed when we compare different environmental status for density (low and high density) and for most of the traits when cactus host (*O. quimilo* and *T. terschekii*) was evaluated since wing aspect exhibited the opposite trend. However, phenotypic value between single and mixed culture that determines the PPI for type
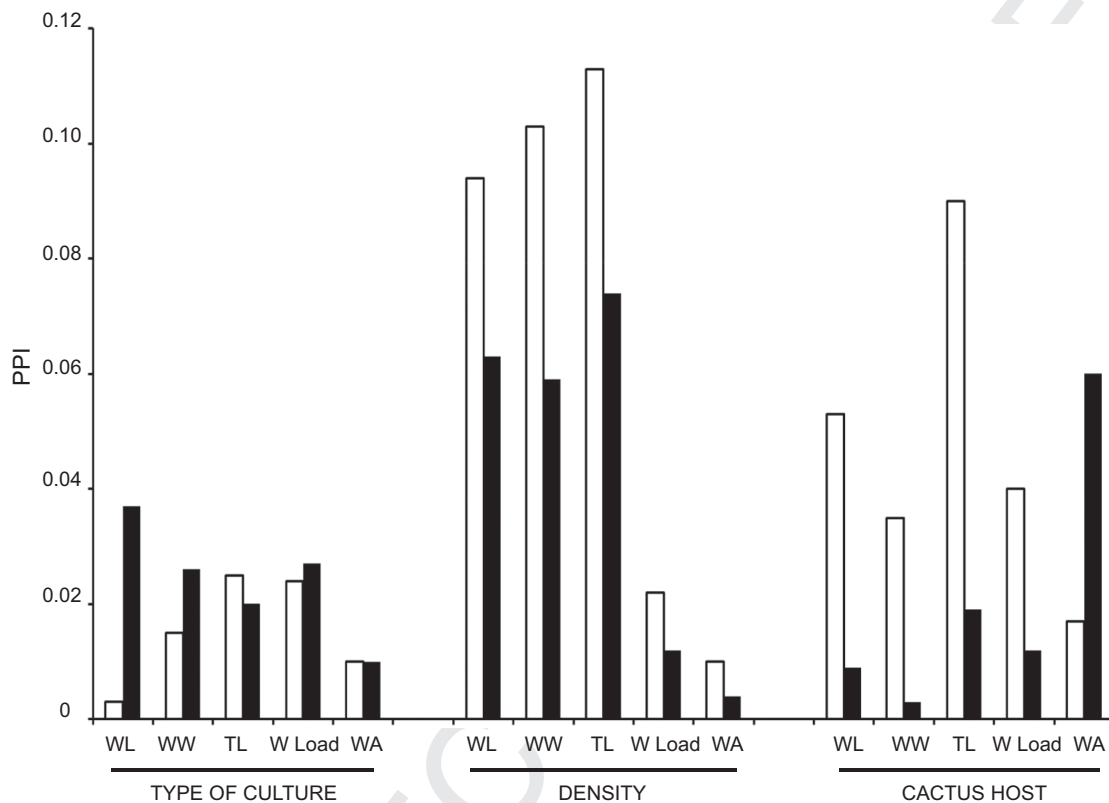
Fig. 2 Phenotypic Plasticity Index (PPI, see text for more details) for wing length (WL), wing width (WW), thorax length (TL), wing loading (WL), and wing aspect (WA) for *D. koepferae* (open bars) and *D. buzzatii* (filled bars) when the environmental heterogeneity is consequence of type of culture (single or mixed), density (40 or 120 larvae per vial) and cactus host (*O. quimilo* or *T. terschekii*) effects.

of culture shows that *D. buzzatii* presents a larger plasticity in WL and WW whereas for the other traits: TL, wing loading and wing aspect the PPI is similar between both *Drosophila* species. It should be noted that for all traits analyzed the major differences between *D. buzzatii* and *D. koepferae* in PPI scores were consequence of cactus host heterogeneity except for WL that was detected in type of culture heterogeneity (Fig. 2).

Discussion

In this study the effect of diverse environments factors were analyzed in different body size-related traits in flies collected from Ruinas de Quilmes population of the cactophilic species *D. koepferae* and *D. buzzatii* revealing not only different response of this species to type of competition (type of culture), crowding conditions (density) and host cactus but trait-specific outcome depending on the environmental. The trends of the PPI showed that, on average, *D. koepferae* exhibited a larger phenotypic plasticity

than *D. buzzatii* for the environmental variables analyzed. The results indicated that different environmental factors generated diverse allometric changes in *D. buzzatii* and *D. koepferae,* as was observed in *D. melanogaster* (Shingleton *et al.*, 2009), suggesting that flies from this population of both *Drosophila* cactophilic species differ in their pattern of variation in body size-related traits as consequence of environmental change. Moreover, body size-related traits of each *Drosophila* cactophilic species responded differently depending on the environmental heterogeneity analyzed.

Several studies have investigated the ecological factors affecting the election of the host cacti and/or the range of distribution of these cactophilic species (Fanara *et al.*, 1999, 2004, 2006; Fanara & Hasson, 2001; Werenkraut *et al.*, 2008; Soto *et al.*, 2012). Most of these studies propose that variation in chemical environment would be responsible for the differences detected in adaptive traits (including body size-related traits) among cacti host (Fogleman & Danielson, 2001; Corio *et al.*, 2013; Soto *et al.*, 2014). Our results suggest that different breeding

sites (*O. quimilo* and *T. terschekii*) would not induce differences in body size-related traits in *D. buzzatii*. It can be argued that the lack of effect of cacti host in *D. buzzatii* was observed in a particular crowding condition that could be not representative of what occurs in nature. Unfortunately there is not data about density conditions in which both species are reared in natural conditions. On the other hand, the higher PPI of both *Drosophila* species was detected under different crowding conditions suggesting that the density factor plays a major role for phenotypic plasticity.

A lower wing loading, as was observed in *D. koepferae*, is associated to a superior flying ability since flight becomes more energetically efficient when wings are larger relative to body size (Berwaerts *et al.*, 2002). In general, organisms with this characteristic are expected to have slower flight and sometimes they combine flying with soaring (Betts & Wootton, 1988). On the other hand, *D. koepferae* presents higher wing aspect than its sister species. Interestingly the wing aspect exhibited nonsignificant interactions involving *Drosophila* species factor suggesting that the genetic differences between *D. buzzatii* and *D. koepferae* are independent of the environmental factors analyzed here. A higher wing aspect is consequence of long, narrow wings that is generally associated with fast-flapping flight, while broad wings that are characteristics of low wing aspect is associated with gliding flight (Wootton, 1992). Diverse studies demonstrated that a better flight performance (low wing loading and high wing aspect) improves dispersal ability (Betts & Wootton, 1988; Gibb *et al.*, 2006; Arribas *et al.*, 2012). Actually, Gu and Barker (1995) suggested that species displaying superior flight ability are better adapted for colonizing. Then, it can be hypothesized that *D. koepferae* would have a wider distribution than *D. buzzatii* if flight performance, estimated by wing loading and wing aspect, plays a major role during colonization of new areas. However, according to the records of distribution of both species the hypothesis clearly cannot be supported because of *D buzzatii* has a subcosmopolitan distribution while *D. koepferae* is localized in a much smaller area (Northwestern of Argentina and South-Central area of Bolivia). Accordingly, an alternative justification should be addressed to explain this outcome: there is another effect affecting dispersal ability. During colonization of new areas, interspecific competition and/or oviposition behavior are also important features that should be taken into consideration. Werenkraut *et al.* (2008) demonstrated that the success of colonization by *D. buzzatii* cannot be attributable to differential competitive ability. Thus, it is possible that the differences in the fecundity schedule between *D. buzzatii* and *D. koepferae* (Fanara *et al.,* 1999; Soto *et al.*, 2012) could

be relevant in the colonization pattern of these cactophilic *Drosophila* species. Besides, Hurtado and Hasson (2013) demonstrated that the proportion of the sperm load that remains available for egg fertilization is almost 3 times lower in *D. koepferae* than *D. buzzatii* indicating that *D. buzzatii* has more chance to lay eggs when females detect a novel resource.

Diverse studies have addressed the ecological consequences of phenotypic plasticity considering to both the range of the ecological distribution of a particular species as the stability and local biodiversity of population and communities (Richards *et al.*, 2006; Sexton *et al.*, 2009; Chevin *et al.*, 2013; Kovach-Orr & Fussmann, 2013). In fact, it was argue that phenotypic plasticity enhances ecological niche breadth because plastic responses allow organisms to express advantageous phenotypes in a broader range of environments (Richards *et al.*, 2005; Ghalambor *et al.*, 2007; Chevin & Lande 2011; Fallis *et al.,* 2011; Overgaard *et al.,* 2011). However, our results shown that in flies collected in a sympatric populations *D. koepferae* is more plastic species but *D. buzzatii* presents a wider range of ecological distribution that is the opposite pattern which is predicted. Certainly, the conclusions from common "garden" experiments only hold strictly for the specific traits under investigation and for the specific conditions under which the experiments were performed (Sultan, 1995). Clearly, a better understanding and prediction of the interplay of phenotypic plasticity, dynamics of adaptive traits, range of the ecological distribution and evolution of interacting species can only be reached by confronting studies of natural populations to experimental evolution in the laboratory (Kawecki *et al.*, 2012). In this sense, the cactophlic species *D. buzzatii* and *D. koepferae* represent an attractive model system to understand the complex system involved in adaptation and colonization in natural populations.

Disclosure

The authors have no conflict of interest to declare.

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