

Correlations among size-related traits are affected by chromosome inversions in an adaptive polymorphism in *Drosophila buzzatii*

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Genetic variation in correlations among size-related traits of head, thorax and wings was examined in *Drosophila buzzatii*, by comparing the correlation pattern of the phenotypic correlation matrix ($CP-R_p$) between inversion karyotypes of the second chromosome. $CP-R_p$ differed between some karyotypes in a natural population. $CP-R_p$ in homokaryotypic classes of wild-reared flies, but not in heterokaryotypes, differed from the whole population represented by laboratory-reared flies. Similarity in $CP-R_p$ was highly significant for a same homokaryotype in two populations. In one of them, the chromosome is polymorphic for four inversions. In the other population, one of the inversions is almost fixed. $CP-R_p$ was significantly similar between these populations, illustrating that similarity of $CP-R_p$ may even occur between populations which have greatly diverged in frequencies of some genotypes affecting correlation patterns. It is suggested that chromosomal inversions are factors affecting genetic correlations among traits known to be phenotypically correlated with fitness components.

Keywords: chromosome inversions, *Drosophila*, phenotypic correlations, size-related traits.

Introduction

Positive phenotypic correlations of body size with adult fitness components have recently been found in wild populations of some *Drosophila* species, including the cactophilic fly *D. buzzatii*. In this species, such a correlation has been detected for three fitness components: mating success (Santos *et al.*, 1988, 1992; Leibowitz *et al.*, 1995; Norry *et al.*, 1995a), fecundity (Santos *et al.*, 1992) and longevity (Santos *et al.*, 1992; Hasson *et al.*, 1993). Recent studies have also shown evidence for the presence of heritable variation in size-related morphometric traits in several wild populations of the same species (Prout & Barker, 1989; Ruiz *et al.*, 1991; Thomas & Barker, 1993; Leibowitz *et al.*, 1995). Genetic responses to size-related selection would therefore be expected in *D. buzzatii* populations, if there is a genetic correlation between such heritable variation and the true target(s) of size-related selection.

Evolution towards larger adult body size does not appear, however, to be in progress, suggesting that genetic correlations between traits could be a possible factor affecting the response to current selection on size (Leibowitz *et al.*, 1995); for example, there is direct evidence for a negative genetic correlation between adult size and pre-adult survival in *D. melanogaster* (Partridge & Fowler, 1993).

Given that genetic correlations yield correlated responses to selection (Falconer, 1989; ch. 19), it is of interest to detect factors affecting genetic correlations among traits phenotypically correlated with fitness components. Chromosomal inversions could be one of such factors in *D. buzzatii*, because the second chromosome inversions affect body size and morphometric traits correlated with it (Ruiz *et al.*, 1991; Hasson *et al.*, 1992; Norry *et al.*, 1995b). This hypothesis is examined in the present study. Specifically, we examine genetic variation in correlations among traits of head, thorax and wings, by comparing the phenotypic correlation matrix (R_p) between

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inversion karyotypes within and between populations. If karyotypes (genotypes) differ in the correlation pattern of R_p (CP- R_p) because of genetic causes in wild flies, this would indicate that inversions are factors affecting genetic correlations through their effects on size-related traits.

Materials and methods

The data

To remove any effects of longevity in wild adults, karyotypic variation in R_p was examined in newly emerged wild flies (NEWFs). They were collected in April 1990 from a population breeding on *Opuntia vulgaris* at Arroyo Escobar (34°4'S, 58°7'W), Province of Buenos Aires, Argentina. This population is polymorphic for four inversions on the second chromosome, namely standard (st), j, jz³ and jq⁷ (Hasson *et al.*, 1991). Detailed information on the data gathering methods can be found in Norry *et al.* (1995b), and a brief description follows.

Flies emerging from rotting cladodes of *O. vulgaris* were collected daily, sexed and crossed individually with flies of a homokaryotypic stock. The cytological analysis of eight larvae of the progeny from each cross allowed inference of the karyotype of the wild parent. In total, 354 NEWFs were karyotyped and scored for five traits: thorax length (TL), wing length (WL), wing width (WW), head width (HW) and face width (FW) (see Norry *et al.*, 1995a for details about measurements). An exploratory analysis (see Results) indicated that sample sizes (N) larger than 25 NEWFs permit a relatively precise estimation of CP- R_p for these traits. Then, only karyotypic classes with $N > 25$ NEWFs were examined. After imposing this constraint the data set contained 30 flies for karyotype j/st, 141 for karyotype j/j, 136 for karyotype j/jz³ and 29 for karyotype jz³/jz³.

The same traits were also scored in laboratory-reared flies (LRFs), derived from: (i) the Arroyo Escobar population; (ii) the Quilmes population (26°6'S, 65°9'W), where inversion j is almost fixed (inversion frequency = 0.98, Hasson *et al.*, 1995). These flies were the offspring of a random mating performed with the laboratory F₂ generation of 70 (Arroyo Escobar) or 48 (Quilmes) isofemale lines from wild-inseminated females collected over banana bait buckets. The random mating was performed by releasing three flies of each sex and isofemale line (420 and 288 flies, respectively, for each population) into an egg-collecting chamber (100 × 200 × 300 mm). Samples of 30–40 first-instar larvae were collected daily from this chamber and

transferred to 95 × 20 mm shell vials with 5 mL of David's (1962) medium for optimal growth at 25 ± 1°C. For each population, 100 randomly chosen flies emerging from these cultures were measured.

Statistical analysis

All measurements (in ocular units) were log_e-transformed and corrected to remove sexual dimorphism in each trait. This correction was performed by adding to male measurements the difference between male and female means, allowing the pooling of data of both sexes (Schluter & Smith, 1986). Prior to this, no significant difference in correlations was found between sexes. R_p was estimated using the Pearson product-moment correlation between traits. Significance levels were adjusted using the sequential Bonferroni test (Rice, 1989).

Severe metric collinearity was apparent in NEWFs, so, therefore, multivariate-normal tests for analyses of covariance matrices do not apply. This study is concerned, not with particular correlations, but with the pattern of R_p (CP- R_p). Therefore, a randomization procedure free from distributional assumptions, Mantel's test, was applied to compare CP- R_p s by testing the null hypothesis of no matrix correlation. The test statistic is the Pearson correlation coefficient (r) calculated by treating the off-diagonal elements of two matrices as paired observations. In all cases, 1500 R_p permutations were run, using program MXCOMP of the NTSYS package (Rohlf, 1988). The P -value reported is the proportion of random permutations with a r -value as high as, or higher than, that observed.

Results

Phenotypic correlations in NEWFs are given in Table 1 for each karyotype examined. All correlations are positive (Table 1). Although phenotypic correlations were typically higher in wild flies than in LRFs (Table 1), Mantel's test did reveal significant similarity of R_p between NEWFs of Arroyo Escobar (the total sample of 354 NEWFs) and LRFs derived from both populations, Arroyo Escobar ($r = 0.60$, $P < 0.05$) and Quilmes ($r = 0.80$, $P < 0.01$).

In NEWFs of Arroyo Escobar, significant or marginally significant similarity of CP- R_p was verified among some karyotypes: j/j, j/jz³ and j/st (Table 2). However, no similarity in CP- R_p was detected between homokaryotypes (Table 2), and karyotype jz³/jz³ differs from the remaining ones (see below). Heterokaryotypes in this natural population, but not homokaryotypes, show a CP- R_p similar to

the whole population represented by LRFs (LRF-AE, Table 2).

Given that R_p for karyotype j/j was estimated using a fairly large sample size (141 NEWFs), very precise estimates were available for the comparisons between this karyotype in NEWFs ($N = 141$) and LRFs ($N = 100$). First, the karyotypic influence on CP- R_p in Arroyo Escobar was also verified by the result that NEWFs carrying the j/j karyotype exhibit no matrix similarity with LRFs representing the whole population of Arroyo Escobar (LRF-AE, Table 2), where CP- R_p would also be affected by the remaining inversions. Secondly, highly significant similarity was verified only in the comparison between NEWFs carrying the j/j karyotype in Arroyo Escobar and LRFs derived from Quilmes (Table 2), as expected by the fact that inversion j is almost fixed in Quilmes (see Materials and methods).

An analysis of empirical results on the statistical power

The permutation test allows the H_0 hypothesis of independence to be tested without relying on formal

null distributions by evaluating the probability of obtaining a r -value as high or higher than that obtained with the observed data. When H_0 is rejected ($P < 0.05$), it cannot be ascertained whether the matrices are equal, proportional or merely similar in pattern to one another (Cowley & Atchley, 1992), so that results in Table 2 may imply karyotypic variation conservatively suggested. However, the test does not consider the precision with which the elements of the matrices are estimated. Hence, Mantel's test will have low statistical power if it is applied to matrices with poorly estimated elements (Cowley & Atchley, 1992). In order to evaluate whether this bias associated with the sample size (N) is expected to be severe in Table 2, ten independent samples were obtained (from Arroyo Escobar) of 25 NEWFs each. The R_p matrix for each sample was obtained (data not shown). Each of these R_p s was compared with the overall R_p obtained by pooling the nine other samples (excluding each sample from the pooled one in each of the ten comparisons). Using Mantel's test, the ten R_p s estimated for these samples ($N = 25$) were all significantly similar to their respective overall R_p

Table 1 Phenotypic correlations between traits are given for (a) homokaryotypes and (b) heterokaryotypes of the second chromosome in a sample of wild *Drosophila buzzatii* emerging from *Opuntia* cladodes taken at Arroyo Escobar. (c) Correlations are also shown for laboratory-reared flies (LRF) representing two whole populations: Arroyo Escobar (LRF-AE) and Quilmes (LRF-Q). Abbreviations of traits are explained in the text. P -values were adjusted by the sequential Bonferroni method

	TL	WL	WW	HW	FW
(a) Homokaryotypes: j/j (below); jz^3/jz^3 (above)					
TL		0.824***	0.898***	0.879***	0.757***
WL	0.775***		0.843***	0.791***	0.844***
WW	0.801***	0.777***		0.873***	0.804***
HW	0.776***	0.727***	0.712***		0.762***
FW	0.697***	0.681***	0.651***	0.795***	
(b) Heterokaryotypes: st/j (below); j/jz^3 (above)					
TL		0.845***	0.815***	0.815***	0.918***
WL	0.774***		0.784***	0.715***	0.749***
WW	0.897***	0.860***		0.672***	0.699***
HW	0.860***	0.741***	0.782***		0.840***
FW	0.914***	0.749***	0.795***	0.920***	
(c) LRF-AE (below); LRF-Q (above)					
TL		0.449*	0.603**	0.511**	0.398*
WL	0.506**		0.332*	0.258	0.249
WW	0.368*	0.497**		0.392*	0.268
HW	0.405*	0.196	0.355*		0.669***
FW	0.532**	0.347*	0.375*	0.739***	

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.005$.

Table 2 Matrix correlations (r) measuring similarity in the pattern of \mathbf{R}_p s for second chromosome karyotypes in newly emerged wild *Drosophila buzzatii* of Arroyo Escobar, and between these karyotypic classes and laboratory-reared flies (LRF) representing two whole populations: Arroyo Escobar (LRF-AE) and Quilmes (LRF-Q). P -values indicate the probability of obtaining a r -value as high as or higher than that observed. 1500 matrix permutations were performed for all tests

	st/j	j/j	j/jz ³	jz ³ /jz ³	LRF-AE
j/j	<i>r</i>	0.50			
	<i>P</i>	(0.07)			
j/jz ³	<i>r</i>	<i>0.64</i>	<i>0.69</i>		
	<i>P</i>	(0.05)	(0.04)		
jz ³ /jz ³	<i>r</i>	-0.14	0.28	-0.13	
	<i>P</i>	(0.38)	(0.22)	(0.40)	
LRF-AE	<i>r</i>	<i>0.69</i>	0.41	<i>0.67</i>	-0.43
	<i>P</i>	(0.03)	(0.18)	(0.02)	(0.09)
LRF-Q	<i>r</i>	<i>0.72</i>	<i>0.78</i>	<i>0.68</i>	0.11
	<i>P</i>	(0.03)	(0.005)	(0.03)	(0.44)
					<i>0.62</i>
					(0.03)

Values in italic indicate significant correlations between \mathbf{R}_p s.

($N = 225$): $0.87 > r > 0.65$, $P < 0.05$, 1500 random permutations were performed for all ten tests. This indicates that severe bias in Table 2 is unlikely, because only karyotypic classes with $N > 29$ NEWFs were included in the study (see Materials and methods).

The definition of the rejection zone in Mantel's test, on the other hand, suggests that a high and negative matrix correlation (r) will generate a low P -value. This is confirmed in Table 2, for example, for the comparison between jz^3/jz^3 and LRF-AE. However, the H_0 hypothesis (the two matrices are not correlated) is tested against the H_1 hypothesis that the two matrices are *positively* correlated. This implies that negative r -values reported in Table 2 should, in fact, be associated to higher P -values than positive r -values. It should be noted, however, that P -values generated by Mantel's test for negative r -values were still 'nonsignificant' at the usual 0.05 level (Table 2), indicating a lack of overall similarity between \mathbf{R}_p s. In fact, what is clear here is that r -values may be negative if the examined matrices differ in the correlation pattern.

Discussion

The phenotypic correlation pattern for a suite of size-related traits of head, thorax and wings, is heterogeneous between inversion karyotypes of the

second chromosome in a wild population of *D. buzzatii*. Because any effects of age were experimentally removed, these results do not confound direct karyotypic effects with indirect effects caused by differential longevity related to body size (see Ruiz *et al.*, 1991; Norry *et al.*, 1995b).

Although morphometric effects of chromosome inversions have been observed in some insects, including *Drosophila* species (Krimbas, 1967; Prevosti, 1967; Stalker, 1980; Ruiz *et al.*, 1991; Bitner-Mathe *et al.*, 1995), to our knowledge, no study has examined the possible effects on the correlation among traits. Because phenotypic correlations are the weighted sums of genetic and environmental correlations (Falconer, 1989), the finding that CP- \mathbf{R}_p may differ greatly between inversion genotypes (karyotypes) within and between populations (Table 2) strongly suggests that inversions are factors affecting the genetic correlation among traits. In addition, the data also suggest that CP- \mathbf{R}_p was not altered by environmental correlations, which are the correlations attributable to environmental deviations plus nonadditive genetic deviations (Falconer, 1989). First, phenotypic correlations are notably higher in NEWFs than in LRFs (Table 1), but CP- \mathbf{R}_p was highly significantly similar both between NEWFs and LRFs representing the whole population and between karyotype j/j in NEWFs and the same karyotype in LRFs derived from Quilmes. Thus, whereas the results suggest that the natural environment is much more variable than the laboratory one, at least for karyotype j/j (and for the set of measured traits), environmental deviations in nature do not substantially alter CP- \mathbf{R}_p . This finding does not imply that \mathbf{R}_p is independent of environmental deviations, but supports the hypothesis that homo-karyotypic variation in CP- \mathbf{R}_p is not only an environmental variation, but partially genetic. Nonadditive effects of the second chromosome inversions, on the other hand, would be apparently very weak on size-related traits in *D. buzzatii*, as most of the phenotypic variance among karyotypes is explained by a linear regression of trait on chromosome dose (Ruiz *et al.*, 1991; Hasson *et al.*, 1992; Norry *et al.*, 1995b). Secondly, phenotypic correlations among morphometric traits often show correlation patterns similar to their genetic counterparts, indicating that CP- \mathbf{R}_p is not typically altered by environmental deviations and/or nonadditive genetic deviations (Cheverud, 1988; Roff, 1995, 1996; Simons & Roff, 1996).

In *D. buzzatii*, at least a fraction of the heritable variation in size-related traits would be determined by the additive contribution of the second chromosome inversions to the phenotypic variance in body

size (Ruiz *et al.*, 1991; Hasson *et al.*, 1992; Norry *et al.*, 1995b). However, although size-related selection is substantial in wild *D. buzzatii* populations, the selection response depends, not only on the heritabilities of traits considered singly, but also on the genetic correlations among all the traits of which the phenotype is composed (Lande, 1979; Falconer, 1989). In the Arroyo Escobar population, the five traits studied here are genetically correlated with one another (Norry *et al.*, 1997), as expected by considering that the inversion polymorphism contributes to their respective additive genetic variances (Norry *et al.*, 1995b). In addition, these traits phenotypically covary with mating success and longevity, and face width would be a direct target of size-related sexual selection (Norry *et al.*, 1995a; Norry & Vilardi, 1996). A correlated response to such selection could then be partially influenced by chromosome inversions if, as suggested here, they also affect the genetic correlation among size-related traits. The importance of such an effect is amplified by the fact that these chromosome arrangements are also differentially correlated with preadult and adult survival in the same population (Hasson *et al.*, 1991; Norry *et al.*, 1995b). This information combined with the present data indicates that inversions also affect genetic correlations among preadult survival and size-related adult traits. Overall, it was previously demonstrated that these chromosome arrangements additively affect adaptive traits and fitness components in wild populations of *D. buzzatii* (Ruiz *et al.*, 1986, 1991; Hasson *et al.*, 1991; Norry *et al.*, 1995b). Therefore, these chromosome arrangements may influence the genetic correlation among adaptive traits, as suggested in this morphometric study. This is exactly what the adaptive basis of the inversion polymorphism would imply.

Because genetic correlations are sensitive to changes in gene frequencies (Turelli, 1988; Falconer, 1989), variation in genetic correlations and $CP-R_p$ would be expected between populations such as Arroyo Escobar and Quilmes, which differ greatly in inversion frequencies and have diverged, genetically, in body size and shape (Norry, 1995). Yet, $CP-R_p$ is similar between these populations (Table 2), illustrating that similarity of $CP-R_p$ may even occur between populations which have greatly diverged in frequencies of some genotypes affecting correlation patterns. In order to test hypotheses about the dynamics of genetic covariance patterns (see Turelli, 1988), the next step of this work would be to compare estimates of these genetic parameters between populations which differ in inversion frequencies.

Acknowledgements

We thank J. Fanara and C. Rodriguez for their assistance in field and laboratory work. We wish to thank an anonymous reviewer for constructive comments on an early version of the manuscript. F.M.N. is a fellow and J.C.V. and E.H. are members of Consejo Nacional de Investigaciones Científicas y Técnicas (Argentina). This work was supported by University of Buenos Aires grant EX 050 and 099 to E.H.

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