species (see Palmer and Strobeck, 1986, for a review), chromosome inversions in *Drosophila* were largely unexplored in relation to FA. Here, we compare the level of FA (in wing length) among inversion karyotypes (genotypes) in wild-reared flies of the cactophilic species *Drosophila buzzatii*.

Table 1. Asymmetry of the wing length is given for karyotypes of the second chromosome in wild-reared *D. buzzatii* flies. Values (in mm x 10^3) are given for data pooled across sexes. Statistics are also shown for data pooled within homokaryotypes (Homo-k) as well as heterokaryotypes (Hetero-k). N is the sample size.

	Karyotypes						
Statistics	j / st	j / j	jz3 / st	jz3 / j	jz3 / jz3	Homo-k	Hetero-k
N	27	105	17	104	20	125	148
Mean	4.02	3.84	5.47	5.66	4.65	3.97	5.34
SD	6.92	7.06	7.63	8.38	8.85	7.34	8.03

Material and Methods: A population breeding on *Opuntia vulgaris* at Arroyo Escobar (34°4' S; 58°7' W), Buenos Aires (Argentina), was sampled for this study. This population is polymorphic for inversions on the second chromosome, namely *standard* (st), j, jz^3 and jq^7 (Hasson *et al.*, 1991). During April 1 to 15, 1991, wild-reared flies were collected from rotting cladodes of *Opuntia vulgaris*, as described in Norry *et al.* (1995a). These flies were immediately sexed, placed in vials with culture medium and individually crossed with flies of a homokaryotypic stock as described in Norry *et al.* (1995a). The cytological analysis of eight larvae of the progeny from each cross allowed us to infer the karyotype of the wild parent. Only karyotypic classes with sample sizes larger than 17 individuals were analyzed.

Wing length was scored as the distance from anterior crossvein to distal tip of vein III (see Norry *et al.*, 1995b). Both wings were measured on a microscope slide at 100× magnification, using a Wild M-20 compound microscope. Asymmetry scores were obtained by subtracting the measurement of the left side from that of the right side.

Results and Conclusions: No sexual dimorphism in FA of wing length was detected by the Mann-Whitney test (MEAN $RANK_{MALES}$ = 137; MEAN $RANK_{FEMALES}$ = 135; P = 0.87). The results are therefore reported for data pooled across sexes. Summary statistics for wing asymmetry in wild flies are given for each examined karyotype in Table 1. Among karyotypes, no significant variation in FA was detected by the non-parametric Kruskal-Wallis test (H = 3.14; P = 0.54). Nor was there evidence of karyotypic variation in FA when data were pooled within homo- and hetero-karyotypic classes (both karyotypic classes were compared using the Mann-Whitney test: MEAN $RANK_{homo\text{-}k}$ = 142; MEAN $RANK_{hetero\text{-}k}$ = 131; P = 0.23).

These results suggest that the inversion polymorphism is adaptively independent of developmental stability, as no significant variation in FA was detected among karyotypes. We conclude that developmental stability (as indexed by wing asymmetry) is independent of: (i) heterozygosity at the karyotypic level of chromosomal variation, and (ii) any possible genetic coadaptation attributable to these chromosome inversions.

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Hodge, Simon [1], **and Paul Mitchell**[2]. [1]Department of Entomology and Animal Ecology, P.O. Box 84, Lincoln University, Canterbury, New Zealand; [2]Division of Biology, Staffordshire University, College Road, Stoke-on-Trent, ST4 2DE, UK. The effect of resource quantity and water content, and atmospheric humidity, on the interaction between *Drosophila hydei* and *D. melanogaster*.

Introduction: It has long been known that the form taken by the interaction between two species can be influenced by the abiotic environment (*e.g.*, Park, 1954). Many environmental variables have been found to affect interactions between drosophilids, including; temperature (*e.g.*, Moore, 1952; Ayala 1966), age of resource (Merrel, 1951; Miller, 1954; Mitchell and Arthur, 1990), light intensity (Moth and Barker, 1976; but see Arthur, 1986), ethanol concentration (Arthur, 1980) and amount of resource (Arthur, 1986).

This study investigated how the amount of resource presented to the larvae, the resource water content and the atmospheric humidity affected the interaction between *D. melanogaster* and *D. hydei*. All these factors are associated with resource desiccation, which is known to affect the performance and behaviour of these two species (Arthur, 1996;

Table 1. Interactions between *D. melanogaster* and *D. hydei* based on pair-wise comparisons in mixed and monocultures of (a) larval survival, (b) wing length, and (c) mean development time. (symbol on left represents effect of *D. hydei* upon *D. melanogaster*)

(a)

Humidity	Liquidity	Mass of IDM 0.5g	Mass of IDM 0.8g
Low	Low	0,-	0,0
	High	0,0	0,0
High	Low	0,0	0,0
	High	0,0	0,0

(b)

Humidity	Liquidity	Mass of IDM 0.5g	Mass of IDM 0.8g
Low	Low	0,-	0,0
	High	0,-	-,-
High	Low	0,-	0,-
	High	0,0	0,0

(c)

Humidity	Liquidity	Mass of IDM 0.5g	Mass of IDM 0.8g
Low	Low	0,-	0,-
	High	+,0	+,0
High	Low	0,-	+,0
	High	0,0	0,0

Arthur and Cassey, 1992; Hodge and Wilson, 1997). In addition to examining the interaction under different environmental conditions, different performance measures of the populations have been used to examine how this led to variation in how the interactions were perceived.

Methods: The experiment used standard glass vials (75mm × 25mm diameter) stoppered with foam bungs to house the drosophilids. Two masses (0.5g and 0.8g) of ground Instant *Drosophila* Medium (IDM; Blades Biological Ltd., UK) were used as a resource. The IDM was hydrated with distilled water, using either a 4:1 or 6:1 by mass water:IDM ratio. The relative humidity was either 'high' (RH 45-50%), or 'low' (RH 30-35%), the high value being the ambient humidity in the incubator and the low humidity being maintained using trays of silica gel which were replaced every 24 hours. By combining these parameters factorially, eight 'environments' were created. A temperature of 25^{o}C and a light:dark regime of 16:8 hours light:dark were used in all cases.

The experiment used wild-type stocks of both species: 'Kaduna' from Nigeria for *D. melanogaster* and a stock reared from British flies for *D. hydei*. For each environment, monocultures were set up using 40 first instar larvae. Mixed cultures were set up using 40 first instar larvae of each species, *i.e.*, 80 larvae in total. Between 8 and 11 replicates of each treatment were used. Emerged adults were removed from vials every 24 hours and stored in 70% alcohol. The body size of the flies was estimated by a measure of female wing length, using the distance from the anterior cross vein to the wing tip along vein 3, with 10 specimens taken from each vial if available. The mean development time was calculated using all the emergent adults from each vial.

Results: The effects of the various environmental factors on performance have been analyzed factorially and discussed elsewhere (Hodge, 1995). This paper concerns itself solely with how the populations performed in mixed cultures compared to mono-cultures within each environment. This has been achieved simplistically, using a series of pairwise ANOVAs, differences being declared significant at $P < 0.05$. Data for survival were arcsine transformed before analysis.

Survival of larvae was robust, being unaffected by the presence of the other species in the large majority of cases (Table 1a). Therefore, the interaction between *D. hydei* and *D. melanogaster* based on larval survival tended to be 'neutral', with one amensal interaction occurring when conditions were severe for *D. hydei* (dry atmosphere, 0.5g IDM).

Wing length was a more sensitive measure (Table 1b). Although 'non-effects' still dominated, there appeared four amensal, one competitive and three neutral interactions. *D. melanogaster* only responded to the presence of *D. hydei* on one occasion, whereas *D. hydei* was negatively affected by *D. melanogaster* in over half of the environmental conditions used.

When considering development time, *D. hydei* was found to facilitate *D. melanogaster* on three occasions, *i.e.* development time of *D. melanogaster* was shortened (Table 1c). *D. hydei* on the other hand was, if anything, negatively affected by *D. melanogaster*, the development time being extended under some environmental conditions. This extension of *D. hydei* development time appeared more likely when the resource had a low water content.

Discussion: Inferences made about the interaction between these two species of *Drosophila* were dependent upon the larval environment and which performance measure was used. Generally, *D. hydei* seemed unsuited to dry conditions (see also Arthur, 1986; Hodge, 1995; Hodge and Wilson, 1997) and in the environments which were prone to drying (small amounts of resource, low water content, low humidity), *D. hydei* tended to be inhibited by *D. melanogaster*. The frequency of this inhibition was related to the sensitivity of the parameter used; for example, using survival, inhibition became manifest only in the driest environment, but when using wing size the inhibition of *D. hydei* became a more general phenomenon. In the 'wettest' environments this inhibition did not appear for any of the parameters used.

In some instances the different population measures were contradictory. For example, the effect of *D. hydei* on *D. melanogaster* in the 0.8g, low humidity, high water environment could be neutral, inhibitive or facilitative, depending on what measure was used. In this case, it is possible that development time was shortened as an 'escape response' from

an unfavourable environment, producing smaller adults because the feeding time of the larvae was curtailed. In these situations, conclusions about the interaction must be subjective. A reduction in body size may lower the reproductive output of the female but, when considering animals whose natural habitat is ephemeral and unpredictable, a reduction in development time may represent an important facilitative effect.

The interaction which occurs between two species can be very specific to a given set of conditions (Thompson, 1988; Dunson and Travis, 1991), and it appears that describing the interaction between these two *Drosophila* species in a single manner is almost meaningless (see Arthur, 1986; Hodge, 1995). Compared to variability in nature, only a narrow band of different environments have been used here and these produced four of the six theoretical outcomes between a pair of interacting species. Experiments such as this one produce useful information on the possible range of interactions that can occur between two species and may aid in clarifying the mechanisms via which the interspecific effects are produced (see Tilman, 1987). It is then desirable to put the results into a more realistic context and determine which scenarios are most likely to occur under natural conditions.

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Gandarela, Manuel R., and Emilio Valadé. Dpto. de Bioloxía Fundamental, Facultad de Bioloxía, Universidade de Santiago de Compostela, Spain. Estimation of duplication time between genes *scute* and *asense*.

The *achaete-scute* gene complex (AS-C) is involved in the development of sensory organs and the central nervous system of *Drosophila*. The AS-C is a gene family containing four genes with neurogenic functions: *achaete(ac)*, *scute* (*sc*), *lethal of scute* (*l'sc*) and *asense* (*ase*). AS-C genes encode related proteins containing the basic-helix-loop-helix (bHLH) domain characteristic of a family of transcriptional regulators. Their products confer on cells the capacity to become neural precursors. Besides its neurogenic function, *sc* is also involved in the establishment of the X:A ratio.

It is possible to estimate the date of the duplication event which gave rise to these two members of the gene family. Li and Graur (1991) describe a method to estimate the duplication time of two paralogous genes from the sequences of these two genes from two species when the divergence time between these species is known. In this work we give an estimation of the duplication time between *sc* and *ase*.

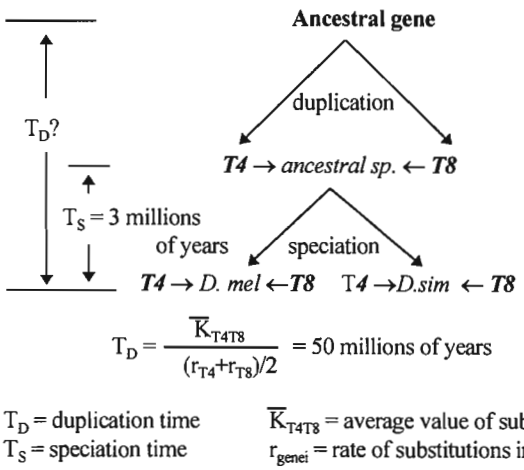

Figure 1. Model for estimating the time of the gene duplication event (Li and Graur, 1991). The matrix of Kimura's two-parameters distances (Table 1) were used to estimate T_D. We consider 3 MYA as the time of speciation between *D. melanogaster* and *D. simulans* (Cariou, 1987).

We amplified by PCR and sequenced a conserved region of *sc* gene from one strain of *D. melanogaster* (Toonda, Australia) and another one of *D. simulans* (Leticia, Colombia). To estimate the duplication time we included two sequences of *ase* obtained from literature: *D. melanogaster* Canton S (Villares and Cabrera, 1988) and *D. simulans* CA-1 (Hilton *et al.*, 1994). We used 3 million years ago (MYA) as the time of divergence between *D. melanogaster* and *D. simulans*. This value is an average of several estimates based on paleo-biogeographic, allozymic, inmunological and nucleotide data (Cariou, 1987).