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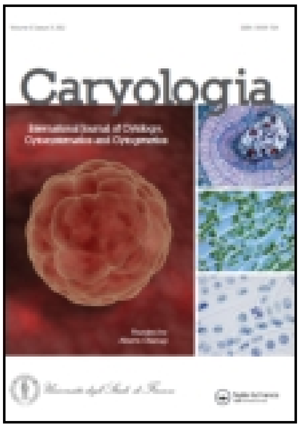

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# Environment-dependent regime of longevity selection in the chromosomally polymorphic species Leptysma argentina (Acrididae: Orthoptera)

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# Environment-dependent regime of longevity selection in the chromosomally polymorphic species *Leptysma argentina* (Acrididae: Orthoptera)

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In previous papers it was reported that a Robertsonian translocation (centric fusion) affected external phenotype in the grasshopper *Leptysma argentina* and that thorax height was the target of adult viability selection. In the present paper two populations of *L. argentina* at different latitudes, with different centric fusion frequencies, were studied. It was demonstrated that selection acts on roughly the same targets but in opposite directions. In the northernmost population longevity selection acted primarily on thorax height (TH), leading to an *increase* of that variable. In the southern population, longevity selection leads to an increased femur length (FL) but to a *decreased* body size (including TH). Longevity selection affects karyotype frequency, leading to an increase of fusion homozygote frequency; however, fusion 3/6 significantly increases FL. This is consistent with an increase in fusion frequency along the season. The fact that longevity selection in one population increases and in another decreases body size is interpreted as an interaction between environment and body size, of the sort already detected in laboratory strains of *Drosophila melanogaster.*

**Keywords:** adult survival; centric fusion; grasshoppers; phenotypic and genotypic selection; selection analysis

## Introduction

Body size is a relevant parameter to the study of natural selection, and it has been demonstrated to affect different fitness components in arthropods, such as longevity (Santos et al. 1988; Hasson et al. 1993; Norry et al. 1995; Norry and Colombo, 1999, Rosetti et al. 2008) and mating success (Partridge, Ewing et al. 1987; Partridge, Hoffman et al. 1987; Santos et al. 1988; Remis et al. 2000; Colombo et al. 2001, 2004). The grasshopper *Leptysma argentina* has been thoroughly studied from the point of view of population cytogenetics; it bears polymorphisms for a centric fusion, a supernumerary segment and a B chromosome (Bidau and Hasson 1984; Colombo 1989). It has been demonstrated that the centric fusion 3/6 enhances body size in its carriers, both in males (Colombo 1989, 1997) and in females (Colombo et al. 2004). Moreover, it has been shown that body size in this species increases adult viability (longevity) in males (Norry and Colombo 1999) and mating success in both sexes (Colombo et al. 2004); therefore centric fusion indirectly but significantly affects these selection components.

In the present work we aim to detect the possible morphological targets of longevity selection, taking advantage of the fact that this species is univoltine at this latitude and generations are discrete and synchronised (Colombo 1993). Furthermore, given that the shift in mean body size within a generation is mathematically equivalent to the covariation between relative fitness and the corresponding trait (Arnold and Wade 1984), we evaluated the effects of selection on different traits, applying a method employed by Rosetti et al. (2008) in another grasshopper that consists of comparing phenotypic traits between age classes. The outcome shows that the effect of body size on adult viability is not constant over the whole distribution area of *L. argentina*, but femur length is important both for natural and sexual selection in all cases so far studied in this species.

## Materials and methods

In this study, 201 males from Otamendi Natural Reserve (Buenos Aires Province, Argentina) (34°10′ S, 58°52′ W), and 213 males from El Palmar National Park (Entre Ríos province, Argentina) (31°50′ S, 58°17′ W) of *L. argentina* were sampled in October and December 2007, roughly coinciding with the onset and the end of the adult life span for this species. Generations are synchronised, so it can be assumed that all individuals in a sample are of the same age. Of the 201 males from Otamendi, 107 were collected in October and 94 in December 2007; of the 212 males from El Palmar, 115 were collected in October and 98 in December 2007. Karyotype was determined as described in Colombo

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(1993). The fusion polymorphism involving chromosomes 3 and 6 will be referred to as F. FF and UF are the fusion homozygotes and heterozygotes, respectively, and UU are the basic, unfused homozygotes. In the Otamendi (southern) population, sited 282 km south of the other population, given that fusion frequency is high, only one UU individual was found, which was pooled for analysis with the UF individuals. Average annual minimum temperature in El Palmar is 11.93°C and in Otamendi is 10.08°C.

### *Morphometric study*

All males were measured for five morphological traits with an ocular micrometer (1 mm: 48 ocular units): TL – length from the extreme of the head to the third coxa; FL – third femur length; TiL – third tibia length; TxL – thorax length; TH – thorax height. The effects of karyotype on these variables were assessed by means of a multiple analysis of variance (MANOVA) with population and selection (0 for young males, 1 for older males) as factors. Statistical analyses were performed with the Statistica package (Statistical Statsoft 1996).

## Results

### *Effects of polymorphisms on morphometrical variables*

When we studied the effect of centric fusion on morphometric characters by means of a MANOVA (Wilk's lambda 0.889, $p \ll 0.01$), in the October sample the variables in FF individuals from Otamendi were consistently larger than those in UF individuals, but only FL was significantly affected (F = 6.76, $p < 0.05$). In the December sample, only TL was significant (F =8.43, $p \ll 0.01$). In El Palmar FF individuals were bigger than UF individuals, UU males being the smallest of them all (Wilk's lambda 0.793, $p < 0.01$). TL (F = 7.83, $p < 0.01$) and TH (F = 5.93, $p < 0.05$) were the only significant variables for this population in October. In the December sample, only TL was significant (F = 7.96, $p < 0.01$). In general, all variables are correlated with each other in both samples. All these results agree with previous studies in other populations (Colombo 1989, 1997).

When different age classes were included in the analysis, it was evident that: (i) in El Palmar larger individuals were favoured, with HTx as the most significantly affected variable (F = 6.02, $p < 0.01$); (ii) In Otamendi, smaller, but leggier, individuals were favoured; femur length increase was the most significant result (F = 9.82, $p \ll 0.01$), followed by thorax height decrease (F = 4.98, $p < 0.05$) (Table 1). An interesting result is that there is a highly significant interaction between longevity (L) and population (P) (F = 10.66, $p \ll 0.01$).

With respect to the effect of karyotype on survival, we performed a contingency chi-square test comparing karyotype frequencies in each sample (Table 2). In Otamendi, the frequency of FF individuals increases at the expense of UF males in December, when compared with the October sample (Table 2). The same result was observed for El Palmar individuals. Therefore survival selection acts on karyotype, favouring fusion homozygotes.

## Discussion

Body size and longevity are traits related to fitness in insects. Unlike longevity, body size is not a fitness component itself, but increased size often appears to confer an important advantage for fecundity and survival in adult *Drosophila* (for references, see Partridge and Fowler 1993). Morphometric characters may be the targets of natural and/or sexual selection; they may be correlated with fitness components, both under laboratory conditions and in the wild, as was consistently found among flies (Santos et al. 1988; Hasson et al. 1993; Norry et al. 1995) and grasshoppers (Norry and Colombo 1999; Remis et al. 2000; Colombo et al. 2001, 2004). However, the effects of chromosome rearrangements on morphologic variables has only been studied in the last 30 years (Butlin et al. 1982; Ruiz et al. 1986; Hasson et al. 1992) in flies and grasshoppers (Colombo 1989, 1997; Remis 1997), after the pioneering work of White and Andrew (1960) and White et al. (1963).

The comparison of age classes is the most direct way to detect natural selection in the wild; other, more indirect, methods include the significant departure from null models, e.g. Hardy-Weinberg or gametic phase equilibria

Table 1. Means (in millimetres) and standard errors (between parentheses) for all five morphometric traits analysed here in males of *Leptysma argentina*. Both populations (O: Otamendi and EP: El Palmar) were included in the analysis.

| | TL | FL | TH | TiL | TxL | N |
|---|---|---|---|---|---|---|
| O young | 13.122 (0.823) | 11.951 (0.911) | 3.016 (0.264) | 10.318 (1.78) | 4.106 (0.431) | 107 |
| O aged | 13.015 (1.034) | 12.141 (1.306) | 2.965 (0.329) | 10.401 (2.54) | 4.126 (0.288) | 94 |
| EP young | 11.055 (0.764) | 10.456 (0.877) | 2.636 (0.190) | 9.629 (1.23) | 3.890 (0.316) | 115 |
| EP aged | 11.800 (0.652) | 10.955 (0.951) | 2.967 (0.203) | 10.001 (0.925) | 4.027 (0.516) | 98 |
| Longevity (L) | $p < 0.01$ | $p < 0.01$ | $p = 0.1085$ ns | $p = 0.2118$ ns | $p = 0.3848$ ns | |
| Population (P) | $p < 0.05$ | $p < 0.01$ | $p < 0.01$ | $p < 0.05$ | $p = 0.0939$ ns | |
| L × P | $p = 0.3283$ ns | $p = 0.5876$ ns | $p < 0.01$ | $p = 0.6857$ | $p = 0.4323$ ns | |

Abbreviations: TL = length from the extreme of the head to the third coxa; FL = third femur length; TiL = third tibia length; TxL = thorax length; TH = thorax height; ns = not significant

Table 2. Chi-square test comparing fusion 3/6 karyotypes in the pre- and post-selective samples (October and December, respectively) in the populations of *Leptysma argentina* analysed here. In the Otamendi population, the only fusion homozygote of October was pooled with fusion heterozygotes in order to prevent small numbers.

| | UU | UF | FF | Total |
|---|---|---|---|---|
| *Otamendi population* | | | | |
| October | 1 | 24 | 91 | 108 |
| December | — | 9 | 90 | 99 |
| Total | 1 | 29 | 177 | 207 |
| $X^2_{(1)} = 4.47$ | | | | $p < 0.05$ |
| *El Palmar population* | | | | |
| October | 48 | 50 | 7 | 105 |
| December | 48 | 51 | 21 | 120 |
| Total | 96 | 101 | 28 | 225 |
| $X^2_{(2)} = 6.02$ | | | | $p < 0.05$ |

Abbreviations: UU = homozygotes without the 3/6 fusion; UF = fusion heterozygotes; FF = fusion homozygotes.

(Endler 1986). Previous and present evidence of age class comparison showed that fusion 3/6 is subject to natural selection (Colombo 1993, 2000, this paper), whereas the supernumerary segment showed evidence of departure from null models (Colombo 2000).

However, the identification of selection targets is often troublesome. In another population of *L. argentina*, Norry and Colombo (1999) demonstrated that, among the morphometric variables considered, only TH seemed to show positive directional selection by using the cubic splines regression technique (Schluter 1988; Schluter and Nychka 1994). In the present study, a different statistical approach was followed; however, the results were consistent in the El Palmar population, showing that the increases in TH and FL are the only significant ones among the measured variables; in Otamendi, on the other hand, FL increased significantly, whereas TH decreased significantly. Furthermore, chi-square analysis showed that karyotype frequency is under selection in both cases, increasing the frequency of fusion homozygotes (Table 2).

The population from Otamendi belongs to the species' southernnmost boundary of distribution (34°10′ S); the El Palmar population lies further north (31°50′ S), with smaller individuals. This agrees with previous experience: it is something of a universal rule among ectotherms that body size increases at lower developmental temperatures (Karl and Fischer 2008). Additionally, body size is usually correlated with longevity (see Partridge and Fowler 1993 for a review). This correlation, however, may be significantly affected by temperature; in *Drosophila* the correlation between body size and longevity changes its sign at low temperature (Norry and Loeschcke 2002). These authors showed that longevity increased with body size in flies at 25°C but, surprisingly, longevity decreased with body size at 14°C. We propose that the longevity selection regime in *L. argentina*, here and elsewhere described, might be another case of temperature-dependent correlation of body size with fitness, as suggested by the interaction between longevity and population.

In other cases it may prove difficult to find selection acting on karyotypes; here we have too many effects. However, all studies converge in showing that: (i) the frequency of fusion 3/6 is indirectly affected, due to the selection on correlated characters; (ii) the fusion is favoured within generations by different components of selection (Colombo 1993; Norry and Colombo 1999; Colombo et al. 2001, 2004); (iii) femur length seems to be an important variable for fitness in this species, given that it was shown that this variable was positively selected in sexual selection studies, both among males and females (Colombo et al. 2001, 2004); and (iv) the frequency of fusion 3/6 is constant among generations. This implies that there must be other fitness components, so far undetected, that negatively affect the fusion frequency. Future studies will focus on such components in order to have a more complete pattern of selection acting on the karyotypic variability in this highly polymorphic species.

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