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Author: Remis, Maria Isabel

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Population differentiation in the grasshopper *Sinipta dalmani*: body size varies in relation to karyotype and climatic conditions

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MARIA ISABEL REMIS

Depto. Ecología, Genética y Evolución, Fac. Cs. Exactas y Naturales. Univ. Buenos Aires. C1428EHA Buenos Aires, Argentina. Fax: (54 11) 45763384. Email: mariar@ege.fcen.uba.ar

Abstract

Sinipta dalmani is an Argentine grasshopper whose chromosome polymorphisms have been widely studied through cytogenetic and fitness-component analyses. This paper reviews the available information on its body-size variations as they relate to differences between sexes, karyotype and mating success, and shows a preliminary analysis of a pattern of geographic variation. A significant body-size sexual dimorphism was evident, with females being significantly larger than males. Polymorphic populations for M_4 pericentric inversion showed considerable variation in both adult male and adult female sizes, a variation in part related to this chromosomal rearrangement, which has a negative effect on body size. Simultaneous cytogenetic, morphometric and fitness analyses showed direct evidence of phenotypic directional selection within populations favoring larger males and smaller females. The patterns of body-size differentiation among populations in relation to geographic conditions suggest local adaptation. Our results in *S. dalmani* demonstrate significant variation in body size within polymorphic populations and among geographical populations, which may be explained under a selective scenario.

Key words

morphometric traits, Orthoptera, body size, karyotype, grasshopper

Introduction

Body-size variation has been the center of many evolutionary studies because it may be a target of natural selection. In insects, size-related traits are often correlated with adult fitness components such as fertility, fecundity, and viability (Taylor & Kekic 1988; Santos *et al* 1988, 1992; Hasson *et al*. 1993; Norry *et al*. 1995; Perfectti *et al.* 2000; Colombo *et al.* 2001, 2004).

Chromosome rearrangements can cause phenotype effects in insects (White & Andrew 1960; White *et al*. 1963; Butlin *et al*. 1982; Hasson *et al.* 1992; Colombo 1997, 2002; Werle & Klekowaki 2004). Therefore the presence of phenotypic variation resulting from chromosome constitution may produce further intraspecific body-size variation on which selection may act.

In Orthoptera, chromosome polymorphisms are frequently encountered. Several recent studies in grasshoppers have shown a significant relationship among karyotype, body size, and fitness components (Perfectti *et al.* 2000; Norry & Colombo 1999; Colombo *et al.* 2001, 2004; Rosetti *et al.* 2007). *Sinipta dalmani* is an Argentine grasshopper for which chromosomal polymorphisms have been widely analyzed (Remis 1989, 1990, 1993). Early cytogenetic studies demonstrated that some natural populations from Entre Rios Province showed a temporally stable polymorphism for a pericentric inversion in the M_4 chromosome pair, which affects chiasma frequency and distribution intra- and interchromosomally (Remis 1989, 1990).

In this paper I review body-size variation in *S. dalmani* as it relates to sex, karyotype and mating success, and I present a preliminary analysis of geographic pattern of body-size variation in order to investigate possible mechanisms underlying phenotypic variation in nature.

Materials and Methods

Morphometric measurements.—Adult males of *S. dalmani* were collected during November-December of 2001 and 2002 from four natural Argentine populations (Table 1). All individuals were measured for five morphometric traits: Total Length: length from the fastigium to the articulation between the third coxa and third femur; Femur Length: length of third femur; Tibia Length: length of third tibia; Thorax Length: length of prothorax; Tegmen Length: length of tegmen. Morphometric traits were measured on the right side of the insect with an ocular micrometer. The results were compared with previous data (Remis 1997, Remis *et al*. 2000, Pensel & Remis 2007).

Data analysis.—We tested for statistical significance among populations through conventional one-way ANOVAs, considering the population as the independent factor and morphometric traits as dependent variables. The phenotypic variation among karyotypes was also evaluated through one-way ANOVAs, considering the population as the independent factor. Differences among karyotypes were also evaluated through the nonparametric Kruskal Wallis test. Variation of body-size related traits due to the M_4 inversion dosage, was analyzed by means of the Kendall correlation. To analyze population variation on a reduced set of independent variants, principal component analyses (PCA) of morphometric variables were also performed. We tested for variation in principal components (PCs) by means of one-way ANOVAs, considering the population as the independent factor and PCs as dependent ones.

The relationships between morphometric traits with respect to geographic (latitude, longitude) and some climatic variables (mean annual precipitation, mean annual temperature, maximum temperature, minimum temperature) were analyzed by means of Kendall nonparametric correlation analysis using STATISTICA (STATISTICS STATSOFT Inc., 1996). Climatic data were obtained through the Local Climate Estimator from www.fao.org/sd/dim_en3/en3_051002_en.

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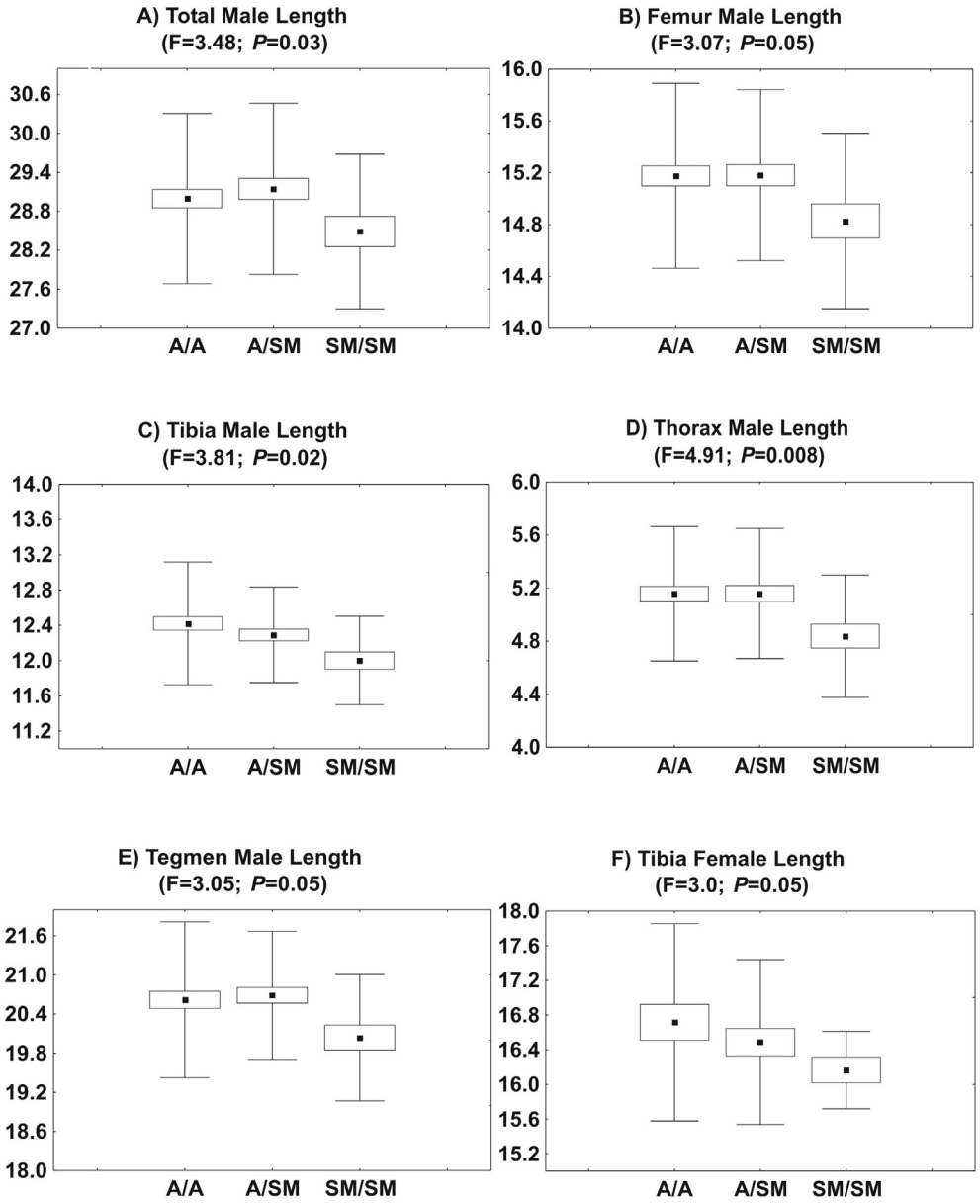


Fig. 1. Mean lengths (points) (in mm), standard errors (boxes) and standard deviations (bars) for morphometric traits in standard homozygotes (A/A), heterozygotes (A/SM) and homozygotes for the inversion M4 (SM/SM) in *S. dalmani*. A-E: data from Remis 1997. F: data from Pensel & Remis 2007.

Results

Relationship between body-size related traits and karyotype.—Populations of *S. dalmani* from National Park "El Palmar" were polymorphic for a pericentric inversion in the M_4 chromosome pair. In a previous work I analyzed morphometric variation pattern in relation to karyotype: morphometric and cytogenetic simultaneous studies were performed in wild individuals from three population samples (Remis 1997). The mean values for five body-size-related traits in individuals with different karyotypes are shown in Fig. 1. Generally, inversion homozygotes produced a decrease in body size.

The individual ANOVAs for each trait in males demonstrated significant and highly significant differences among karyotypes for total, tibia and thorax lengths (Fig. 1A, C, D), and marginally significant differences for femur and tegmen lengths (Fig. 1B, E). Females exhibited the same tendency, with inversion homozygotes being smaller than nonhomozygous individuals, but only tibia length was marginally significant (Fig. 1E). Likewise, the individual Kruskal Wallis ANOVAs demonstrated significant differences among karyotypes for thorax, femur and tibia lengths (χ^2_2=6.34, p=0.04; χ^2_2= 10, p=0.007; χ^2_2= 12,30, p=0.002, respectively) in males, and only for tibia length in females (χ^2_2=6.52, p=0.038).

To analyze the effect of the inversion M_4 on phenotype, Kendall Tau correlations between inversion dosage and each morphometric trait were performed. Significant and highly significant associations were detected between thorax, femur, tibia and tegmen lengths and the dose of inverted chromosomes in males (Z=-2.46, p=0.01, Z=-2.46, p=0.01, Z=-2.46, p=0.01, Z=-2.46, p=0.01) (Remis 1997). In

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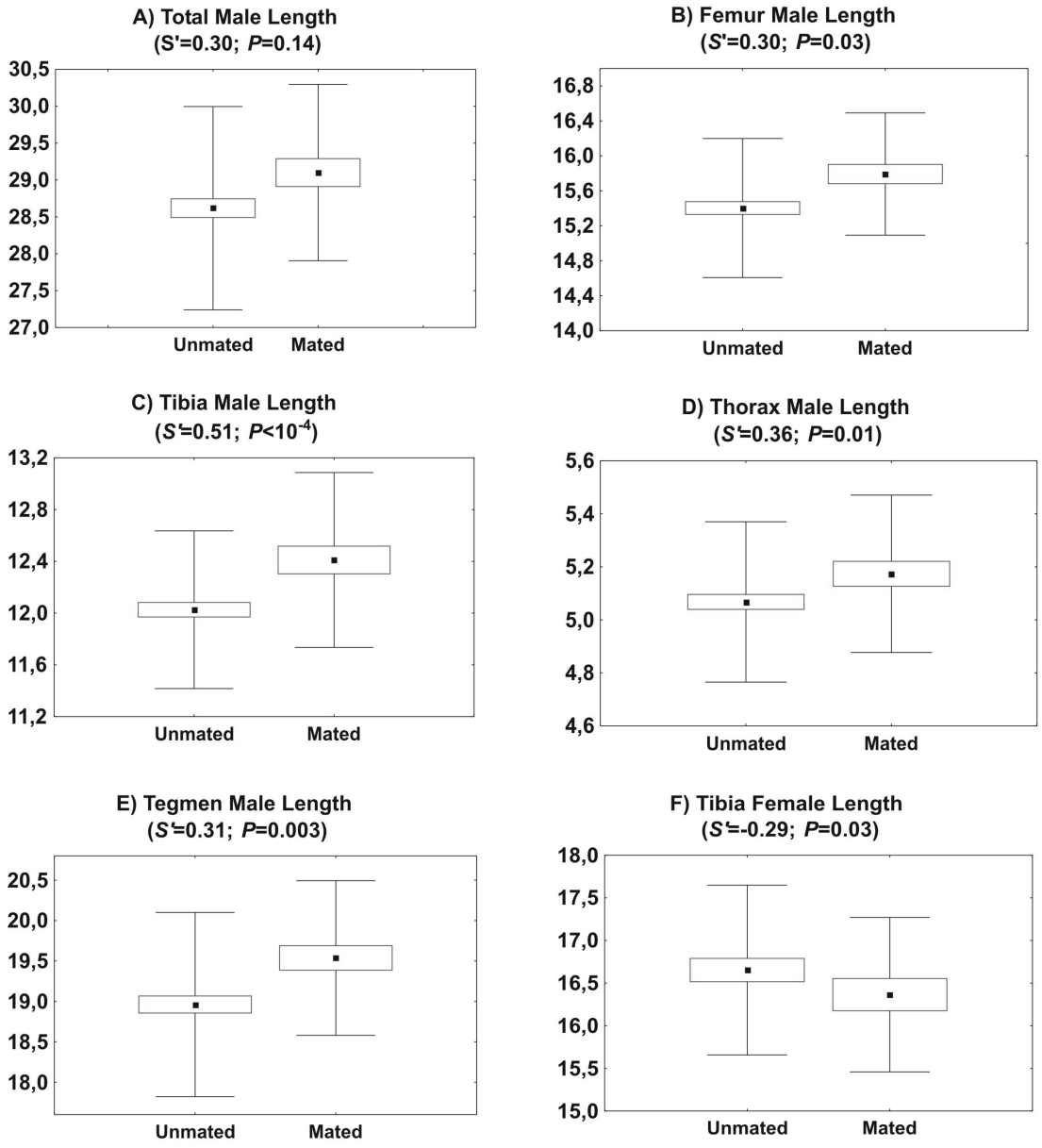


Fig. 2. Mean lengths (points) (in mm), standard errors (boxes) and standard deviations (bars) for morphometric traits in mated males, unmated males, and females of *S. dalmani*. A-E: data from Remis *et al* 2000. F: data from Pensel and Remis 2007.

females, the only significant differences were detected for tibia length (Z=-2.46, p=0.01) (Pensel & Remis 2007). These results suggest that tibia length exhibits an inversion dose effect in both sexes.

To analyse population variation on a reduced set of independent variants, principal component analyses (PCA) were also performed. The first three principal components (PC) for males accounted for about 90% of total variance (Table 2). The PC1 is negatively related with all five body-size related traits and may be considered as a measure of overall size. The PC2 is positively associated with tibia length whereas total and thorax lengths mainly define PC3. The individual ANOVAs revealed highly significant differences among karyotypes only for PC1. The analysis of principal components in females did not render statistically significant differences for any PC (Table 2).

Relationships between body-size related traits and mating success.—We analyzed directional selection on male mating success in competition cages using a unisexual approach during three consecutive years (one female and several males per each competition cage) (Remis *et al*. 2000). In general, mated males are bigger than unmated males (Fig. 2A-E). The univariate study of mating success through the analysis of standardized differentials, showed that directional selection might be acting on four out of the five analyzed traits, favoring bigger individuals.

Female mating success in relation to chromosome and body-size related traits was scored from competition cages using a bisexual approach during two consecutive years (approximately equal number of males and females in each competition cage) (Pensel & Remis

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Table 1. Population mean length (in mm), standard errors in parentheses, for five body-size related traits, and geographic and climatic data for natural populations of *S. dalmani* collected in Argentina. N=sample size, M=males, F=females

Location		Total	Femur	Tibia	Tegmina	Thorax	N	Latitude	Longitude	Max. Temp (°C)	Min. Temp (°C)	Mean Temp (°C)	Mean Ppt. (mm)
El Palmar (EPAM)*	M	13.2 (0.069)	15.5 (0.063)	12.1 (0.052)	19.1 (0.091)	5.09 (0.024)	153	31° 59'S	58° 18'W	24.3	12.6	18.2	102
	F	17.4 (0.14)	21.4 (0.17)	16.7 (0.13)	25.4 (0.22)	7.20 (0.061)	95						
Colón (COLO)	M	10.0 (0.13)	13.1 (0.23)	9.9 (0.15)	15.7 (0.13)	3.81 (0,055)	13	32° 13'S	58° 09'W	23.7	12.2	17.9	101
Isla Talavera (ISTA)	M	9.2 (0.23)	13.0 (0.25)	10.2 (0.21)	16.2 (0.15)	3.93 (0.065)	14	34° 02'S	58° 58'W	21.2	13.5	16.6	75
Escobar (ESCO)	M	9.8 (0.12)	12.6 (0.14)	9.7 (0.11)	15.5 (0.13)	3.75 (0.051)	29	34° 23'S	58° 45'W	22.2	10.2	16.2	87
Tandil (TAND)	M	9.4 (0.16)	14.0 (0.13)	10.9 (0.21)	17.6 (0.98)	4.17 (0.045)	19	37° 19'S	59°09'W	19.8	6.7	12.9	62

* data from Pensel & Remis 2007.

2007). The analysis of standardized selection differentials revealed only directional selection on tibia length favoring females (Fig. 2F).

To distinguish direct and indirect effects of directional selection, we analyzed mating success through a multivariate approach. The analysis of the logistic multiple regression showed tibia length may be considered as a target of sexual selection in both males (α= 1.46, *P*=0.0001) and females (α= -1.67, p=0.01). The effects on the other body-size related traits in males might be considered as indirect effects because of correlated influences.

Variation in body size among populations.—To analyze morphometric variation patterns, the same morphometric traits were scored in individuals from all the studied populations (Table 1). The multivariate analysis of variance (MANOVA) showed highly significant differences among populations ($p<10^{-4}$). The individual ANOVAs also showed highly significant differences among populations in all five morphometric traits (total length $F_{4;229}= 269.14$ $p< 10^{-4}$; 3rd femur $F_{4;229}= 152.03$, $p< 10^{-4}$; 3rd tibia $F_{4;229}= 143.73$, $p< 10^{-4}$; thorax $F_{4;229}= 245.75$, $p< 10^{-4}$; and tegmen $F_{4;229}= 53,92$, $p< 10^{-4}$). Accordingly, the individual Kruskal Wallis ANOVAs for each trait also demonstrated highly significant differences among populations (total length $H_4= 161.7$ $p< 10^{-4}$; 3rd femur $H_4= 153.1$, $p< 10^{-4}$; 3rd tibia $H_4= 146.5$, $p< 10^{-4}$; thorax $H_4= 161.7$, $p< 10^{-4}$; and tegmen $H_4= 141.4$, $p< 10^{-4}$).

To analyze population variation on a set of independent variables, a PCA was also performed. The first three principal components accounted for nearly 95% of the total variation (Table 3). The PC1 is negatively associated with all morphometric traits analyzed and may be considered as a measure of overall size. The tegmen length mainly defines PC2. A positive association with tibia length and a negative association with total length mainly define the third PC, showing that this PC may be considered as a measure of the body shape. The individual ANOVAs showed highly significant differences among populations for PC1 and PC3 (Table 3).

As a general rule, a decrease in morphometric traits was evident when latitude increased and mean temperature decreased (Table 1). Mean values for femur length were correlated negatively with latitude (Z= -2.04, p= 0.04) and positively with mean temperature (Z= 2.04, p= 0.04). The ISTA population was removed from the analysis.

Discussion

The grasshopper *S. dalmani* shows, as do many insect species, body-size sexual dimorphism, with females being significantly larger than males. Sexual dimorphism is considered the result of differences in selection processes acting on body size in both sexes. Sexual selection and fecundity selection have been invoked as the main factors molding such sex differences (Gwynne 1984, Freeman & Herron 1998, Preziosi & Fairbairn 2000).

Additionally, in natural populations of *S. dalmani*, we detected significant body-size variation related to the M_4 pericentric inversion polymorphism. This rearrangement is associated with a significant decrease in body-size related traits, and is most evident in males (Remis 1997, Pensel & Remis 2007). ANOVA's revealed a chromosome (genetic) component in the determination of total and thorax length in males and tibia length in both sexes. Thus it is possible to analyze the variation among different karyotypes with the genetic variance of the trait under study (Ruiz *et al.* 1991). The analysis of the relationships between body-size-related traits and karyotype, revealed a chromosome-dose effect only for tibia length in both sexes. This last result suggests that the variation in tibia length associated with the M_4 is largely additive. Genetic additive variation is essential to evolutionary changes because it represents the material on which selective factors act.

Our experiments also demonstrated that the above phenotypic traits influenced fitness. The analysis of male mating success during three consecutive years, revealed that phenotypic directional selection seemed to favor bigger males and standard homozygotes seemed to be the fittest karyotype (Remis *et al.* 2000). Analyses of mating success in females during two consecutive years, established the opposite effects of phenotypic sexual selection to those detected in males, favoring smaller females (Pensel & Remis 2007). Analysis of the selection gradient demonstrated that tibia length might be considered as the most probable target of selection in both sexes. Thus directional selection acts in opposite directions, favoring males with larger tibias and females with smaller tibias. In this species, females often fight, jump, and repel suitors. Males with larger tibias might be better able to secure and subsequently maintain a hold upon struggling females. Smaller females, with smaller tibia, may possibly have less ability to repel suitors. However, we do not

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Table 2. Factor loadings on the three first principal components (PCs) for males and females of *S. dalmani* from the polymorphic population of "El Palmar" and "F" values from individual ANOVAs performed to test phenotypic differences among karyotypes. Bold-type values show the traits with the highest factor loading on each PC.

	Males			Females		
	PC1	PC2	PC3	PC1	PC2	PC3
Total	**-0.853**	0.0415	**0.387**	**-0.785**	**0.333**	**0.375**
Femur	**-0.867**	-0.2700	-0.041	**-0.845**	0.055	**-0.375**
Tibia	**-0.627**	**0.740**	-0.237	**-0.751**	**-0.487**	**0.369**
Tegmina	**-0.909**	0.015	0.203	**-0.814**	**-0.325**	**-0.277**
Thorax	**-0.796**	**-0.350**	**-0.415**	**-0.809**	**0.399**	-0.037
Eigen values	**3.333**	**0.745**	**0.422**	**3.211**	**0.616**	**0.496**
Cumulative % Variance	**66.7**	**81.6**	**90.0**	**64.2**	**76.5**	**86.5**
$F_{(2,173)}$	**4.94**	**0.48**	**1.17**	**0.08**	**1.45**	**0.89**
p	**0.008**	**0.62**	**0.31**	**0.92**	**0.24**	**0.41**

know at this time if these morphological differences actually do relate to differences in mating success, or how they might relate to signals affecting sex preference. Moreover, our observations are laboratory-based, and may be invalid in nature.

In spite of these differences, the M_4 polymorphism seems to be stable over time, suggesting that it may influence trade-offs between detrimental and favorable properties on different fitness components (Remis et *al.* 2000, Pensel & Remis 2007). Sexual selection for larger males and smaller females does not explain sexual dimorphism in body size in this species. Selective processes related to body-size dimorphism may be much more complex and may involve other fitness components, which remain unstudied in this species.

Many species of arthropod exhibit body-size variation among populations and such variation has often been related to adaptation to different environmental conditions (for review see Blanckenhorn & Demont 2004). In grasshoppers and crickets, there are many examples in which body size decreases with latitude or altitude, exhibiting a converse pattern to Bergmann's rule (Masaki 1967, Telfer & Hassall 1999, Mousseau & Roff, 1989, Colombo 2002, Bidau & Marti 2007). Moreover in some cases, the genetic basis of the population differences have been demonstrated in common-garden laboratory conditions (Masaki 1967, 1972; Mousseau & Roff 1989). At higher altitudes and latitudes, temperatures are likely to be lower, reducing the duration of the growing season (Masaki 1967). Individuals from lower-temperature habitats sometimes develop faster and are smaller when reared under identical conditions with conspecific individuals from high-temperature habitats (Orr 1996).

In the present preliminary analysis of genetic variation in body size in *S. dalmani*, we detected significant differences among populations in all studied body-size related traits. Moreover, total length, as a general index of body size, correlates negatively with latitude and positively with mean annual temperature in this species. Thus, the analyzed populations of *S. dalmani* followed the converse of Bergman's rule. Mean annual temperature may have a main impact on phenotypic patterns, because it constitutes a good indicator of the duration of suitable conditions for development and reproduction (Roff & Mousseau 2005). The detected decrease in body size at higher latitudes (lower temperature) may be another example of selection for shorter development time.

In *S. dalmani* we demonstrated adaptive changes in body size at two levels. Firstly, changes in body size occur within polymorphic populations and may be achieved through directional selection on chromosome polymorphism with phenotype effects. Secondly, body size varies among populations, and thus may be the result of climatic selection on genes that affect phenotype.

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Table 3. Factor loadings on the three first principal components (PCs) for *S. dalmani* males and "F" values from individual ANOVAs performed to test phenotypic differences among populations. Bold type values show the traits with the highest factor loading on each PC.

	PC1	PC2	PC3
Total	**-0.908**	-0.120	**-0.376**
Femur	**-0.943**	-0.131	0.184
Tibia	**-0.939**	-0.091	**0.244**
Tegmina	**-0.793**	**0.609**	-0.013
Thorax	**-0.942**	-0.174	-0.052
Eigen values	4.106	0.441	0.237
Cumulative % Variance	82.11	90.94	95.68
$F_{(4,229)}$	**313.7**	**1.95**	**24.5**
p	**$<10^{-4}$**	**0.10**	**$<10^{-4}$**

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