

Spatial Variation in Body Size and Wing Dimorphism Correlates With Environmental Conditions in the Grasshopper *Dichroplus vittatus* (Orthoptera: Acrididae)

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Subject Editor: Darrell Ross

Received 21 November 2017; Editorial decision 29 January 2018

Abstract

Wing dimorphism occurs widely in insects and involves discontinuous variation in a wide variety of traits involved in flight and reproduction. In the current study, we analyzed the spatial pattern of wing dimorphism and intraspecific morphometric variation in nine natural populations of the grasshopper *Dichroplus vittatus* (Bruner; Orthoptera: Acrididae) in Argentina. Considerable body size differences among populations, between sexes and wing morphs were detected. As a general trend, females were larger than males and macropterous individuals showed increased thorax length over brachypterous which can be explained by the morphological requirements for the development of flight muscles in the thoracic cavity favoring dispersal. Moreover, when comparing wing morphs, a higher phenotypic variability was detected in macropterous females. The frequency of macropterous individuals showed negative correlation with longitude and positive with precipitations, indicating that the macropterous morph is more frequent in the humid eastern part of the studied area. Our results provide valuable about spatial variation of fully winged morph and revealed geographic areas in which the species would experience greater dispersal capacity

Key words: wing dimorphism, morphometric traits, Orthoptera, environmental condition

Many studies demonstrated the relevance of the relationship between morphological variation and adaptation to environmental and ecological variables in animals (Masaki 1972, Karr and James 1975, Johansson et al. 2001, Rikiya et al. 2002). Dispersal capacity by flight is an important adaptive trait in insects, because it allows individuals to locate new food sources and favorable habitats for their survival and reproduction (Johnson 1969). Wing dimorphism is a widespread phenomenon in many insect groups and has ecological and evolutionary consequences (Harrison 1980, Roff 1986). Wing dimorphic populations are represented by two classes of individuals with different wing lengths. Short-winged or brachypterous are adapted to prompt reproduction in a suitable habitat whereas long-winged or macropterous show a delay in the onset of reproduction and reduced fecundity, however, they can migrate between habitats in response to adverse environmental conditions, and hence this morph has a potential advantage when the environment is temporally and spatially heterogeneous (Southwood 1962, Dingle 1980, Harrison 1980, Roff 1990, Denno et al. 1991). Dispersal capacity by flight is an important adaptive trait in insects, in this regard, it was suggested that there is a trade-off between flight and reproduction in wing polymorphic insects (Roff 1986, Zera and Denno 1997, Tanaka and Suzuki 1998, Guerra and

Pollack 2007, Guerra 2011), where females of flying morph reduce reproductive performance as a cost of their increased dispersal capability. The trade-off in wing dimorphic males is less evident; however there are some studies where the relationship between wing morphs includes calling effort (Crnokrak and Roff 1995), gonad development spermatophore size (Sakaluk 1997, Zeng and Zhu 2012), courtship behavior and mating system (Guerra and Pollack 2007, Steenman et al. 2015). In Orthoptera, several wing dimorphic species are predominantly brachypterous whereas in other species macropterous is the most common morph (Van Dyck and Matthysen 1999; Steenman et al. 2013, 2015). Changes in morphological traits related to flight can vary with latitude or habitat due to differences in climate. In other cases, macropterous is the most common morph.

Species with widespread, latitudinal and longitudinal geographic ranges are useful models for analyzing body size distribution at intraspecific levels; in addition flight-related morphological changes may be complex processes and vary with climatic and geographic variables (Feng et al. 2016).

Dichroplus vittatus (Bruner; Orthoptera: Acrididae) is a South American grasshopper with agronomic importance in Argentina that is found in either the short-winged (brachypterous) or fully-winged

(macropterous) morphs. Brachypterous form (tips of tegmina barely reaching fifth abdominal tergite) is the most frequent morph in populations (Turk and Barrera 1979, Cigliano and Otte 2003) and may be considered as the original morph.

Previous studies analyzed geographic body size variation in populations of South America. In males it were verified a converse latitudinal Bergmann cline and an increase in body size variation which may be explained by a combination of a shorter growing season, increasing seasonality limiting available resources, and sexual size dimorphism resulting, partially, from protandry (Bidau and Marti 2007).

In order to give deeper insights about intraspecific variation associated with body size in this wing dimorphic species we analyze populations of *D. vittatus* from Central West Argentina. The particular objectives were: 1) analyze morphometric variation in natural populations related with geographic location, sex and wing morph; 2) characterize morphometrically different morphs for tegmen length; 3) evaluate morphometric differences in body size between wing morphs; 4) analyze pattern of spatial variation in wing morph incidence.

Materials and Methods

Biological Material and Body Size Measurements

A total of 273 adult males and females were collected in nine Argentinian natural populations of the grasshopper *D. vittatus* belonging to Pampeana (Castex [CAS], Winifreda [WIN], Santa Rosa [SRO]); Espinal (Santa Rosa de ConLara [CLA], Tilisarao [TIL], La Toma [LTA], Parque Luro [PLU]) and Monte (Lihuel Calel [LIH], Puelches [PUE]) biogeographic provinces (Fig. 1A, Table 1 Supplemental Material). All individuals were measured for five morphometric traits total body, third femur, third tibia, tegmen, and thorax lengths. Total body size was measured from the fastigium to the third coxa (according to Colombo et al. 2004). All measurements were performed on the right side of the insect, with a stereoscopic microscope and an ocular micrometer (1 mm = 48 ocular units).

Statistical Analysis

All statistical analyses were performed considering two main datasets: 1) the measurements of all nine analyzed populations where brachypterous individuals were present and 2) the measurements from four polymorphic populations where brachypterous and macropterous individuals coexist. We performed a multivariate analysis of variance (MANOVA) to estimate morphometric differences among populations and between sexes for the five morphometric traits measured in group 1. The analysis was carried out among populations, sexes and wing morphotypes comparing the mean values of four morphometric traits (we excluded tegmen length for this analysis) for group 2. We also tested for statistical significance among populations, wing size morphs and sexes through three-way ANOVAs, considering population, and sex as the independent factors for group 1 and population, wing size and sex for group 2; and body size related traits as the dependent variables. We analyzed population variation on a reduced set of independent variables, to avoid the problem of pseudoreplication. Principal Components Analyses (PCA) of body size related variables were also performed. We tested for variation in the first principal components (PCs) by means of individuals ANOVAs considering the population, wing size and sex as the independent factors and PCs as dependent ones. All analyses were carried out using InfoStat software (InfoStat 2008).

Furthermore, we performed a Principal Coordinates analysis (PCoA) to explore and visualize similarities or dissimilarities of morphometric dataset. PCoA starts with a distance matrix and assigns for each variable a location in a low-dimensional space. In order to define clusters according wing morph and sex, we performed a PCoA using Gower distance matrices in PAST software (Hammer et al. 2001).

In order to understand more deeply the relationship between morphometric traits and wing polymorphism we analyzed the coefficient of variation (CV), which represents the ratio of the standard deviation to the mean and it is a useful statistic for comparing the degree of variation from different data sets. We assess the differences in the extent of variability among populations and between sexes

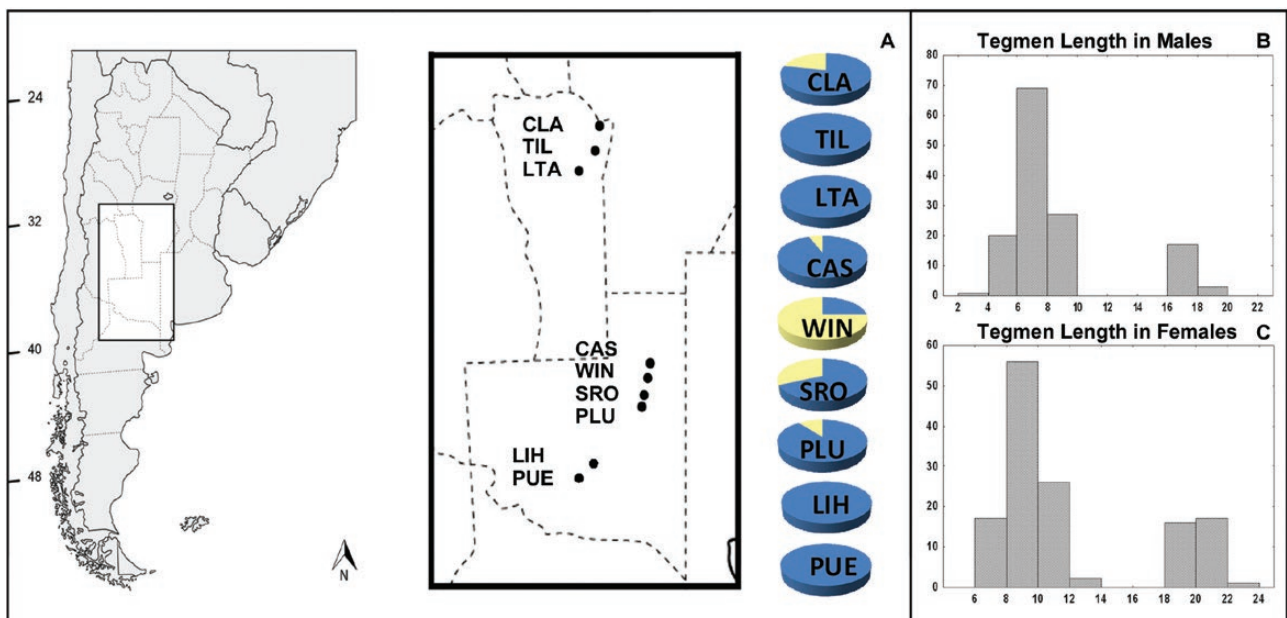


Fig. 1. Geographical distribution of the nine analyzed populations of *D. vittatus* indicating relative frequencies of macropterous (yellow online/white in printed version) and brachypterous individuals (blue on line/grey in printed version) in pie diagrams (A). Histograms showing bimodal distribution for tegmen length for males (B) and females (C).

Table 1. Mean length values (in mm) and standard error in brackets for five body size related traits of brachypterous and macropterous individuals in 9 natural populations of *D. vittatus*

			Total	Thorax	Femur	Tibia	Tegmen	N
Brachypterous	CAS	Males	7.23 (0.55)	3.96 (0.19)	11.11 (0.59)	8.93 (0.58)	7.69 (0.50)	16
		Females	9.28 (0.68)	5.57 (0.41)	15.14 (0.89)	12.42 (0.47)	10.48 (0.72)	16
	SRO	Males	7.86 (0.21)	4.09 (0.15)	11.06 (0.61)	8.67 (0.45)	8.00 (0.71)	14
		Females	8.34 (0.31)	5.96 (0.18)	13.97 (0.66)	11.29 (0.95)	10.17 (0.84)	18
	PLU	Males	8.08 (0.12)	3.96 (0.13)	10.97 (0.44)	8.47 (0.35)	7.99 (0.99)	22
		Females	8.49 (0.18)	5.97 (0.22)	14.27 (0.45)	11.79 (0.68)	9.51 (0.45)	12
	WIN	Males	8.02 (0.17)	3.89 (0.11)	10.97 (0.45)	8.29 (0.36)	7.46 (0.71)	6
		Females	8.68 (0.12)	5.83 (0.21)	15 (0.55)	11.87 (0.63)	10.69 (0.48)	3
	CLA	Males	7.84 (0.28)	3.86 (0.22)	10.66 (0.61)	8.45 (0.36)	7.06 (0.73)	11
		Females	8.56 (0.25)	4.96 (0.16)	14.24 (0.71)	11.80 (0.86)	9.13 (0.78)	11
	TIL	Males	7.71 (0.26)	3.71 (0.23)	9.46 (0.70)	7.79 (0.46)	6.42 (0.74)	5
		Females	8.68 (0.21)	4.95 (0.17)	13.52 (0.49)	11.90 (0.32)	8.43 (0.30)	10
	LTA	Males	8.02 (0.12)	3.92 (0.12)	10.28 (0.13)	8.35 (0.21)	7.08 (0.55)	3
		Females	8.68 (0.17)	5.07 (0.15)	13.82 (0.31)	10.63 (0.42)	8.96 (0.47)	12
	PUE	Males	6.21 (0.51)	3.70 (0.28)	9.98 (0.69)	7.77 (0.56)	5.75 (0.63)	24
		Females	7.94 (0.44)	4.82 (0.23)	12.31 (0.66)	9.73 (0.80)	7.81 (0.59)	19
	LIH	Males	6.61 (0.39)	3.54 (0.17)	9.97 (0.39)	7.32 (0.58)	5.42 (0.38)	7
		Females	7.67 (0.50)	3.84 (0.17)	10.36 (0.21)	8.16 (0.24)	6.94 (0.17)	5
Macropterous	CAS	Males	—	—	—	—	—	—
		Females	9.27 (1.32)	5.63 (0.88)	15.21 (0.59)	12.50 (0.29)	20.10 (0.15)	2
	SRO	Males	8.07 (0.26)	4.22 (0.32)	11.09 (0.66)	8.96 (0.45)	17.71 (0.78)	4
		Females	8.41 (0.48)	6.00 (0.21)	14.42 (0.68)	11.38 (1.07)	20.02 (0.59)	11
	PLU	Males	8.23 (0.15)	4.16 (0)	11.25 (0.29)	8.85 (0.44)	16.98 (0.15)	2
		Females	8.54 (0.29)	6.14 (0.15)	14.69 (0.44)	11.98 (1.62)	20.11 (1.33)	2
	WIN	Males	8.04 (0.18)	3.96 (0.14)	11.27 (0.40)	8.60 (0.39)	17.46 (0.98)	10
		Females	8.69 (0.26)	5.90 (0.18)	13.86 (0.91)	11.20 (1.17)	20.31 (0.77)	17
	CLA	Males	7.86 (0.10)	3.96 (0.29)	10.88 (1.16)	8.49 (0.35)	16.82 (0.49)	4
		Females	8.85 (0.44)	5.21 (0.29)	13.33 (0.29)	10.94 (0.74)	20 (1.47)	2

N = sample size.

and wing morphotypes taken into account the same partitioning of the data set in two main groups as above, by means of nonparametric Mann-Whitney *U* tests, using InfoStat software (InfoStat 2008).

The relationships between body size related traits and climatic variables (mean, maximum and minimum temperature and annual precipitations) were analyzed using Spearman partial correlations. Climatic data were obtained through the Local Climate Estimator from www.fao.org/sd/dim_en3/en3_051002_en. Bonferroni's test for multiple comparisons was applied, using Statistica software (Statistica Statsoft Inc. 1996).

Results

Differences in Body Size Among Populations, Between Sexes and Between Wing-Morphs

There is an extensive variation in tegmen length in males and females proving a bimodal distribution (Fig. 1B and C). We verified the existence of two distinct wing morphs: brachypterous and macropterous. In males the mean tegmen lengths were 17.24 mm and 6.96 mm in macropterous and brachypterous individuals respectively whereas the mean length values of macropterous and brachypterous females were 20.17 mm and 9.09 mm correspondingly.

We found a considerable body size variation in brachypterous individuals among populations (Wilks' $\lambda_{8,212} = 0.066$, $P < 10^{-4}$) and sexes (Wilks' $\lambda_{1,212} = 0.087$, $P < 10^{-4}$). The individual ANOVAs reveal highly significant differences in both levels (population and sexes) in all analyzed body size related traits (Table 2) including tegmen length demonstrating that brachypterous individuals exhibited

Table 2. *F* statistic values and their significance levels (*P*) from one-way ANOVAs achieved to analyze differentiation among populations and between sexes in nine populations where brachypterous individuals were present

	Population		Sex	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Total	44.3	<10⁻⁴	239.1	<10⁻⁴
Thorax	50.2	<10⁻⁴	1691.6	<10⁻⁴
Femur	36.6	<10⁻⁴	1133.4	<10⁻⁴
Tibia	31.5	<10⁻⁴	986.7	<10⁻⁴
Tegmen	51.6	<10⁻⁴	387.2	<10⁻⁴

Significant values are in bold type.

significant variation in the length of the short-wing. As a general factor female are larger than males.

In a second examination we analyze phenotype variation in the four wing polymorphic populations in which macropterous and brachypterous individuals were found in both sexes (WIN, SRO, PLU and CLA) (Table 1). The PCoA described the phenotypic variation graphically (Fig. 2). The PCoA revealed four groups: macropterous males, macropterous females, brachypterous males and brachypterous females, thus, the scatterplot effectively showed that both wing morph and sexes are strongly differentiated within each population. In addition, it was also observed that macropterous females occupied a larger area in the scatterplot suggesting highest phenotypic variability.

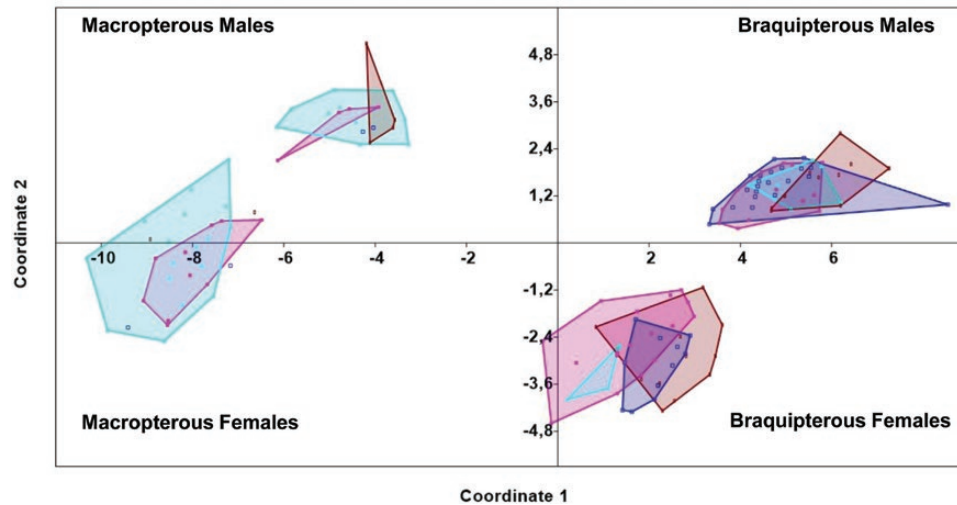


Fig. 2. PCoA applied to the Euclidean distance matrix describing similarities/dissimilarities among four wing dimorphic populations of *D. vittatus*, based on four morphometric traits. Convex polygons encompass the individuals from the Santa Rosa, Winifreda, Parque Luro, Santa Rosa de Conlara populations, respectively.

The MANOVA considering four morphometric traits as indexes of body size (total length, and lengths of thorax, third tibia and third femur) revealed variation among populations (Wilks' $\lambda_{3;148} = 0.36$, $P < 10^{-4}$), sexes (Wilks' $\lambda_{1;148} = 0.065$, $P < 10^{-4}$) and wing morphs (Wilks' $\lambda_{1;148} = 0.88$, $P = 0.001$). Individual ANOVAs showed significant variation among populations for total and thorax lengths, between sexes for all analyzed traits and between wing morphs for thorax lengths (Table 3). In order to describe phenotypic variation in each sex we performed MANOVAs and ANOVAs for females and males separately. MANOVA analysis for females showed significant variation among populations (Wilks' $\lambda_{3;75} = 0.18$, $P < 10^{-4}$) and between wing morphs (Wilks' $\lambda_{1;75} = 0.82$, $P = 0.012$). Individuals ANOVAs demonstrated significant differentiation among populations for total and thorax lengths and between wing morphs for thorax length (Table 4). The MANOVA using male dataset indicated significant differentiation among populations (Wilks' $\lambda_{3;72} = 0.54$, $P < 10^{-4}$). Individual ANOVAs showed significant variation among populations for total and thorax lengths and between wing morphs for thorax and tibia lengths (Table 4). The analyses demonstrated again that females are larger than males and as a general tendency that macropterous individuals were larger than brachypterous in both sexes (Fig. 3).

We also studied morphometric variation on a reduced set of independent variables with PCA. The analysis considering brachypterous individuals in all studied populations showed that first PC (PC1) accounted for about 90% of total variation whereas the PCA study taken into account polymorphic populations demonstrated that PC1 explained 93.1% of total variation. The first PC in both cases was highly and positive correlated with all body size related traits allowing us to consider this component as an adequate estimator of overall body size (Table 5A and B). The individual ANOVAs using PC1 instead of original data revealed highly significant differences among populations ($F_{8;212} = 368.7$, $P \leq 0.0001$) and between sexes ($F_{1;212} = 968.5$, $P \leq 0.0001$) for brachypterous individuals from all analyzed populations. Additionally, highly significant differences among populations ($F_{3;148} = 78.8$, $P \leq 0.0001$), between sexes ($F_{1;148} = 2371.2$, $P \leq 0.0001$) and wing morphs ($F_{1;148} = 49.2$, $P \leq 0.0001$) were detected when we analyzed the differentiation in wing dimorphic populations.

Table 3. *F* statistic values and their significance levels (*P*) from one-way ANOVAs achieved to analyze differentiation among populations, between sexes and wing morphs in four polymorphic populations

	Population		Sex		Wing morph	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Total	2.97	0.034	98.19	<10⁻⁴	3.22	0.075
Thorax	39.52	<10⁻⁴	1756.62	<10⁻⁴	9.28	0.002
Femur	2.46	0.065	508.76	<10⁻⁴	0.081	0.772
Tibia	0.65	0.583	306.83	<10⁻⁴	0.04	0.851

Significant values are in bold type.

For brachypterous morph the levels of variation differed significantly between sexes being males significantly more variable than females for tegmen length ($Z = -2.61$, $P = 0.008$). For macropterous individuals the pattern is inverted and females show significantly greater variability than males for total ($Z = 2.02$, $P = 0.043$) and tibia lengths ($Z = 2.31$, $P = 0.021$) (Fig. 4). No significant variation was observed between male wing morphs ($P \geq 0.05$ in all cases). The nonparametric comparisons showed that macropterous females are marginally more variable than brachypterous ones for total length ($Z = -1.73$, $P = 0.07$) and tibia length ($Z = -1.73$, $P = 0.08$) (Fig. 4).

Spatial Variation in the Frequencies of the Different Wing-Morphs

The frequency of brachypterous and macropterous forms varied between the nine analyzed populations from Argentina (Fig. 1). Five out of the nine analyzed populations are wing dimorphic, while the remaining four are composed only of brachypterous individuals. Among polymorphic populations, WIN showed the higher frequency of macropterous individuals. The frequency of macropterous individuals, which varied ranging from 0 to 75%, correlated negatively with longitude ($r = -0.77$; $P = 0.009$) and positively with precipitations ($r = 0.85$; $P = 0.001$). This result indicated that macropterous morph is more frequent in the humid eastern environment of the studied area.

Discussion

Wing dimorphism is usually viewed as a response to heterogeneous environments in which no single morph is favored (Zeng and Zhu 2014). In general, reduced wing morph is most frequent in stable habitats; winged morph is common in unstable habitats whereas both wing morphs are usually present in heterogeneous habitats of intermediate quality establishing a dimorphic population (Javinen and Vepsäläinen 1976, Denno 1994, Denno et al. 1996).

Table 4. F statistic values and their significance levels (P) from one-way ANOVAS to analyze differentiation among populations and between wing morphs for females and males in four polymorphic populations

	Population		Wing morph	
	F	P	F	P
Females				
Total	3.73	0.015	1.12	0.294
Thorax	43.19	<10⁻⁴	4.15	0.045
Femur	1.48	0.227	1.62	0.207
Tibia	0.61	0.613	0.97	0.328
Males				
Total	4.20	0.008	2.93	0.092
Thorax	5.27	0.002	5.24	0.025
Femur	1.01	0.392	1.53	0.221
Tibia	2.50	0.067	4.55	0.036

Significant values are in bold type.

The dataset of the present paper verified that *D. vittatus* exhibit two different wing morphs brachypterous and macropterous that occurred in both sexes, in Central-West Argentina. In *D.vittatus* brachypterous form is the most frequent morph in populations (Turk and Barrera 1979, Cigliano and Otte 2003) and may be considered as the ancestral morph. Out of the nine analyzed populations, four were found to be dimorphic for wing size, while the rest of the populations are composed exclusively of brachypterous individuals, which suggests a stable habitat for those locations. It is generally accepted that macropterous individuals exhibit higher mobility and dispersal range than brachypterous individuals. Thus, macropterous individuals can occupy new habitats and expand faster than brachypterous morphs (Zera and Denno 1997). Among the four polymorphic populations, WIN showed higher frequency of macropterous than brachypterous, this allowed us to assume that WIN could represent the most unfavorable habitat or one of recent colonization.

In several insect species winged and wing reduced morphs have been shown to differ in a variety of traits involving body proportions and size, survival, development time and pattern of egg production (e.g., Roff 1984, Zera 1984, Dingle 1985). In insects, wing length is assumed to reflect a trade-off between dispersal and fecundity (for review see Guerra 2011). Macropterous individuals are flight-capable at the expense of reproduction, while brachypterous cannot fly, are less mobile, but have greater reproductive output. The macropterous female exhibits a variety of characteristics associated with flight, including fully developed thoracic wing musculature and heavy sclerotization of head and thorax. The brachypterous female

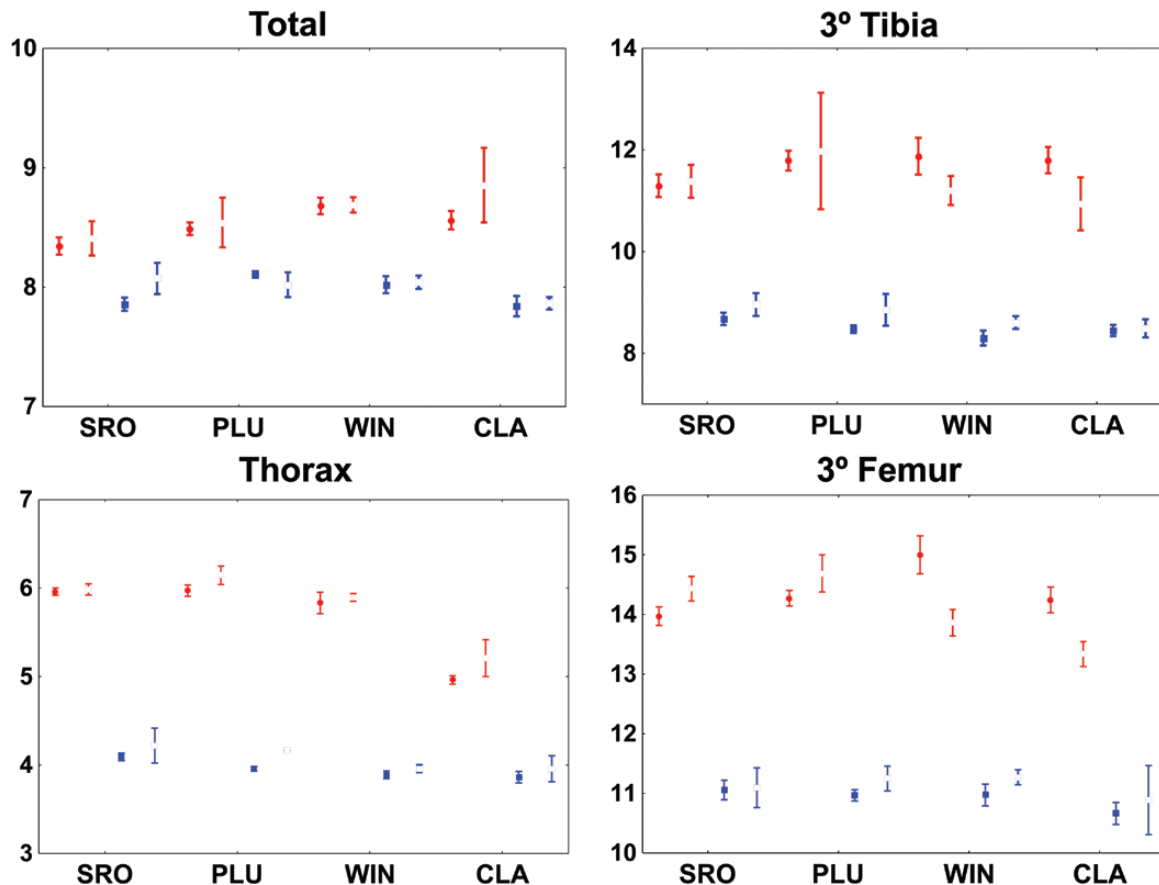


Fig. 3. Mean values (primary symbols) and standard errors (bars) for four morphometric traits in males (squares) and females (circles) belonging to four dimorphic populations (solid symbols: brachypterous; open symbols: macropterous).

Table 5. Factor loadings, eigenvalues, and cumulative percentage of variance on the two PCs for (A) nine populations where brachypterous individuals are present and (B) four polymorphic populations

(A)	PCA1	PCA2
Total	0.41	0.84
Thorax	0.45	-0.43
Femur	0.46	-0.24
Tibia	0.46	-0.21
Tegmen	0.45	0.12
Eigenvalues	4.50	0.32
Cumulative percentage of variance	90	97
(B)		
Total	0.47	0.86
Thorax	0.50	-0.44
Femur	0.51	-0.21
Tibia	0.51	-0.16
Eigenvalues	3.72	0.21
Cumulative percentage of variance	93	98

The highest loading of each trait in bold type.

produces no wings or wing rudiments and smaller or inactive thoracic muscles (Kalmus 1945, Kring 1977, Kawada 1987, Tsuji and Kawada 1987). In a comparison of winged and non-winged species of craneflies Byers (1969) noted that in the brachypterous forms (non-winged) the ovaries extend into the thoracic cavity, which in macropterous forms (winged) is filled with the flight muscles. In some cricket species (e.g., *Gryllus firmus* Scudder (Orthoptera: Gryllidae)) the musculature of thorax was found to be significantly weaker in brachypterous females but the genitalia were more developed; thus a trade-off of these characters was suggested (Roff 1986, Roff and Bradford 1996, Zera et al. 1997).

D. vittatus showed significant differentiation in body size among populations and female biased body size dimorphism as reported before (Bidau and Marti 2007). We also demonstrated significant differences in body size between wing morphs within each sex, macropterous females are larger than brachypterous for thorax length and macropterous males are larger comparing with brachypterous males for thorax and third tibia lengths. In an evolutive context, several examples pointed out that macropterous phenotype differs from the brachypterous morph, as mentioned before by showing higher mobility and dispersal range,

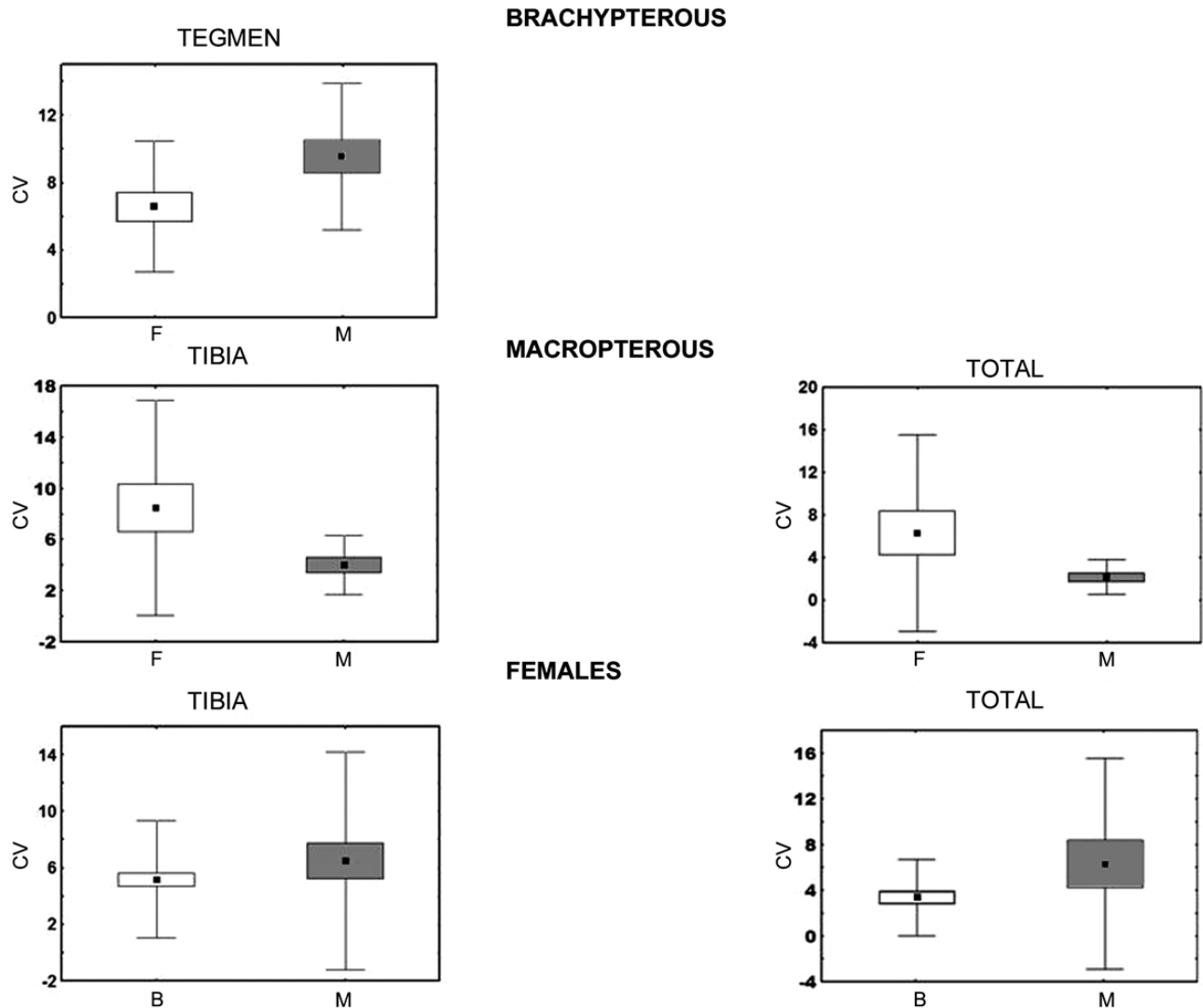


Fig. 4. Mean CV (primary symbols), standard error (boxes), and confidence interval (bars) for significant different morphometric traits between wing morphs and sexes.

and moreover by displaying a longer developmental time, longer reproductive period, smaller eggs, lower offspring production and prolonged longevity (MacKay and Wellington 1975, Zeng and Zhu 2012, Steenman et al. 2015). In *D. vittatus*, though dispersal range of different morphs still remains to be studied. However, the fact that macropterous males and females are larger than brachypterous can be related with the morphological requirements for the development of flight muscles in the thoracic cavity favoring dispersal from the current habitat.

Previous studies analyzing pattern of morphometric variation in populations with reduced wing individuals of *D. vittatus* showed a decrease in male body size with a simultaneous increase in morphometric variables with latitude. These patterns were attributed to some factors such as the period of growing season, the increasing seasonality and protandry (Bidau and Marti 2007, 2008). Moreover, the authors showed that the degree of SSD increased significantly with general body size and most analyzed traits scaled allometrically according to the converse of Rensch's rule suggesting a larger phenotypic variation in females than male size (Bidau and Marti 2008). We found that within brachypterous phenotype (the ancestral morph), males tend to be the most variable sex for tegmen length, following the tendency observed in other protandry species of grasshopper, whereas for macropterous we detected an opposite tendency being females the most variable for total and third tibia lengths. The analysis of the differences in body size variability among wing morph within each sex may clarify some aspects. The data provide by Steenman et al. (2013) in *Tetrix subulata* sustained the idea that derived wing morph (brachypterous morph in this case), which may occur by a switch from one development program to another, will exhibited major phenotypical variation. In the studied area, we detected that males do not evidence differences in morphological variation between macropterous and brachypterous, while macropterous females were the most phenotypic diverse supporting the hypothesis mentioned above.

Wing morph differences can be attributed to variation in genotype and/or, response to variation in the environment (Zera 2016). In hemimetabolous insects in general and in Orthopteran in particular, are generally controlled by polygenic inheritance (Roff and Fairbairn 2007) so that wing morph can result most commonly from a combination of both genetic and environmental variation (Harrison 1980, Zera and Denno 1997, Zera and Brisson 2015).

The relative contribution of genetic and environmental components can vary among different genetic systems and factors that affect adaptation (Zera and Denno 1997, Ikeda and Sota 2011). Thus, the different flight ability can be maintained in heterogeneous spatiotemporal conditions based on the particular trade-off between dispersal capability and reproduction in each biological model (Roff and Fairbairn 1991, Zera and Denno 1997, Roff et al. 1999, Fox and Czesak 2000, Jonsson 2003).

There are several examples of diverse environmental conditions affecting the frequencies of wing morphotypes such as temperature, photoperiod, rains etc. (Ingrisch and Köhler 1998, Rikiya et al. 2002, Nardi et al. 2008, Perner and Simpson 2009, Poniatowski and Fartmann 2009). Wing dimorphism in *D. vittatus* might be influenced by both precipitation and longitude. Thus, higher proportions of macropterous occurred in eastern populations of the studied area with higher humidity in an attempt to find drier and suitable environments, this may be due to the greater nutritional value of the vegetation that grows in the most arid places for these insects. The seasonality and/or growing season which vary at longitudinal scale can also be a factor that increases the production of macropterous individuals in eastern populations, since they are responsible for

population dispersal and colonization of new favorable areas. In this scenario, the increase in thorax length and in body size variation in fully winged individuals can be seen as a parallel effect in the attempt of the population of reaching more suitable environments for reproduction.

The most widely accepted physiological mechanism to explain wing polymorphism is related mainly with hormones. Ecdysteroids and specially juvenile hormone have been proposed as key regulators of the expression of morph-specific traits during the juvenile and adult stages (Zera 2016). The insects for which detailed information is available on the endocrine mechanisms underlying morph determination are the *Gryllus* crickets (Zera 2009, 2016; Zera and Brisson 2015).

In this point it was recognized the importance to examine the expression of genes known to be involved in the metabolism and transport of juvenile hormone to explain the differences in the level of this hormone in different wing morphs. In addition to being environmentally determined, aphid wing dimorphism has also been shown to be under epigenetic control (Simpson et al. 2011). The role of epigenetics in wing dimorphism will most certainly be addressed with enthusiasm in future studies (Zera and Brisson 2015).

Our results provide valuable information about spatial variation of fully winged morph and revealed geographic areas in which the species would experience greater dispersal capacity. Further studies in *D. vittatus* regarding the distribution of wing dimorphism at macrogeographic scale are necessary to gain deeper insight about the importance of environmental influence in wing morph.

Acknowledgments

Funding provided by CONICET (<http://dx.doi.org/10.13039/501100002923>) under award number 11220130100492CO and Universidad de Buenos Aires (<http://dx.doi.org/10.13039/501100005363>) under award number 20020130100358BA through grants to Dr. M. I. Remis is gratefully acknowledged.

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

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