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Morphometric differentiation in a field population of *Dichroplus maculipennis* (Orthoptera: Acrididae: Melanoplinae) under outbreak and non-outbreak situations

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Abstract

Dichroplus maculipennis is one of the most damaging grasshopper species of Argentina. Individuals of this species at high density are historically known to show aggregation behavior and dispersal flights, attributes that might suggest that it does exhibit to some extent phase polyphenism in relation to population density. Phase polyphenism is a complex phenomenon and the amplitude of phase change is usually species-dependent. Morphological differences between gregarious and solitarious locusts can be measured and analyzed in order to characterize the phase status. The objective of this study was to evaluate morphometric differences between individuals of a *D. maculipennis* field population in the southern Pampas region of Argentina during non-outbreak and outbreak conditions including the magnitude of sexual size dimorphism related to variation in density. Collected individuals in the outbreak condition totaled 804 (422 females, 382 males) and those in non-outbreak condition were 325 (141 females, 184 males). Six morphometric characters were measured and two ratios (F/C and E/F) usually used to discriminate between solitarious and gregarious individuals in true locust species were calculated. Results show that size traits of *D. maculipennis* change over time at the population level, and that these changes correlate with outbreak *vs* non-outbreak populations. Females and males of *D. maculipennis* in outbreak conditions are significantly larger than in non-outbreak conditions. Furthermore, significant change over time was recorded in values of the two ratios calculated. *D. maculipennis* showed female biased sexual size dimorphism in both outbreak and non-outbreak conditions. There is a smaller difference in body size among females and males in outbreak conditions than in females and males in non-outbreak conditions. These results may be an indication of the presence of density-dependent phenotypic plasticity in this species, but additional experiments are required in order to establish a causal relationship between population density and changes in size traits.

Key words

agricultural pest, phase polyphenism, grasshopper, locust, morphometric traits, Pampas region

Introduction

Locusts are among the most striking examples of density-dependent phase polyphenism, a process in which solitarious and cryptically colored grasshoppers can turn into gregarious and conspicuously colored individuals in response to an increase in population density (Latchininsky 2010, Song 2011). Individuals may be either of two extreme phenotypes: solitarious or gregarious at low or high population density, respectively, or intermediate forms between the two extremes depending on the direction of the transformation due to the process being reversible (Lecoq *et al.* 2011). The transition from solitarious to gregarious involves a series of continuously varying features of morphological, anatomical, reproductive, developmental, physiological, biochemical, molecular, behavioral and ecological changes (Uvarov 1966, Deng *et al.* 1996, Sword 2003, Song & Wenzel 2008, Pener & Simpson 2009, Gray *et al.* 2009, Ben Hamouda *et al.* 2011, Gotham & Song 2013). Locust phase polyphenism is a complex phenomenon that primarily depends on density and where the magnitude of the change of a given phase is species-specific. Song (2011) listed 24 Acrididae species belonging to six different subfamilies that show elements of density-dependent polyphenism. Many of these species have a tendency to aggregation and migration but show rudimentary phase polyphenism, thus the expression of density-dependent polyphenism may be subtle and not overtly manifested as in model locusts such as *Schistocerca gregaria* (Forskål) and *Locusta migratoria* (Linnaeus) (Uvarov 1966, 1977, Jago 1985, Simpson *et al.* 1999, Song 2011). These species may be considered as less typical locusts, aggregating grasshoppers or non-model locusts (Pener & Simpson 2009, Song 2011).

The grasshopper *Dichroplus maculipennis* (Blanchard), a polyphagous and univoltine melanopline (Mariottini *et al.* 2011a, b), is one of the most widely distributed species of the genus, occurring in most of Argentina, southern Brazil (Rio Grande do Sul), Chile, and Uruguay (Cigliano & Otte 2003, Carbonell *et al.* 2006). It is one of the most harmful grasshopper species in Argentina, mainly in areas of the Pampas and Patagonia regions (Liebermann 1972, Lange *et al.* 2005, Cigliano *et al.* 2014), where it is considered a major pest of several crops (barley, rye, oats, wheat, flax, lucerne) and forages on natural pastures (COPR 1982, Carbonell *et al.* 2006). *Dichroplus maculipennis* showed a drastic recession in the Pampas region during recent decades (Cigliano *et al.* 1995, Torrusio *et al.* 2002, Cigliano *et al.* 2002, De Wysiecki *et al.* 2004) but a major outbreak covering approximately 2.5 million ha occurred from late 2008 to early 2010 in the southern Pampas where densities reached 75 inds/m^2 and swarm-like, aggregative dispersal flights were observed (Mariottini *et al.* 2012). This event is congruent with earlier reports (Joan 1927, Schiuma 1938, Daguerre 1940, Liebermann & Schiuma 1946, Liebermann 1972).

Whether a given grasshopper species displays density-dependent phase polyphenism is difficult to demonstrate and usually requires controlled experimentation (Song 2011). However, some elements such as morphometric features can be measured and analyzed in order to detect the eventual occurrence of phase transformation of an individual or a population and if so to estimate its magnitude (Uvarov 1966, Bouachi & Simpson 2003, Franc *et al.* 2005, Pener & Simpson 2009, Ben Hamouda *et al.* 2011, Song 2011). Morphometric charts have been used to monitor the gregarization process over generations (Dirsh 1953, Uvarov 1966, Pener 1991).

The main objective of this study was to evaluate morphometric differences between individuals of a *D. maculipennis* field population during non-outbreak and outbreak conditions including the magnitude of sexual size dimorphism related to density variations.

Materials and methods

Sampling and morphometric measurements.—Adult males and females of *D. maculipennis* (n = 1131) were collected with entomological nets in natural and improved pastures of Laprida county (36°02'S, 59°06'W), Buenos Aires province, in the southern Pampas region as defined by Morrone (2006). Collecting was from December to February for five successive seasons (2005-06 through 2009-10). The condition of the population at each collecting time (non-outbreak versus outbreak) was determined by estimating density (individuals/m^2) through the rings method developed by Onsager & Henry (1977). The non-outbreak condition extended from December 2005 through January 2008 and the outbreak one lasted from December 2008 through February 2010 (Mariottini *et al.* 2012). Collected individuals in outbreak condition totaled 804 (422 females, 382 males) and those in non-outbreak were 327 (141 females, 184 males).

Six morphometric characters that are of value for determination of sexual size dimorphism in species of *Dichroplus* (Bidau & Marti 2007a, b, 2008) were measured and two ratios normally used to discriminate between solitarious and gregarious individuals in true locust species were calculated (Uvarov 1966, Pener 1991, Pierozzi & Lecoq 1998, Bouachi & Simpson 2003, Pener & Simpson 2009). Morphometric characters were total body length (BL), length of hind femur (F), length of tegmina from axial region to apex (E), mid-dorsal length of pronotum (PL), height of pronotum (PH), and maximum width of head (C) from cheek to cheek. Ratios were E/F and F/C. Measurements were taken with an electronic digital caliper (Stainless Hardened; resolution: 0.01mm; accuracy: ± 0.02 (< 100mm) range: 0-150mm).

Morphometric data analysis.—Since *D. maculipennis*, like most Caelifera, exhibits female biased sexual size dimorphism (females larger than males) (Hochkirch & Gröning 2008), all analyses that were performed needed to take into account such attribute. Principal component analyses (PCA) on a matrix of variance and covariance of the six morphometric traits and two ratios were carried out independently for females and males. PCA analyses were conducted using PAST (Hammer *et al.* 2001). Multivariate statistical methods were used to delimit groups of specimens of the same sex, including morphometric features that may represent the variation under different density conditions. In order to analyze homogeneity of variances, Levene's test was utilized. Since some characters were not distributed normally, they were $\log_{10}$ transformed before the one-way ANOVA analysis. When data departed from normality a Kruskal-Wallis test was performed. These tests were performed within the same sex for each trait using density as factor and within the same density condition using sex as factor.

Sexual size dimorphism (SSD) was estimated for each density situation (outbreak and non-outbreak) as the ratio between the logarithm of each measured character of females and the corresponding of males (log F/M) following Smith (1999). The homogeneity of variance was evaluated with Levene's test, and the statistical significance with ANOVA or Kruskal-Wallis' test; significance was detected at $\alpha=0.05$. Due to the difference in number of specimens between the two population density conditions (outbreak, non-outbreak) and sex (males, females) the analyses were based on a subset of the data (141 individuals for each category). Statistical analyses were estimated using 'lawstats' package (Gastwirth *et al.* 2013) in R 3.0.3 software.

Results

Morphometric differences between individuals of the same sex under different density conditions.—PCA performed for males showed that the first three PCs accounted for 96.56% of the total variation (74.75, 15.98, and 5.84, respectively) while in females these accounted for 97.25% of the total variation (80.22, 13.14, and 3.89, respectively). In both analyses, PC_1 was positively associated to all morphometric variables, except to the ratios in males (Table 1). PCA for males and females revealed similar results, where PC_1 and PC_2 had significant

Table 1. Loadings, eigenvalues, and cumulative percentage of variance for the first three PCA extracted for males and females of *D. maculipennis* at outbreak *vs* non-outbreak conditions. Length of tegmina (E), femur length (F), maximum head width (C), dorsal length of pronotum (PL), height of pronotum (PH) and total body length (BL).

	Males			Females		
	I	II	III	I	II	III
E	0.494	0.836	-0.207	0.638	0.645	-0.395
F	0.340	0.013	0.883	0.334	0.183	0.844
C	0.113	-0.043	0.038	0.090	0.017	-0.028
PL	0.115	0.052	0.133	0.130	0.080	0.222
PH	0.096	-0.002	0.107	0.100	0.049	0.099
BL	0.778	-0.538	-0.294	0.668	-0.734	-0.102
F/C	-0.003	0.041	0.200	0.014	0.033	0.214
E/F	-0.006	0.069	-0.141	0.007	0.025	-0.128
Eigenv	4.483	0.958	0.350	7.603	1.245	0.368
% Var	74.746	15.976	5.839	80.221	13.137	3.888
%VA	74.746	90.722	96.561	80.221	93.358	97.246

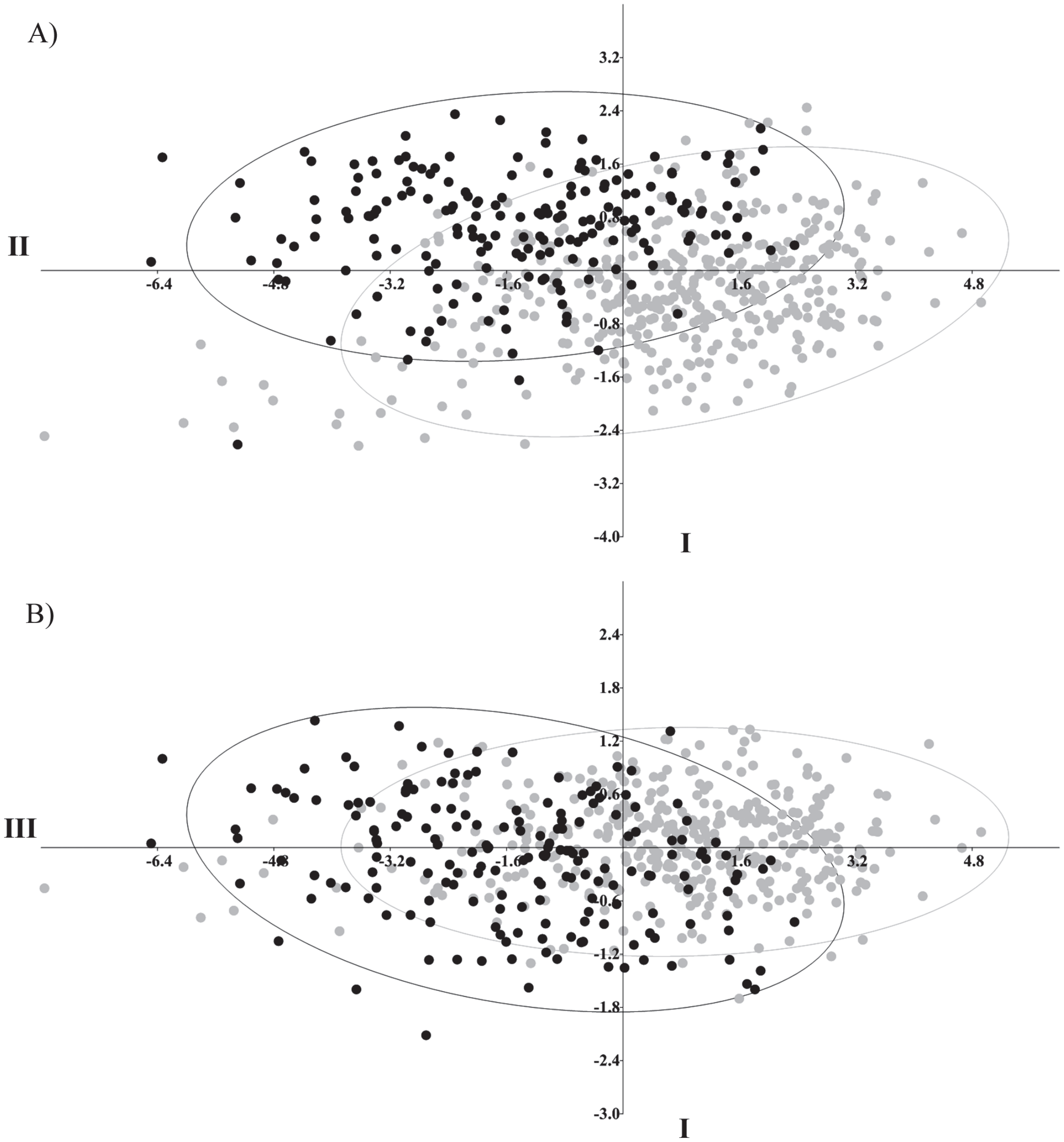

Fig. 1. Biplot from PCA for males of *Dichroplus maculipennis* for outbreak (grey dots) and non-outbreak (black dots) condition. A) PC1 *vs* PC2, B) PC1 *vs* PC3.

representation from tegmina length (E) and body size (BL), while femur length (F) was the variable that most contributed to the variation of PC$_3$ (Table 1).

PCA for females and for males showed that specimens in outbreak and non-outbreak conditions were plotted as a continuum into the same cloud in the multivariate space. However, in the scatterplots a displacement to the right (along PCA$_2$ and PCA$_3$) of individuals in outbreak situations was noticeable which would indicate a variation in body size (mostly given by the variation of the length of tegmina, femur and body) between specimens from the different situations (Figs 1, 2). While in the analysis for males the displacement to the right is more evident, in the analysis of females a larger dispersion of the specimens was observed (Figs 1, 2).

Results obtained from the analyses of morphometric variables were consistent with the PCA. Females in outbreak condition were significantly larger than females in non-outbreak condition. Five out of the six morphometric variables were significantly higher in females in outbreak condition, and only the length of pronotum was similar between females from both situations (Table 2). Similarly, males in outbreak condition were larger than males in non-outbreak condition. In this case, all estimated morphometric variables were significantly higher in males under outbreak condition except for tegmina length (E) (Table 2).

The E/F ratio was significantly higher in outbreak condition for females compared with those in non-outbreak. In males, the opposite was observed where the E/F ratio was higher in non-outbreak situations, indicating that the femur has a greater development relative to tegmina in outbreak condition.

The F/C ratio was significantly higher among individuals in non-outbreak condition for both sexes (Table 2), revealing a greater relative development of maximum width of head over the femur length.

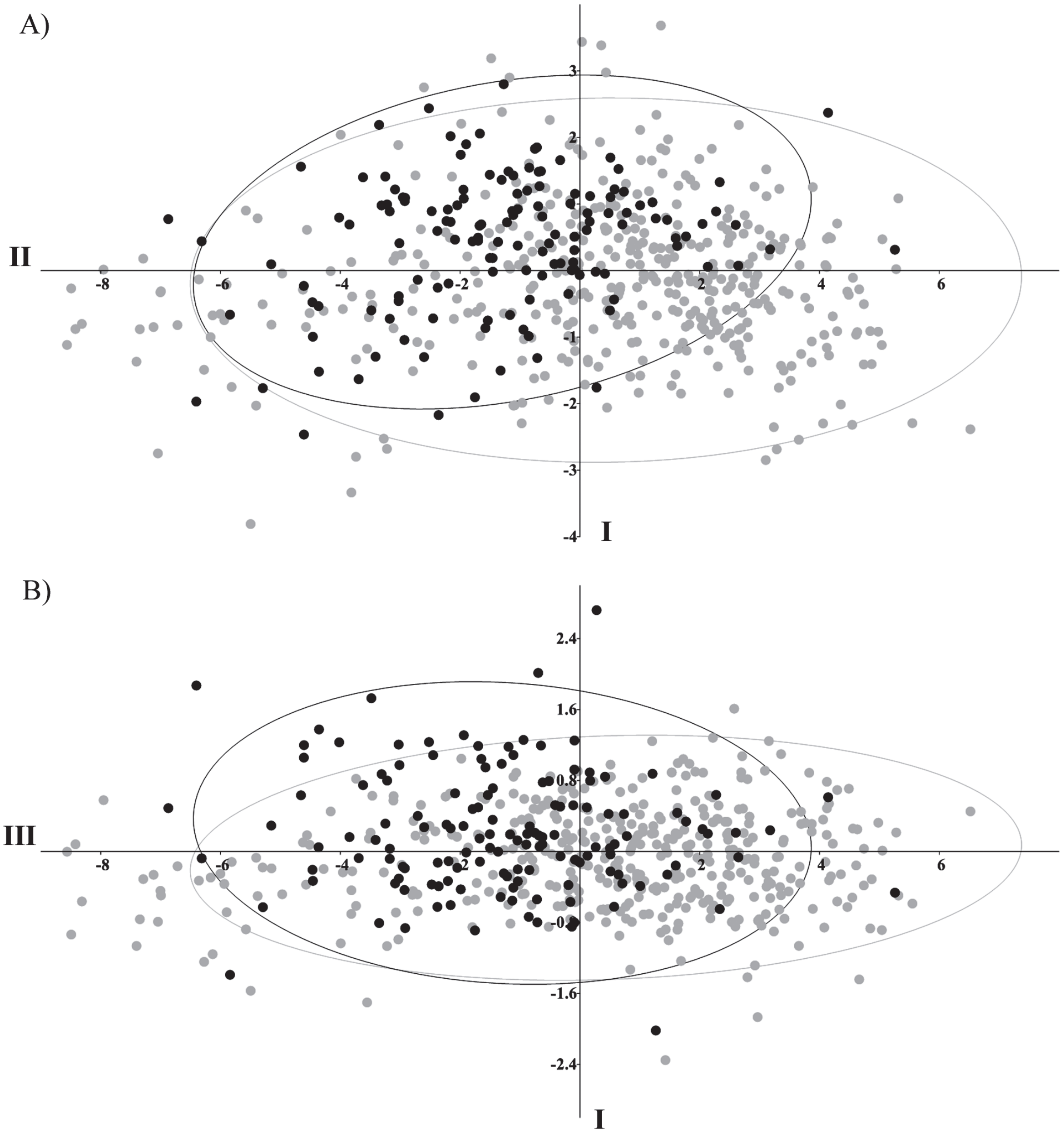

Fig. 2. Biplot from PCA for females of *D. maculipennis* in outbreak (grey dots) and non-outbreak (black dots) condition. A) PC1 *vs* PC2, B) PC1 *vs* PC3.

Morphometric differences between individuals of different sex under the same density situation.—Results obtained related to sexual size dimorphism under each density situation showed that females displayed significantly higher values than males in every trait (C, F, E, PL, PH) except body length (Table 3, Figs 3, 4). Males showed significantly larger body length values (BL) than females under outbreak conditions (Table 3).

Results showed that sexual size dimorphism ratios (SSD) were significantly different for all traits between outbreak and non-outbreak conditions (Table 4, Fig. 5). During non-outbreak conditions the sexual size dimorphism value was higher in all variables except tegmina length, while it was higher only in tegmina length during outbreak conditions.

Discussion

Results of this study indicate that in *D. maculipennis* there is significant body size variation in individuals of the same sex under different density conditions (outbreak *vs* non-outbreak). Adults of *D. maculipennis* in outbreak conditions are normally larger than in non-outbreak conditions. The size of an individual adult locust depends on species, sex, nutrition, and phase (Hunter 1989, Pener 1991, Yerushalmi *et al.* 2001, Bouachi & Simpson 2003, Franc *et al.* 2005, Gray *et al.* 2009, Jannot *et al.* 2009, Pener & Simpson 2009, Ben Hamouda *et al.* 2011, Gotham & Song 2013, among others). However, in different locust species, phase-dependent changes in size are strongly dissimilar. There are species that show changes in the size of both sexes. For example, solitarious females of *L. migratoria*, *S. gregaria*, and *Nomadacris septemfasciata* (Serville) are larger than conspecific gregarious females. While in adult males the situation is reversed, solitarious individuals are smaller than gregarious ones

Table 2. Morphometric values and ratios (mean ± SE) in males and females of *D. maculipennis* at outbreak and non-outbreak condition. Length of tegmina (E), femur length (F), maximum head width (C), dorsal length of pronotum (PL), height of pronotum (PH) and total body length (BL). Coefficient of variability (C.V) * significant differences between the two density conditions, F: values from ANOVA, KW: values from Kruskal Wallis test. ** p < 0.01, *** p < 0.001.

		Outbreak		**non Outbreak**		
		Mean ± SE	**C.V.**	**Mean ± SE**	**C.V.**	**Significance**
Males	E	20.11 ± 0.070	6.82	19.89 ± 0.092	6.26	F = 3.43
	F	12.46 ± 0.041	6.48	11.54 ± 0.054	6.31	F = 171.70***
	C	4.06 ± 0.014	6.58	3.67 ± 0.020	7.27	F = 265.00***
	PL	4.52 ± 0.018	7.64	4.35 ± 0.028	8.74	F = 30.94***
	PH	3.66 ± 0.015	8.25	3.38 ± 0.021	8.39	F = 113.60***
	BL	24.72 ± 0.070	5.54	22.56 ± 0.111	6.68	F = 288.70***
	F/C	3.07 ± 0.010	6.08	3.16 ± 0.018.	7.82	KW = 11.98***
	E/F	1.62 ± 0.004	5.26	1.73 ± 0.008	6.60	KW = 126.98***
Females	E	22.53 ± 0.095	8.64	21.70 ± 0.141	7.74	F = 20.59***
	F	13.85 ± 0.054	8.03	13.56 ± 0.079	6.94	F = 7.91**
	C	4.55 ± 0.015	6.97	4.24 ± 0.025	6.91	F = 105.30***
	PL	5.10 ± 0.025	9.90	5.10 ± 0.035	8.12	F = 0.011
	PH	4.21 ± 0.021	10.18	4.10 ± 0.031	9.03	F = 8.165***
	BL	24.34 ± 0.099	8.36	22.75 ± 0.118	6.17	KW = 80.76***
	F/C	3.05 ± 0.009	6.01	3.21 ± 0.020	7.53	KW = 55.13***
	E/F	1.63 ± 0.004	4.94	1.60 ± 0.008	6.16	KW =9.15**

(Pener & Simpson 2009). There are also species in which the size is different for only one sex. Gregarious males of *Chortoicetes terminifera* (Walker) are larger than solitarious, while in females this difference is scarcely observable (Uvarov 1977). Gotham & Song (2013) observed that in the non-swarming grasshopper *Schistocerca americana* (Drury), the isolated females were larger than crowded ones, but the same pattern was not recorded for males. Similar to the pattern registered in this study for *D. maculipennis*, gregarious adults of *Dociostaurus maroccanus* (Thunberg) and *Locustana pardalina* (Walker) are larger than solitarious adults of the same sex (Uvarov 1966, 1977). The above examples suggest that there is no general trend that relates the size of an adult grasshopper to the phase.

Locust phase transformation is accompanied by shifts in the F/C and E/F ratios (Pener & Simpson 2009). The absolute values of these ratios and he amplitude of their shifts depend strongly not only on the species and sex but also on the subspecies or geographic range (Deng *et al.* 1996, Bouachi & Simpson, 2003, Franc *et al.* 2005, Song 2011). Accordingly, Pener & Simpson (2009) indicated that the ratios should be considered as exact indicators of phase state only when they are obtained from a definite population. In this sense, we feel it is of central relevance to note that in our study we conducted the whole work with field individuals coming from the very same collecting area and thus presumably from the same population. Significant density-dependent change was recorded in values of the two ratios (F/C and E/F). The F/C ratio is generally regarded as the most appropriate for differentiating between solitarious and gregarious locust phases (Uvarov 1966, Deng *et al.* 1996, Franc *et al.* 2005). This ratio is higher in solitarious than in gregarious locusts for *S. gregaria*, *L. migratoria*, *N. septemfasciata*, and *L. pardalina* (Yerushalmi *et al.* 2001, Franc *et al.* 2005, Pener & Simpson 2009). In *D. maculipennis*, the F/C ratio for both sexes

Table 3. Results from analysis of variance (ANOVA) and Kruskal-Wallis test for sexual size dimorphism under each density situation. Length of tegmina (E), femur length (F), maximum head width (C), dorsal length of pronotum (PL), height of pronotum (PH) and total body length (BL).** p < 0.01, *** p < 0.001.

	Outbreak		**non Outbreak**	
	ANOVA	**KW**	**ANOVA**	**KW**
E		305.90***		96.30***
F		315.40***		172.70***
C		354.90***	333.30***	
PL		109.90***	250.10***	
PH		134.10***		166.00***
BL		6.72**	1.27	

Table 4. Results of analysis of variance (ANOVA) of sexual size dimorphism ratios (SSD) between the logarithm of each morphometric trait of females and males at each density condition (outbreak vs. non-outbreak): a) Length of tegmina (E), b) femur length (F), c) maximum head width (C), d) dorsal length of pronotum (PL), e) height of pronotum (PH) and f) total body length (BL).
*p < 0.05, ** p < 0.01, *** p < 0.001.

	ANOVA
E	F = 5.44*
F	F = 13.74***
C	F = 7.40**
PL	F = 4.19*
PH	F = 4.07*
BL	F = 8.49**

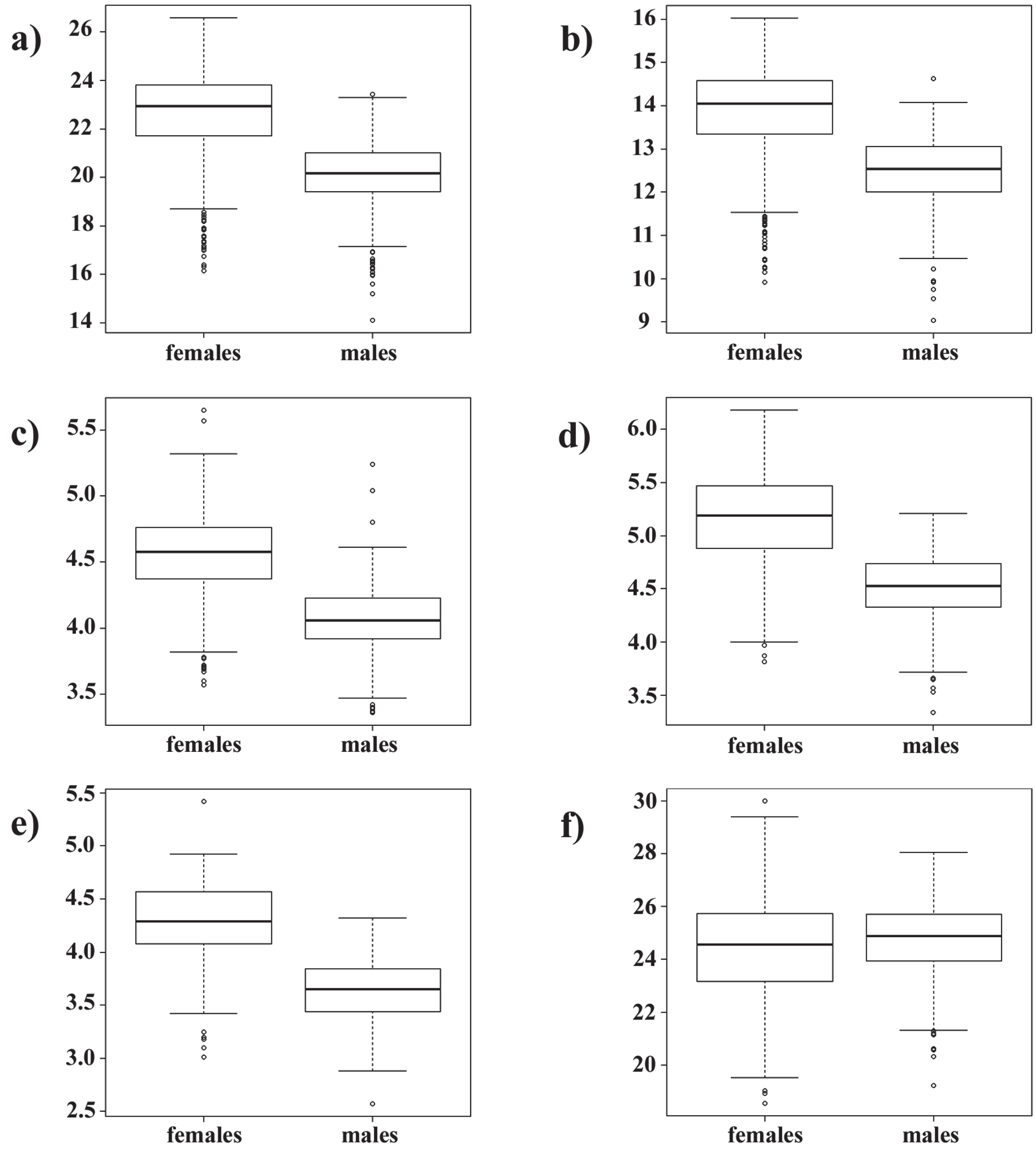

Fig. 3. Results of Kruskal-Wallis test between females and males of *D. maculipennis* in outbreak condition: a) Length of tegmina (E), b) femur length (F), c) maximum head width (C), d) dorsal length of pronotum (PL), e) height of pronotum (PH) and f) total body length (BL).

shifted following the same trend as in true locust (*i.e.*, being higher in what would be solitarious than would be gregarious individuals), indicating a higher relative growth of maximum head width over femur length. On the other hand, the E/F ratio is considered to be a less reliable phase indicator than the F/C ratio (Deng *et al.* 1996, Yerushalmi *et al.* 2001, Pener & Simpson 2009) and it is higher in gregarious than in solitarious locusts. Similarly to those species considered as true locusts, the E/F ratio was significantly higher in *D. maculipennis* females in outbreak condition than non-outbreak. However, the opposite situation was recorded for males (higher E/F in non-outbreak condition), indicating that the femur had a greater development relative to tegmina in outbreak males.

Although it is admittedly difficult to demonstrate the presence of density-dependent phase polyphenism without controlled experimentation, the recent detailed review by Song (2011) where four "expressions" (nymphal color, morphometric ratios, physiology, behavior) are used to determine the scope of density-dependent phase polyphenism among 24 species of Acrididae in six subfamilies, provides a suitable framework for an assessment of the situation regarding *D. maculipennis*. Our results revealing significant size differences for outbreak and non-outbreak individuals of the same field population fulfill the morphometric "expression", which is arguably one of the main attributes that historically defined classic or model locusts (Uvarov 1977). Although quantitative information is not available, earlier contributions (Joan 1927, Schiuma 1938, Daguerre 1940, Liebermann & Schiuma 1946, Liebermann 1972, COPR 1982, Mariottini *et al.* 2012) and our own recent observations on obvious nymphal and adult aggregation, including group oviposition and swarm-like displacements of up to 50 km, attest to behavioral "expression". Likewise, studies under experimental, controlled conditions determined that females from outbreak conditions have a shorter lifespan and are less fecund than females from non-outbreak conditions (Mariottini *et al.* 2011c), conceivably accounting for the physiology "expression". Since no color differences were observed in more than 1500 juveniles at outbreak and non-outbreak conditions (Mariottini *et al.* 2015) and no records (even anecdotal or circumstantial) exist in the earlier literature that mention coloration changes in nymphs, nymphal color "expression" is the only lacking characteristic preventing *D. maculipennis* from exhibiting the complete set of evidence of density-dependence phase polyphenism.

Among the Melanoplinae, one of the largest subfamilies of Acrididae (more than 1100 species) with a Holarctic-Neotropical

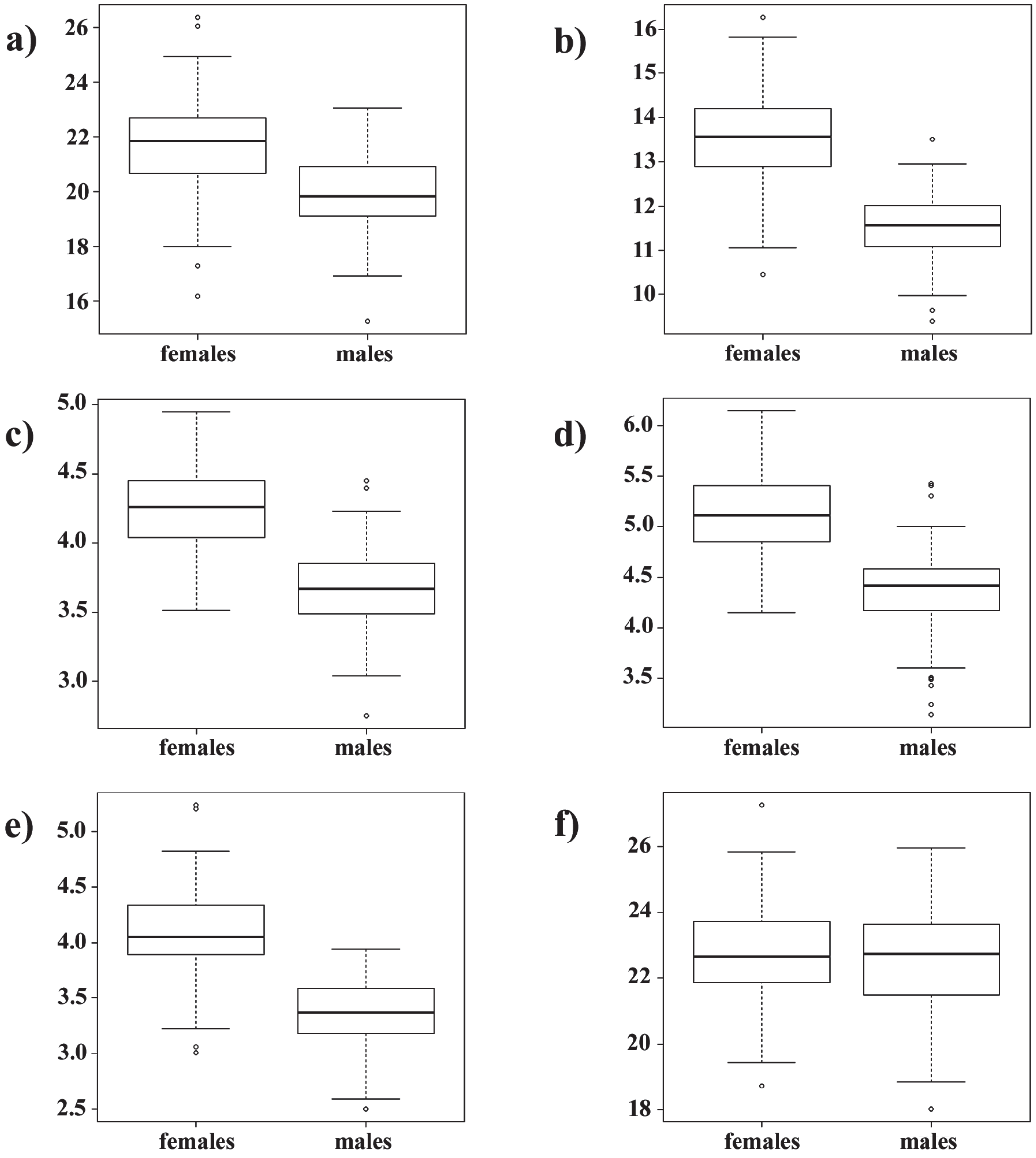

Fig. 4. Results of ANOVA and Kruskal-Wallis test between females and males of *D. maculipennis* in non-outbreak condition: a) Length of tegmina (E), b) femur length (F), c) maximum head width (C), d) dorsal length of pronotum (PL), e) height of pronotum (PH) and f) total body length (BL).

distribution (Chintauan-Marquier *et al.* 2011, Eades *et al.* 2015), very few species are known to express some level of density-dependent polyphenism. Nearctic *Melanoplus sanguinipes* (Fabricius), *M. differentialis* (Thomas), and *M. spretus* (Walsh) have been reported to display hopper bands and adult swarms that migrate (Lockwood & DeBrey 1990, Pener & Simpson 2009). Fielding & Defoliart (2005) recorded that crowding induces melanization in nymphs of *M. sanguinipes*. Thus the Melanoplinae should be added to the other acridid subfamilies (Cyrtacanthacridinae, Oedipodinae, Gomphocerinae, Calliptaminae; Song, 2011) where density-dependent phase polyphenism has evolved, strengthening the view that this phenomenon evolved multiple times within the Acrididae.

Leaving model or classic locusts aside (*i.e.*, those seven species that depict all four "expressions"), our study showed that *D. maculipennis* is one of the acridids that probably expresses density-dependent phase polyphenism to a great extent. However, in order to obtain conclusive results on this, it would be necessary to rear in the laboratory individuals of *D. maculipennis* under different densities for multiple generations to quantify the effect of rearing density in terms of morphometry, color and behavior. Similar studies were carried out to corroborate or quantify phase polyphenism in other species (Deng *et al.* 1996, Yerushalmi *et al.* 2001, Franc *et al.* 2005, Gray *et al.* 2005, Jannot *et al.* 2009, Gotham & Song 2013).

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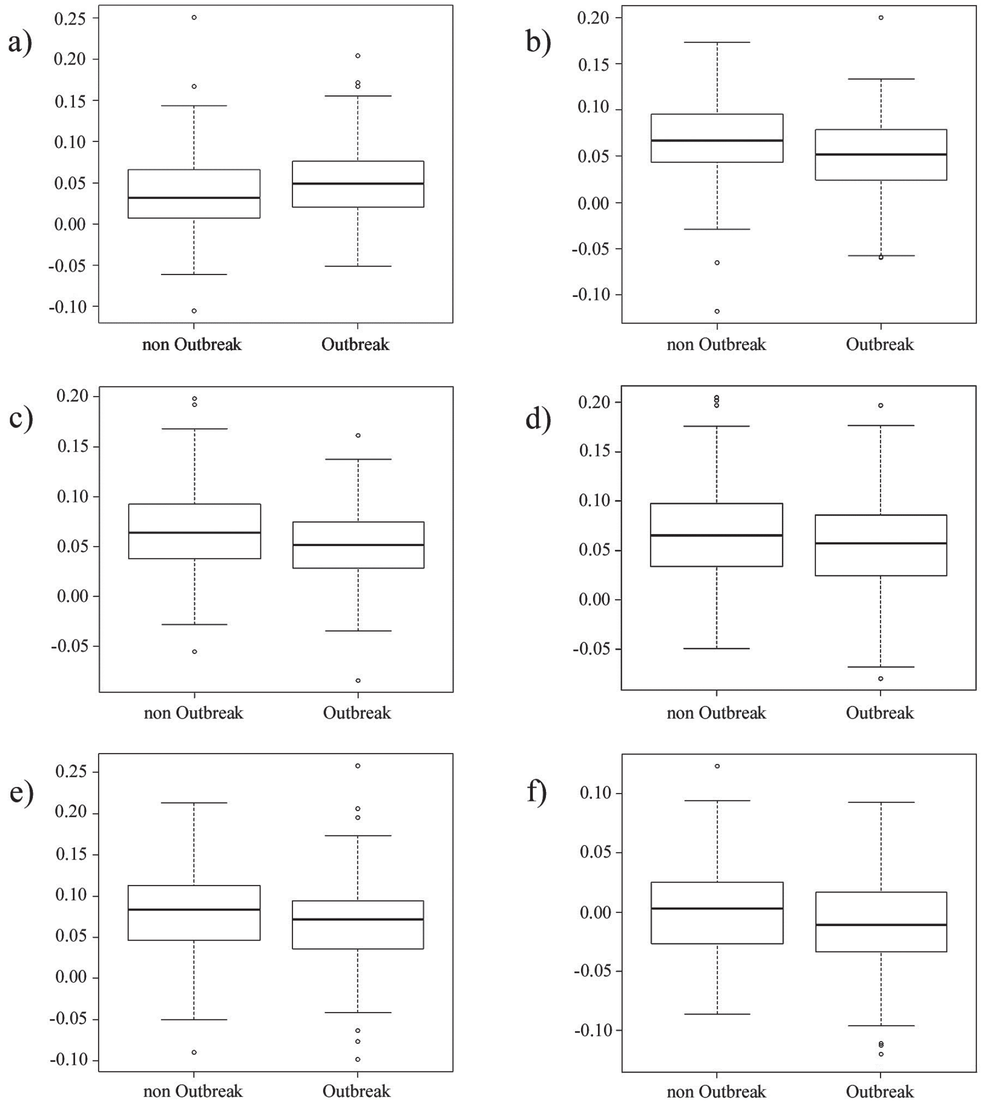

Fig. 5. Results of analysis of variance (ANOVA) of sexual size dimorphism ratios (SSD) between the logarithm of each morphometric trait of females and males at each density condition (outbreak *vs* non-outbreak): a) Length of tegmina (E), b) femur length (F), c) maximum head width (C), d) dorsal length of pronotum (PL), e) height of pronotum (PH) and f) total body length (BL).

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