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# Contrasting patterns of sexual size dimorphism in the grasshoppers *Dichroplus vittatus* and *D. pratensis* (Acrididae, Melanoplinae)\*

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\*Dedicated with love to: Claudio Jr., Pablo, Julieta, Juan Bautista, Emiliano, Franco and Rodrigo, our sons.

## Abstract

Sexual size dimorphism (SSD) can be the result of sexual selection (SS) or natural selection (NS). Due to male-male competition for access to females, SS could favor an increase in male body size. On the other hand, larger size in females could be favored by NS, since egg production is directly correlated with body size. Rensch's rule states that SSD increases with increasing body size in animals, where males are the larger sex, and decreases when females are larger than males. Thus, Rensch's rule predicts that in those insects where females are larger than males, SSD should decrease with increasing body size, when comparing populations and species. We analyzed SSD in 19 Argentine populations of the grasshoppers *Dichroplus vittatus* and 25 of *D. pratensis*. Both species show latitudinal and altitudinal variation in body size, following the converse to Bergmann's rule: body size decreases with increasing latitude and decreasing ambient temperature. SSD occurs in both species across their geographical distribution ranges, also involving differences in allometry and shorter developmental times in males. In *D. vittatus*, the degree of SSD increased significantly with general body size, whereas in *D. pratensis* SSD decreased as body size increased. A plausible explanation of SSD is that SS favors a differential increase in female body size related to a preference by males for more fecund females. Given the close phylogenetic relationship between both species, the differences in SSD between them may be the result of differential natural and sexual selective pressures. In *D. vittatus* both sexes could be reacting differently to environmental conditions regarding body size, while in *D. pratensis* protandry could be the main factor behind SSD.

## Key words

allometry, *Dichroplus vittatus*, *Dichroplus pratensis*, grasshopper, Reduced Major Axis regression, Rensch's rule, sexual size dimorphism

## Introduction

Sexual dimorphism (SD) results from morphological differences between the sexes. According to Wilson (1975) SD is, "any consistent difference between males and females beyond the basic functional portions of the sex organs". In many animal species, the sexes differ in size (sexual size dimorphism or SSD) (Fairbairn 1990, 1997; Shine 1990; Andersson 1994; Badyaev 2002; Lindenfors 2002). Body size is correlated with many life history traits and can be the target of both sexual and natural selection (Blackburn *et al.* 1999). In many mammals and birds SSD is male biased, but in the majority of ectotherms, it is female biased, although with many exceptions (Ralls 1976, Andersson 1994, Monnet & Cherry 2002, Schulte-Hostedde *et al.* 2002, Teder & Tammaru 2005). Differences between females and males in the intensity and/or direction of sexual selection can

generate differences in SSD (Darwin 1871; Spencer & Masters 1992; Andersson 1994; Fairbairn & Preziosi 1994; Ding & Blanckenhorn 2002; Kraushaar & Blanckenhorn 2002; Szekely *et al.* 2004; Teder & Tammaru 2005, 2005). In most insects, females are larger, perhaps because larger females are more fecund than smaller ones (Andersson 1994, Honek 1993). In addition, small males may also be selected for in species where scramble competition polygyny, and not male contests, is the main form of sexual competition between males (Thornhill & Alcock 1983, Schwagmeyer 1988, Andersson 1994, Bidau & Martí 2007b).

However, natural selection can also explain sex differences in body size if males and females have different niches (Butler *et al.* 2000, Myerud 2000, Blondel *et al.* 2002, Pérez-Barbería *et al.* 2002). Differences in emergence and maturation times between females and males could explain SSD. A common phenomenon in many cases where adult males are smaller than adult females is protandry. Early emergence of males could evolve by natural selection because males that mature earlier than females could have an advantage in mate competition (Darwin 1871). Also, early emergence of small males could be advantageous when scrambles and early arrival to mating grounds are the main mode of competition for mates (Andersson 1994, Zonneveld 1996, Morbey & Ydenberg 2001, Matsuura 2006). For protandry to evolve it must be heritable and populations must be univoltine, or have nonoverlapping generations (Bradshaw *et al.* 1997). Selection for protandry could cause female-biased SSD if males and females realize the same preadult growth rates. In this case, SSD would result from sexual selection (Singer 1982). Alternatively, SSD could result from natural selection if large females attain higher fecundity, but large males received no particular sexual or reproductive advantage (Thornhill & Alcock 1983). Protandry also could be a female reproductive strategy to minimize the prereproductive period (Fagerström & Wiklund 1982).

SSD is a fundamental component of intra- and interspecies morphological variation. In species with a large latitudinal and/or altitudinal distribution range, body size may show significant variation (*e.g.*, Bergmann's rule, Bergmann 1847) that can be correlated with environmental variables (*e.g.*, Rensch's rule; Rensch 1960, Bidau & Martí 2007b). Moreover, patterns of SSD may be inherited from a common ancestor, thus being relevant to determinate monophyletic groups (Baker & Wilkinson 2001).

The main goal of this study was to quantify the degree of SSD in two closely related grasshopper species with large and partially overlapping geographic distribution. According to Rensch's rule (Rensch 1950, 1960) in taxa in which males are the larger sex, the degree of SSD tends to increase with increasing average body size, and decreases with body size in those taxa where females are larger than males (Abouheif & Fairbairn 1997). This tendency has been

**Table 1a.** Means and standard errors of six morphometric characters in males in populations of *D. vittatus* and *D. pratensis*. Populations are those indicated in Fig. 1. Lat (S): latitude; Lon (W): longitude; A: altitude (meters above sea level); N: number of individuals; BL: total body length; F3L: left femur 3 length; T3L: left tibia 3 length; Tel: tegmina length; PL: pronotum length; PH: pronotum height; s $\bar{x}$ : standard error of the mean.

| Population          | Lat (S) | Lon (W) | A    | N  | BL $\pm$ s $\bar{x}$ | F3L $\pm$ s $\bar{x}$ | T3L $\pm$ s $\bar{x}$ | Tel $\pm$ s $\bar{x}$ | PL $\pm$ s $\bar{x}$ | PH $\pm$ s $\bar{x}$ |
|---------------------|---------|---------|------|----|----------------------|-----------------------|-----------------------|-----------------------|----------------------|----------------------|
| <i>D. vittatus</i>  |         |         |      |    |                      |                       |                       |                       |                      |                      |
| 1. Huacalera        | 23° 26' | 65° 21' | 2758 | 25 | 17.3 $\pm$ 0.14      | 9.6 $\pm$ 0.10        | 8.0 $\pm$ 0.08        | 6.0 $\pm$ 0.13        | 3.7 $\pm$ 0.04       | 2.8 $\pm$ 0.03       |
| 2. La Viña          | 25° 28' | 65° 35' | 1265 | 2  | 21.6 $\pm$ 0.28      | 11.9 $\pm$ 0.35       | 9.9 $\pm$ 0.23        | 7.7 $\pm$ 0.02        | 4.7 $\pm$ 0.29       | 3.4 $\pm$ 0.08       |
| 3. S. del Estero    | 26° 01' | 62° 22' | 174  | 10 | 20.3 $\pm$ 0.28      | 11.5 $\pm$ 0.15       | 9.4 $\pm$ 0.13        | 8.0 $\pm$ 0.19        | 4.5 $\pm$ 0.10       | 3.1 $\pm$ 0.06       |
| 4. C. del Valle     | 26° 22' | 65° 57' | 1662 | 3  | 19.8 $\pm$ 0.50      | 11.1 $\pm$ 0.40       | 9.1 $\pm$ 0.45        | 7.0 $\pm$ 0.24        | 4.4 $\pm$ 0.10       | 3.1 $\pm$ 0.03       |
| 5. Tafi del Valle   | 26° 52' | 65° 43' | 2014 | 24 | 20.1 $\pm$ 0.17      | 11.0 $\pm$ 0.08       | 9.0 $\pm$ 0.09        | 7.5 $\pm$ 0.09        | 4.6 $\pm$ 0.05       | 3.2 $\pm$ 0.04       |
| 6. Miraflores       | 28° 36' | 65° 41' | 537  | 4  | 19.0 $\pm$ 0.36      | 10.2 $\pm$ 0.35       | 9.0 $\pm$ 0.48        | 5.7 $\pm$ 0.49        | 4.1 $\pm$ 0.09       | 3.0 $\pm$ 0.03       |
| 7. Chumbicha        | 28° 52' | 66° 14' | 376  | 10 | 20.0 $\pm$ 0.29      | 10.3 $\pm$ 0.15       | 8.6 $\pm$ 0.12        | 6.8 $\pm$ 0.20        | 4.1 $\pm$ 0.11       | 3.1 $\pm$ 0.06       |
| 8. La Rioja         | 29° 05' | 66° 40' | 521  | 4  | 20.3 $\pm$ 0.19      | 10.9 $\pm$ 0.05       | 9.0 $\pm$ 0.08        | 7.3 $\pm$ 0.25        | 4.3 $\pm$ 0.07       | 3.1 $\pm$ 0.04       |
| 9. Valle Fértil     | 30° 38' | 67° 27' | 828  | 14 | 18.6 $\pm$ 0.23      | 10.2 $\pm$ 0.16       | 8.3 $\pm$ 0.13        | 6.1 $\pm$ 0.14        | 3.9 $\pm$ 0.05       | 2.9 $\pm$ 0.04       |
| 10. V. Rosario      | 31° 34' | 63° 32' | 248  | 25 | 19.2 $\pm$ 0.14      | 10.4 $\pm$ 0.09       | 8.5 $\pm$ 0.08        | 6.9 $\pm$ 0.12        | 4.1 $\pm$ 0.04       | 3.1 $\pm$ 0.03       |
| 11. Guido           | 32° 52' | 69° 15' | 2099 | 8  | 19.5 $\pm$ 0.29      | 10.5 $\pm$ 0.14       | 8.5 $\pm$ 0.11        | 6.6 $\pm$ 0.18        | 4.1 $\pm$ 0.09       | 3.0 $\pm$ 0.04       |
| 12. Potrerillos     | 32° 57' | 69° 11' | 1469 | 2  | 17.9 $\pm$ 0.55      | 9.9 $\pm$ 0.17        | 8.0 $\pm$ 0.36        | 5.9 $\pm$ 0.41        | 3.9 $\pm$ 0.07       | 3.0 $\pm$ 0.10       |
| 13. Cacheuta        | 33° 02' | 69° 07' | 1310 | 3  | 18.6 $\pm$ 0.47      | 9.9 $\pm$ 0.24        | 8.3 $\pm$ 0.15        | 6.8 $\pm$ 0.12        | 4.0 $\pm$ 0.08       | 2.9 $\pm$ 0.03       |
| 14. Compuertas      | 33° 03' | 69° 04' | 1063 | 10 | 19.6 $\pm$ 0.39      | 10.4 $\pm$ 0.20       | 8.4 $\pm$ 0.21        | 6.4 $\pm$ 0.13        | 4.2 $\pm$ 0.09       | 3.1 $\pm$ 0.04       |
| 15. La Punilla      | 33° 08' | 65° 05' | 942  | 4  | 18.9 $\pm$ 0.42      | 10.3 $\pm$ 0.23       | 8.4 $\pm$ 0.21        | 6.5 $\pm$ 0.35        | 4.2 $\pm$ 0.10       | 2.9 $\pm$ 0.04       |
| 16. El Morro        | 33° 13' | 65° 29' | 993  | 6  | 18.4 $\pm$ 0.39      | 10.1 $\pm$ 0.18       | 8.3 $\pm$ 0.17        | 7.2 $\pm$ 0.18        | 4.1 $\pm$ 0.07       | 2.9 $\pm$ 0.03       |
| 17. Olmos           | 33° 30' | 63° 10' | 117  | 10 | 18.5 $\pm$ 0.40      | 10.2 $\pm$ 0.22       | 8.5 $\pm$ 0.19        | 6.7 $\pm$ 0.20        | 3.8 $\pm$ 0.10       | 3.1 $\pm$ 0.03       |
| 18. Toay            | 36° 40' | 64° 21' | 174  | 9  | 16.8 $\pm$ 0.43      | 9.5 $\pm$ 0.24        | 7.6 $\pm$ 0.20        | 5.3 $\pm$ 0.34        | 3.7 $\pm$ 0.11       | 2.6 $\pm$ 0.08       |
| 19. Playa Unión     | 43° 04' | 65° 03' | 36   | 17 | 16.4 $\pm$ 0.23      | 9.1 $\pm$ 0.16        | 7.6 $\pm$ 0.13        | 5.6 $\pm$ 0.57        | 2.8 $\pm$ 0.06       | 3.6 $\pm$ 0.06       |
| <i>D. pratensis</i> |         |         |      |    |                      |                       |                       |                       |                      |                      |
| 20. Volcán          | 23° 55' | 65° 27' | 2474 | 27 | 22.4 $\pm$ 0.24      | 12.0 $\pm$ 0.14       | 9.8 $\pm$ 0.11        | 11.6 $\pm$ 0.18       | 4.9 $\pm$ 0.04       | 3.9 $\pm$ 0.05       |
| 21. E. Mazán        | 28° 44' | 66° 29' | 646  | 22 | 23.8 $\pm$ 0.23      | 12.6 $\pm$ 0.14       | 10.0 $\pm$ 0.13       | 14.5 $\pm$ 0.23       | 5.2 $\pm$ 0.07       | 4.2 $\pm$ 0.07       |
| 22. Carrizal        | 28° 54' | 67° 33' | 522  | 5  | 24.0 $\pm$ 0.50      | 12.8 $\pm$ 0.23       | 10.1 $\pm$ 0.21       | 14.6 $\pm$ 0.21       | 5.2 $\pm$ 0.16       | 4.2 $\pm$ 0.12       |
| 23. Las Juntas      | 30° 41' | 67° 35' | 1203 | 5  | 21.8 $\pm$ 0.39      | 11.6 $\pm$ 0.13       | 8.9 $\pm$ 0.09        | 13.5 $\pm$ 0.17       | 4.5 $\pm$ 0.12       | 3.9 $\pm$ 0.08       |
| 24. C. Machado      | 31° 28' | 63° 35' | 314  | 15 | 25.6 $\pm$ 0.28      | 14.0 $\pm$ 0.17       | 11.5 $\pm$ 0.13       | 17.5 $\pm$ 0.26       | 5.6 $\pm$ 0.08       | 4.3 $\pm$ 0.07       |
| 25. Guido           | 32° 52' | 69° 15' | 2099 | 12 | 25.1 $\pm$ 0.47      | 13.4 $\pm$ 0.31       | 10.6 $\pm$ 0.24       | 16.8 $\pm$ 0.31       | 5.3 $\pm$ 0.13       | 4.3 $\pm$ 0.09       |
| 26. Potrerillos     | 32° 56' | 69° 11' | 1469 | 28 | 23.8 $\pm$ 0.20      | 12.6 $\pm$ 0.10       | 9.9 $\pm$ 0.11        | 15.8 $\pm$ 0.17       | 5.0 $\pm$ 0.26       | 4.0 $\pm$ 0.04       |
| 27. Cacheuta        | 33° 02' | 69° 07' | 1310 | 16 | 23.5 $\pm$ 0.26      | 12.5 $\pm$ 0.16       | 9.9 $\pm$ 0.17        | 15.6 $\pm$ 0.36       | 5.1 $\pm$ 0.07       | 4.0 $\pm$ 0.06       |
| 28. Compuertas      | 33° 03' | 69° 04' | 1063 | 10 | 26.4 $\pm$ 0.38      | 14.1 $\pm$ 0.25       | 10.9 $\pm$ 0.21       | 17.3 $\pm$ 0.22       | 5.6 $\pm$ 0.11       | 4.3 $\pm$ 0.12       |
| 29. La Punilla      | 33° 08' | 65° 05' | 942  | 4  | 24.2 $\pm$ 0.28      | 13.5 $\pm$ 0.16       | 10.5 $\pm$ 0.03       | 17.0 $\pm$ 0.53       | 5.2 $\pm$ 0.06       | 3.5 $\pm$ 0.10       |
| 30. Achiras         | 33° 09' | 65° 00' | 838  | 12 | 23.8 $\pm$ 0.30      | 13.2 $\pm$ 0.16       | 10.2 $\pm$ 0.15       | 15.3 $\pm$ 0.34       | 5.1 $\pm$ 0.08       | 4.1 $\pm$ 0.06       |
| 31. Saladillo       | 33° 13' | 65° 52' | 840  | 6  | 25.0 $\pm$ 0.21      | 13.7 $\pm$ 0.14       | 10.9 $\pm$ 0.15       | 17.4 $\pm$ 0.19       | 5.3 $\pm$ 0.08       | 4.3 $\pm$ 0.10       |
| 32. El Morro        | 33° 13' | 65° 29' | 993  | 5  | 24.7 $\pm$ 0.51      | 13.6 $\pm$ 0.23       | 10.9 $\pm$ 0.16       | 17.0 $\pm$ 0.23       | 5.2 $\pm$ 0.11       | 3.7 $\pm$ 0.07       |
| 33. La Granja       | 33° 30' | 63° 17' | 577  | 15 | 26.0 $\pm$ 0.70      | 14.1 $\pm$ 0.49       | 11.3 $\pm$ 0.53       | 18.4 $\pm$ 0.79       | 5.7 $\pm$ 0.27       | 4.3 $\pm$ 0.33       |
| 34. Manantiales     | 33° 33' | 63° 20' | 580  | 15 | 26.1 $\pm$ 1.41      | 14.5 $\pm$ 0.56       | 11.6 $\pm$ 0.52       | 18.2 $\pm$ 1.12       | 5.6 $\pm$ 0.33       | 4.4 $\pm$ 0.42       |
| 35. Don Tomás       | 36° 41' | 64° 20' | 175  | 15 | 24.2 $\pm$ 0.25      | 13.5 $\pm$ 0.09       | 10.9 $\pm$ 0.12       | 17.5 $\pm$ 0.21       | 5.3 $\pm$ 0.05       | 4.1 $\pm$ 0.07       |
| 36. Olavarría       | 36° 55' | 60° 17' | 162  | 15 | 22.6 $\pm$ 0.23      | 12.6 $\pm$ 0.11       | 10.1 $\pm$ 0.0        | 16.6 $\pm$ 0.15       | 4.8 $\pm$ 0.10       | 3.7 $\pm$ 0.09       |
| 37. C. Pringles     | 37° 59' | 61° 22' | 846  | 15 | 23.4 $\pm$ 0.75      | 13.0 $\pm$ 0.50       | 10.4 $\pm$ 0.42       | 16.8 $\pm$ 0.77       | 4.9 $\pm$ 0.28       | 3.8 $\pm$ 0.30       |
| 38. C. Ceferino     | 38° 06' | 61° 48' | 853  | 15 | 23.3 $\pm$ 0.90      | 13.1 $\pm$ 0.70       | 10.2 $\pm$ 0.48       | 16.5 $\pm$ 1.12       | 5.0 $\pm$ 0.37       | 4.0 $\pm$ 0.27       |
| 39. I. Ameghino     | 42° 30' | 64° 32' | 55   | 20 | 22.2 $\pm$ 0.22      | 12.2 $\pm$ 0.16       | 10.1 $\pm$ 0.3        | 15.5 $\pm$ 0.23       | 4.8 $\pm$ 0.07       | 3.7 $\pm$ 0.06       |
| 40. P. Madryn       | 42° 49' | 65° 03' | 18   | 20 | 22.6 $\pm$ 0.20      | 12.7 $\pm$ 0.15       | 10.3 $\pm$ 0.12       | 15.6 $\pm$ 0.2        | 5.1 $\pm$ 0.07       | 4.4 $\pm$ 0.09       |
| 41. K 1430. NR 3    | 43° 04' | 65° 12' | 36   | 6  | 22.5 $\pm$ 0.50      | 12.4 $\pm$ 0.19       | 10.3 $\pm$ 0.25       | 15.7 $\pm$ 0.45       | 4.7 $\pm$ 0.15       | 3.9 $\pm$ 0.15       |
| 42. Lago Musters    | 45° 30' | 69° 08' | 261  | 17 | 19.5 $\pm$ 0.30      | 11.4 $\pm$ 0.19       | 9.4 $\pm$ 0.12        | 13.4 $\pm$ 0.20       | 4.2 $\pm$ 0.09       | 3.1 $\pm$ 0.09       |
| 43. D. Argentina    | 45° 47' | 67° 40' | 326  | 16 | 19.3 $\pm$ 0.28      | 11.1 $\pm$ 0.15       | 8.7 $\pm$ 0.14        | 13.1 $\pm$ 0.18       | 3.7 $\pm$ 0.10       | 2.9 $\pm$ 0.09       |
| 44. V. Rada Tilly   | 45° 57' | 67° 32' | 0    | 7  | 18.2 $\pm$ 0.45      | 10.7 $\pm$ 0.40       | 8.7 $\pm$ 0.39        | 13.5 $\pm$ 0.35       | 3.8 $\pm$ 0.27       | 3.0 $\pm$ 0.21       |

documented both across and within species.

We were interested in analyzing intraspecific patterns of SSD in two related species because most of the information on the occurrence of Rensch's rule in nature is interspecific. Although recently a number of intraspecific studies have been published, between-species comparisons of related species are uncommon (Fairbairn 2005), and it is not known if the underlying mechanisms, both proximate and evolutionary, are comparable to those that have been proposed for interspecific SSD variation (Fairbairn 2005).

Furthermore, proximate mechanisms may be entirely different in vertebrates *vs* invertebrates, or endo- *vs* ectotherms (Blanckenhorn *et al.* 2007).

In acridoid grasshoppers, the degree of female-biased SSD varies widely between families and genera (Uvarov 1966, 1977). The South American Melanoplinae and especially the widespread genus *Dichroplus*, exhibit moderate to pronounced SSD as well as other aspects of sexual dimorphism such as differences in coloration (Cigliano & Otte 2003, Bidau & Martí 2007b). We therefore analyzed SSD in

Table 1b. Means and standard errors of six morphometric characters for females of *D. vittatus* and *D. pratensis*. See Table 1a caption for legend.

| Population          | N  | BL $\pm$ s $\bar{x}$ | F3L $\pm$ s $\bar{x}$ | T3L $\pm$ s $\bar{x}$ | TeL $\pm$ s $\bar{x}$ | PL $\pm$ s $\bar{x}$ | PH $\pm$ s $\bar{x}$ |
|---------------------|----|----------------------|-----------------------|-----------------------|-----------------------|----------------------|----------------------|
| <i>D. vittatus</i>  |    |                      |                       |                       |                       |                      |                      |
| 1. Huacalera        | 18 | 21.7 $\pm$ 0.31      | 12.4 $\pm$ 0.11       | 10.4 $\pm$ 0.12       | 7.7 $\pm$ 0.19        | 5.3 $\pm$ 0.08       | 3.8 $\pm$ 0.06       |
| 2. La Viña          | 11 | 28.1 $\pm$ 0.31      | 15.6 $\pm$ 0.18       | 13.5 $\pm$ 0.22       | 11.0 $\pm$ 0.58       | 6.7 $\pm$ 0.20       | 4.9 $\pm$ 0.21       |
| 3. S. del Estero    | 10 | 24.8 $\pm$ 0.29      | 13.4 $\pm$ 0.15       | 10.5 $\pm$ 0.16       | 8.6 $\pm$ 0.25        | 5.5 $\pm$ 0.21       | 3.8 $\pm$ 0.21       |
| 4. C. del Valle     | 2  | 25.4 $\pm$ 1.67      | 14.6 $\pm$ 0.67       | 12.2 $\pm$ 0.62       | 9.2 $\pm$ 0.55        | 6.2 $\pm$ 0.28       | 4.6 $\pm$ 0.16       |
| 5. Tafi del Valle   | 21 | 25.7 $\pm$ 0.19      | 14.0 $\pm$ 0.11       | 11.8 $\pm$ 0.10       | 9.4 $\pm$ 0.15        | 6.2 $\pm$ 0.06       | 4.4 $\pm$ 0.05       |
| 6. Miraflores       | 3  | 25.7 $\pm$ 0.18      | 14.1 $\pm$ 0.18       | 12.0 $\pm$ 0.12       | 8.9 $\pm$ 0.28        | 6.2 $\pm$ 0.06       | 4.1 $\pm$ 0.05       |
| 7. Chumbicha        | 5  | 23.7 $\pm$ 0.62      | 13.1 $\pm$ 0.25       | 11.4 $\pm$ 0.28       | 8.3 $\pm$ 0.58        | 5.7 $\pm$ 0.40       | 4.2 $\pm$ 0.13       |
| 8. La Rioja         | 9  | 27.4 $\pm$ 0.25      | 14.6 $\pm$ 0.33       | 12.4 $\pm$ 0.26       | 10.3 $\pm$ 0.26       | 6.3 $\pm$ 0.06       | 4.6 $\pm$ 0.06       |
| 9. Valle Fértil     | 4  | 24.7 $\pm$ 0.29      | 13.6 $\pm$ 0.14       | 11.2 $\pm$ 0.09       | 8.1 $\pm$ 0.29        | 5.8 $\pm$ 0.09       | 3.9 $\pm$ 0.10       |
| 10. V. Rosario      | 25 | 26.1 $\pm$ 0.17      | 14.3 $\pm$ 0.13       | 12.0 $\pm$ 0.16       | 9.4 $\pm$ 0.13        | 6.2 $\pm$ 0.06       | 4.3 $\pm$ 0.03       |
| 11. Guido           | 10 | 23.5 $\pm$ 0.25      | 12.8 $\pm$ 0.28       | 10.3 $\pm$ 0.25       | 7.1 $\pm$ 0.25        | 5.4 $\pm$ 0.07       | 3.9 $\pm$ 0.07       |
| 12. Potrerillos     | 5  | 22.8 $\pm$ 0.67      | 12.2 $\pm$ 0.39       | 10.3 $\pm$ 0.31       | 6.8 $\pm$ 0.39        | 5.4 $\pm$ 0.23       | 3.8 $\pm$ 0.16       |
| 13. Cacheuta        | 5  | 21.7 $\pm$ 0.71      | 11.6 $\pm$ 0.38       | 9.7 $\pm$ 0.31        | 6.6 $\pm$ 0.43        | 5.3 $\pm$ 0.25       | 3.7 $\pm$ 0.19       |
| 14. Compuertas      | 2  | 22.0 $\pm$ 1.28      | 12.2 $\pm$ 0.56       | 10.2 $\pm$ 0.33       | 6.8 $\pm$ 0.31        | 5.5 $\pm$ 0.38       | 3.9 $\pm$ 0.18       |
| 15. La Punilla      | 4  | 23.7 $\pm$ 0.42      | 13.0 $\pm$ 0.30       | 10.8 $\pm$ 0.35       | 8.0 $\pm$ 0.30        | 5.8 $\pm$ 0.40       | 3.7 $\pm$ 0.24       |
| 16. El Morro        | 6  | 23.2 $\pm$ 0.49      | 13.3 $\pm$ 0.15       | 10.8 $\pm$ 0.16       | 8.1 $\pm$ 0.30        | 5.5 $\pm$ 0.28       | 3.9 $\pm$ 0.25       |
| 17. Olmos           | 10 | 22.7 $\pm$ 0.22      | 12.7 $\pm$ 0.27       | 10.7 $\pm$ 0.28       | 8.4 $\pm$ 0.22        | 5.3 $\pm$ 0.10       | 3.8 $\pm$ 0.05       |
| 18. Toay            | 9  | 20.8 $\pm$ 0.20      | 11.8 $\pm$ 0.27       | 9.6 $\pm$ 0.18        | 6.5 $\pm$ 0.19        | 5.4 $\pm$ 0.08       | 3.9 $\pm$ 0.05       |
| 19. Playa Unión     | 16 | 20.3 $\pm$ 0.42      | 11.3 $\pm$ 0.20       | 9.6 $\pm$ 0.16        | 6.2 $\pm$ 0.18        | 4.8 $\pm$ 0.09       | 3.4 $\pm$ 0.08       |
| <i>D. pratensis</i> |    |                      |                       |                       |                       |                      |                      |
| 20. Volcán          | 7  | 24.3 $\pm$ 0.45      | 14.0 $\pm$ 0.34       | 11.4 $\pm$ 0.40       | 12.6 $\pm$ 0.28       | 5.8 $\pm$ 0.08       | 4.9 $\pm$ 0.10       |
| 21. E. Mazán        | 23 | 26.5 $\pm$ 0.31      | 14.3 $\pm$ 0.15       | 11.6 $\pm$ 0.05       | 15.1 $\pm$ 0.23       | 6.1 $\pm$ 0.07       | 5.0 $\pm$ 0.07       |
| 22. Carrizal        | 5  | 28.2 $\pm$ 0.20      | 15.2 $\pm$ 0.13       | 12.1 $\pm$ 0.07       | 16.0 $\pm$ 0.29       | 6.2 $\pm$ 0.18       | 5.0 $\pm$ 0.13       |
| 23. Las Juntas      | 6  | 25.7 $\pm$ 0.27      | 14.1 $\pm$ 0.17       | 11.2 $\pm$ 0.19       | 15.1 $\pm$ 0.56       | 5.7 $\pm$ 0.08       | 4.6 $\pm$ 0.11       |
| 24. C. Machado      | 13 | 27.7 $\pm$ 0.32      | 15.7 $\pm$ 0.24       | 13.0 $\pm$ 0.18       | 18.7 $\pm$ 0.26       | 6.2 $\pm$ 0.11       | 5.0 $\pm$ 0.09       |
| 25. Guido           | 7  | 26.9 $\pm$ 0.62      | 14.7 $\pm$ 0.36       | 11.9 $\pm$ 0.32       | 17.4 $\pm$ 0.32       | 5.8 $\pm$ 0.18       | 4.7 $\pm$ 0.13       |
| 26. Potrerillos     | 32 | 23.8 $\pm$ 0.21      | 13.2 $\pm$ 0.15       | 10.5 $\pm$ 0.4        | 14.7 $\pm$ 0.27       | 5.2 $\pm$ 0.07       | 4.3 $\pm$ 0.05       |
| 27. Cacheuta        | 14 | 24.9 $\pm$ 0.45      | 13.7 $\pm$ 0.25       | 11.1 $\pm$ 0.20       | 15.3 $\pm$ 0.30       | 5.5 $\pm$ 0.09       | 4.3 $\pm$ 0.11       |
| 28. Compuertas      | 15 | 27.2 $\pm$ 0.35      | 15.1 $\pm$ 0.19       | 12.0 $\pm$ 0.16       | 17.53 $\pm$ 0.39      | 5.9 $\pm$ 0.07       | 4.7 $\pm$ 0.07       |
| 29. La Punilla      | 4  | 25.8 $\pm$ 0.60      | 14.5 $\pm$ 0.36       | 11.6 $\pm$ 0.17       | 17.0 $\pm$ 0.40       | 5.7 $\pm$ 0.14       | 4.2 $\pm$ 0.13       |
| 30. Achiras         | 9  | 26.7 $\pm$ 0.34      | 15.0 $\pm$ 0.21       | 11.7 $\pm$ 0.14       | 15.8 $\pm$ 0.30       | 5.8 $\pm$ 0.07       | 4.7 $\pm$ 0.08       |
| 31. Saladillo       | 6  | 25.7 $\pm$ 0.71      | 14.6 $\pm$ 0.40       | 11.5 $\pm$ 0.14       | 16.5 $\pm$ 0.60       | 5.6 $\pm$ 0.11       | 4.4 $\pm$ 0.17       |
| 32. El Morro        | 3  | 24.5 $\pm$ 0.17      | 13.8 $\pm$ 0.38       | 11.0 $\pm$ 0.40       | 16.3 $\pm$ 0.46       | 5.6 $\pm$ 0.12       | 3.9 $\pm$ 0.13       |
| 33. La Granja       | 15 | 26.8 $\pm$ 0.22      | 14.8 $\pm$ 0.20       | 11.8 $\pm$ 0.19       | 17.8 $\pm$ 0.21       | 5.9 $\pm$ 0.11       | 4.6 $\pm$ 0.10       |
| 34. Manantiales     | 15 | 26.9 $\pm$ 0.24      | 14.9 $\pm$ 0.20       | 11.9 $\pm$ 0.18       | 19.8 $\pm$ 0.20       | 5.9 $\pm$ 0.12       | 4.7 $\pm$ 0.09       |
| 35. Don Tomás       | 15 | 25.4 $\pm$ 0.23      | 14.1 $\pm$ 0.23       | 11.4 $\pm$ 0.23       | 17.1 $\pm$ 0.24       | 5.4 $\pm$ 0.10       | 4.4 $\pm$ 0.07       |
| 36. Olavarría       | 15 | 24.3 $\pm$ 0.27      | 14.0 $\pm$ 0.18       | 11.2 $\pm$ 0.14       | 16.9 $\pm$ 0.22       | 5.5 $\pm$ 0.09       | 4.2 $\pm$ 0.09       |
| 37. C. Pringles     | 15 | 25.3 $\pm$ 0.28      | 14.4 $\pm$ 0.17       | 11.6 $\pm$ 0.15       | 16.8 $\pm$ 0.22       | 5.5 $\pm$ 0.10       | 4.4 $\pm$ 0.08       |
| 38. C. Ceferino     | 15 | 25.2 $\pm$ 0.30      | 14.4 $\pm$ 0.16       | 11.5 $\pm$ 0.15       | 16.7 $\pm$ 0.21       | 5.2 $\pm$ 0.11       | 4.5 $\pm$ 0.07       |
| 39. I. Ameghino     | 20 | 24.1 $\pm$ 0.44      | 13.7 $\pm$ 0.12       | 11.4 $\pm$ 0.16       | 16.1 $\pm$ 0.17       | 5.0 $\pm$ 0.05       | 4.4 $\pm$ 0.04       |
| 40. P. Madryn       | 20 | 25.2 $\pm$ 0.41      | 14.4 $\pm$ 0.21       | 11.7 $\pm$ 0.17       | 16.8 $\pm$ 1.17       | 5.4 $\pm$ 0.09       | 4.2 $\pm$ 0.13       |
| 41. K 1430. NR 3    | 15 | 22.3 $\pm$ 0.32      | 13.4 $\pm$ 0.22       | 11.1 $\pm$ 0.29       | 15.5 $\pm$ 0.38       | 4.9 $\pm$ 0.16       | 4.1 $\pm$ 0.14       |
| 42. Lago Musters    | 16 | 23.5 $\pm$ 0.36      | 13.7 $\pm$ 0.28       | 11.3 $\pm$ 0.20       | 15.5 $\pm$ 0.30       | 5.2 $\pm$ 0.11       | 3.9 $\pm$ 0.11       |
| 43. D. Argentina    | 16 | 22.2 $\pm$ 0.35      | 13.3 $\pm$ 0.16       | 11.2 $\pm$ 0.13       | 15.3 $\pm$ 0.27       | 5.0 $\pm$ 0.16       | 3.7 $\pm$ 0.09       |
| 44. V. Rada Tilly   | 21 | 23.2 $\pm$ 0.34      | 13.9 $\pm$ 0.19       | 11.5 $\pm$ 0.18       | 15.8 $\pm$ 0.26       | 5.0 $\pm$ 0.08       | 3.9 $\pm$ 0.09       |

two closely related South American grasshoppers, *Dichroplus vittatus* (Figs 4, 5; Plate IV) and *D. pratensis* (see Figs 2, 3 of paper p. 149 this issue; Plate IV). Both species have ample overlapping latitudinal and altitudinal geographic distributions, occupying many different habitats (Liebermann 1963; Cigliano & Otte 2003; Bidau & Martí 2002, 2007a, b). Both species show body-size variation and follow the converse to Bergmann's rule (Bidau & Martí 2007a, b). Our central hypothesis was that the degree of SSD was similar in both sister species and that Rensch's rule was verified in both.

## Materials and methods

Population samples of *D. vittatus* were obtained at 19 Argentine localities spanning almost 20 degrees of latitude and 36 to 2758 m above sea level (Fig. 1., Table 1). Twenty five samples of *D. pratensis* were collected at localities from Argentina spanning 22 degrees of latitude and 0 to 2474 m elevation (Fig. 1, Table 1). Using a precision caliper (0.01 mm), we measured a) body length (BL), b) length of left hind femur (F3L), c) length of left hind

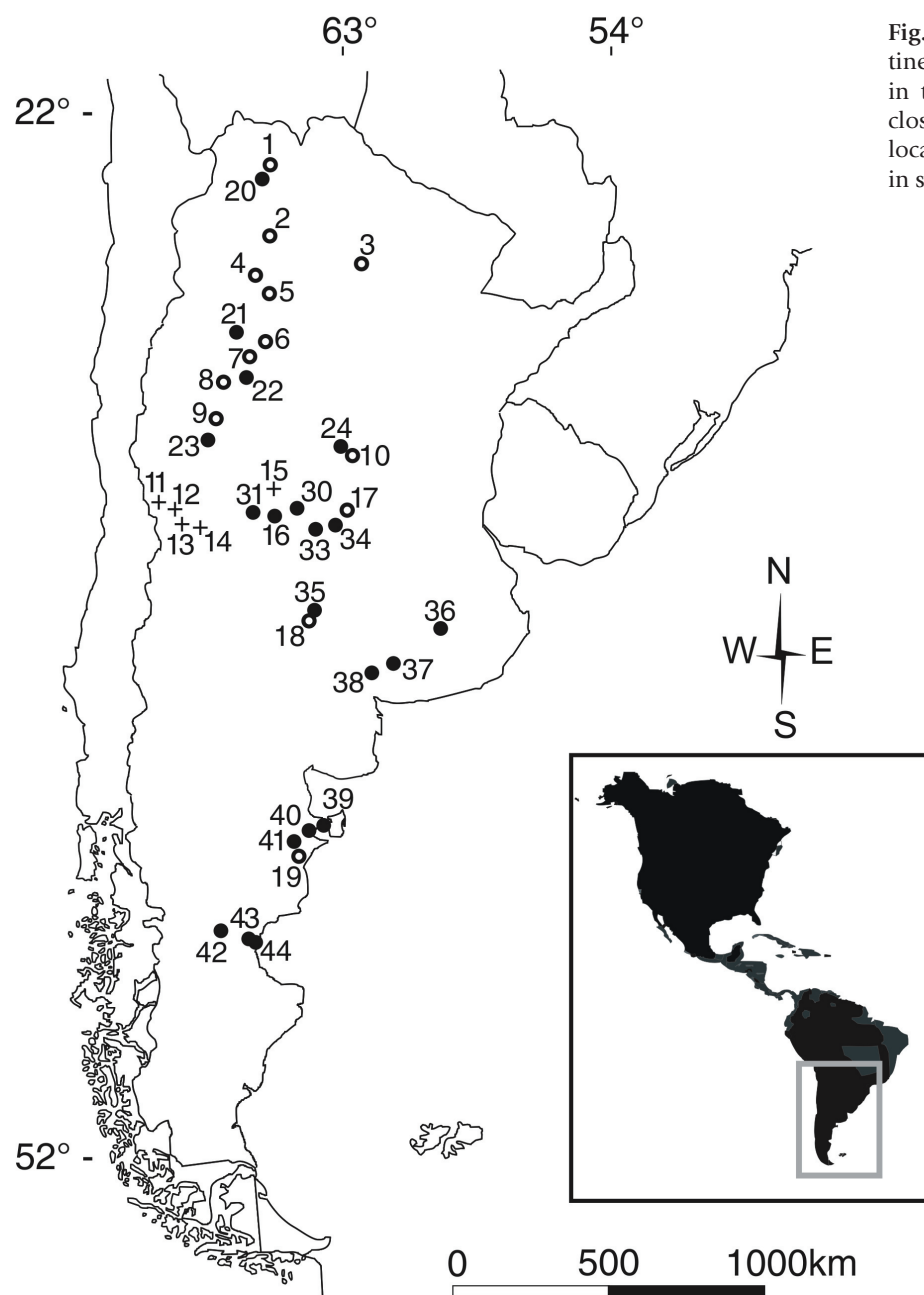


Fig. 1. Geographic distribution of Argentine grasshopper populations analyzed in this paper. Open circles, *D. vittatus*; closed black circles, *D. pratensis*; crosses, localities where both species were found in sympatry.

tibia (T3L), d) length of tegmina (TeL), e) mid-dorsal length of pronotum (PL) and f) height of pronotum (PH) of female and male preserved specimens. We used these measurements because they are standard, and because males and females of *Dichroplus* and other Melanoplinae usually differ conspicuously for them. Prior to statistical analysis, all measurements were log transformed and then tested for normality using the Kolmogorov-Smirnov test, to determine the appropriateness of subsequent parametric analysis. No variable departed from normality. Coefficients of variation for each analyzed trait were calculated as  $CV = s \times 100 / \bar{x}$  (Zar 1999). A General Linear Model (GLM) was employed for determining size differences between species, populations and sexes for all six morphometric traits. Within species, one-way ANOVAs were performed for each trait, using population or sex as factors.

SSD was calculated for each population as the ratio between the arithmetic mean of each measured character of females, and the

corresponding mean of males (Smith 1999), in order to visualize directly deviations from 1 (*i.e.*, from isometry). The scaling of SSD with body size was described by regressing  $\log_{10}$  (male size) on  $\log_{10}$  (female size) for the six traits (Fairbairn & Preziosi 1994; Abouheif & Fairbairn 1997; Fairbairn 1997, 2005). Thus, Rensch's rule applies when the slope of the regression line is greater than 1.0, whereas slopes smaller than 1.0 signal its converse (Fairbairn 1997).

Ordinary, least squares regression (OLS) is not adequate for this type of analysis because  $x$  (in this case, female body size) is not fixed and is estimated with error, with the consequence that the slope  $b$  and its confidence interval, are estimated with error (Fairbairn 1997). In these cases, type II regression is recommended (Sokal & Rohlf 1995). We thus used reduced major-axis regression (RMA) to estimate slopes for the relationship between  $\log_{10}$  of male size and  $\log_{10}$  of female size. For this purpose we used the software for RMA (Java version, Bohonak & van der Linde 2004). Clarke's  $T$

**Table 2a.** Summarized results of a General Linear Model performed on *D. vittatus* and *D. pratensis* specimens, considering all six morphometric traits as dependent variables with species (spp), sex, population (pop), sex  $\times$  pop and spp  $\times$  sex  $\times$  pop, as covariates.

| Trait | F      | df | p      | r <sup>2</sup> |
|-------|--------|----|--------|----------------|
| BL    | 157.10 | 5  | <0.001 | 0.46           |
| F3L   | 43.91  | 5  | <0.001 | 0.19           |
| T3L   | 69.74  | 5  | <0.001 | 0.27           |
| TeL   | 587.69 | 5  | <0.001 | 0.76           |
| PL    | 204.61 | 5  | <0.001 | 0.53           |
| PH    | 141.89 | 5  | <0.001 | 0.44           |

statistic, with adjusted degrees of freedom, was used for testing the hypothesis that  $\beta_{\text{RMA}} = 1.0$  (Clarke, 1980). Allometric relationships within the sexes of both species were also investigated by regressing traits on total body length using the same statistical procedures described above as in Fairbairn (2005).

## Results

To determine the sources of body-size variation in *D. vittatus* and *D. pratensis*, we performed a multivariate GLM, considering all six morphometric traits as dependent variables and species (spp), sex, population (pop), sex  $\times$  pop and spp  $\times$  sex  $\times$  pop, as covariates (Table 2a). All six traits showed highly significant ( $p < 0.001$ ) differences between species, sexes (except TeL, where  $p = 0.364$ ), populations (except TeL, where  $p = 0.591$ ; PL was significant at the 5% level,  $p = 0.037$ ) and spp  $\times$  sex  $\times$  pop (except for F3L, where  $p = 0.198$ ). No significant differences were observed for sex  $\times$  pop.

In view of the former results we performed one-way ANOVAs for each species separately, using sex or population as the independent variable (Table 2b). In both species, differences between sexes and populations were highly significant, with the exception of TeL of *D. pratensis*, where significance was borderline (Table 2b). All analyzed populations of *D. vittatus* and *D. pratensis* thus showed SSD across their respective distribution ranges, although the degree of SSD was variable (Fig. 2). For the six morphological traits, females were larger than males (Fig. 2). SSD in *D. vittatus* was greater than in *D. pratensis* (Fig. 2).

The mean size of the six morphological traits was highly correlated between sexes in both species (Table 3). In order to assess if SSD increased or decreased between populations of each species, we analyzed the RMA between-sex allometric slopes of the six measured traits in both species, under the null hypothesis of  $\beta = 1$  (isometry). A slope significantly greater than 1.0 indicates agreement with Rensch's rule, while  $\beta < 1.0$  indicates a trend which is its converse. In *D. pratensis*, all 6 RMA slopes were highly significantly greater than 1, signaling agreement with Rensch's rule (Table 3; Fig. 3a). Conversely, in *D. vittatus*, all measurements showed RMA slopes  $< 1.0$  (Table 3, Fig. 3a). Of these, four showed statistical significance and one, TeL, was marginally significant while PL was nonsignificant, indicating between-sex isometry (Table 3).

Allometric relationships differed among traits, sexes and species. TeL showed hyperallometry in both sexes, although in female *D. pratensis* the slope was not statistically significant (Table 4; Fig. 3b,c). In males of *D. pratensis* the size of F3L and T3L scaled isometrically with body length. Nevertheless females of this species showed significant hypoallometry (Table 4, Fig. 3b). Larger females have relatively shorter third legs than smaller ones. On the other hand, in both sexes of *D. vittatus*, F3L and T3L scaled isometrically

**Table 2b.** One-way ANOVAs for each morphometric trait of *D. vittatus* and *D. pratensis* using sex or population as factors. F= F-statistic; df= degrees of freedom; p= probability; r<sup>2</sup>= coefficient of determination. For meaning of trait abbreviations see Materials and Methods.

| Species             | Factor     | Trait | F      | df      | p      |
|---------------------|------------|-------|--------|---------|--------|
| <i>D. vittatus</i>  | Sex        | BL    | 56.25  | 1, 293  | <0.001 |
|                     |            | F3L   | 182.09 | 1, 293  | <0.001 |
|                     |            | T3L   | 76.08  | 1, 293  | <0.001 |
|                     |            | TeL   | 191.51 | 1, 293  | <0.001 |
|                     |            | PL    | 183.04 | 1, 293  | <0.001 |
|                     |            | PH    | 513.68 | 1, 293  | <0.001 |
|                     | Population | BL    | 10.32  | 18, 275 | <0.001 |
|                     |            | F3L   | 3.00   | 18, 275 | <0.001 |
|                     |            | T3L   | 6.06   | 18, 275 | <0.001 |
|                     |            | TeL   | 6.39   | 18, 275 | <0.001 |
|                     |            | PL    | 6.30   | 18, 275 | <0.001 |
|                     |            | PH    | 11.41  | 18, 275 | <0.001 |
| <i>D. pratensis</i> | Sex        | BL    | 29.40  | 1, 615  | <0.001 |
|                     |            | F3L   | 30.81  | 1, 615  | <0.001 |
|                     |            | T3L   | 27.25  | 1, 615  | <0.001 |
|                     |            | TeL   | 3.17   | 1, 615  | 0.076  |
|                     |            | PL    | 73.75  | 1, 615  | <0.001 |
|                     |            | PH    | 24.19  | 1, 615  | <0.001 |
|                     | Population | BL    | 513.68 | 24, 592 | <0.001 |
|                     |            | F3L   | 56.25  | 24, 592 | <0.001 |
|                     |            | T3L   | 182.09 | 24, 592 | <0.001 |
|                     |            | TeL   | 76.08  | 24, 592 | <0.001 |
|                     |            | PL    | 191.51 | 24, 592 | <0.001 |
|                     |            | PH    | 183.04 | 24, 592 | <0.001 |

with body length (Table 4, Fig. 3c). Males of *D. pratensis* exhibited hyperallometry for PL, whereas females and males exhibited hyperallometry for PH (Table 4, Fig. 3b); in *D. vittatus*, both traits scaled isometrically with body length in both sexes (Table 4, Fig. 3c).

In *D. vittatus* the coefficients of variation of all measurements are higher in females than in males, whereas in *D. pratensis* the coefficients of variation are higher in males than females. The only inversion of this pattern occurs in *D. pratensis* where PH is less variable in males than in females (Table 5). The highest populational mean BL for females in *D. vittatus* was 28.13 mm at La Viña, and the lowest 20.26 mm at Playa Unión, giving a range of 7.87 mm. In the case of males, the highest and lowest mean BLs occurred in the same populations (21.62 and 16.43 mm, respectively) producing a range of 5.19 mm. In *D. pratensis* the values of the mean BL ranges were inverted with respect to *D. vittatus*, 6.05 mm for females (28.23 mm at Carrizal and 22.18 mm at Diadema, Argentina) and 7.47 mm for males (26.38 mm at Compuertas and 18.91 mm at Villa Rada Tilly).

To evaluate if SSD was correlated to variability of morphometric traits, we estimated linear and nonlinear relationships between the CVs of each trait of males and females, and SSD. The results are shown in Table 6. In *D. vittatus*, most relationships showed a negative tendency, and four were statistically significant. Conversely, in *D. pratensis* significant correlations were basically positive except for PH of females.

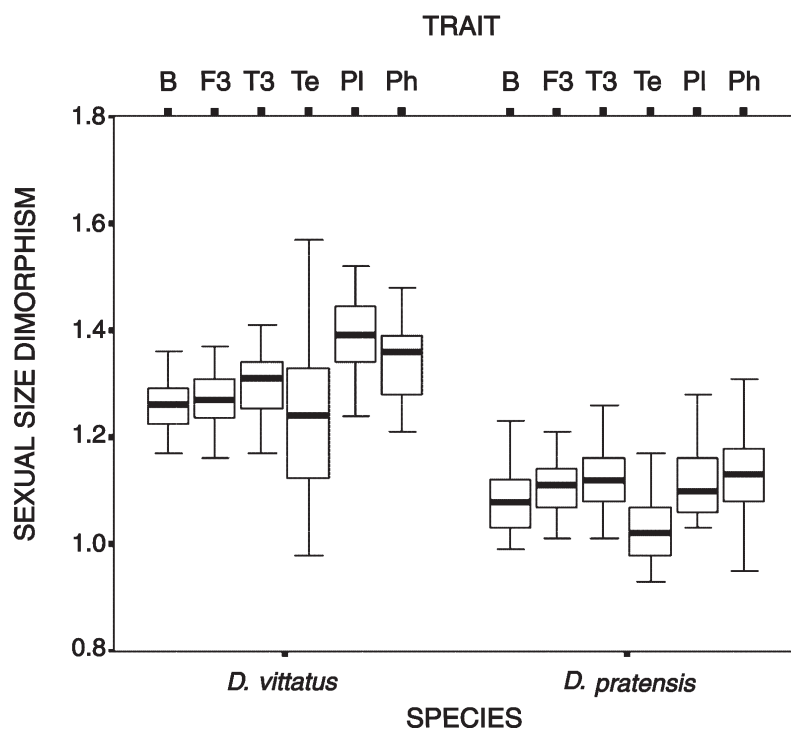


Fig. 2. Box-plots of geographic variation in sexual size dimorphism of six morphometric traits in *D. vittatus* (left) and *D. pratensis* (right). Each box represents the median, quartiles, and extreme values for each morphometric variable. B=body length; F3=Femur3 length; T3=Tibia3 length; Te=Tegmina length; Pl=Pronotum length; Ph=Pronotum height.

Table 3. Results of reduced major-axis regression of log (male size) on log (female size) for population means of six morphological traits from 25 and 19 populations of *D. pratensis* and *D. vittatus* respectively. For abbreviations of traits see Materials and Methods.  $r$ =Pearson's correlation coefficient;  $t$ =Student's  $t$  statistic;  $\beta$ =slope of the RMA regression line;  $T$ =Clarke's  $T$  statistic;  $df$ =degrees of freedom;  $^{1}df$ =Clarke's adjusted degrees of freedom for  $T$ ;  $a$ =intercept of the RMA regression line; 95% CI=95% confidence intervals; SE=standard error;  $p$ =probability. For meaning of trait abbreviations see Materials and Methods.

| Correlation coefficient |       |      |      |    |                    | RMA slope                    |      |                 |                    |              | RMA intercept          |                   |
|-------------------------|-------|------|------|----|--------------------|------------------------------|------|-----------------|--------------------|--------------|------------------------|-------------------|
| Species                 | Trait | r    | t    | df | p                  | $\beta$<br>( $s_{\bar{x}}$ ) | T    | df <sup>1</sup> | p                  | 95% CI       | a<br>( $s_{\bar{x}}$ ) | 95% CI            |
| <i>D. pratensis</i>     | TBL   | 0.79 | 6.12 | 23 | 2*10 <sup>-5</sup> | 1.328<br>(0.171)             | 2.60 | 20.33           | 0.0085             | 0.975, 1.681 | -0.493<br>(0.239)      | -0.988,<br>0.002  |
|                         | F3L   | 0.65 | 4.06 | 23 | 0.00024            | 1.770<br>(0.282)             | 4.94 | 21.86           | 0.0003             | 1.187, 2.353 | -0.936<br>(0.325)      | -1.609,<br>-0.263 |
|                         | T3L   | 0.48 | 2.73 | 23 | 0.00596            | 1.886<br>(0.345)             | 4.95 | 23.52           | 0.0003             | 1.172, 2.600 | -0.993<br>(0.367)      | -1.751,<br>-0.235 |
|                         | TeL   | 0.84 | 6.38 | 23 | 1*10 <sup>-6</sup> | 1.458<br>(0.163)             | 4.18 | 19.70           | 0.0002             | 1.121, 1.795 | -0.568<br>(0.197)      | -0.976,<br>-0.156 |
|                         | PL    | 0.71 | 4.88 | 23 | 0.00003            | 1.620<br>(0.237)             | 4.31 | 21.14           | 0.0002             | 1.130, 2.109 | -0.512<br>(0.177)      | -0.877,<br>-0.147 |
|                         | PH    | 0.66 | 4.18 | 23 | 0.00018            | 1.739<br>(0.273)             | 4.80 | 21.74           | 4*10 <sup>-5</sup> | 1.173, 2.304 | -0.706<br>(0.204)      | -1.128,<br>-0.284 |
| <i>D. vittatus</i>      | TBL   | 0.83 | 6.15 | 17 | 5*10 <sup>-6</sup> | 0.767<br>(0.104)             | 2.40 | 15.38           | 0.0147             | 0.549, 0.986 | 0.221<br>(0.143)       | -0.080,<br>0.522  |
|                         | F3L   | 0.81 | 5.78 | 17 | 0.00001            | 0.753<br>(0.106)             | 1.80 | 15.52           | 0.0457             | 0.529, 0.976 | 0.173<br>(0.119)       | -0.077,<br>0.423  |
|                         | T3L   | 0.79 | 5.26 | 17 | 0.00003            | 0.701<br>(0.105)             | 2.06 | 15.74           | 0.0282             | 0.480, 0.923 | 0.202<br>(0.109)       | -0.029,<br>0.432  |
|                         | TeL   | 0.67 | 3.68 | 17 | 0.00093            | 0.712<br>(0.129)             | 1.63 | 16.73           | 0.0609             | 0.440, 0.984 | 0.172<br>(0.117)       | -0.075,<br>0.420  |
|                         | PL    | 0.77 | 4.98 | 17 | 0.00006            | 0.876<br>(0.134)             | 0.82 | 15.88           | 0.2122             | 0.590, 1.162 | -0.049<br>(0.102)      | -0.266,<br>0.167  |
|                         | PH    | 0.75 | 4.66 | 17 | 0.00011            | 0.658<br>(0.106)             | 2.19 | 16.06           | 0.0218             | 0.435, 0.882 | 0.078<br>(0.064)       | -0.056,<br>0.213  |

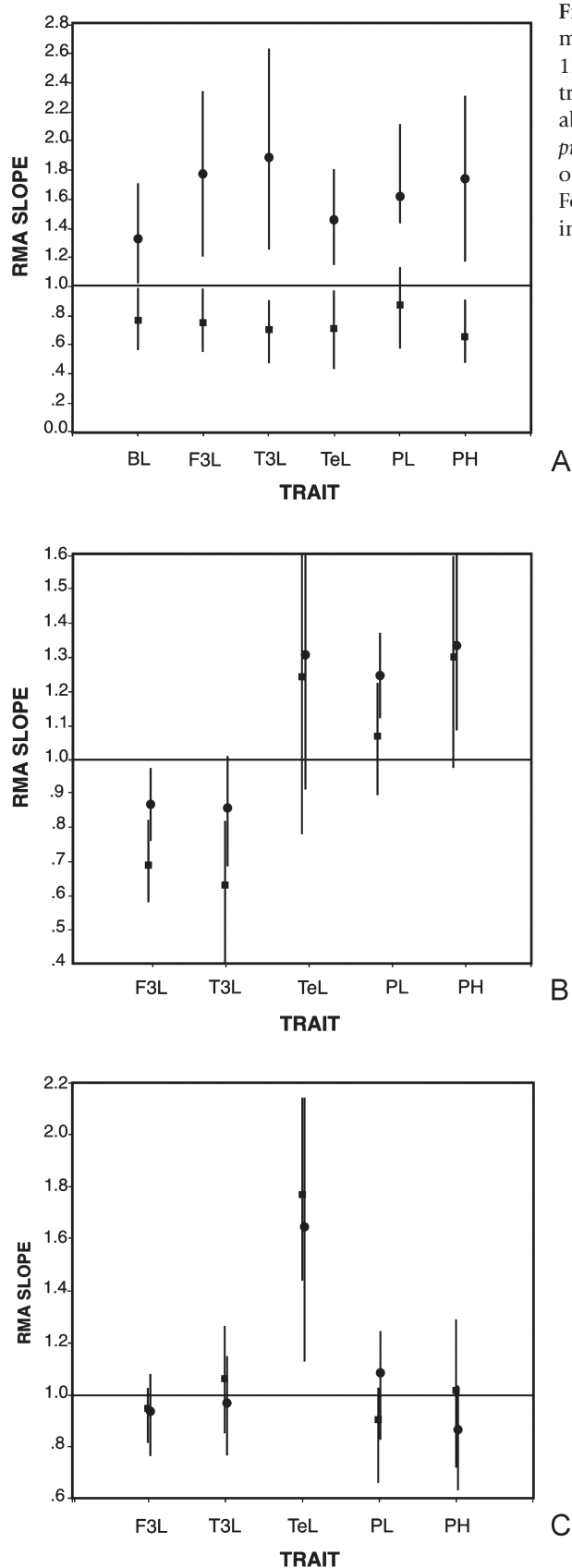
**Table 4.** Results of reduced major-axis regression of log (mean trait size) on log (mean body length) for male and female *D. pratensis* (25 populations) and *D. vittatus* (19 populations). For abbreviations of traits see Materials and Methods.  $r$ =Pearson's correlation coefficient;  $t$ =Student's  $t$  statistic;  $\beta$ =slope of the RMA regression line;  $T$ =Clarke's  $T$  statistic;  $df$ =degrees of freedom;  $^1df$ =Clarke's adjusted degrees of freedom for  $T$ ;  $a$ =intercept of the RMA regression line; 95% CI=95% confidence interval;  $s_{\bar{x}}$ =standard error;  $p$ =probability. For meaning of trait abbreviations see Materials and Methods.

|                     |     | Correlation coefficient |      |       |    | RMA slope          |                                  |      |                 |                    | RMA intercept |                        |                   |
|---------------------|-----|-------------------------|------|-------|----|--------------------|----------------------------------|------|-----------------|--------------------|---------------|------------------------|-------------------|
| Species             | Sex | Trait                   | r    | t     | df | p                  | $\beta$<br>( $s_{\bar{\beta}}$ ) | T    | df <sup>†</sup> | p                  | 95% CI        | a<br>( $s_{\bar{a}}$ ) | 95% CI            |
| <i>D. pratensis</i> |     | F3L                     | 0.96 | 17.21 | 23 | 10 <sup>-6</sup>   | 0.872<br>(0.049)                 | 0.65 | 18.40           | 0.2619             | 0.771, 0.973  | -0.085<br>(0.067)      | -0.224,<br>0.053  |
|                     |     | T3L                     | 0.80 | 6.29  | 23 | 10 <sup>-6</sup>   | 0.855<br>(0.081)                 | 1.17 | 20.24           | 0.1278             | 0.688, 1.022  | -0.160<br>(0.011)      | -0.388,<br>0.068  |
|                     | ♂   | TeL                     | 0.78 | 5.88  | 23 | 3*10 <sup>-6</sup> | 1.304<br>(0.172)                 | 2.35 | 20.46           | 0.0117             | 0.948, 1.660  | -0.587<br>(0.235)      | -1.074,<br>-0.101 |
|                     |     | PL                      | 0.97 | 19.34 | 23 | 10 <sup>-6</sup>   | 1.243<br>(0.062)                 | 4.94 | 18.32           | 5*10 <sup>-5</sup> | 1.114, 1.372  | -1.004<br>(0.085)      | -1.180,<br>-0.828 |
|                     |     | PH                      | 0.86 | 7.94  | 23 | 10 <sup>-6</sup>   | 1.334<br>(0.144)                 | 3.17 | 19.56           | 0.0025             | 1.037, 1.631  | -1.234<br>(0.197)      | -1.641,<br>-0.828 |
|                     |     | F3L                     | 0.91 | 10.24 | 23 | 10 <sup>-6</sup>   | 0.682<br>(0.060)                 | 3.67 | 19.02           | 0.0008             | 0.558, 0.807  | 0.197<br>(0.084)       | 0.022,<br>0.372   |
|                     |     | T3L                     | 0.76 | 5.45  | 23 | 8*10 <sup>-6</sup> | 0.628<br>(0.087)                 | 2.74 | 20.77           | 0.0062             | 0.448, 0.808  | 0.181<br>(0.122)       | -0.072,<br>0.434  |
|                     | ♀   | TeL                     | 0.50 | 2.76  | 23 | 0.0056             | 1.239<br>(0.224)                 | 1.35 | 23.34           | 0.0950             | 0.776, 1.701  | -0.527<br>(0.314)      | -1.176,<br>0.122  |
|                     |     | PL                      | 0.93 | 11.98 | 23 | 10 <sup>-6</sup>   | 1.063<br>(0.082)                 | 0.83 | 18.77           | 0.2085             | 0.893, 1.233  | -0.745<br>(0.115)      | -1.068,<br>-0.421 |
|                     |     | PH                      | 0.82 | 6.88  | 23 | 10 <sup>-6</sup>   | 1.299<br>(0.155)                 | 2.56 | 19.96           | 0.0093             | 0.978, 1.619  | -1.176<br>(0.217)      | -1.626,<br>-0.728 |
| <i>D. vittatus</i>  |     | F3L                     | 0.95 | 12.11 | 17 | 10 <sup>-6</sup>   | 0.931<br>(0.073)                 | 0.91 | 14.43           | 0.1889             | 0.777, 1.084  | -0.174<br>(0.093)      | -0.370,<br>0.022  |
|                     |     | T3L                     | 0.93 | 6.79  | 17 | 2*10 <sup>-6</sup> | 0.972<br>(0.086)                 | 0.33 | 14.55           | 0.3731             | 0.791, 1.153  | -0.311<br>(0.109)      | -0.541,<br>-0.080 |
|                     | ♂   | TeL                     | 0.82 | 5.89  | 17 | 9*10 <sup>-6</sup> | 1.643<br>(0.229)                 | 3.17 | 15.48           | 0.0031             | 1.161, 2.125  | -1.280<br>(0.292)      | -1.896,<br>-0.664 |
|                     |     | PL                      | 0.93 | 10.22 | 17 | 10 <sup>-6</sup>   | 1.035<br>(0.094)                 | 0.40 | 14.59           | 0.3475             | 0.837, 1.233  | -0.710<br>(0.120)      | -0.963,<br>-0.456 |
|                     |     | PH                      | 0.88 | 7.48  | 17 | 10 <sup>-6</sup>   | 0.870<br>(0.102)                 | 1.14 | 15.01           | 0.1361             | 0.655, 1.084  | -0.636<br>(0.130)      | -0.910,<br>-0.361 |
|                     |     | F3L                     | 0.97 | 15.5  | 17 | 10 <sup>-6</sup>   | 0.949<br>(0.059)                 | 0.84 | 14.27           | 0.2074             | 0.824, 1.074  | -0.188<br>(0.081)      | -0.359,<br>-0.016 |
|                     |     | T3L                     | 0.93 | 10.71 | 17 | 10 <sup>-6</sup>   | 1.063<br>(0.093)                 | 0.74 | 14.53           | 0.2355             | 0.868, 1.259  | -0.424<br>(0.128)      | -0.693,<br>-0.155 |
|                     | ♀   | TeL                     | 0.92 | 10.84 | 17 | 10 <sup>-6</sup>   | 1.771<br>(0.158)                 | 8.87 | 14.57           | 10 <sup>-6</sup>   | 1.436, 2.105  | -1.530<br>(0.218)      | -1.990,<br>-1.070 |
|                     |     | PL                      | 0.93 | 10.69 | 17 | 10 <sup>-6</sup>   | 0.906<br>(0.082)                 | 1.07 | 14.59           | 0.1510             | 0.733, 1.080  | -0.493<br>(0.113)      | -0.731,<br>-0.254 |
|                     |     | PH                      | 0.85 | 9.92  | 17 | 10 <sup>-6</sup>   | 1.014<br>(0.128)                 | 0.11 | 15.20           | 0.4569             | 0.743, 1.284  | -0.793<br>(0.197)      | -1.166,<br>-0.420 |

## Discussion

We analyzed SSD at the intraspecific level in two species of *Diachroplus* grasshoppers. Both species showed significant female-biased SSD across their geographic distribution ranges. In *D. pratensis* the six morphometric traits followed Rensch's rule, whereas in *D. vittatus*, which exhibited greater SSD than *D. pratensis*, the converse to Rensch's rule was verified. Moreover, allometric relationships differed between species and sexes.

Since male and female sizes covary, there is an allometric relationship between female and male body size of the type  $\log(\text{female size}) = a + \beta \times \log(\text{male size})$ , where, if  $\beta > 1.00$ , SSD decreases when females are larger than males (hypoallometry; Rensch's rule), whereas, if  $\beta < 1.00$ , SSD increases according to an increase in body size (hyperallometry; the converse to Rensch's rule in female-biased SSD). *D. pratensis* shows the typical case of larger females and  $\beta > 1.00$ . *D. vittatus*, although having larger females than males and exhibiting stronger SSD than *D. pratensis*, shows  $\beta < 1.00$ . *D. pra-*



**Fig. 3 A.** Plot of Reduced Major Axis (RMA) regression slopes ( $\beta$ ) of  $\log_{10}$  mean male size on  $\log_{10}$  mean female size for six morphometric traits of 19 and 25 populations of *D. vittatus* and *D. pratensis*, respectively. For each trait,  $\beta$  (black circle) and its confidence interval, are represented. All  $\beta$  values above 1.0 correspond to *D. pratensis*, those below 1.0 to *D. vittatus*. **B.** *D. pratensis*; **C.** *D. vittatus*. Plots of RMA regression slopes ( $\beta$ ) of  $\log_{10}$  mean male or female trait size on  $\log_{10}$  mean male or female body length, respectively. For each trait,  $\beta$  (black circle, male; black square, female) and its confidence interval, are represented.

*tensis* follows Rensch's rule while *D. vittatus* follows its converse. It must be noted that in a previous paper (Bidau & Martí 2007b), we considered *D. pratensis* as following the converse to Rensch's rule but this conclusion was based on a restricted definition of the rule. Thus in *D. pratensis* SSD decreases with increasing body size while in *D. vittatus* the opposite trend occurs.

A recent study (Teder & Tammaru 2005) examined the extent and direction of SSD and its conforming to Rensch's rule in 158 insect species comprising all the major orders, including six orthopterans, five of them acridoidea (Walton 1980, Lewis 1984, Sword & Chapman 1994, Willott & Hassall 1998). Eighty-two percent of these showed female-biased SSD and 70% of them followed Rensch's rule (including the four acridoidea species considered in the definitive analyses); 30% followed its converse according to the criteria defined by the authors. Most data in Teder & Tammaru's (2005) analysis were obtained from experimental studies of insects reared under different environmental conditions, but not necessarily from different geographical localities. Thus, in this case, most differences in SSD are probably ontogenetic. However, the results are relevant for the assessment of body-size responses of either sex to environmental variation, and may be useful to interpret situations in the wild. Nevertheless, different species in the same monophyletic group, including the same genus may show very different SSD tendencies (Fairbairn 1997). The latter appears to be the case in the only two *Dichroplus* species studied until now, *D. vittatus* and *D. pratensis*.

Why do insects in which females are larger than males tend to follow Rensch's rule? In general, it is probable that larger females have a fecundity advantage over smaller ones (Honek 1993, Andersson 1994), while small males may benefit in scrambles over females, which is a frequent form of male competition in insects (Andersson 1994).

Two further processes may explain Rensch's rule in these cases. On one side, it is possible that large female size is favored if females compete actively for males, although this does not seem to be the case in these *Dichroplus* species. Second, female size could be more sensitive to change of environmental conditions, as suggested by the results of Teder & Tammaru (2005). Thus, as conditions improve, females could achieve their optimal size more readily than in poorer conditions. The latter is plausible, especially in species with a large geographical distribution such as *D. vittatus*.

As shown elsewhere (Bidau & Martí, in prep.), *D. vittatus* displays great latitudinal variation in average body size. This species inhabits arid to semi-arid habitats across more than 20 degrees of latitude and about 3000 m of elevation (Cigliano *et al.* 2000, Cigliano & Otte 2003), and these habitats show great variability in plant diversity and host-plant density. Furthermore, populations from high-latitude localities usually have shorter reproductive seasons than those from lower latitudes (Cigliano & Otte 2003, Bidau & Martí, unpub. results), probably resulting from physical and ecological constraints (*i.e.*, temperature and food quality and quantity).

On the other hand, although *D. pratensis* also shows large levels of body-size variation along its latitudinal and altitudinal distribu-

**Table 5.** Means and coefficients of variation of six morphometric traits of males and females of *D. vittatus* and *D. pratensis*. N= number of populations. For meaning of trait abbreviations see Materials and methods.

|      | <i>D. vittatus</i> |       |       | <i>D. pratensis</i> |       |       |
|------|--------------------|-------|-------|---------------------|-------|-------|
|      | N                  | Mean  | CV    | N                   | Mean  | CV    |
| BLM  | 17                 | 19.02 | 7.22  | 23                  | 23.30 | 7.82  |
| BLF  | 17                 | 23.94 | 9.57  | 19                  | 25.14 | 7.03  |
| F3LM | 17                 | 10.39 | 6.87  | 23                  | 12.77 | 7.78  |
| F3LF | 17                 | 13.19 | 9.14  | 19                  | 14.21 | 4.80  |
| T3LM | 17                 | 8.57  | 7.15  | 23                  | 10.20 | 7.70  |
| T3LF | 17                 | 11.03 | 10.34 | 19                  | 11.52 | 4.45  |
| TeLM | 17                 | 6.60  | 11.82 | 23                  | 15.68 | 11.41 |
| TeLF | 17                 | 8.19  | 17.06 | 19                  | 15.99 | 8.19  |
| PLM  | 17                 | 4.10  | 7.62  | 23                  | 4.96  | 10.72 |
| PLF  | 17                 | 5.71  | 8.70  | 19                  | 5.54  | 7.56  |
| PHM  | 17                 | 3.00  | 6.21  | 23                  | 3.00  | 6.40  |
| PHF  | 17                 | 4.05  | 9.67  | 19                  | 4.03  | 9.91  |

tion (Bidau & Martí 2007b), SSD decreases as average body size increases, as shown in this paper. In both species however, larger size is achieved in ecologically central populations, which are usually less protandrous, since sexual maturity tends to be more synchronized due to longer developmental time and the possibility that females could achieve their optimal size more readily in central ecological conditions. Thus, ecologically central populations would tend to be less protandrous and show lower levels of SSD than marginal ones.

Intraspecific Rensch's rule in this case could possibly be related to protandry, but only in *D. pratensis*, since in *D. vittatus* central populations that exhibit larger body sizes, are in fact more dimorphic.

Protandry is the phenomenon observed in many insects and other animals, where males emerge and/or reach sexual maturity before females (Nylin *et al.* 1993, Zonneveld 1996, Cueva del Castillo & Núñez-Farfán 1999, Crowley & Johansson 2002, Candolin & Voigt 2003, Møller 2004, Morbey & Ydenberg 2001). The evolutionary origin of protandry may be related to an advantage for males reaching early sexual maturity and gaining early access to virgin females (Andersson 1994, Morbey & Ydenberg 2001). However, in *D. pratensis*, due to the large geographic range, developmental time and emergence of males and females is strongly affected by climatic conditions. The single annual adult season is much shorter in marginal environments where body size is smaller, than in central ones where average sizes reach their maximum (Bidau & Martí 2002, 2005). Nevertheless, protandry is the rule in all studied populations, females reaching the adult stage when environmental conditions reach their optimum. Thus, in marginal habitats males should be proportionally much smaller than females, while in central areas of the species range, longer development time would allow males to reach larger sizes closer to the females' optimum (Bidau & Martí 2005). If environmental conditions affect body size in *D. pratensis*, it is thus possible, contrary to what we proposed for *D. vittatus*, that both sexes show similar responses.

Correlation analysis between the CVs of each trait for males and females of both species, and the degree of SSD of each trait, further reinforces the idea of different proximate mechanisms operating on SSD of each species. In *D. vittatus*, with a single exception, the

**Table 6.** Correlation coefficients (r) and regression equations between the coefficients of variation (CV) of six morphometric traits of males (M) and females (F) and the degree of sexual size dimorphism (SSD) in 19 and 25 populations of *D. vittatus* and *D. pratensis* respectively. In the case of nonsignificant correlations, the sign (+/-) of r is indicated. For meaning of trait abbreviations see Materials and methods.

| Species             | Trait | r     | p      | Regression equation                                                                                  |
|---------------------|-------|-------|--------|------------------------------------------------------------------------------------------------------|
| <i>D. vittatus</i>  | MBL   | -0.48 | 0.037  | CVMBL= 1.05*(0.007**SSDBL)                                                                           |
|                     | MF3L  | -NS   |        |                                                                                                      |
|                     | MT3L  | -NS   |        |                                                                                                      |
|                     | MTeL  | -NS   |        |                                                                                                      |
|                     | MPL   | +NS   |        |                                                                                                      |
|                     | MPH   | -NS   |        |                                                                                                      |
|                     | FBL   | -0.70 | 0.001  | CVFBL= 1.5 - 7.5*SSDBL<br>CVFF3L= 1.3 - 5.4*SSDF3L                                                   |
|                     | FF3L  | -0.63 | 0.016  |                                                                                                      |
|                     | FT3L  | -NS   |        |                                                                                                      |
|                     | FTeL  | -NS   |        | CVFPL= 1.9 - 7.5*SSDPL                                                                               |
|                     | FPL   | -0.70 | 0.008  |                                                                                                      |
|                     | FPH   | -NS   |        |                                                                                                      |
|                     |       |       |        |                                                                                                      |
| <i>D. pratensis</i> | MBL   | -NS   |        |                                                                                                      |
|                     | MF3L  | 0.46  | 0.022  | CVMF3L= 0.5 + 2.5*SSDF3L + 923.5*SSDPL**2<br>CVMT3L= 0.4 - 20.9*SSDT3L - 406.0*SSDT3L**2 + 2243.3**3 |
|                     | MT3L  | 0.57  | 0.040  |                                                                                                      |
|                     | MTeL  | +NS   |        |                                                                                                      |
|                     | MPL   | 0.73  | <0.001 | CVMPL= 6.6 - 64.9*SSDPL +<br>CVMPL= 0.9 - 1.1*SSDPH - 44.1*SSDPH**2 + 636.7**3                       |
|                     | MPH   | 0.70  | 0.002  |                                                                                                      |
|                     | FBL   | +NS   |        |                                                                                                      |
|                     | FF3L  | -NS   |        | CVFPH= 1.1 - 3.9*SSDPH - 79.9*SSDPH**2 + 942.9**3                                                    |
|                     | FT3L  | -NS   |        |                                                                                                      |
|                     | FTeL  | -NS   |        |                                                                                                      |
|                     | FPL   | +NS   |        |                                                                                                      |
|                     | FPH   | -0.76 | 0.003  |                                                                                                      |
|                     |       |       |        |                                                                                                      |

CVs of all traits were negatively associated with SSD in both sexes, indicating that high SSD implies low morphometric variation. This could be expected if a depletion of genetic variation occurs because of selection for increasingly larger body sizes in females. Conversely, in male *D. pratensis*, four significant and one nonsignificant correlations were positive, indicating that in populations where males are smaller, they are morphometrically more variable: this could be due to a plastic response to marginal conditions and more variability in early emergence. The latter could be why no clear pattern of CV/SSD was found for *D. pratensis* females: the only significant correlation was for PH, a measurement that shows an atypical behavior regarding variability, as described above. Thus, in *D. pratensis* longer development time of males would homogenize body size and produce lower CVs, as well as lower SSD.

No detailed studies on ontogenetic development have been conducted in *Dichroplis* species, thus any conclusions about static allometric relationships as found in this paper are speculative. However, it is interesting that these two species, which show a very close phylogenetic relationship as demonstrated by morphometric and molecular studies (Cigliano & Otte 2003, Colombo *et al.* 2005), exhibit different allometric patterns.

Although in both species the tegmina show hyperallometry, no direct explanation for this fact can be advanced. Both species (and especially *D. vittatus* which is brachypterous) are flightless and have very low vagility. However, tegmina-length allometry might be related to thermoregulation: tegmina of both species are relatively longer at lower latitudes where mean annual and summer temperatures are higher, and where ambient energy is higher as measured by potential evapotranspiration (Bidau & Martí 2007a,b). Thus, tegmina may act as control devices for thermal insulation and thermoregulation (including behavioral thermoregulation) and relatively longer tegmina may be selected for in such environments.

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Fig. 4. *Dichroplus vittatus* female, La Punilla, San Luis, Argentina. Photo by Dardo A. Marti. See Plate IV.



Fig. 5. *Dichroplus vittatus* male, La Punilla, San Luis, Argentina. Photo by Dardo A. Marti. See Plate IV.