

CHANGE OF MORPHOMETRIC AND ALLOMETRIC PATTERNS  
ON WINGS OF BANDED DEMOISELLE  
(*CALOPTERYX SPLENDENS*) MALES  
IN CASE OF ECOLOGICALLY DIFFERENT WATERCOURSE TYPES

LÁSZLÓ JÓZSEF SZABÓ, CSILLA VAJDA\*, PETRA ÉVA SZALAY  
OLGA KIS, MARGIT MISKOLCZI and GYÖRGY DÉVAI

*Department of Hydrobiology, University of Debrecen, H-4032 Debrecen, Egyetem tér 1, Hungary*  
E-mails: szlj55@gmail.com; <https://orcid.org/0000-0002-1222-4576>  
roheryn89@gmail.com; <https://orcid.org/0000-0001-8678-0308>; \*corresponding author  
pe.szalay@gmail.com; <https://orcid.org/0000-0002-8346-2440>  
kisolgie@gmail.com; <https://orcid.org/0000-0001-7737-8587>  
miskolczi.margit@science.unideb.hu; <https://orcid.org/0000-0001-6422-3260>  
devai.gyorgy@science.unideb.hu; <https://orcid.org/0000-0002-9989-9460>

In nature, dragonfly larvae living in watercourses are exposed to a complex system of environmental influences. Different watercourse types (creeks, brooks, streams, little rivers and medial rivers) are known to provide different conditions for larval development (water depth, flow rate, temperature, oxygen content, substrate type, nutrient supply, etc.). These conditions can vary significantly between watercourse types but can be very similar within types. This work examines the body sizes and wing morphometric characteristics of males of *Calopteryx splendens* reared from different watercourse types (brook, stream, creek, little river, medial river). Although there were no significant differences in body size depending on watercourse types, significant differences were found in the wing features. We found the greatest number of differences between the individuals reared from streams and creeks and the individuals reared from a stream and medial river. Our results show that the individuals reared from different watercourse types were different on the two wings. The results also suggest significant differences in the number and pattern of allometric features on the wings of individuals reared from different watercourse types.

Key words: damselflies, allometry, wing features variations, NE Hungary

## INTRODUCTION

It is well known that insects living in watercourses are sensitive to different abiotic (CORBET 1999) and biotic (CORBET 1999, MIKOLAJEWSKI *et al.* 2005) factors. Among abiotic factors, the abundance of larvae and the composition of species assemblages can be significantly influenced by the hydrolytic conditions of the water body (MCLELLAND *et al.* 1996), turbidity and conductivity (D'AMICO *et al.* 2004, STEWART & DOWNING 2008). The last two factors may affect the choice of the oviposition site (BERNÁTH *et al.* 2002). In these habitats, the influence of temperature and discharge can also be significant on aquatic organisms, and these effects can be very complex and interactive (NAIMAN

*et al.* 2002, PETTS 2000). Temperature affects the physiology, phenology and seasonality of larvae (HASSALL & THOMPSON 2008). Moreover, dissolved oxygen affects the behaviour, metabolism and survival of Odonata larvae at a given temperature and pressure (CORBET 1999). In larvae of odonates the rate of oxygen consumption increases with the rate of waterflow (AMBÜHL 1959, ZAHNER 1959).

In a given watercourse the factors mentioned above act in a complex manner. From this point of view, studies of adults are particularly interesting because individuals have accumulated environmental effects during the larval stages. MINOT *et al.* (2019) pointed out that their study “underscore the importance of taking into account larval growth in order to better understand the adult straits of Odonates”. In the species of the genus *Calopteryx*, the morphology of specimens reflects population response to environmental factors (SVENSSON *et al.* 2004, TAYLOR & MERRIAM 1995). In *Agria sedule*, STEWART and VODOPICH (2018) found differences in wing shape and body size among most environments examined. Some studies suggest that habitat type (OUTOMURO *et al.* 2013) and habitat fragmentation (TAYLOR & MERRIAM 1995) affect adults’ wing shape.

The females of the *Calopteryx splendens* prefer watercourses with dense herbaceous vegetation but avoid the sections with tree coverage along the bank (WARD & MILL 2005). The larvae strongly prefer muddy bottoms with silt and detritus, but this is not a necessity (GOODYE 2000). Based on many studies, *C. splendens* specimens are attached to the watercourse they emerged from and migrated only within small distances (STETTNER 1996, WARD & MILL 2007). Mating and oviposition take place on or close to the water surface (CORBET 1999). The results of a mark-release-recapture study showed that more than 80% of the recaptured adults moved within a distance of 100 m or less, and only 1.3% of the individuals moved farther than 500 m (WARD & MILL 2007). During our fieldwork, we observed that even though *C. splendens* has dispersing specimens that fly quickly along the watercourse, a significant number of individuals only populate sections of watercourses with a defined habitus, where they show a strong territorial behaviour. CHAPUT-BARDY *et al.* (2010) found that the proportion of dispersing individuals is smaller in males than in females. Due to the small migration distance, it can be presumed that male adult specimens developed in the same waterbody at which they were captured. In Hungary, larvae of *C. splendens* can be found in every clear and less polluted watercourse except for the epirithral reaches of highland brooks.

Studies demonstrate differences in body length, wing size, wing shape and wing spot size in different populations (e.g. MERTENS *et al.* 1992, OUTOMURO *et al.* 2013, SADEGHI *et al.* 2009). Such differences can be evolved in a population by phenological ways (HARDERSEN 2010). However, we have little information on the morphometric properties of adults reared from different

types of watercourses. Larvae developing in ecologically different waterbody types are exposed to different influences, leading to different body structures and morphology of adults (DMITRIEW *et al.* 2007).

Morphometric traits correlate with body length, so they are allometric traits (DUBOIS 1897). If two traits are measured in the same stage, there is static allometry (SCHLICHTING & PIGLIUCCI 1998, SHINGLETON *et al.* 2007). This can result from two processes: autonomic specification of the organ and determination of the final size of the organ based on the total weight (STERN & EMLÉN 1999). In case of static allometry, the equation  $Y = b \cdot X^a$  describes the correlation between the two body size, which is  $\log(Y) = \log(b) + a \cdot \log(X)$  in logarithmic form. The extents of the allometric effects were examined using the latter equation. The 'a' (gradient) is the allometric coefficient (HUXLEY 1924, SHEA 1985). Very little information about the regulation of static allometry is available, but this mechanism is a basic developmental process (SHINGLETON *et al.* 2007).

Static allometry can be well examined on organisms with discrete stages, such as insects (KLINGENBERG & ZIMMERMANN 1992). In the case of insects, the allometric changes occur after larvae have finished feeding. Imaginal tissues in holometabolous insects start growing in the stage of pupa (WILLIAMS 1980). By hemimetabolous insects (mayflies, damselflies), the process is different. In an Australian mayfly, the allometric changes do not occur in the same larval stage but at the end of the nymphal stage (CAMPBELL 1991).

SACCHI and HARDERSEN (2012) found different allometries between damselflies (Zygoptera) and dragonflies (Anisoptera) and also among Zygoptera families.

It appears that the allometric traits are not constant. Variation in growth is also affected by genetic differences among specimens, differences among habitats and the interaction of these two factors (SHINGLETON *et al.* 2007). In addition, HORENSTEIN *et al.* (2010) pointed out that the environment can significantly affect the allometric pattern and body size.

Our observations also suggested that the size and shape of the wings, particularly the wing spot of males, vary in great detail. However, the individuals from the same waterbody are alike and can be separated from individuals from other populations.

Based on the above, the following questions were asked: are there differences in (i) body length or (ii) wing features, and (iii) allometric features and allometric patterns of the individuals reared from different ecological watercourse types?

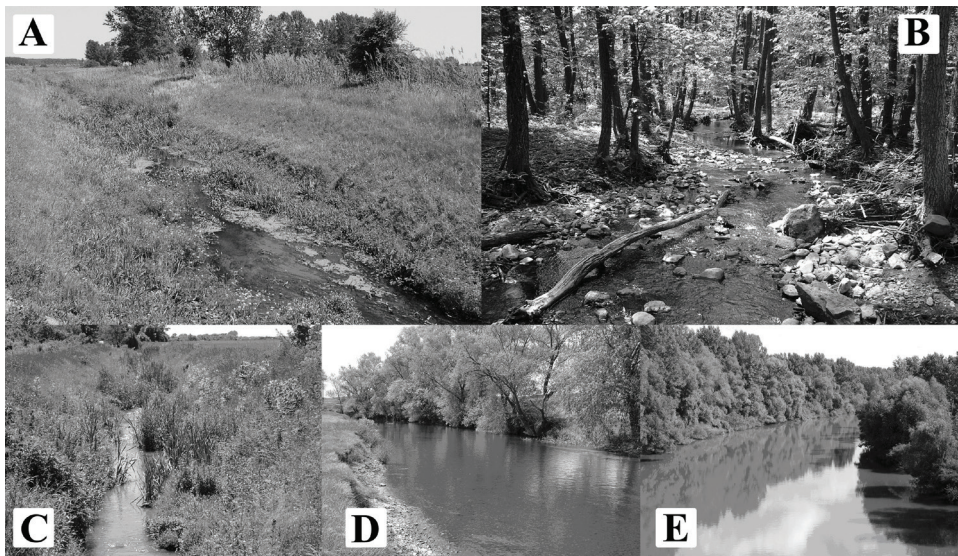
## MATERIAL AND METHODS

Five male adults were collected from 45 watercourses in NE Hungary with an insect net. The total number of male specimens was 225. The watercourses were classified into 5

types: brook, stream, creek, little river, medial river, according to DÉVAI (1976), LAJTER *et al.* (2010), DÉVAI *et al.* (2001). These types are different in appearance (Fig. 1) and in several characteristics (Table 1), ensuring different conditions for the larvae to develop. Among the main characteristics listed in Table 1, the following watercourse characteristics may affect the development and morphology of larvae: geographical position, flow velocity, substrate type and debris accumulation (see Introduction). The specimens were collected between 27 May and 12 August 2012. The result of the two-way NPMANOVA showed that both the time (month) and watercourse type had a significant effect on the characteristics of the wing. Therefore, to exclude the effect of time, further studies were performed only on the individuals collected in June. In this month, individuals were collected from every type of watercourse. As a result, the number of water bodies (populations) decreased to 29 and was distributed as follows: 3 creeks, 5 brooks, 11 streams, 9 little rivers and 3 medial rivers. Based on the above, the number of specimens included in the comparative study was 155. The number of specimens from each watercourse type was as follows: creeks: 15 specimens, brooks: 25 specimens, streams: 55 specimens, little rivers: 45 specimens, medial rivers: 15 specimens.

Specimens were kept in ethanol (70 V/V%) till analysis. Measurements were taken with a digital calliper (to the nearest 0.01mm) in case of total body length and Image Tool software 7 in case of wing traits. For the measurements in Image Tool the right fore and hind wings were cut off, and digital photos were taken with an Olympus SZX 16 microscope. 12 traits were measured on the wing: 7 were related to the size and shape of the whole wing and 5 to the size and position of the wing spot (Figs 2A, B).

The nomenclature of the wing venation was based on DUMONT (1991), and the distances were measured between the landmarks of SADEGHI *et al.* (2009). The wing features were the distances between the given landmarks (Table 2). Since the edge of the wing spot is not sharp, the X and Y points are marked where 50% of the cell above the vein is pigmented.



**Fig. 1.** The typical appearance of watercourse types in Northeast Hungary (A = creek, B = brook, C = stream, D = little river, E = medial river). (Photo: Miskolczi, M.)

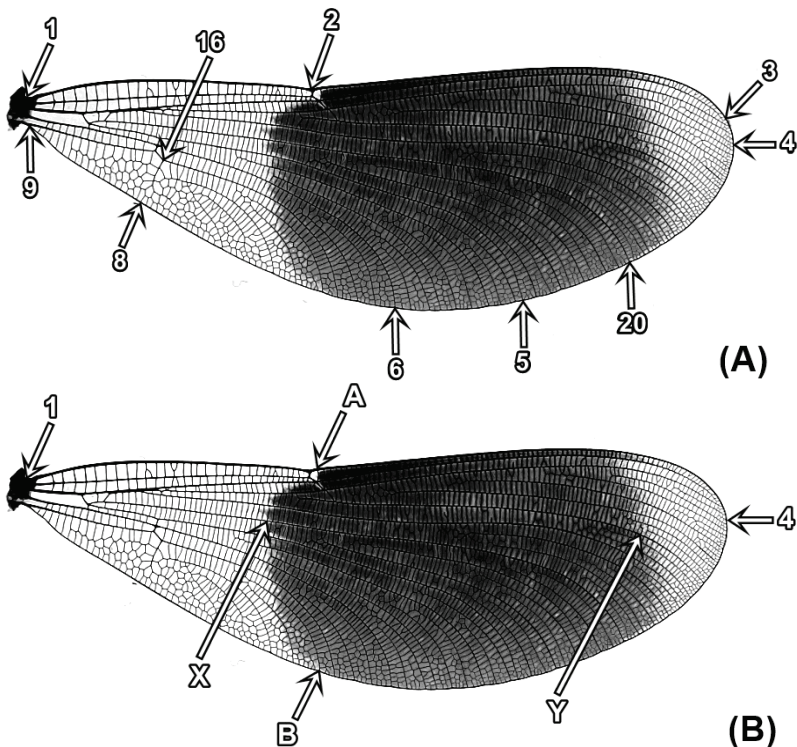
**Table 1.** The main characteristics of watercourse types in NE Hungary (based on LAJTER *et al.* 2010, DÉVAI *et al.* 2001).

| Main type  | Small watercourses |   |                         |                 | Rivers                         |                |                 |
|--|--------------------|---|-------------------------|-----------------|--------------------------------|----------------|-----------------|
|  | Subtype            | Brook                                   | Stream                  | Creek           | Little river                   | Medial         | Grand           |
| Length of watercourse (km)                                 |                    | <50                                     | <50                     | <50             | 50–250                         | 250–1000       | 1000–2500       |
| Catchment area (km <sup>2</sup> )                          |                    | <500                                    | <500                    | <500            | 500–10 000                     | 10 000–100 000 | 100 000–500 000 |
| Discharge (m <sup>3</sup> /s, according to mean discharge) |                    | <5                                      | <5                      | <5              | 5–50                           | 50–400         | 400–2500        |
| Streamline depth (m, according to mean water-level)        |                    | separation can-<br>not be used          | <3                      | 3-6             | >6                             |                |                 |
| Geographical position                                      |                    | high- and<br>medial-height<br>mountains | foothills and<br>hills  | plains          | separation can-<br>not be used |                |                 |
| Surface slope  |                    | high                                    | moderate                | small           | separation can-<br>not be used |                |                 |
| Flow velocity  |                    | fast                                    | moderate                | slow            | separation can-<br>not be used |                |                 |
| Substrate type   |                    | stony - gravelly                        | gravelly -<br>sandy     | sandy-<br>muddy | separation can-<br>not be used |                |                 |
| Riparian vegetation  |                    | along the river-<br>side                | along the bed<br>margin | in the<br>bed   | separation can-<br>not be used |                |                 |
| Debris accumulation  |                    | little                                  | moderate                | great           | separation can-<br>not be used |                |                 |

The watercourse types were compared with PCA separately on both wings for populations. The fore and hind wings were compared with the Mantel test and PCA (for all individuals). Since there were differences in magnitude between the values measured on the wings, the raw data were standardised with the range before applying multivariate methods. This means that all data were divided with the range of the watercourse type to retain variability (measured via standard deviation) and set up a range for all variables equal to 1 (JAJUGA & WALESIAK 2000).

Normal distribution of raw data of body length and wing features was examined with the Shapiro & Wilk test, and the homogeneity of variances was tested by the Levene test. The watercourse types were compared with one-way ANOVA and Tukey post hoc tests (normal distributions), or Kruskal & Wallis and Mann & Whitney tests (non-normal distributions).

For the investigation of wing traits allometry, the raw data were log<sub>10</sub>-transformed for the regression analyses. Similarly to SACCHI and HARDERSEN'S (2012) study, the allometric slopes for wing traits were calculated with the standardised major axis regression (SMA). We preferred this method over ordinary least square regression (OLS), because when the independent variable has error variance, the SMA, unlike OLS, does not underestimate slope (SACCHI & HARDERSEN 2012, WARTON *et al.* 2006). We ran the SMA for all features of each watercourse type and tested slope differences from 1 by r-statistic. When the correlation was not significant, r-statistics were not performed. This procedure was carried



**Fig. 2.** Measuring points on the right fore wing of *Calopteryx splendens* males (A = landmarks related to size and shape measurements, B = landmarks related to measurements on the wing spot) based on the work of SADEGHI *et al.* (2009)

**Table 2.** Differences among watercourse types by features (bold: significant differences).

| Feature | Fore wing     |               |                     |                   | Hind wing     |               |                     |                   |
|---------|---------------|---------------|---------------------|-------------------|---------------|---------------|---------------------|-------------------|
|         | one-way ANOVA |               | Kruskal-Wallis test |                   | one-way ANOVA |               | Kruskal-Wallis test |                   |
|         | F             | p             | Chi <sup>2</sup>    | p                 | F             | p             | Chi <sup>2</sup>    | p                 |
| 1-2     |               |               | <b>23.89</b>        | <b>&lt;0.0001</b> |               |               | <b>23.56</b>        | <b>&lt;0.0001</b> |
| 2-3     | <b>2.487</b>  | <b>0.0459</b> |                     |                   | <b>2.509</b>  | <b>0.0443</b> |                     |                   |
| 1-4     |               |               | <b>15.38</b>        | <b>0.004</b>      | <b>4.089</b>  | <b>0.0036</b> |                     |                   |
| 2-6     |               |               | <b>10.79</b>        | <b>0.029</b>      | <b>3.976</b>  | <b>0.0043</b> |                     |                   |
| 9-16    |               |               | <b>15.37</b>        | <b>0.004</b>      | <b>3.344</b>  | <b>0.0118</b> |                     |                   |
| 16-8    |               |               | <b>25.70</b>        | <b>&lt;0.0001</b> | <b>3.543</b>  | <b>0.0086</b> |                     |                   |
| 9-8     |               |               | <b>10.50</b>        | <b>0.0327</b>     |               |               | <b>14.22</b>        | <b>0.0066</b>     |
| 1-X     | 2.189         | 0.0729        |                     |                   | 1.500         | 0.2051        |                     |                   |
| X-Y     | 1.551         | 0.1905        |                     |                   | 1.036         | 0.3907        |                     |                   |
| Y-4     | 1.925         | 0.1091        |                     |                   |               |               | 4.64                | 0.3257            |
| 1-A     | <b>4.796</b>  | <b>0.0011</b> |                     |                   |               |               | <b>15.40</b>        | <b>0.0039</b>     |
| 1-B     | <b>3.782</b>  | <b>0.0058</b> |                     |                   |               |               | <b>15.73</b>        | <b>0.0034</b>     |

out in both wings. The differences of distribution of allometric traits among watercourse types were analysed by Fisher's exact test (fore and hind wing separately).

The statistical analyses were performed using Microsoft Excel 2003, Past 2.16 software (HAMMER *et al.* 2001) and smart (WARTON *et al.* 2012) package in software R (ver. 2.13.1, R CORE TEAM 2018).

## RESULTS

In the first step, morphometric measurements were performed on all individuals. The results of the two-way NPMANOVA performed on the data showed that both the watercourse type ( $F = 2.23$ ,  $p = 0.0001$ ) and the time (month) ( $F = 2.75$ ,  $p = 0.0001$ ) had a significant effect on the morphometric characteristics (but the interaction was not significant). Therefore, in the further analyses, we used only the specimens caught in June.

In all ecologically different watercourse types the average body length values showed normal distribution (Shapiro & Wilk  $W = 0.940$ – $0.974$ ;  $p = 0.120$ – $0.701$ ). Moreover, for each type, the differences in total body length of the individuals and their means of body lengths were very similar (the means: creeks: 47.49 mm; brooks 46.83 mm; streams: 47.05 mm, little rivers: 47.55 mm; medial rivers: 47.95 mm) (Fig. 3), and there were no significant differences among watercourse types (ANOVA  $F = 1.79$ ;  $p = 0.135$ ).

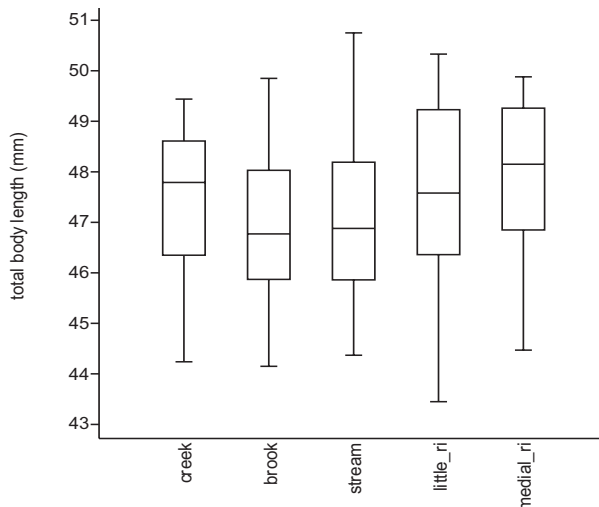
In contrast, the one-way ANOVAs and Kruskal & Wallis tests for the morphometric features of the wing showed significant differences in most of the cases on both wings (Table 2). Only three characteristics connected to the

patch's position (1-X, X-Y and Y-4) showed no significant differences among watercourse types. In investigating the differences between watercourse types pairwise (Table 3), the same three characteristics (1-X, X-Y and Y-4) and one feature (2-3) of the whole wing measurements showed no significant differences in any pairings. The most significant differences (6 out of 10 pairings) were in features 1-2 on both wings and features 9-16, 1-4, and 16-8 on the fore wing, and 9-8 on the hind wing (Table 3). In total, the features of the fore wing distinguished significantly more pairings of watercourses (38) than of the hind wing (26).

The creeks, streams and medial rivers showed the highest number of significant differences with other watercourses (Table 4). Interestingly there were only 2 features that differed significantly between the creeks and medial rivers, while the greatest number of differences were between the stream and the creek (fore wing: 9, hind wing: 7 features), and between the stream and the medial river (fore wing: 7: hind wing: 7) (Table 4). It is also notable that no or only one feature differed significantly between brook, stream, and little river.

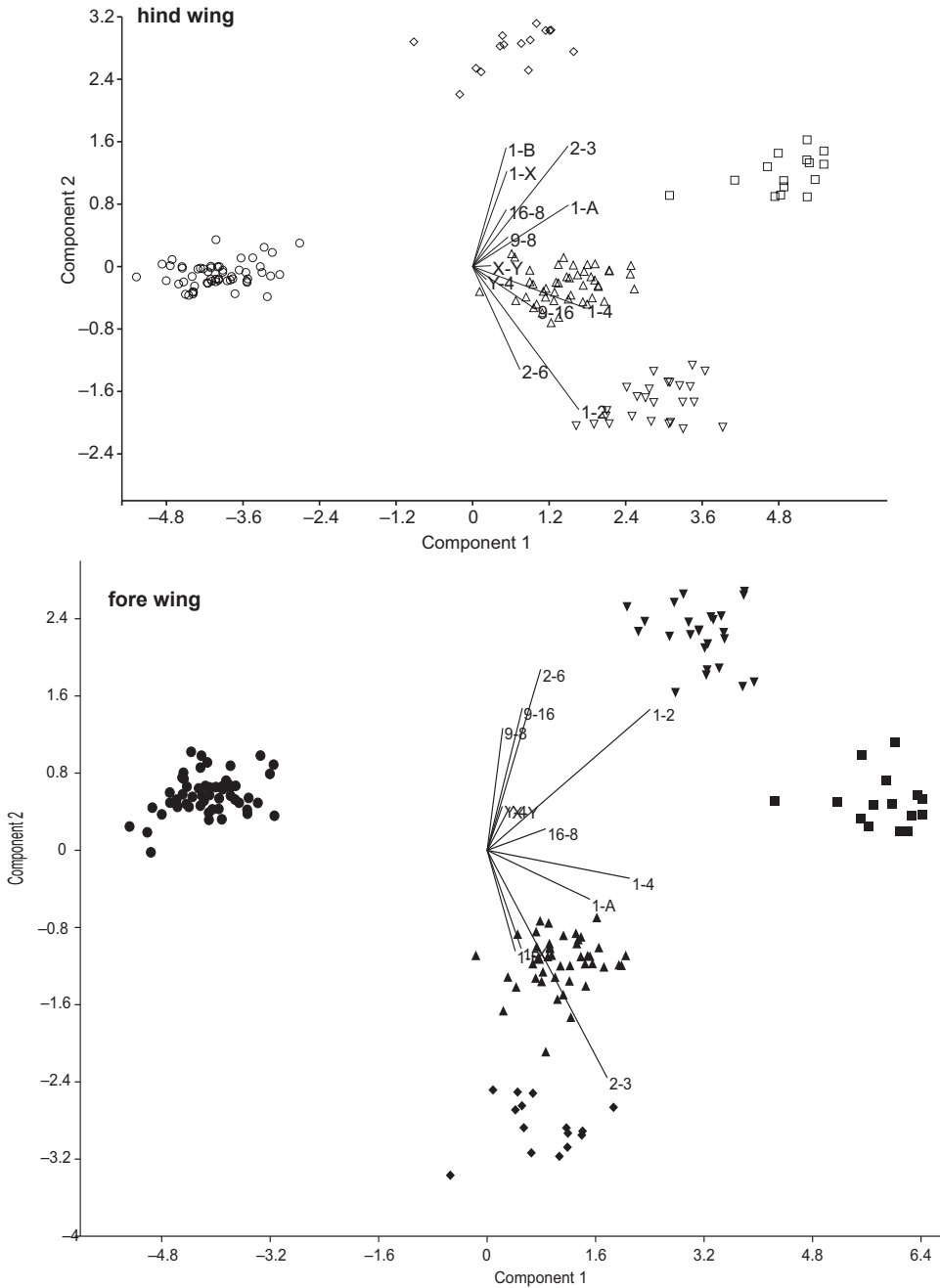
According to the PCA based on the features of the fore wing (Fig. 4), the first two principal components explained 89.28% of total variances (75.11 and 14.17%). The streams and medial rivers were separated from each other along with the first principal component. This separation was mainly caused by features 1-2 and 16-8. The other three types were separated along with the second principal component. The separation of brooks is mainly caused by features 9-8, 9-16 and 2-6, and the separation of creeks by features 1-X, 1-B and 2-3.

PCA performed for the features of the hind wing (Fig. 4) showed that the first two principal components explained 87.90% of total variances (77.85 and 10.05%). Unlike in the fore wing, the separation between streams and medial



**Fig. 3.** Boxplot of total body lengths at different watercourse types





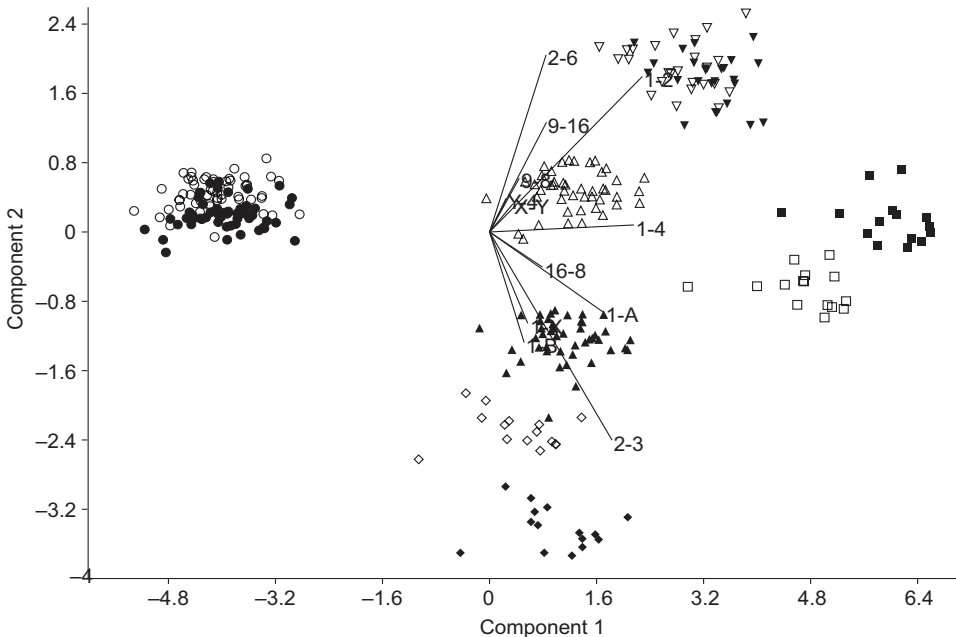
**Fig. 4.** Results of PCAs (fore wing: 1. component = 75.11%, 2. component = 14.17%; hind wing: 1. component = 77.85%, 2. component = 10.05%). Symbols: ◆ = creek, ▼ = brook, ● = stream, ▲ = little river, ■ = medial river

**Table 3.** The number of significantly different pairings between watercourse types by feature (max. 10 pairs).

|           | Feature |     |     |     |      |      |     |     |     |     |     |     |
|-----------|---------|-----|-----|-----|------|------|-----|-----|-----|-----|-----|-----|
|           | 1-2     | 2-3 | 1-4 | 2-6 | 9-16 | 16-8 | 9-8 | 1-X | X-Y | Y-4 | 1-A | 1-B |
| Fore wing | 6       | 0   | 5   | 2   | 6    | 5    | 3   | 1   | 1   | 1   | 4   | 4   |
| Hind wing | 6       | 0   | 2   | 2   | 2    | 2    | 5   | 0   | 0   | 0   | 4   | 3   |

**Table 4.** The number of significantly different features between watercourse types (max. 12).

|           |              | fore wing |       |        |              |              |
|-----------|--------------|-----------|-------|--------|--------------|--------------|
| type      |              | creek     | brook | stream | little river | medial river |
| hind wing | creek        |           | 3     | 9      | 5            | 2            |
|           | brook        | 3         |       | 1      | 0            | 4            |
|           | stream       | 7         | 0     |        | 1            | 7            |
|           | little river | 3         | 0     | 0      |              | 4            |
|           | medial river | 0         | 3     | 7      | 2            |              |



**Fig. 5.** PCA with watercourse type, for fore and hind wing (1. component = 77.66%; 2. component = 11.70%) (filled symbols: fore wing, empty symbols: hind wing). Symbols: ◆ = creek, ▼ = brook, ● = stream, ▲ = little river, ■ = medial river

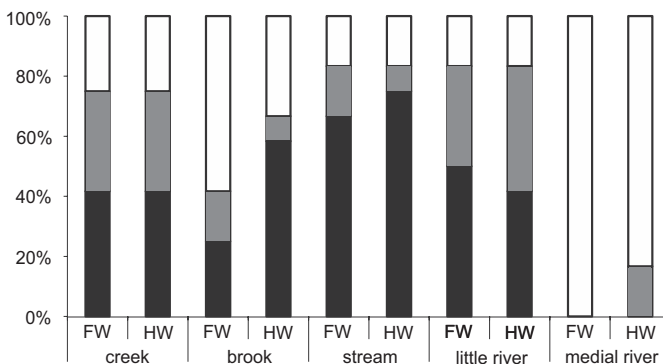
rivers is caused by features 2-3, X-Y and 16-8. Along with the second principal component, the separation of brooks and little rivers was caused by features 1-2, 1-4 and 9-16 and the separation of creeks by features 1-X, 1-B and 16-8.

The results of the Mantel test showed that there were close correlations between the features of the two wings ( $R = 0.979$ ,  $p = 0.0002$ ). However, the result of PCAs performed on individuals differed between watercourse types (Fig. 5). For streams and brooks, the point clouds of fore wings and hind wings were completely overlapping. In contrast, these point clouds were slightly different in the creek and the medial rivers and significantly different for the little rivers.

The results of standardised major axis regression (Table 5) showed significant differences in the number of allometric traits and the type of allometry among watercourse types on both wings (Fisher's exact test: fore wing  $p < 0.0001$ , hind wing  $p = 0.0012$ ) (Fig. 6).

The number and proportion of allometric features were examined for all individuals. In this case, the total number of cases for all characters was 60 (12 features  $\times$  5 types = 60), for features related to the shape and size of the whole wing was 35 (7 features  $\times$  5 types = 35), and for features related to the shape and size of the wing spot was 25 (5 features  $\times$  5 types = 25). Thus, allometric features exceeded 50% of all features in the first four types of watercourse types (fore wing: 34, 56.66%; hind wing: 40, 66.67%). In the case of features related to the shape of the whole wing, these values are much higher (fore wing: 23, 65.71%; hind wing: 28.80%). In contrast, the proportion of allometric features related to the shape and size of the wing spot is much smaller (fore wing: 11.44%; hind wing: 12.48%).

The allometric pattern on the two wings was very similar in all watercourse types, except the brooks, where three features (9-16, 9-8 and 8-16) differed significantly between wings.



**Fig. 6.** Patterns of allometric features at different watercourse types. White bars = no allometry, grey bars = isoallometry, black bars = hyperallometry

**Table 5.** Results of standardised major axis regressions (bold: isoallometry, bold + gray: hyperallometry).

| y      | Fore wing      |                   |              |    |                   | Hind wing      |                   |              |    |                   |
|--------|----------------|-------------------|--------------|----|-------------------|----------------|-------------------|--------------|----|-------------------|
|        | correlation    |                   | H0 – slope=1 |    |                   | correlation    |                   | H0 – slope=1 |    |                   |
|        | R <sup>2</sup> | p                 | r            | df | p                 | R <sup>2</sup> | p                 | r            | df | p                 |
| Creek  |                |                   |              |    |                   |                |                   |              |    |                   |
| 1-2    | <b>0.597</b>   | <b>0.0007</b>     | <b>0.304</b> | 13 | <b>0.2715</b>     | <b>0.485</b>   | <b>0.0039</b>     | <b>0.344</b> | 13 | <b>0.2093</b>     |
| 2-3    | <b>0.444</b>   | <b>0.0067</b>     | <b>0.504</b> | 13 | <b>0.0556</b>     | <b>0.337</b>   | <b>0.0233</b>     | <b>0.462</b> | 13 | <b>0.0831</b>     |
| 1-4    | <b>0.534</b>   | <b>0.002</b>      | <b>0.321</b> | 13 | <b>0.2439</b>     | <b>0.420</b>   | <b>0.0089</b>     | <b>0.474</b> | 13 | <b>0.0746</b>     |
| 2-6    | <b>0.746</b>   | <b>&lt;0.0001</b> | <b>0.899</b> | 13 | <b>&lt;0.0001</b> | <b>0.440</b>   | <b>0.007</b>      | <b>0.616</b> | 13 | <b>0.0145</b>     |
| 9-16   | <b>0.612</b>   | <b>0.0006</b>     | <b>0.800</b> | 13 | <b>0.0003</b>     | <b>0.816</b>   | <b>&lt;0.0001</b> | <b>0.898</b> | 13 | <b>&lt;0.0001</b> |
| 16-8   | <b>0.673</b>   | <b>0.0002</b>     | <b>0.864</b> | 13 | <b>&lt;0.0001</b> | <b>0.782</b>   | <b>&lt;0.0001</b> | <b>0.922</b> | 13 | <b>&lt;0.0001</b> |
| 9-8    | <b>0.377</b>   | <b>0.0149</b>     | <b>0.795</b> | 13 | <b>0.0004</b>     | <b>0.620</b>   | <b>0.0005</b>     | <b>0.887</b> | 13 | <b>&lt;0.0001</b> |
| 1-A    | <b>0.416</b>   | <b>0.0094</b>     | <b>0.379</b> | 13 | <b>0.1642</b>     | <b>0.234</b>   | <b>0.068</b>      | <b>0.446</b> | 13 | <b>0.0956</b>     |
| 1-B    | 0.150          | 0.1537            |              |    |                   | <b>0.309</b>   | <b>0.0313</b>     | <b>0.629</b> | 13 | <b>0.012</b>      |
| 1-X    | 0.022          | 0.599             |              |    |                   | 0.066          | 0.3567            |              |    |                   |
| X-Y    | <b>0.423</b>   | <b>0.0087</b>     | <b>0.761</b> | 13 | <b>0.001</b>      | 0.147          | 0.1582            |              |    |                   |
| Y-4    | 0.001          | 0.9364            |              |    |                   | 0.073          | 0.3314            |              |    |                   |
| Brook  |                |                   |              |    |                   |                |                   |              |    |                   |
| 1-2    | <b>0.395</b>   | <b>0.0008</b>     | <b>0.104</b> | 23 | <b>0.6212</b>     | <b>0.351</b>   | <b>0.0018</b>     | <b>0.106</b> | 23 | <b>0.615</b>      |
| 2-3    | 0.055          | 0.2603            |              |    |                   | 0.047          | 0.2993            |              |    |                   |
| 1-4    | <b>0.507</b>   | <b>&lt;0.0001</b> | <b>0.456</b> | 23 | <b>0.022</b>      | <b>0.451</b>   | <b>0.0002</b>     | <b>0.498</b> | 23 | <b>0.0113</b>     |
| 2-6    | 0.036          | 0.3671            |              |    |                   |                |                   |              |    |                   |
| 9-16   | 0.042          | 0.3269            |              |    |                   | <b>0.061</b>   | <b>0.2337</b>     | <b>0.406</b> | 23 | <b>0.0443</b>     |
| 16-8   | 0.038          | 0.3502            |              |    |                   | <b>0.267</b>   | <b>0.0082</b>     | <b>0.856</b> | 23 | <b>&lt;0.0001</b> |
| 9-8    | 0.141          | 0.0645            |              |    |                   | <b>0.061</b>   | <b>0.2328</b>     | <b>0.729</b> | 23 | <b>&lt;0.0001</b> |
| 1-A    | <b>0.265</b>   | <b>0.0085</b>     | <b>0.354</b> | 23 | <b>0.0829</b>     | <b>0.204</b>   | <b>0.0234</b>     | <b>0.453</b> | 23 | <b>0.023</b>      |
| 1-B    | <b>0.433</b>   | <b>0.0004</b>     | <b>0.890</b> | 23 | <b>&lt;0.0001</b> | <b>0.370</b>   | <b>0.0013</b>     | <b>0.842</b> | 23 | <b>&lt;0.0001</b> |
| 1-X    | <b>0.389</b>   | <b>0.0009</b>     | <b>0.922</b> | 23 | <b>&lt;0.0001</b> | <b>0.267</b>   | <b>0.0082</b>     | <b>0.856</b> | 23 | <b>&lt;0.0001</b> |
| X-Y    | 0.058          | 0.2464            |              |    |                   | 0.000          | 0.9393            |              |    |                   |
| Y-4    | 0.125          | 0.0832            |              |    |                   | 0.131          | 0.0756            |              |    |                   |
| Stream |                |                   |              |    |                   |                |                   |              |    |                   |
| 1-2    | <b>0.621</b>   | <b>&lt;0.0001</b> | <b>0.201</b> | 48 | <b>0.1613</b>     | <b>0.653</b>   | <b>&lt;0.0001</b> | <b>0.117</b> | 53 | <b>0.3962</b>     |
| 2-3    | <b>0.399</b>   | <b>&lt;0.0001</b> | <b>0.552</b> | 48 | <b>&lt;0.0001</b> | <b>0.487</b>   | <b>&lt;0.0001</b> | <b>0.470</b> | 53 | <b>0.0003</b>     |
| 1-4    | <b>0.486</b>   | <b>&lt;0.0001</b> | <b>0.237</b> | 48 | <b>0.0982</b>     | <b>0.473</b>   | <b>&lt;0.0001</b> | <b>0.209</b> | 53 | <b>0.1252</b>     |
| 2-6    | <b>0.230</b>   | <b>0.0004</b>     | <b>0.446</b> | 48 | <b>0.0012</b>     | <b>0.381</b>   | <b>&lt;0.0001</b> | <b>0.466</b> | 53 | <b>0.0003</b>     |
| 9-16   | <b>0.218</b>   | <b>0.0006</b>     | <b>0.475</b> | 48 | <b>0.0005</b>     | <b>0.439</b>   | <b>&lt;0.0001</b> | <b>0.526</b> | 53 | <b>&lt;0.0001</b> |

Table 5 (continued)

| y            | Fore wing      |         |              |    |         | Hind wing      |         |              |    |         |
|--------------|----------------|---------|--------------|----|---------|----------------|---------|--------------|----|---------|
|              | correlation    |         | H0 – slope=1 |    |         | correlation    |         | H0 – slope=1 |    |         |
|              | R <sup>2</sup> | p       | r            | df | p       | R <sup>2</sup> | p       | r            | df | p       |
| Stream       |                |         |              |    |         |                |         |              |    |         |
| 16-8         | 0.146          | 0.0061  | 0.523        | 48 | 0.0061  | 0.428          | <0.0001 | 0.543        | 53 | <0.0001 |
| 9-8          | 0.097          | 0.0281  | 0.666        | 48 | 0.0281  | 0.291          | <0.0001 | 0.776        | 53 | <0.0001 |
| 1-A          | 0.429          | <0.0001 | 0.608        | 48 | <0.0001 | 0.481          | <0.0001 | 0.681        | 53 | <0.0001 |
| 1-B          | 0.370          | <0.0001 | 0.809        | 48 | <0.0001 | 0.353          | <0.0001 | 0.717        | 53 | <0.0001 |
| 1-X          | 0.244          | 0.0003  | 0.877        | 48 | <0.0001 | 0.278          | <0.0001 | 0.800        | 53 | <0.0001 |
| X-Y          | 0.055          | 0.1016  |              |    |         | 0.076          | 0.041   | 0.472        | 53 | 0.0003  |
| Y-4          | 0.028          | 0.2488  |              |    |         | 0.063          | 0.065   |              |    |         |
| Little river |                |         |              |    |         |                |         |              |    |         |
| 1-2          | 0.419          | <0.0001 | -0.309       | 43 | 0.0386  | 0.414          | <0.0001 | -0.427       | 43 | 0.0034  |
| 2-3          | 0.260          | 0.0004  | -0.113       | 43 | 0.4595  | 0.386          | <0.0001 | -0.160       | 43 | 0.2948  |
| 1-4          | 0.284          | 0.0002  | 0.061        | 43 | 0.693   | 0.271          | 0.0002  | -0.179       | 43 | 0.24    |
| 2-6          | 0.202          | 0.002   | 0.226        | 43 | 0.135   | 0.244          | 0.0006  | 0.135        | 43 | 0.3757  |
| 9-16         | 0.321          | <0.0001 | 0.459        | 43 | 0.0015  | 0.261          | 0.0003  | 0.183        | 43 | 0.2279  |
| 16-8         | 0.236          | 0.0007  | 0.606        | 43 | <0.0001 | 0.228          | 0.0009  | 0.339        | 43 | 0.0227  |
| 9-8          | 0.218          | 0.0012  | 0.622        | 43 | <0.0001 | 0.222          | 0.0011  | 0.692        | 43 | <0.0001 |
| 1-A          | 0.358          | <0.0001 | -0.160       | 43 | 0.2954  | 0.456          | <0.0001 | 0.084        | 43 | 0.5826  |
| 1-B          | 0.222          | 0.0011  | 0.673        | 43 | <0.0001 | 0.254          | 0.0004  | 0.645        | 43 | <0.0001 |
| 1-X          | 0.126          | 0.0166  | 0.777        | 43 | <0.0001 | 0.215          | 0.0014  | 0.742        | 43 | <0.0001 |
| X-Y          | 0.045          | 0.1599  |              |    |         | 0.051          | 0.1361  |              |    |         |
| Y-4          | 0.000          | 0.957   |              |    |         | 0.030          | 0.2557  |              |    |         |
| Medium river |                |         |              |    |         |                |         |              |    |         |
| 1-2          | 0.252          | 0.0565  |              |    |         | 0.282          | 0.0417  | 0.114        | 13 | 0.6848  |
| 2-3          | 0.111          | 0.2249  |              |    |         | 0.138          | 0.1728  |              |    |         |
| 1-4          | 0.199          | 0.0953  |              |    |         | 0.266          | 0.0489  | 0.141        | 13 | 0.6169  |
| 2-6          | 0.185          | 0.1095  |              |    |         | 0.243          | 0.0621  |              |    |         |
| 9-16         | 0.054          | 0.4035  |              |    |         | 0.112          | 0.2226  |              |    |         |
| 16-8         | 0.101          | 0.2481  |              |    |         | 0.073          | 0.3317  |              |    |         |
| 9-8          | 0.119          | 0.208   |              |    |         | 0.160          | 0.1396  |              |    |         |
| 1-A          | 0.098          | 0.2561  |              |    |         | 0.069          | 0.3434  |              |    |         |
| 1-B          | 0.051          | 0.4182  |              |    |         | 0.094          | 0.2673  |              |    |         |
| 1-X          | 0.000          | 0.9522  |              |    |         | 0.001          | 0.9068  |              |    |         |
| X-Y          | 0.048          | 0.4337  |              |    |         | 0.069          | 0.3462  |              |    |         |
| Y-4          | 0.017          | 0.6441  |              |    |         | 0.094          | 0.2667  |              |    |         |

The specimens reared from medial rivers showed allometry only for two features (1-4 and 2-3) on the hind wing.

Consequently, the following statements apply to only four watercourse types (excluding medial rivers): (1) features 1-4 were isoallometric in 3 types and hyperallometric in little rivers on both wings; (2) features 1-2, 2-3 and 2-6 were mostly isoallometric, but in some cases hyperallometry or no allometry; (3) the 9-16, 9-8 and features 8-16 were mostly hyperallometric on both wings, but features of the fore wing in brooks showed no allometry and features 9-16 of the hind wing in little river showed isometry; (4) features 1-A, 1-B and 1-X were mostly hyperallometric, except that 1-A showed isoallometry in creeks and little rivers on both wings and in brooks on the fore wing, 1-B showed no allometry in creeks on the fore wing, 1-X showed no allometry in creeks on both wings; (5) features X-Y showed no allometry except in creeks on the fore wing and streams on the hind wing where these were hyperallometric. The feature Y-4 was not allometric.

## DISCUSSION

Morphological studies, especially traditional morphometrics (as is the case in this work), have been used for a very long time. Nevertheless, these studies are used for solving taxonomic problems, population characterisations and comparisons. However, although some work deals with differences between populations (OUTOMURO *et al.* 2013, TAYLOR & MERRIAM 1995), we have very little information about adult morphometric differences among watercourse types.

HARDERSEN (2010) and GALLESINI *et al.* (2016) have found that the season affects the morphology and shape of the wing of *C. splendens*.

Other studies showed differences in body length, wing size, wing shape and wing spot size between different populations (e.g. MERTENS *et al.* 1992, OUTOMURO *et al.* 2013, SADEGHI *et al.* 2009). Many factors affect body size in the case of amphibious taxa, especially temperature and quantity of food (MCKIE & CRANSTON 2005, SHINGLETON *et al.* 2007). Larger body size refers to better environmental circumstances in the larval stage (TEDER *et al.* 2008). The large amount of food consumed during the larval stage resulted in larger adult body sizes (MARDEN 1989) and may allow individuals to store a larger volume of fat reserves (MARDEN 1989). This may mean an adaptive shift in the immature stage (PLAISTOW & SIVA-JOTHY 1999). These works also suggest that there may be differences in the body size of adults among biotopes.

In contrast, we have found no significant differences in mean body sizes among watercourse types. Nonetheless, mean body sizes were larger in creeks and medial rivers than in the other three types, and the differences were not significant. This may indicate that the food supply in the studied types is evenly good. However, the data also show that larger individuals

are present with a higher frequency in little and medial rivers. There are two possible reasons for this: (i) competition for food which affects selection to larger body size (BLOMQUIST *et al.* 1997) or (ii) there is a high probability of cannibalism, such that larvae can fall victim (CROWLEY & HOPPER 1994) and their density can significantly decrease (VAN BUSKIRK 1989). Therefore, cannibalism can raise the ratio of large body size and reduce the proportion of small specimens. In some cases, small individuals may be missing.

The environmental circumstances can affect the size, shape and ornamental traits of damselflies wings (RÜPPELL *et al.* 2005). The size and shape of the wing can significantly affect flight performance. Longer wings can increase flight speed, while wider wings can increase the ability to turn quickly (HEDENSTRÖM & ROSÉN 2001). It is known that predation can often cause strong selection and rapid evolutionary change in natural populations (THOMPSON 1998). SVENSSON and FRIBERG (2007) found that predation means a selection pressure for shorter and wider wings in *Calopteryx splendens*.

GALLESI *et al.* (2016) pointed out that the wing shape shows a seasonal variation and the different mating tactics associated with different wing morphologies in both sexes of *C. splendens*. In addition, a positive correlation has also been proved between habitat heterogeneity and morphological traits related to flight (ROFF 1990, TAYLOR & MERRIAM 1995).

In contrast to body sizes, we found significant differences in most of the wing features between individuals reared from different water body types. The differences were significant for all of the size-related features, but only features 1-A (the distance between the wing base and the wing spot's proximal edge on the fore-section of costa) and 1-B (the distance between the wing base and the wing spot's proximal edge on the back-section of costa) were related to the size and shape of the spot.

OTUMURO *et al.* (2012) found a higher evolutionary divergence of hind wing shape in both sexes of *C. splendens*. We found that the number of significant differences detected by post hoc tests was greater in the fore wing (36) than in the hind (25) wing. Our results also suggest that individuals reared from the creeks and medial rivers are different from the others in most features. This can also be explained by the fact that these two types have the lowest flow rate, which may be disadvantageous for larvae (GIBBONS & PAIN 1992, SIVA-JOTHY *et al.* 1995). In contrast, individuals reared from brooks, streams, and little rivers are very similar, with no significant differences in any feature (hind wing) or only in one feature (fore wing).

The PCAs also support these results since the biplot displays different features in different degrees on the two wings distinguishing the watercourse types.

If the two wings and the water body types are examined together, a similarity can be determined between the individuals reared from brooks and streams, while the spot clouds of the fore and hind wings completely overlap.

In contrast, there are significant differences between the two wings for those reared from streams, medial or little rivers, especially little rivers.

It is known that environmental circumstances affect allometric patterns (BATTÁN HORENSTEIN & PERETTI 2011) and stability of development (PALMER & STROBECK 1992, SOTO *et al.* 2008) in larval stages. This can explain our result, which shows that the number and proportion of allometric traits also vary among different watercourse types. This is especially significant if we consider hyperallometric traits. The ratio of allometric features was highest in the individuals reared from creeks, streams and little rivers and did not differ or differed only insignificantly between the two wings. In contrast, the proportion of non-allometric features on the fore wing is very high for those reared from brooks. From this viewpoint, the individuals reared from medial rivers differed most from the others, while the features on the fore wing were not allometric at all, and only two features showed isoallometry on the hind wing.

OUTOMURO and CORDERO-RIVERA (2012) pointed out that wing pigmentation traits of males in species of the family Calopterygidae are hyperallometric. By contrast, studies support that this is not universal (BONDURIANSKY 2007, OUTOMURO *et al.* 2014). We found that wing spot related features were hyperallometric in most cases, but can be isoallometric or non-allometric in some water body types.

We assume that in favourable habitats, the development of wing traits is under strong allometric regulation. This regulation is weaker if the habitat is less favourable for larvae. Thus, differences in larval habitat could result in significant variation of adults. Our work shows that morphometric characteristics and allometric patterns can characterise individuals developed in different ecological watercourse types.

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