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Altitudinal variation of wing length and wing area in *Libellula quadrimaculata* (Odonata: Libellulidae)

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Abstract. The area and length of the right fore and hind wings and the abdomen length were analysed in specimens from two Iberian populations of *Libellula quadrimaculata* Linnaeus, 1758, one on a plateau (782 m a.s.l.) and another in the mountains (1 909 m a.s.l.), with a view to ascertaining whether their morphometric characteristics vary with altitude. Allometric relationships in terms of length and area of the fore and hind wings of both populations were found. The wings are longer and have a greater area in plateau specimens whereas the length of the abdomen did not vary between populations. Between the populations there was an overlap in the wing length measurements. The significance of these parameters in aiding the dragonflies' flight capacity and hence the effects on their lifestyle under different environmental conditions is discussed.

Further key words. Dragonfly, Anisoptera, wing morphology, mountains, plateau, Iberian Peninsula

Introduction

Numerous works have analysed aerodynamics properties of odonate wings with respect to their lifestyle (Kesel 2000; Combes & Daniel 2003; Wang & Sun 2005), such as migratory or non-migratory behaviour (Johansson et al. 2009), etc. However, there has been less analysis of the variation in these features at an intraspecific level with respect to the characteristics of the habitats they occupy (Taylor & Merriam 1995; Hassall et al. 2009).

Most Odonata live in warm areas (Pritchard & Leggott 1987). In view of the fact that temperature falls with altitude, high mountain areas (>1 900 m a.s.l.) are less favourable for them than sites at lower elevations. This is why dragonflies inhabiting mountains have morphological features improving survival in these areas.

Wing aspect ratio AR, *i.e.*, the relationship between wing length and wing width, influences the flight of animals (Norberg 1989), in a way that high AR facilitates greater manoeuvrability and slower speed, and lower AR facilitates swifter straight line flight and greater powers of dispersal. However, there is no consensus that AR always produces these same effects in insects (see Hassall 2015).

Furthermore, the behaviour of every species is attuned to its morphological features. In the Odonata the wings play a decisive role in their manner of flying (Wootton 1991) and in their migratory movements (Johansson et al. 2009; Sacchi & Hardersen 2013). Fore wings vary relative little between species of migratory and non-migratory dragonflies, whereas the hind wings of migratory species typically have an expansion in the anal field which could facilitate gliding (Johansson et al. 2009).

What is more, in migratory species, the lower the body mass/body size ratio, the higher the displacement capacity will be. In Odonata the abdomen constitutes an important part of the body mass meaning that reducing its size results in a reduction in wing loading, thereby potentially increasing dispersal capacity (Hassall et al. 2009).

On the other hand, Bergmann's rule states that endothermic animals inhabiting cooler climates will be larger than related species from warmer climates (Bergmann 1847). It has been suggested that ectothermic animals might follow a converse-Bergmann's rule (Mousseau 1997), where those living in cold climates are smaller than those living in warm climates. Since then there has been a controversy around this rule (see reviews of Blanckenhorn & Demont 2004; Meiri 2011). Specifically in insects, certain authors believe this rule doesn't hold (Shelomi 2012), while others find proof of the same in facultative endothermic species (Scriven et al. 2016).

Libellula quadrimaculata Linnaeus, 1758 is a common species with Holarctic distribution. In the Iberian Peninsula it is found mainly in the northern half, becoming scarce in the South (Boudot et al. 2009). It is regarded as a spring species *sensu* Corbet (1954), as the emergence of 50 % of larvae occurs in 12–20 days (Grand & Boudot 2006). It can live in lower and mountainous areas (Corbet 2004), but in southern Europe the species is rare at low altitudes and is mainly found in higher elevations, and therefore is a suitable species for analysing variations of some biometric traits in relation to altitude.

In cold environments insect flight capacity is lower than in warm environments (Lehmann 1999; Dudley 2002) and body size is smaller (Laiolo et al. 2013). In this study we have measured and compared abdomen length (as an estimate of body size; Samejima & Tsubaki 2010), and area and length of the wings, of *L. quadrimaculata* from a plateau population and another population from higher elevations in the mountains, with a view to ascertaining whether these characteristics are correlated with altitude. If *L. quadrimaculata* follows the above pattern, it could be predicted that the length of the abdomen and the wings should be lower in dragonflies living in mountains than in plateau, and therefore the ratio of body length to wing length should be similar in mountain and plateau and, consequently, there should be no allometric variation. As for wing length, if Bergmann's rule applies to *L. quadrimaculata*, individuals from the mountains should be larger than those living on the plateau, while the opposite should be true if the converse-Bergmann's rule is followed.

Material and methods

The study was conducted in two areas in the centre of the Iberian Peninsula, one located in the mountains and another one on a plateau. Detailed characteristics of the two sites are provided in Table 1. The distance between the two areas was 95 km.

In 2014 we visited the site on the plateau for weekly sampling from 01-iv- to 01-vi-2014. The mountain sampling site was visited weekly from 01-vi- to 20-vii-2016.

We also included in our analysis 25 other males of *Libellula quadrimaculata* from the plateau. The dates of capture were 11-v-2014 (19 males) and 15-v-2014 (6). From the mountain sampling site we analysed 29 males collected on the following dates: 17-vi- (3), 22-vi- (5), 30-vi- (3) and 8-vii-2016 (18).

Table 1. Characteristics of the two sampling areas in the central Iberian Peninsula. Temp. – mean annual temperature; Precip. – mean annual rainfall (from Ninyerola et al. 2005). Datum ETRS89 in UTM coordinates of both sampling areas.

	Sampling area	
	Mountain	Plateau
Municipality	Santiago del Collado	Alba de Yeltes
Province	Ávila	Salamanca
Habitat	Water meadow	Lagoon
UTM X	304763	726734
UTM Y	4477165	4505878
Grid zone	30	29
Elevation [m a.s.l.]	1909	782
Temp. [°C]	7.5	12.5
Precip. [mm]	761	582

Abbreviations

FWL – fore wing length; HWL – hind wing length; FWA – fore wing area; HWA – hind wing area; ARFW – wing aspect ratio in fore wings; ARHW – wing aspect ratio in hind wings; AL – abdomen length.

Of all analysed specimens, right fore and hind wings were flattened by a glass plate and scanned using an HP Scanjet 3770 at 2 400 dpi. Wing length (from the extreme base of the cubitus posterior vein to the wing apex) and wing area (Fig. 1) were measured using software ImageJ (Abramoff et al. 2004). Abdomen length, excluding appendices of segment 10, was measured with a Mitutoyo calliper (precision 0.01 mm). Wing aspect ratio was calculated as the ratio between the square wingspan (expressed as twice wing length) and the wing area (Hassall 2015; Suárez-Tovar & Sarmiento 2016) of fore wings (FWAR) and hind wings (ARHW).

Five variables (FWL, HWL, FWA, HWA, and AL) were log-transformed before analysis (Warton et al. 2006). To analyse what type of allometry the abdomen and wing have, we have plotted FWA and HWA in relation to AL, and FWL and HWL in relation to AL, and test for differences. The same was done for FWL *vs* HWL and FWA *vs* HWA. Common slope and common elevation for populations were assessed using a likelihood ratio test (L) and the Wald test statistic (W), respectively. In this sense, we have followed the approach described by Warton et al. (2006), using the standardised major axis (SMA) regression model. We have used the software R version 2.13.1, for these analyses and the Smatr package (Warton et al. 2011).

While data of five previous variables (HWL, FWL, HWA, ARFW, and ARHW) followed a normal distribution, according to the Shapiro-Wilk test (*P* >0.05 in all cases), the FWA and AL variables did not. When data were normal, we used these variables in a MANOVA to test for size differences and an ANOVA for independent sampling with equal variances (Levene's test) to analyse difference within each variable. When normality was not followed, we used a Kruskal-Wallis test. These analyses were done in STATA version 12.1 and Past version 3.15.

Results

Adults of *Libellula quadrimaculata* were captured in the months of May, June, and July 2014 and 2016. In 2014 on the plateau site the first exuviae were found on the 13-iv- and the last on the 20-v-2014. The emergence curve

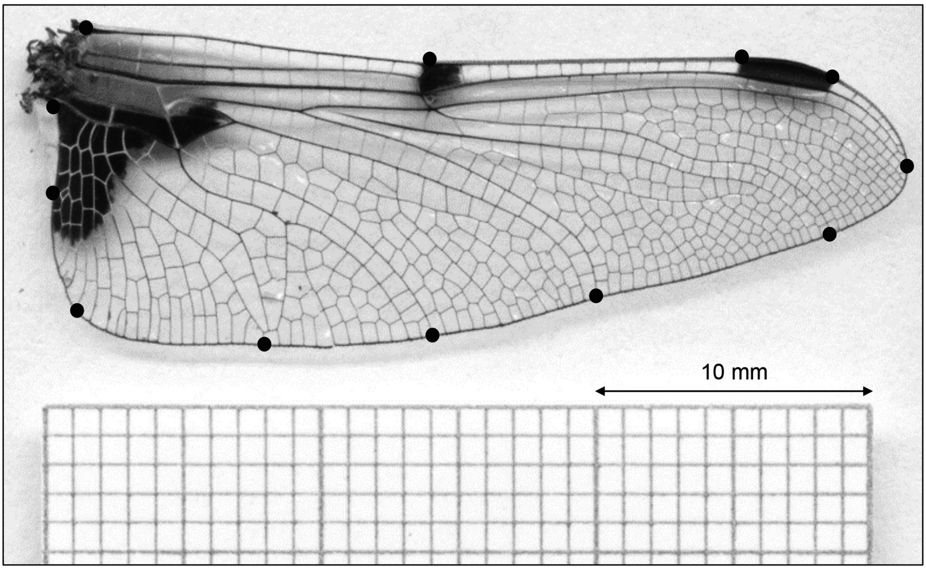

Figure 1. Scanned image of a hind wing of *Libellula quadrimaculata* from a mountain site in the central Iberian Peninsula. Wing area was calculated according to solid points. Points are the same as in Johansson et al. (2009). A scale was incorporated.

fitted the equation $y = -0.0362x^2 + 4.0253x - 8.6285$ ($R^2 = 0.982$, $P<0.000$), according to which 50 % emergence was reached in 18 days. In 2016 no exuviae were recorded from the mountain site and adults of *L. quadrimaculata* were seen from 10-vi- to 20-vii-2016.

We found allometric differences between FWL *vs* HWL and between FWA *vs* HWA for the populations from the plateau and from mountains (Table 2). Other allometric regressions were not significant ($R^2<0.04$ and $P>0.05$, Table 2 and Fig. 2). The slopes and the elevation of the regressions between FWL and HWL (Fig. 2) did not differ between plateau and mountain populations ($L=0.102$, $P=0.841$), where L is a likelihood ratio test, nor did we find differences in elevation (Wald statistic $W=4.447$, $P=0.212$). For FWA and HWA no differences were detected either in the slope ($L=0.523$, $P=0.145$) or elevation (Wald statistic $W=1.631$, $P=0.508$) (Fig. 3).

The slope value between FWL and HWL did not differ from 1 in the plateau (r = 0.1726, $P=0.4095$) and in mountainous areas (r = 0.2045, $P=0.2871$). In FWA and HWA we found a greater difference from 1 for the values from the plateau (r = 0.4277, P = 0.0331) but not in the mountains (r = 0.144, P = 0.556).

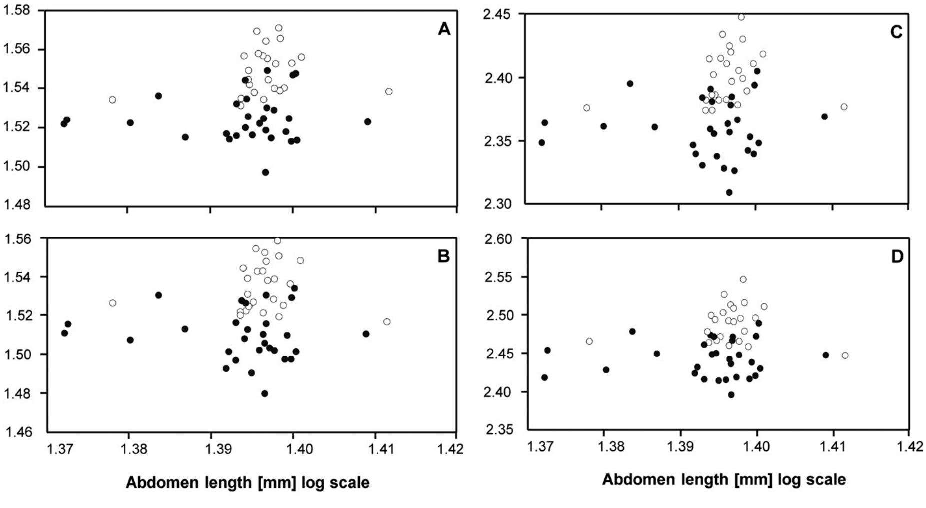

Figure 2. Fore wing (A) and hind wing length (B) [mm], fore wing (C) and hind wing area (D) [mm^2] in relation to abdomen length in *Libellula quadrimaculata* from a plateau (open circles) and a mountain site (solid circles) in the central Iberian Peninsula. All log scale.

Table 2. Values of fit using Standardized Major Axis plotting fore wing length (FWL) *vs* hind wing length (HWL), fore wing area (FWA) *vs* hind wing area (HWA), and abdomen length (AL) *vs* length and area of both wings, in plateau and mountain sampled areas in the central Iberian Peninsula.

Variables		Plateau		Mountain	
		Elevation	Slope	Elevation	Slope
FWL *vs* HWL	Estimated	-0.093	1.051	-0.155	1.091
	Lower limit	-0.292	0.929	-0.429	0.925
	Upper limit	0.106	1.188	0.119	1.286
	R^2	0.920		0.825	
	P-value	0.000		0.000	
FWA *vs* HWA	Estimated	-0.268	1.145	0.001	1.034
	Lower limit	-0.605	1.011	-0.282	0.921
	Upper limit	0.079	1.296	0.285	1.161
	R^2	0.916		0.913	
	P-value	0.000		0.000	
AL *vs* FWL	Estimated	0.724	0.433	0.384	0.661
	Lower limit	0.440	0.287	-0.013	0.450
	Upper limit	1.008	0.654	0.782	0.972
	R^2	0.04		0.001	
	P-value	0.323		0.787	
AL *vs* HWL	Estimated	0.762	0.412	2.309	-0.606
	Lower limit	0.490	0.271	1.949	-0.889
	Upper limit	1.035	0.627	2.66	-0.413
	R^2	0.01		0.001	
	P-value	0.796		0.624	
AL *vs* FWA	Estimated	0.810	0.244	2.201	-0.342
	Lower limit	0.562	0.161	1.882	-0.503
	Upper limit	1.058	0.368	2.519	-0.232
	R^2	0.03		0.001	
	P-value	0.354		0.954	
AL *vs* HWA	Estimated	0.866	0.213	0.586	0.330
	Lower limit	0.638	0.140	0.267	0.225
	Upper limit	1.094	0.323	0.904	0.486
	R^2	0.01		0.001	
	P-value	0.793		0.827	

According to MANOVA, the variables FWL, HWL, FWA, HWA, and AL differ between plateau and mountain populations (Wilks $\lambda = 0.4823$,

$F_{1,48}=10.30$, $P=0.000$). Analysis of each variable separately showed that FWL and HWL were significantly larger in the plateau population than in the mountain population (Table 3). FWA and HWA were also significantly greater in the population from plateau than in the mountainous population. In this case, the value measured from the hind wing was up to 11% larger in plateau dragonflies. AL, in turn, did not vary greatly between the two populations (Table 3).

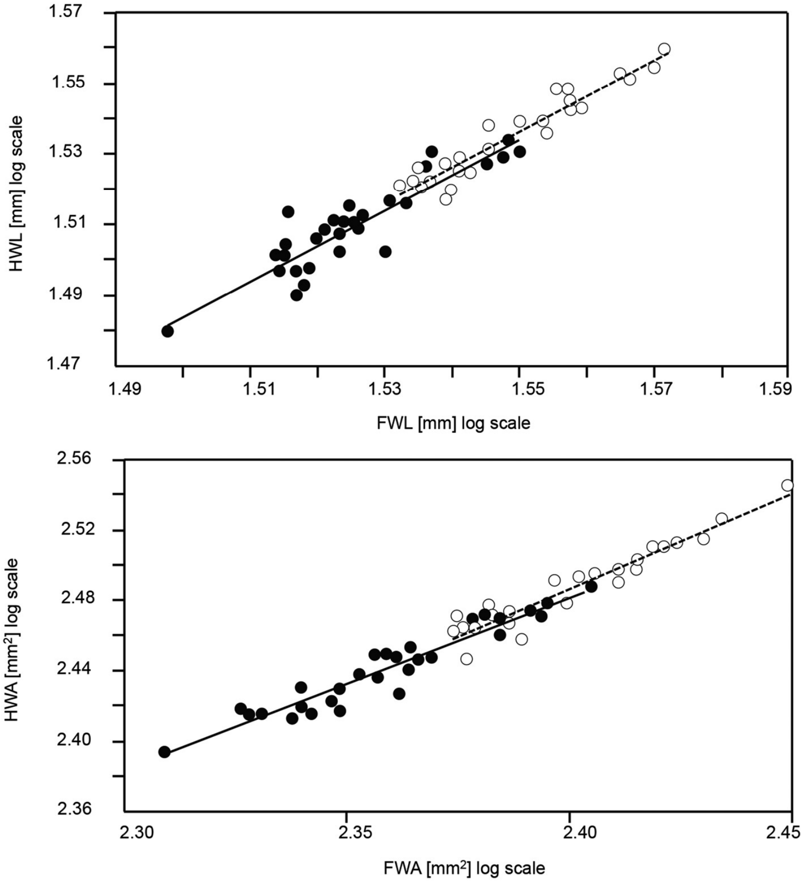

Figure 3. Fore wing length (FWL) and hind wing length (HWL) allometry and fore wing area (FWA) and hind wing area (HWA) allometry in *Libellula quadrimaculata* from a plateau (open circles) and a mountain site (solid circles) in the central Iberian Peninsula.

Table 3. Mean value (±SD) of length [mm] and area [mm²] of fore wing, hind wing, and abdomen of *Libellula quadrimaculata* in specimens from a plateau and a mountain site in the central Iberian Peninsula. Range of values in parentheses. n – sample size; *K* – Kruskal-Wallis test; *F* – ANOVA; *P* – level of significance.

	Plateau n = 25	Mountain n = 29	Test
Fore wing area	252.0±12.5 (236.7–281.7)	229.0±12.3 (203.8–253.9)	$K = 27.27$ $P = 0.001$
Hind wing area	307.8±17.3 (280.0– 351.2)	277.1±15.4 (248.3–308.1)	$F_{1,52} = 52.48$ $P = 0.00001$
Fore wing length	35.4±1.0 (34.0–37.3)	33.5±0.9 (31.4–35.5)	$F_{1,52} = 46.21$ $P = 0.00001$
Hind wing length	34.3±1.0 (32.9–36.2)	32.3±1.0 (30.2–34.2)	$F_{1,52} = 47.21$ $P = 0.00001$
Abdomen length	24.9±0.3 (23.9–25.8)	24.7±0.4 (23.5–25.6)	$K = 0.995$ $P = 0.3183$
Fore wing aspect ratio	9.95±0.20 (9.58–10.62)	9.83±0.24 (9.38–10.45)	$F_{1,52} = 4.037$ $P = 0.0497$
Hind wing aspect ratio	7.65±0.18 (7.24–8.08)	7.55±0.17 (7.21–8.04)	$F_{1,52} = 3.893$ $P = 0.0538$

ARFW was significantly higher on the plateau than in the mountain, while ARHW values did not differ significantly between the two zones (Table 3).

In both populations there were examples of large (≥35 mm) and small FWL (≤34 mm), though the overlap between measurements was small (Fig. 4). The same can be said of the HWL (Fig. 4).

Discussion

To avoid any possible bias owing to sex, only males were taken into account. It is known that in odonates body size decreases as the emergence date increases, particularly in females (Plaistow & Siva-Jothy 1999; Purse & Thompson 2003).

Our data shows that wing length and wing area of *Libellula quadrimaculata* vary with altitude. In the two areas sampled in this work, specimens with large and small wings co-exist (Fig. 4). Okuyama et al. (2015) recorded that smaller species of damselflies flew better than larger species in cool environments. In *L. quadrimaculata* the smaller specimens are probably better adapted to living in the mountain, where flight capacity is reduced (Lehmann 1999; Dudley 2002), whereas the larger ones are better adapted to the plateau.

Migrating species have longer wings than non-migrating species (Sacchi & Hardersen 2013). Generally, larger wings are considered to facilitate gliding ability (Grabow & Rüppell 1995). In Europe, *L. quadrimaculata* is a facultative migrant (Dumont & Hinnekint 1973; Burton 1996) and some swarms can travel hundreds of kilometers. Therefore, populations of *L. quadrimaculata* from the plateau, with longer wings, will probably be more migratory than those found in the mountain. In island populations selection reduces the ability for dispersion (Cox & Moore 1993). It would be interesting to analyse if, in addition to morphological differences, in-

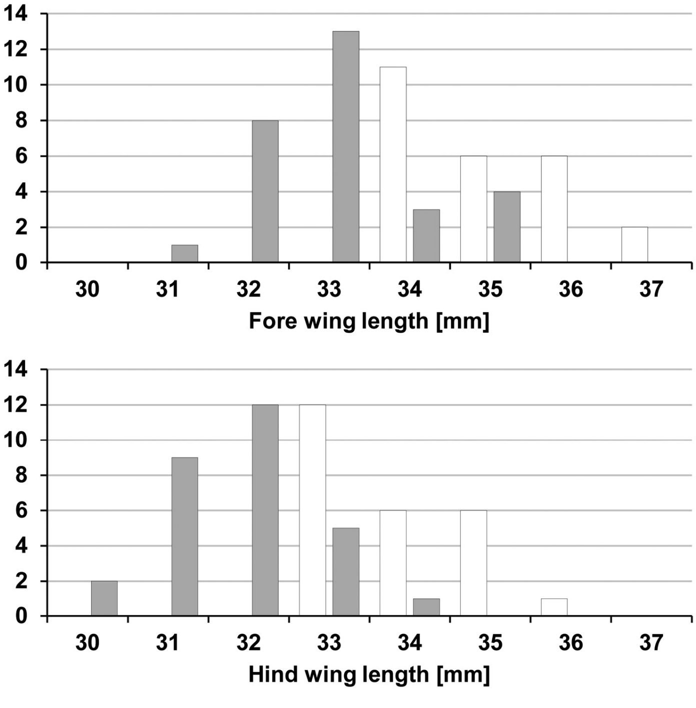

Figure 4. Frequency distribution of *Libellula quadrimaculata* individuals collected on a plateau (white bars) and in the mountains (grey bars) in the central Iberian Peninsula according to the fore and hind wing length.

habiting mountains show genetic isolation derived from their lower gliding ability, as occurs in populations of *Pantala flavescens* (Samways & Osborn 1998). The question would serve to clarify if plateau specimens ascend and reproduce in mountainous areas where the environmental conditions are less favourable for their survival.

The length of the fore wing in *L. quadrimaculata* males from Germany and France measured by Grabow & Rüppell (1995) was 37.3 mm (n = 20). Wakeling (1997) found lengths of the fore wing in males from Great Britain falling between 34.4 and 37.3 mm (n = 6). In turn, Ocharan Larrondo (1987) recorded a mean length of the hind wing of 32.9 mm in 60 males from Spain. Hence, the length of the fore wing of *L. quadrimaculata* seems smaller in our study area than in other countries situated further north, though the aforementioned authors do not specify the altitude where the specimens measured were collected hence comparisons between altitudes are not possible.

Regarding Bergmann's rule, *L. quadrimaculata* seems to follow the converse-Bergmann's rule as the mountain species are smaller in size than those from the plateau. Our study was done on an intraspecific level, as Meiri (2011) recommends. It must be noted that this study was carried out in two relatively close populations (<100 km apart) and it remains to be seen whether the same results will be obtained between populations which are very far apart (*e.g.*, northern and southern Europe) which assume temperature differences such as those stated here. In view of the fact that the geographic distribution of *L. quadrimaculata* is very broad, it seems to be a good species for studies about the validity of this rule in Odonata insects provided that the precautions suggested by Shelomi (2012) are followed to avoid false positives.

In this work we have found that the wings of *L. quadrimaculata* vary with altitude, but not the abdomen. The variation in wing allometry with altitude suggests a subtle adaptation to flight dynamics in response to different environmental conditions. Presumably this acts to optimise resources, whether this be food or survival from predators. It is yet to be explained whether the cause of the variation is the different temperature in the mountains and in the plateau or other causes such as, for example, the number and size of the wing cells (Calboli et al. 2003). More work is required to clarify this matter.

Hassall (2015) showed that the wing aspect ratio in fore wings (ARFW) tends to be higher in populations of *Calopteryx maculata* (Zygoptera) inhabiting areas of low temperature. Our data show the opposite for populations of *L. quadrimaculata* (Anisoptera) living in mountain areas. This result is in agreement with results found by Johansson et al. (2009) and Suárez-Tovar & Sarmiento (2016), where the aspect ratio analysis alone is not an accurate criterion for studying how wing shape influences flight and, at least in the populations studied in this work, it is necessary to take into account other variables.

The variation in wing size in Odonata has been related with variables such as the structure of the habitat (Taylor & Merriam 1995), foraging behaviour (Johansson et al. 2009) or distribution range (Rundle et al. 2007). The present work demonstrates that wing measurements may change according to altitude and that, consequently, it becomes necessary to consider this variable in future studies about intraspecific differences. Whether this aspect should only be assumed in species of the Libellulidae or in the other families of Anisoptera is something which has yet to be clarified.

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