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## The Adaptive Significance of Wing Shape and Dispersal Ability of an Insect



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## ABSTRACT

How does wing shape affect the dispersal ability of flying animals? Is one type of wing shape more suitable for longer dispersal than another? This study asks these two questions, which are crucial if we want to understand how animals track temporal and spatial environmental variability. As a model organism the damselfly, *Lestes sponsa* (Lestidae, Odonata) was studied. A mark-recapture study was carried out at a boreal pond-area in Uppland (Sweden). A total of 2157 individuals were captured, and their wings were marked and photographed. Of these, 796 were recaptured. Using geo-referencing, their dispersal between the initial capture and the recaptures was calculated. Moreover, an estimate of the survival was made using the observed longevity. Wing shape was analyzed using geometric morphometrics. Both fore- and hindwings were studied for both sexes. Statistically significant relationships were found between wing shape and maximum dispersal distance, longevity and wing centroid size in males. The wing shape of males with longer maximum dispersal distance was more elongated and slender and with a narrower wing tip, which is associated with long distance flight dispersal. In the females, statistical significance was found between wing shape and longevity and wing centroid size. A smaller sample size in females might be the reason for the lack of a significant relationship between maximum dispersal distance and wing shape. The observed relationship between wing shape and longevity in both sexes might be related to predator avoidance, although the patterns obtained in wing shape differed from expected. In summary, wing shape can be hypothesized to affect the different behavioral performances in insects, and more specifically, can be adaptive for dispersal ability.

**KEYWORDS:** damselflies, geometric morphometric, *Lestes sponsa*, longevity, sex differences, size

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## INTRODUCTION

Precipitation, temperature and seasonal events, such as droughts and heavy rains, differ from one year to another and can create temporary habitats or make them temporarily uninhabitable. Such seasonal events, in combination with habitat fragmentation and loss of habitat are a challenge for the organisms because of the need to track those changes (Dolman & Sutherland, 1995). In order to be able to predict beforehand how different animals will track these changes it is important to look at different aspects of their behavior, such as dispersal ability. Habitat stability has been found to affect the dispersal ability of organisms (Hof *et al.*, 2012). For example, habitats with lower stability select for a greater capacity for dispersal. Dispersal ability is also a very relevant factor when predicting future population distributions, because of the need of organisms to track the shifting climate and spread to new suitable habitats (Hof *et al.*, 2012; Grewe *et al.*, 2013).

Many animals can disperse by flight. Flight has allowed for longer migration and greater dispersal (Hedenström, 2002), with speeds far exceeding those of terrestrial transportation (Norberg, 1995). Wings have a central role in flight ability and their shape has been found to be affected by different life strategies such as migration and dispersal ability (Norberg & Rayner, 1987; Mönkkönen, 1995; Breuker *et al.*, 2007; Dockx, 2007; Bowlin & Wikelski, 2008; Johansson *et al.*, 2009). In fact, the evolution of wing shape is thought to have developed to maximize flight performance (agility, maneuverability, speed etc.) and wing aerodynamics (lift to drag ratio), balanced between the costs and the benefits (Norberg, 1995). Consequently, variation in wing shape is expected to be adaptive (Köliker-Ott *et al.*, 2003). There have been a number of studies on migratory strategy and its relation to wing shape in different animals (Mönkkönen, 1995; Johansson *et al.*, 2009). However, studies of more subtle intraspecific variation in wing shape, related to dispersal over shorter distances, are largely lacking (Breuker *et al.*, 2007). Knowledge of the evolution of wing shape in relation to dispersal ability can be important for the conservation of flying species, because it can predict how they will react to habitat and climate changes.

Some previously found patterns might be related to the ability to disperse. For instance, butterflies with broader wings have been shown to be more agile, while more slender wings are associated with prolonged, less agile flight (Betts & Wootton, 1988). Similar patterns have been reported in bats; short broad wings allow for slower flight inside of vegetation (Norberg & Rayner, 1987). In migratory birds, butterflies and dragonflies, a pointier wing was reported, in comparison to resident individuals (Mönkkönen, 1995; Dockx, 2007; Johansson *et al.*, 2009). In Odonata, the twisting of the wing in flight has also been found to affect the ability to hover and also has a role in slower flight (Córdoba-Aguilar, 2008). In addition, the position of the nodus in relation to the wing length seems to have an effect on how much the wing twists; the closer it is to the wing base, the more it twists and therefore slower, more agile flight over shorter distance is expected. With the aforementioned information about how wing shape is related to flight performance, a prediction can be made on how the wing shape of an insect varies with regard to dispersal. Individuals that are more dispersive should have longer, more slender wings, with a nodus farther away from the wing base. The forewing tip would also be expected to be pointier in more dispersive individuals. Short distance dispersers should have a broader and rounder wing shape and the nodus should be closer to the wing base.

In the present study, I explored whether wing shape had an adaptive variation related to dispersal. As a model organism, I used a population of the damselfly *Lestes sponsa* (Hansemann, 1823) (Lestidae, Odonata) inhabiting a group of wetlands in a boreal forest area. Damselflies are a good model system for addressing this question for a number of reasons:

they are easy to manipulate, their population densities are usually high and they are highly variable in size due to carry-over effects during their complex life histories (Córdoba-Aguilar, 2008). I was also interested in comparing the dispersal abilities of both sexes, since previous studies have suggested that females may disperse longer distances than males (Beirinckx *et al.*, 2006; Chaput-Bardy *et al.*, 2010). Moreover, I also compared the wing shape variation between the fore- and hindwings. Previous studies in butterflies have suggested that the wing pairs may have a different role in flight, with forewings playing a more important role in the flight mechanism and hindwings a larger part in speed and maneuverability (Jantzen & Eisner, 2008). I used a capture-mark-recapture method to estimate dispersal distance in a complex habitat matrix. This allowed me to estimate individual survival. Therefore, I also studied whether wing shape was related to survival. Previous studies have shown that a certain wing shape (e.g. better flight agility) might improve predator avoidance (Svensson & Friberg, 2007).

I addressed the following specific questions:

- (1) Is wing shape variation related to an individual ability to disperse?
- (2) Does wing shape vary with individual survival?
- (3) And, if so, do the patterns obtained differ between the sexes and between fore- and hindwings within an individual?

## MATERIALS AND METHODS

### *Study species*

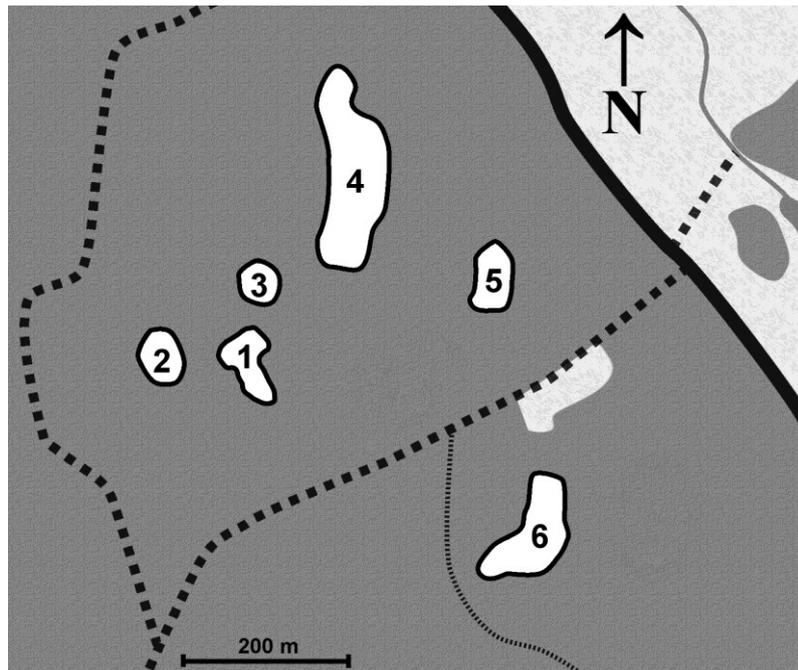
*L. sponsa* inhabits standing pools of water (Dijkstra & Lewington, 2006). Males and females can be easily distinguished by their body colors and sexual appendages.

### *Field work – the location*

I carried out the study in a group of wetlands (Figure 1) located north of Bälinge (Uppland, Sweden, 59° 58' 33" N, 17° 26' 45" E, 60 m a.s.l.) in a boreal forest area. Pond 1 was the only one with exposed water surfaces. The other ponds had more or less extended areas of bog. *L. sponsa* was the dominant lepidopteran species in the study area. *L. sponsa* is a common European species which is not considered endangered in Sweden (Gärdenfors, 2010).

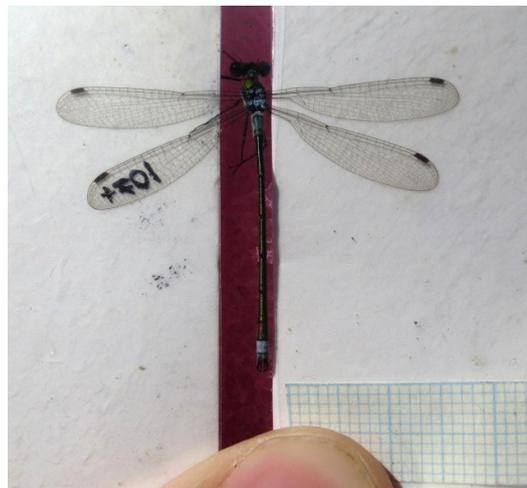
### *Field work – the procedure*

The population was studied using a capture-mark-recapture technique (Cordero-Rivera & Stoks, 2008). A team of four people was involved in the field work. The study was carried out from July 15<sup>th</sup> to August 10<sup>th</sup>, from around 11.30 to about 16.00, six days a week. The study was divided into two phases. Phase I: in ponds 1, 2 and 3 (Figure 1), the damselflies were captured with an entomological net, geo-referenced and marked with a four-digit number. The number was placed on the left hindwing, using a permanent ink marker. As this species does not have ornamental colored features on the wings or sexual displays, marking the wings does not interfere with normal sexual behaviors. Pond 1 was considered as the main source population. Sex was also noted. Moreover, recaptured individuals were also daily geo-referenced the first time they were recaptured that day. Ponds 4, 5 and 6 (Figure 1) were inspected daily for marked individuals, but no marking was done here. Phase II: from August 5<sup>th</sup> until August 10<sup>th</sup>, individuals were only recaptured. During cool days and days with heavy rain, the damselflies were not active. These days were used for data transferring and analysis.



**Figure 1.** Map showing the study area. The boundaries of the ponds are marked with a black border and a number (1-6). Dotted lines mark gravel roads and dirt trails. The solid black line marks a road.

The wings were also photographed *in vivo* and *in situ* using an especially designed device (Figure 2). This handling did not damage the damselflies. The device was composed of a rack in which a camera was mounted and a plate with two transparent sheets of plastic in which the individual was placed, with the wings spread out underneath the sheets. A piece of millimeter paper was also placed to be used in the image scaling, during image processing. Each individual was released at the exact same location it was (re)captured.



**Figure 2.** A marked male in the device used for photographing the wings. In the bottom right corner the millimetre paper is visible.

### ***Data acquisition and analysis***

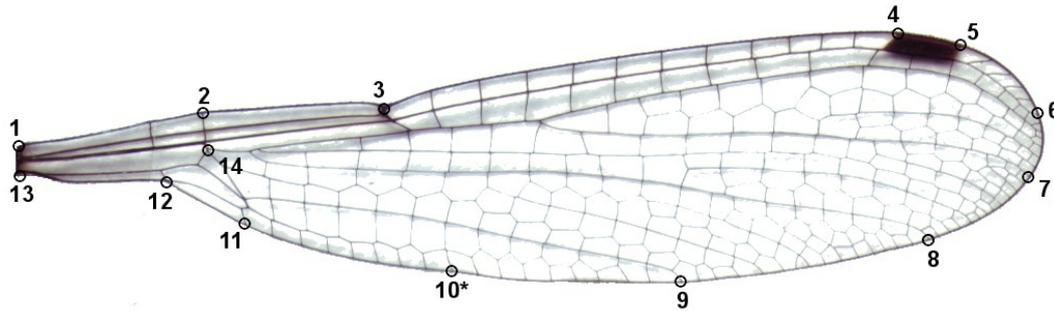
The wing pictures were used to study the wing shape, using geometric morphometric techniques. This tool has a very high statistical power and retains the spatial co-variation among landmarks, keeping mathematically constant the effects of non-shape variation (position, orientation and scale) (Bookstein, 1991; Rohlf & Marcus, 1993; Adams, *et al.*,

2004). Moreover, geometric morphometric techniques also give a good visualization of shape differences (Johansson *et al.*, 2009). For each fore- and hindwing, 13 landmarks and 1 semi-landmark (Figure 3) were digitalized to capture wing shape, using tpsDig2 (Rohlf, 2010a). The semi-landmark was used to capture the posterior wing curvature and was placed on the main hindwing vein, halfway between landmarks 9 and 11. Generalized Procrustes Analysis (GPA) was done on the landmarks and semi-landmark configurations (Rohlf & Slice, 1990), separately for males and females. This method quantifies shape from the landmark coordinates after having been translated to the origin, scaled into unit centroid size and rotated to minimize the total sum-of-squares deviations from all individual configurations to the average configuration. In the GPA, the semi-landmark was made to slide along its tangent direction to minimize procrustes distance between the configurations (Bookstein, 1991). A consensus wing shape (average configuration) was calculated for each sex. Using this wing as a reference, the shape components were calculated (uniform and non-uniform shape components) on tpsRelw (Rohlf, 2010b). Wing centroid size was also calculated and later corrected using the scale of each picture. Because of high correlation found between wing centroid size and body size, this was used as an estimate for body size (Outomuro & Johansson, 2011).

Dispersal was calculated for each recaptured individual. When the same individual was recaptured more than once, the longest distance was used (maximum dispersal distance). The longevity of each individual was estimated as the number of days between it was marked and the last recapture date. Logarithmic transformation for maximum dispersal distance and longevity were done to improve normality. A general linear model was used to analyze the data, separately for each sex. The shape variables (partial warps and the uniform component) were included as dependent variables. Wing (fore- or hindwing) was included as a fixed factor, and maximum dispersal, longevity and wing centroid size were included as covariates. The non-significant interactions between the factor and each covariate were removed from the model one by one. There was no multicollinearity among the continuous variables (for all cases, tolerance > 0.8).

To visualize wing shape variation with the covariates that showed significant effects in the model, tpsRegr was used (Rohlf, 2011). It performs a multivariate multiple regression of the shape components on a continuous variable (e.g. maximum dispersal distance), visualizing wing shape variation along the continuous variable as thin-plate splines.

The nodus position in relation to wing span was calculated from the landmark coordinates. The length of the wing was measured from landmark 1 to landmark 6. The distance from the wing base to the nodus position was then measured (landmark 1 to landmark 3) and divided by wing length to obtain a percentage. The distances were calculated using only the x-coordinate to remove the extra distance caused by the angles (wings were previously aligned along the major axis). A general linear model was used to analyze the data, separately for each sex. The logarithmic transformation of the relative position of the nodus was included as the dependent variable. Wing (fore- or hindwing) was included as a fixed factor, and maximum dispersal, longevity and wing centroid size were included as covariates. Non-significant interactions between the factor and each covariate were removed from the model one by one. There was no multicollinearity among the variables (for all cases, tolerance > 0.8).



**Figure 3.** The 13 landmarks and the semi-landmark (marked with an asterisk) used for the morphological analysis of the damselflies wings. Landmarks are defined as follows: (1) base of C, (2) the crossvein between C and Sc, above arculus, (3) centre of nodus, (4) left side of pterostigma, (5) right side of pterostigma, (6) end of R<sub>1</sub>, (7) end of R<sub>3</sub>, (8) end of R<sub>4</sub>, (9) end of CuP, (10\*), (11) crossvein between A<sub>1</sub> and posterior margin underneath the start of CuP, (12) junction between A<sub>1</sub> and posterior margin, (13) base of A<sub>1</sub>, (14) centre of arculus. C: coastal vein, Sc: subcoastal vein, R: radius, CuP: Cubitus posterior, A: anal vein.

## RESULTS

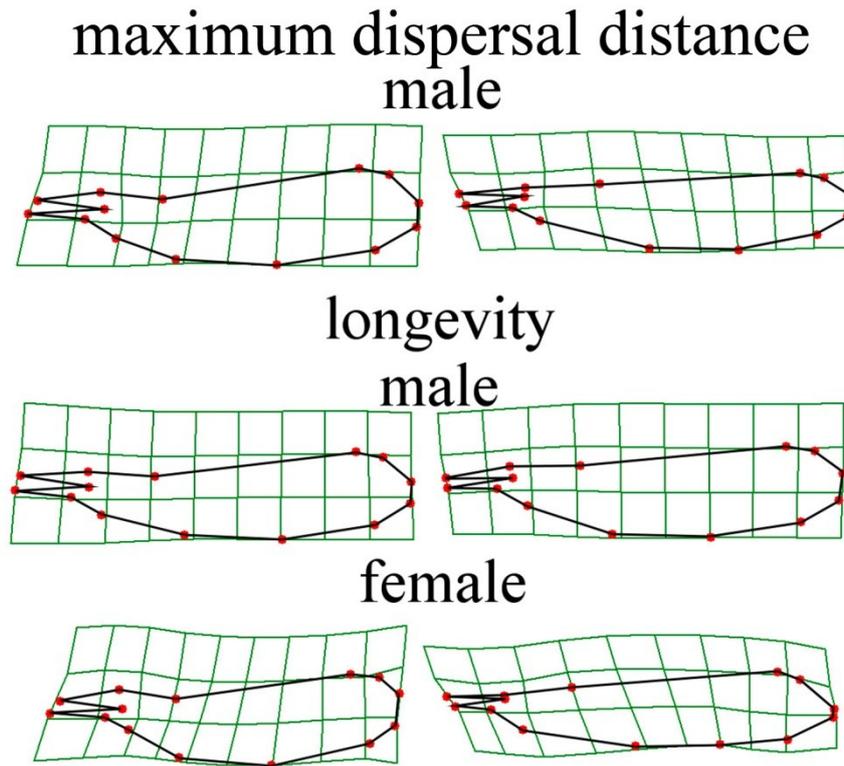
During a total of 22 days of fieldwork 2158 damselflies were caught (1811 males and 347 females), marked and photographed. Of these, 796 were recaptured at least once (756 males (~41.7%) and 40 females (~11.5%). Among all recaptured specimens, 686 males and 36 females were possible to analyze.

### *Males*

I found that maximum dispersal distance had statistically significant effects on wing shape (Table 1). The wing shape of males with longer dispersal distance was longer and more slender with a relatively straight front edge (Figure 4). The wing base was also a bit more slender as well as the wing tip, which was pointier. The wing shape of individuals with shorter dispersal distance was shorter, more crooked and with a narrower wing base. Longevity also showed a significant effect on wing shape (Table 1). The wing shape of individuals with shorter longevity was more slender at the node and showed a somewhat straighter wing base compared to those with longer longevity (Figure 4). Finally, I also found statistically significant differences between the fore- and the hindwing shape (Table 1). Moreover, the allometry of wing shape differed between fore- and hindwings, since we found a significant interaction between wing (fore- or hindwing) and wing centroid size (Table 1). The shape of the forewing was longer and more slender at smaller centroid size and rounder and shorter at larger centroid size (Figure 5). The base of the wing was also bent upwards at larger centroid size and straighter at smaller centroid size. By contrast, hindwing shape followed a pattern somewhat opposite to that shown by forewings (Figure 5). Hindwings were rounder and shorter at smaller centroid size and longer and more slender at larger sizes.

**Table 1.** Results from the general linear model ran on wing shape for males.

Effect	Wilks' $\lambda$	$F_{24,1343}$	P-value
Wing (fore-/hindwing)	0.874	8.073	<0.001
Wing centroid size	0.896	6.520	<0.001
Longevity	0.973	1.544	0.045
Maximum dispersal distance	0.970	1.771	0.012
Wing x Wing centroid size	0.907	5.705	<0.001



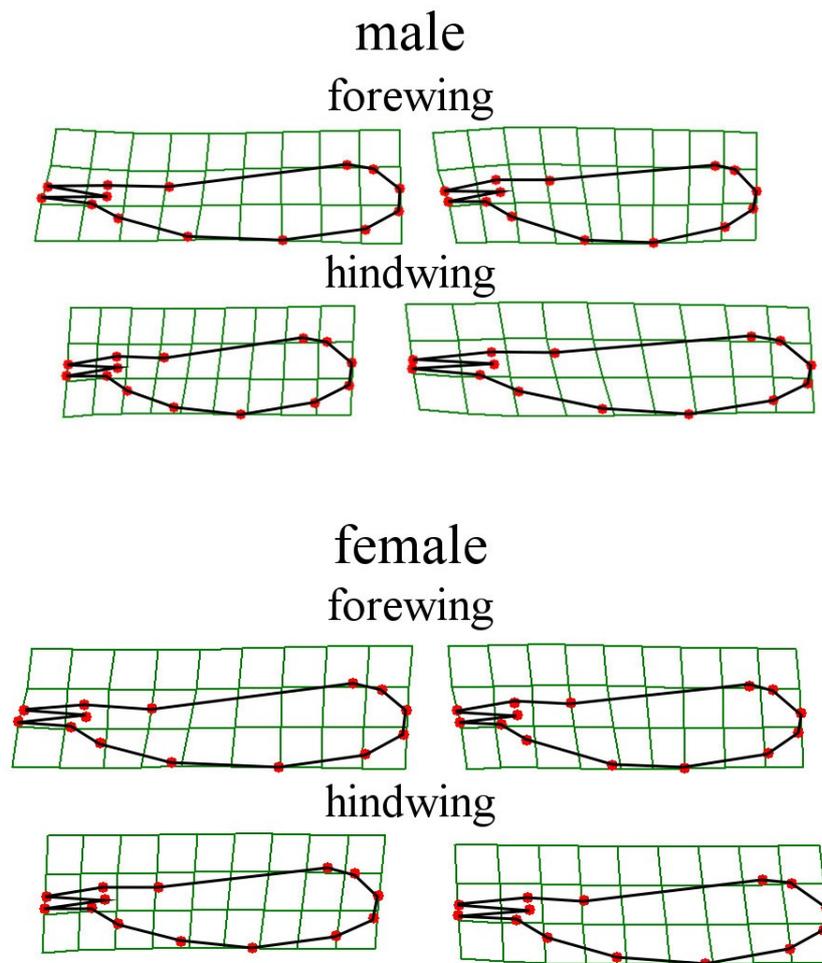
**Figure 4.** Deformation grids, visualizing the different wing shapes at the two extremes of variation (low to the left and high to the right) of maximum dispersal distance (top) and longevity (bottom). The relationships were similar in fore- and hindwings, so only forewings are shown. The deformation grids are exaggerated 10 times, to enhance the morphological differences. The images do not represent wing size, but shape variation.

### *Females*

Longevity, but not maximum dispersal distance, showed a significant effect on wing shape (Table 2). The wing shape of females with shorter longevity was shorter, rounder and had a more bent wing base, while the wing shape of females with longer longevity was longer, more slender, had a straighter front edge and a very straight wing base (Figure 4). As for males, I found significant differences in wing shape between fore- and hindwings of females (Table 2). Wing centroid size showed also a significant effect on wing shape variation. The wing shape variation between larger and smaller centroid size differed between the fore- and hindwings, similarly to the males (Figure 5). However, those differences were possibly not as strong in females as in males, since I did not find a significant interaction between wing (fore- or hindwing) and wing centroid size in the model.

**Table 2.** Results from the general linear model ran on wing shape for females.

Effect	Wilks' $\lambda$	$F_{24,44}$	P-value
Wing (fore-/hindwing)	0.072	23.632	<0.001
Wing centroid size	0.416	2.568	0.003
Longevity	0.506	1.787	0.047
Maximum dispersal distance	0.541	1.553	0.101



**Figure 5.** Deformation grids, visualizing the different wing shapes at the two extremes of variation (low to the left and high to the right) of wing centroid size. The effect is exaggerated 3 times, to enhance the morphological differences. The images do not represent wing size, but shape deformation.

### *Nodus*

The nodus relative position showed a relationship with maximum dispersal distance that was close to significance in males (Table 3) and non-significant in females (

Table 4). No relationship was found for longevity in both sexes and for wing centroid size in females.

**Table 3.** Results from the general linear model ran on the nodus relative position for males.

Effect	d.f.	SS	F	P-value
Wing (fore-/hindwing)	1	0.081	387.079	<0.001
Wing centroid size	1	0.004	21.189	<0.001
Longevity	1	<0.001	0.209	0.648
Maximum dispersal distance	1	0.001	3.106	0.078
Error	1365	<0.001		

**Table 4.** Results from the general linear model ran on the nodus relative position for females.

Effect	d.f.	SS	F	P-value
Wing (fore-/hindwing)	1	0.005	24.730	<0.001
Wing centroid size	1	<0.001	2.198	0.143
Longevity	1	<0.001	0.137	0.712
Maximum dispersal distance	1	<0.001	1.362	0.247
Error	67	<0.001		

## DISCUSSION

The results supported my predictions about wing shape in relation to dispersal distance. I also found a link between wing shape and longevity. Furthermore, the results also showed a relationship between wing shape and size which differed between fore- and hindwings. However, regarding the relative position of the nodus, I only found a nearly significant relationship with maximum dispersal distance in males.

### *Dispersal distance*

Wing shape was related to maximum dispersal distance; a longer dispersal distance was correlated with a more elongated, slender wing and narrower wing tip in males. This is in agreement with my predictions based on previous studies on migrating birds and butterflies (Mönkkönen, 1995; Dockx, 2007). Moreover, in butterflies, longer and more slender wings were associated with prolonged flight (Betts & Wootton, 1988). Thus, the wing shape reported in this study is probably advantageous for dispersing. In fact, pointier wings in migratory birds, combined with other factors (wing loading, avoidance of high winds and turbulence) were showed to reduce the flight cost (Bowlin & Wikelski, 2008). This might also be true for damselflies but since these two groups differ in many anatomical flight characteristics more studies are needed. The size difference between birds and damselflies might also affect the Reynolds numbers, which have a large impact on predicting optimal flight performance (Dudley, 2002), although previous studies on butterflies give support to my results (Betts & Wootton, 1988).

Contrary to males, females did not show a relationship between maximum dispersal distance and wing shape. Past studies have shown that females disperse further than males (Beirinckx, *et al.*, 2006). The reason for the absence of a relationship in my study might be that my sample size for females was too small in comparison to males. Because of their more camouflaged color and their less conspicuous behavior, females are harder to detect; correspondingly, the number of captures and recaptures for females was much lower than for males. I also note that the females tended to reside more in the forest and only arrive to the ponds to mate, and in general therefore they were more dispersive than the males. In fact, most of the captured females were mating, only a very few were caught flying solitarily. Previous studies (reviewed in Cordero-Rivera & Stoks, 2008) have shown that recapture rates in my study species are lower for females (13.2 ±1.4%) than for males (29.3±1.2%). In the present study, the recapture rate for males (41.7%) was higher than previously reported, and slightly lower than reported for females (11.5%).

Regarding my predictions on the relative position of the nodus of the wing, I found close to significant results only in males. If the nodus is closer to the wing base, the wing will twist more in flight (Córdoba-Aguilar, 2008). Wing twisting is important when flying slowly and

hovering (Córdoba-Aguilar, 2008); both could be assumed to be associated with shorter dispersal. Therefore, my results may point towards this hypothesis in males. Again, this might be due to the sample size difference.

### ***Longevity***

I showed that wing shape had an effect on the longevity of individuals, but when looking at the deformation grids of the two extremes, the differences were subtle in males, but clearer in females (Figure 4). If a certain shape gives better agility, maneuverability or similar benefits, it might increase an individual's chance of evading an attacking predator and thus lead to a longer life (Svensson & Friberg, 2007). Shorter and broader wings are usually related to better flight agility (Betts & Wootton, 1988) and thus to improved predator avoidance (Svensson & Friberg, 2007). However, my results are in the opposite direction, since wings of the individuals that lived the longest were more slender and longer. Moreover, I did not find a relationship between relative nodus position and longevity. I currently lack an explanation for this pattern. I note that the estimation of individuals' longevity is often underestimated when using the method that I applied (Córdoba-Aguilar, 2008). The values could also be skewed because the marking took place over three weeks, so individuals that were marked in the first days had the potential for greater longevity scores, compared to individuals marked on the last day. Even though these limitations are evident, capture-mark-recapture studies are the best way to estimate longevity (Cordero-Rivera & Stoks, 2008).

### ***Wing centroid size***

There was a difference in the allometric patterns of wing shape between fore- and hindwings of both males and females, but the difference was only significant for males. This is a very interesting result since it implies that the allometric patterns of the wings within the individual are somehow partially decoupled. This is an issue that certainly deserves further research.

## **CONCLUSIONS**

In the introduction I asked three questions. (1) *Is wing shape variation related to the individual ability to disperse?* The answer is yes, since I showed that wing shape was elongated and more slender and with a tendency to have the nodus located farther away from the wing base in individuals with longer dispersal. My results were not significant for females due probably to the smaller sample size. (2) *Does wing shape vary with individual survival?* Again the answer is yes, since wing shape was correlated to the longevity, both for males and females. However, the patterns reported differed from the expected patterns according to previous studies. (3) *Do the patterns obtained differ between the sexes and between fore- and hindwings within an individual?* Differences were found between the sexes. Moreover, a different relationship between fore- and hindwings and the wing centroid size was found, clear in males, more subtle in females.

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