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Sexual Dimorphism and Allometric Effects Associated With the Wing Shape of Seven Moth Species of Sphingidae (Lepidoptera: Bombycoidea)

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ABSTRACT. Sexual dimorphism is a pronounced pattern of intraspecific variation in Lepidoptera. However, moths of the family Sphingidae (Lepidoptera: Bombycoidea) are considered exceptions to this rule. We used geometric morphometric techniques to detect shape and size sexual dimorphism in the fore and hindwings of seven hawkmoth species. The shape variables produced were then subjected to a discriminant analysis. The allometric effects were measured with a simple regression between the canonical variables and the centroid size. We also used the normalized residuals to assess the nonallometric component of shape variation with a t-test. The deformations in wing shape between sexes per species were assessed with a regression between the nonreduced shape variables and the residuals. We found sexual dimorphism in both wings in all analyzed species, and that the allometric effects were responsible for much of the wing shape variation between the sexes. However, when we removed the size effects, we observed shape sexual dimorphism. It is very common for females to be larger than males in Lepidoptera, so it is expected that the shape of structures such as wings suffers deformations in order to preserve their function. However, sources of variation other than allometry could be a reflection of different reproductive flight behavior (long flights in search for sexual mates in males, and flight in search for host plants in females).

Key Words: Dilophonotini, geometric morphometric, Macroglossini, Philampelini, sexual selection

Morphological differences between males and females are forms of widespread intraspecific variation in Lepidoptera (Allen et al. 2010). Among this variation, there are, for example, the antennae morphology (e.g., filiform in females and pectinate in males; Symonds et al. 2012), body size (smaller in males and larger in females; Stillwell et al. 2010), genitalia morphology (Rutowski 1997), and wing shape and color (Allen et al. 2010). Such dimorphic traits may have reproductive (e.g., fecundity and mate attraction and location; Wiklund 2003, Sanderford 2009) or nonreproductive reasons (e.g., mimetic color pattern; Brown 1981) (Allen et al. 2010). Regarding reproductive functions, the wing shape is an important feature to consider as wing size and shape can be selected to minimize costs of mate searching, increasing the performance in flight-based mating tactics (Wiklund 2003). For example, in the butterfly *Pararge aegeria* (Linneaus 1758) the aspect ratio (wing length²/wing area) was positively related to acceleration capacity only in males (Berwaerts et al. 2002).

Taking into consideration structural differences, sexual dimorphism may arise as size dimorphism, shape dimorphism or by the dependence of shape in relation to size (i.e., allometry) (Shingleton et al. 2008, Tobler and Nijhout 2010). Thus, changes in the size of a structure should be accompanied by changes in its shape, to preserve the original function of the structure (Peters 1983), and therefore, this should be evaluated in the context of sexual dimorphism (Benítez et al. 2013). Such dimorphic aspect can be particularly important in flying animals, such as lepidopterans. This type of locomotion requires high-energy costs (Norberg 1990, 1994; Marinello and Bernard 2014), and lepidopteran species usually exhibit female-biased sexual size dimorphism, weighing up to two times more than males (Allen et al. 2010). Thus, allometry may be classified in relation to the cause of variation in size that gives rise to the allometric relationship. If individuals of the same

species are examined at the same stage of development (i.e., adults), both ontogenetic and evolutionary causes, sources of "dynamic" variation, are controlled, and the remaining variation is static allometry (Klingenberg 1996, Benítez et al. 2013).

Traditionally, moths of the family Sphingidae are considered an exception to the many cases of sexual dimorphism found in other moths and butterflies. Although in other families there are clearly distinguishable morphological wing features (e.g., size, shape, and color) between males and females, differences in sphingids between sexes are often very discreet, with great overlap of wing size ranges (see Martin et al. 2011). However, there is a size sexual dimorphism in which females tend to be slightly larger than males (Janzen 1984).

This family evolved with an exclusive set of features, which may represent an evolutionary constriction, including nocturnal behavior, an adult life span that can last months (due to the capacity to feed) and a long and fast migratory flight (Kitching and Cadiou 2000). This latter feature represents a significant part of their biology and dispersal capacity, as many species have wide distribution and may be present on entire continents (Kitching and Cadiou 2000). Moreover, as wing shape can be an important feature regarding reproductive aspects (Wiklund 2003), different behavior between sexes related to reproductive fitness must be taken under consideration. For example, although males of this moth family are committed to find sexual mates through long flights, females tend to concentrate their flight efforts in searching host plants for oviposition (Janzen 1984). Although there is some parallelism between patrolling done by males in search of females and by females in search of host plants, as each plant will receive one or a few eggs depending on their ability to supply food (Janzen 1984), the males have more to gain in fitness with increased speed, which could explain the

male's greater flight power (Kitching and Cadiou 2000). In theory, such behavior can be translated in different wing morphology.

No study with the specific objective of evaluating sexual dimorphism in the wing shape of this family has been performed. As males and females present very similar wings (at least visually), geometric morphometrics can be an useful tool for detecting and quantify subtle differences, as this technique describes variation in shape by assessing the covariation of measures at specific points of a structure (Birch 1995). For example, studies that used geometric morphometrics in other groups identified sexual dimorphism in bat species where other studies had failed to do so (Camargo and Oliveira 2012), bees (Benítez et al. 2013), and moths of Geometridae family (Benítez et al. 2011).

Therefore, in this study we aimed to use geometric morphometric techniques to describe and quantify size and shape sexual dimorphism in the fore and hindwings of moth species of Sphingidae. Our specific objectives were: 1) assess the contribution of static allometry to the variation in wing shape between males and females, and 2) evaluate specific adaptations in the wing shape of males and females regardless of possible allometric effects. In relation to the allometric contribution in wing shape, we expected that sexual size dimorphism would present an allometric effect to preserve flight function. As seen for several lepidopteran species (e.g., Stillwell et al. 2010), moths of the family Sphingidae also tend to a female-biased sexual size dimorphism (e.g., Janzen 1984, Tobler and Nijhout 2010). Additionally, we also expected that different reproductive behaviors between sexes (males searching for sexual mates and females searching for host plants; Janzen 1984) should be reflected in adaptive differences in wing shape.

Materials and Methods

Data Acquisition. Specimens used in this study come from the Entomological Collection of Embrapa Cerrados. In it are catalogued 142 species of Sphingidae, which represents 77% of the estimated richness for the group in Brazil (Amorim et al. 2009). Females are much rarer than males in entomological collections, possibly due to the patrolling behavior of males (Janzen 1984). Thus, we chose only species that were represented in the collection by both sexes to further analyses. Among these species were *Enyo ocypete* (Linnaeus 1758) (Macroglossinae: Dilophonotini), *Erinnyis ello* (Linnaeus 1758) (Macroglossinae: Dilophonotini), *Erinnyis oenotrus* (Cramer 1780) (Macroglossinae: Dilophonotini), *Isognathus menechus* (Boisduval [1875]) (Macroglossinae: Dilophonotini), *Pseudosphinx tetrio* (Linnaeus 1771) (Macroglossinae: Dilophonotini), *Eumorpha anchemolus* (Cramer 1779) (Macroglossinae: Philampelini), and *Xylophanes chiron* (Cramer 1777) (Macroglossinae: Macroglossini).

To obtain the morphological data, the right fore and hindwings of all individuals of these species were photographed using a Sony Cyber-shot camera (DSC-W650 16.1 megapixels) mounted on a tripod (Sony VCT-R100, New York city, NY). When the right wing was damaged, the left wing was used and then flipped (e.g., Bai et al. 2011, Benítez et al. 2013). Each specimen was fixed on a mount board at a distance of 8 cm from the camera lens and no zoom effects were used, so wing size could be estimated. To distinguish males and females, we first observed the frenulum, which is a brush of bristles in females and a single bristle in males. In addition to this, we also moved the scales of the last abdominal segment with the aid of a brush to verify the presence of anal buds in females or valve in males (Kitching and Cadiou 2000).

To evaluate the wing shape, 16 type 1 landmarks on the extremities and junctions of veins were digitalized using program TpsDig 1.18 (Rohlf 1999a). The following parts of the wing were not sampled: the region bounded by the costal margin and the Radial 3 vein (Rs3) and part of the region bounded by Radial 3 vein (Rs3) to its insertion in Radial 4 (Rs4), part of the region bounded by the inner edge and the anal vein (2A + 3A) in the forewing; the costal margin and subcostal and radial veins (SC + R) and part of the region bounded by the inner margin and the anal vein (2A) on the hindwing (details in Fig. 1). Landmarks in these regions were not chosen, as it would be difficult to ensure homologies
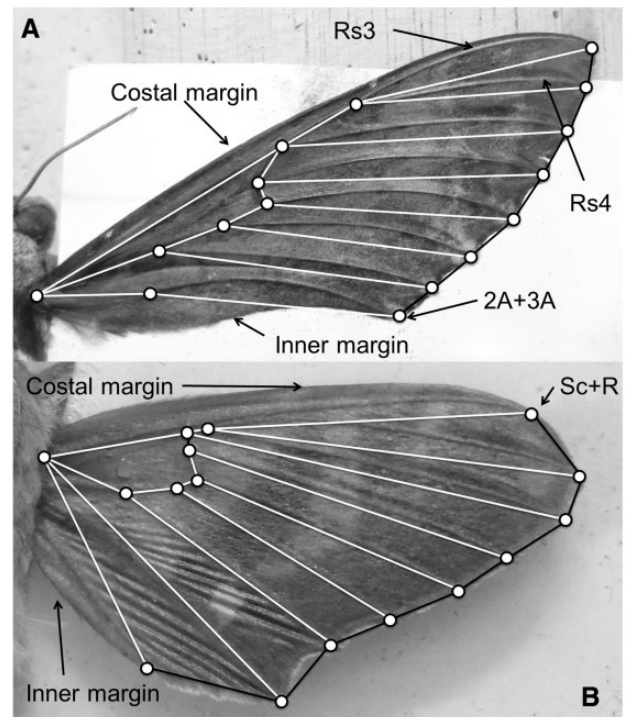

Fig. 1. Dorsal face of the forewing (A) and the ventral face of the hindwing (B) of a Sphingidae, showing the 16 selected type 1 landmarks, connected by lines that highlight the sampled region of the wings. Wing vein's and regions' names follow Moré et al. (2005).

Table 1. Discriminant analysis results for fore and hindwings of males and females of seven Sphingidae species

Species	Wilk's λ	F	P
Forewings			
E. ocypete (19,16)	0.026	8.09	<0.05
Er. ello (51,54)	0.108	22.41	<0.001
Er. oenotrus (63,9)	0.230	5.13	<0.0001
Eu. anchemolus (49,13)	0.263	3.30	<0.05
I. menechus (49, 8)	0.187	4.34	<0.0001
P. tetrio (42,36)	0.283	4.43	<0.0001
X. chiron (63,17)	0.158	9.50	<0.0001
Hindwings			
E. ocypete (19,16)	0.012	17.15	<0.05
Er. ello (50,52)	0.127	17.93	<0.0001
Er. oenotrus (61,9)	0.234	4.79	<0.0001
Eu. anchemolus (49,13)	0.186	5.16	<0.0001
I. menechus (48,8)	0.334	1.92	<0.05
P. tetrio (42,36)	0.291	4.27	<0.001
X. chiron (63,17)	0.158	9.71	<0.001

The index of Wilk's λ indicates this analysis ability to separate the groups using the variables. The closer to 0 the greater the difference between males and females. Numbers in parenthesis in front of species names indicate males and females, respectively.

between points on those curvatures (landmark type 2), and complex explanations derived from them would be less reliable (Bookstein 1991).

To make the veins more visible without damaging the entomological material, xylene was applied along the wings. The anatomic landmarks were obtained from the dorsal face of the forewings and the ventral face of the hindwings (Fig. 1), so that the entire wing could be photographed and the overlap between them did not hinder full visualization of the structures.

The variables that describe wing shapes (uniform components and partial warps) were acquired using TPSRELW v.1.18 (Rohlf 1999b).
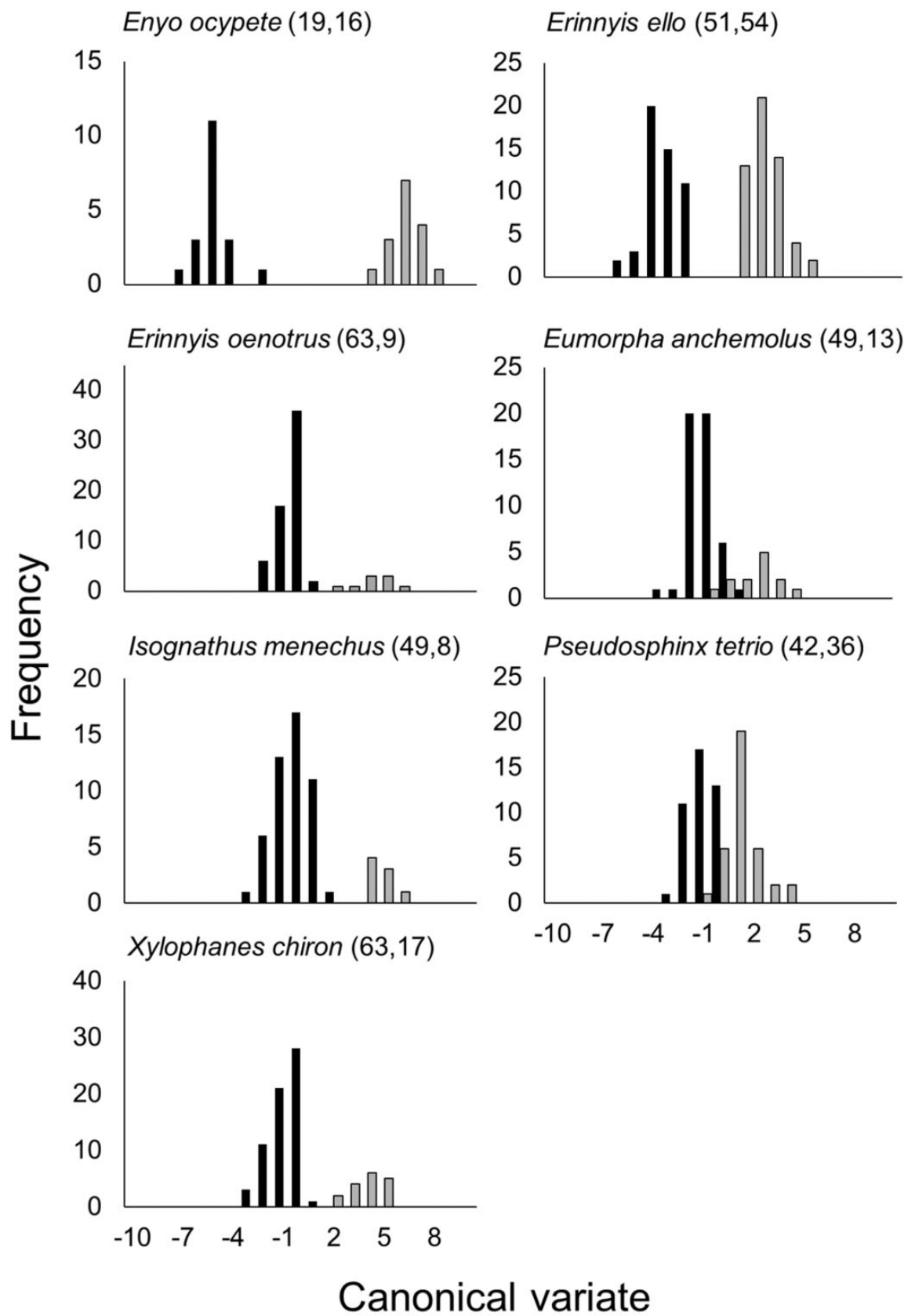
Fig. 2. Canonical variate frequencies generated in the forewing discriminant analysis. In the parentheses, in order, are the number of males and females analyzed in each species. Black bars represent males and gray bars represent females.
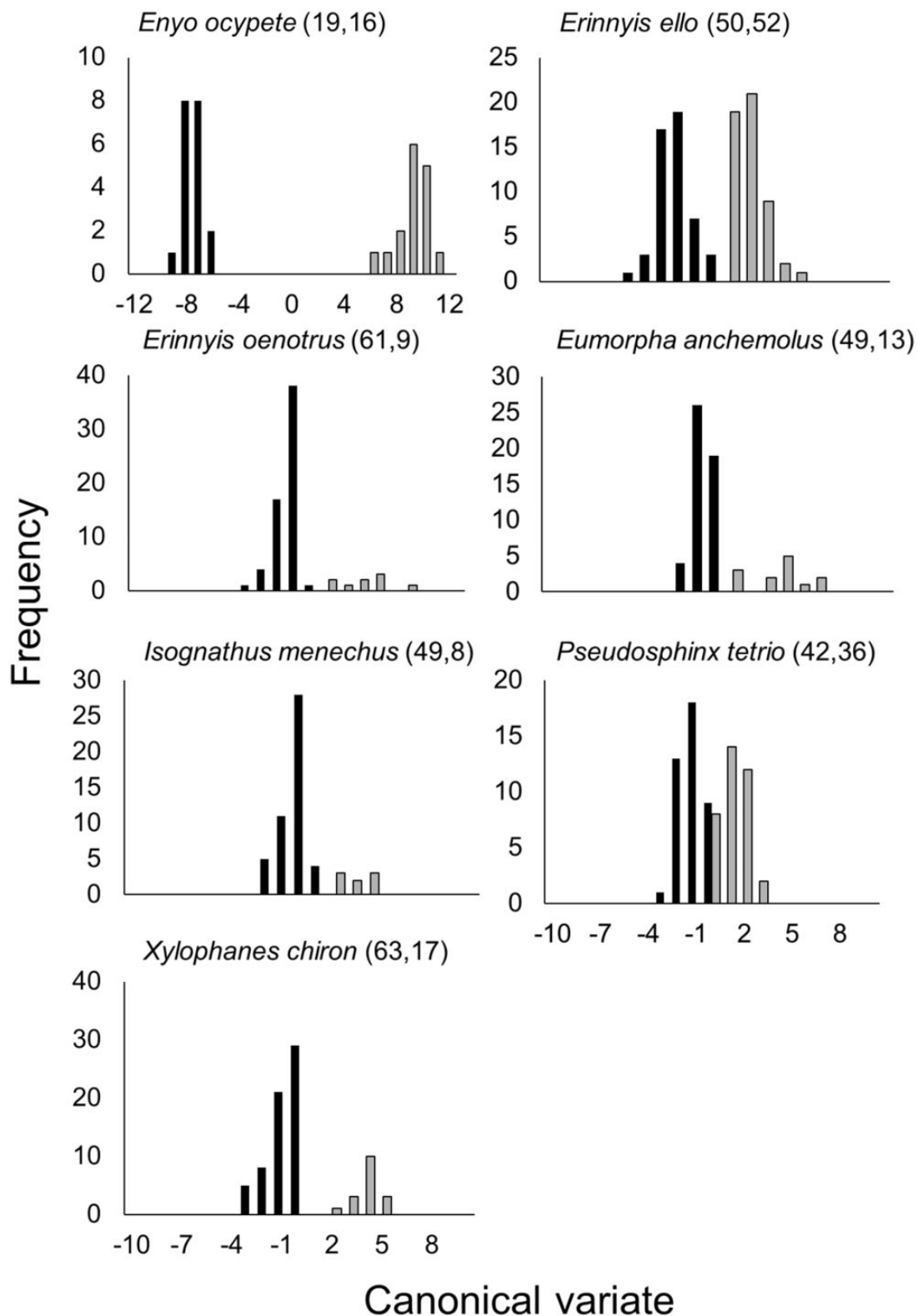
Fig. 3. Canonical variate frequencies generated in the hindwing discriminant analysis. In parentheses, in order, are the number of males and females analyzed in each species. Black bars represent males and gray bars represent females.

This method involves superimposition, centralization, and minimization of the Euclidean distances between anatomical landmarks to compare the shapes of the structures (Bookstein 1991). This method eliminates any information related to the position and orientation of the points (i.e., rotation, translation, and mathematic scale).

Additionally, the software also provides a multivariate isometric wing size estimator called the centroid size, defined as the square root of the sum of the squares of the distances from each anatomic landmark to the center of mass of each configuration (Bookstein 1991). The resulting variable is used as a single measurement that accounts for the multivariable
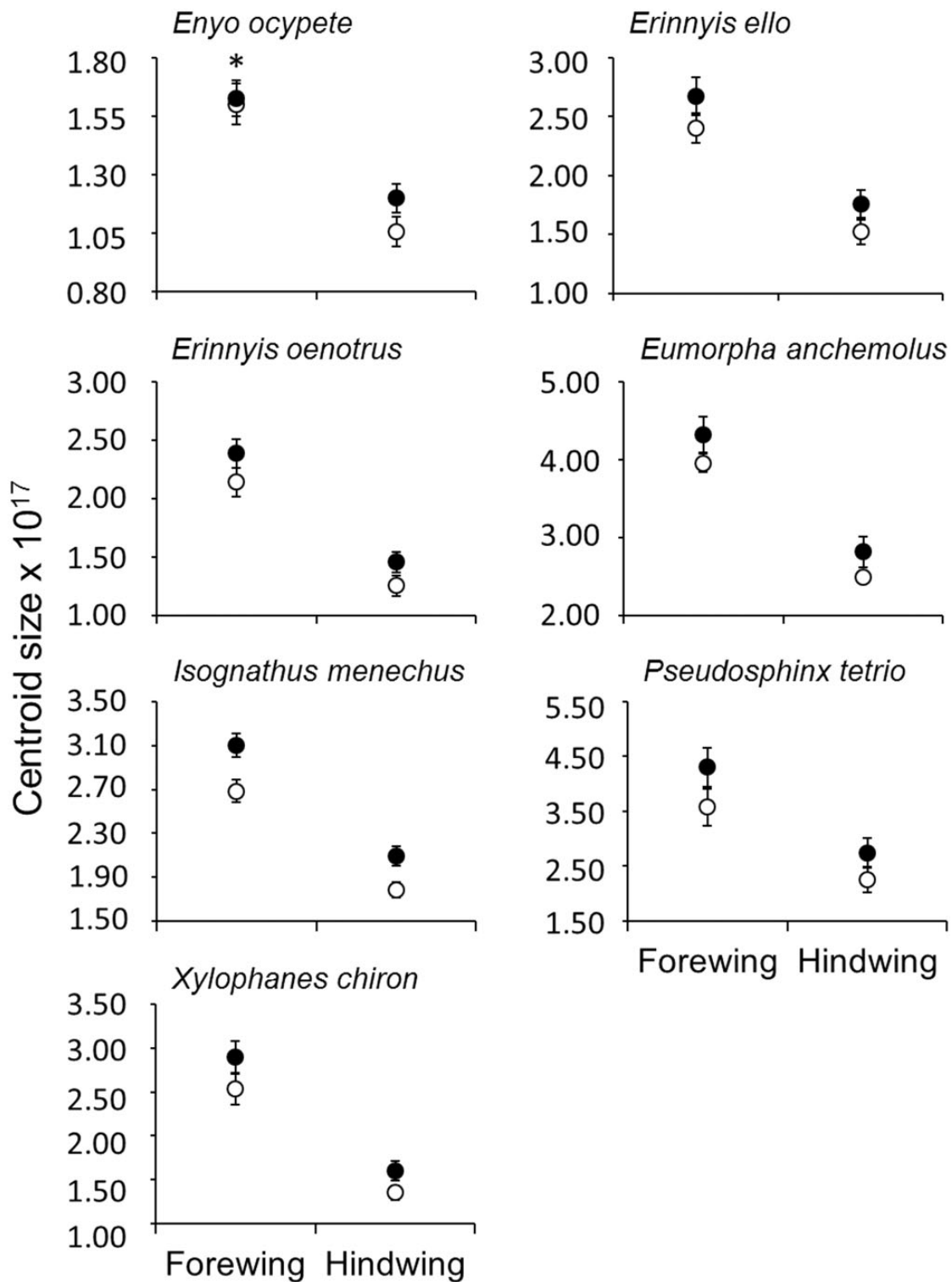
Fig. 4. Centroid size comparisons (*t*-test) of fore and hindwings of males (white symbols) and females (black symbols). Horizontal bars indicate standard deviation. Asterisk in *E. ocypete* indicates not significant difference for the forewing.

nature of the wing size in all subsequent analyzes. This procedure removes only the effects of isometric size. Therefore, the configurations keep both shape variations unrelated to size and allometric variations.

Statistical Analyses. Wing shape variation of each species was assessed by discriminant analysis of the uniform components and partial warps scores, using specimens grouped by sex for acquiring the canonical variables that summarize the set of original variables in each grouping (i.e., males and females). We also performed an analysis of

correct classifications by stepwise through klaR package (Weihs et al. 2005) of the software R 2.13.1 to verify the ability of discriminant analysis to classify individuals in males and females. Additionally, to evaluate the presence of size sexual dimorphism, we performed a *t*-test on centroid size of males and females.

Then, allometric effects in wing shape of each species were measured with simple regression analyses between the canonical variate as dependent variables and the log-transformed values of centroide size as

Table 2. *t*-Test results comparing the centroid size of fore and hindwings of males and females of seven Sphingidae species

Species	*t*-Value	P
Forewings		
E. ocypete (19,16)	−1.698	**>0.05**
Er. ello (51,54)	8.138	<0.001
Er. oenotrus (63,9)	−3.556	<0.001
Eu. anchemolus (49,13)	−6.266	<0.001
I. menechus (49, 8)	−10.686	<0.001
P. tetrio (42,36)	−8.924	<0.001
X. chiron (63,17)	−5.288	<0.001
Hindwings		
E. ocypete (19,16)	−2.611	<0.05
Er. ello (50,52)	9.246	<0.001
Er. oenotrus (61,9)	−4.621	<0.001
Eu. anchemolus (49,13)	−5.583	<0.001
I. menechus (48,8)	−10.209	<0.001
P. tetrio (42,36)	−9.058	<0.001
X. chiron (63,17)	−6.300	<0.001

Numbers in parenthesis in front of species names indicate males and females, respectively.
Numbers in bold indicate not significant results.

Table 3. Simple regression between log-transformed centroid size and the canonical variate obtained with the discriminant analysis that reduced the original wing shape variables

Species	R^2	P	Slope ± SE	P-slope
Forewings				
E. ocypete (35)	0.16	<0.05	2.01 ± 0.80	**>0.05**
Er. ello (105)	0.49	<0.001	1.82 ± 0.18	<0.001
Er. oenotrus (72)	0.25	<0.001	1.61 ± 0.29	<0.05
Eu. anchemolus (62)	0.40	<0.001	−1.05 ± 0.17	<0.001
I. menechus (57)	0.51	<0.001	1.79 ± 0.24	<0.05
P. tetrio (78)	0.52	<0.001	1.28 ± 0.14	<0.05
X. chiron (80)	0.31	<0.001	1.70 ± 0.22	<0.05
Hindwings				
E. ocypete (35)	0.08	**>0.05**	2.93 ± 1.65	**>0.05**
Er. ello (102)	0.38	<0.001	−2.89 ± 0.23	<0.001
Er. oenotrus (70)	0.20	<0.001	−0.93 ± 0.22	<0.001
Eu. anchemolus 62)	0.45	<0.001	−1.52 ± 0.21	<0.001
I. menechus (56)	0.60	<0.001	−1.31 ± 0.15	<0.001
P. tetrio (78)	0.60	<0.001	−1.41 ± 0.13	<0.001
X. chiron (80)	0.31	<0.001	−1.28 ± 0.21	<0.001

R^2 indicates the variation in wing shape that can be attributed to allometric effects. *P*-values in the second column indicate probabilities of regressions. *P*-slope in the fourth column indicates probability of slopes differing from 1 (i.e., allometry). SE indicates Standard Error of the slopes. Numbers in bold indicate not significant results. Numbers in parenthesis in front of species names indicate total of analyzed individuals.

Table 4. *t*-Test results comparing the fore and hindwings residuals of males and females of seven Sphingidae species

Species	Males $\bar{x} \pm \sigma$	Females $\bar{x} \pm \sigma$	t
Forewings			
E. ocypete (19,16)	−0.80 ± 0.48	0.95 ± 0.40	−11.62**
Er. ello (51,54)	−0.68 ± 0.72	0.64 ± 0.78	8.97**
Er. oenotrus (63,9)	−0.27 ± 0.70	1.91 ± 0.52	−9.04**
Eu. anchemolus (49,13)	0.32 ± 0.60	−1.20 ± 1.12	6.30**
I. menechus (49, 8)	0.25 ± 0.04	0.48 ± 0.10	−9.93**
P. tetrio (42,36)	−0.43 ± 0.70	0.50 ± 1.03	−4.66**
X. chiron (63,17)	−0.37 ± 0.70	1.36 ± 0.67	−9.05**
Hindwings			
E. ocypete (19,16)	−0.85 ± 0.32	1.00 ± 0.28	−17.98**
Er. ello (50,52)	0.69 ± 0.71	−0.67 ± −0.73	−9.60**
Er. oenotrus (61,9)	0.29 ± 0.62	−2.0 ± 0.62	10.29**
Eu. anchemolus (49,13)	0.33 ± 0.69	−1.24 ± 0.99	6.60**
I. menechus (48,8)	0.11 ± 0.87	−0.67 ± 0.95	2.14*
P. tetrio (42,36)	0.41 ± 0.90	−0.48 ± 0.87	4.45**
X. chiron (63,17)	0.39 ± 0.67	−1.44 ± 0.56	10.34**

Residuals were obtained by regressions between wing shape variables (uniform components and partial warps) and centroid size (see Statistical Analyses for more details). Numbers in parenthesis in front of species names indicate the number of males and females analyzed, respectively. $\bar{x}$, mean; σ, standard deviation, t, t-test.
*$P < 0.05$; **$P < 0.001$.

Results

The results showed a significant difference between the wing shape of males and females of all seven species, both in the forewings and in the hindwings (Table 1). The landmarks produced 28 variables that the discriminant analysis reduced to a single canonical variate for each individual. The frequencies of male and female across the canonical variates for each species are shown in Figs. 2 (forewings) and 3 (hindwings). Our analyses regarding classification of groups (i.e., males and females) showed high levels of correct classification for both fore and hindwings (species = proportion of correct classification of forewings, proportion of correct classification of hindwings − *E. ocypete* = 1.00, 1.00; *Er. ello* = 0.89, 0.97; *Er. oenotrus* = 0.94, 0.92; *Eu. anchemolus* = 0.87, 0.92; *I. menechus* = 0.96, 0.94; *P. tetrio* = 0.86, 0.80; *X. chiron* = 0.90, 0.99). Each canonical variate presented two distinct distributions for each sex in the seven species, with minimal overlap in the forewings of *Eu. anchemolus* and *P. tetrio* (Figs. 2 and 3). Larger separation was observed in *E. ocypete*. Our results comparing centroid sizes between sexes showed that females present larger wings than males in most species, with the exception of forewings of *E. ocypete* (Fig. 4; Table 2). The regression between each canonical variate and the centroid size indicated a significant allometric effect on most species wings, with the single exception of hind and forewings of *E. ocypete* (Table 3). For this species, although a significant but week association between wing size and shape for the forewings was found, the slope did not statistically differ from 1 (Table 3).

The *t*-test with residuals grouped by sex showed a significant difference of wing shape for both sexes in all species and for both fore and hindwings regardless of size effects (Table 4). According to the regression using allometric residuals and wing shape variables (uniform components and partial warps), it was verified that forewings of males tended to be straighter, with more triangular tips, whereas their hindwings were wider and shorter. The females had thinner forewings with rounder extremities whereas their hindwings were thinner than males, although longer (Figs. 5 and 6).

Discussion

Although sphingid moths are considered not to present sexual dimorphism in wings (Janzen 1984), in our study we found wing shape differences comparing sexes. The allometric effects we found suggest that this factor can be important in intraspecific variation of wing shape in Sphingidae, representing up to 60% of the explanation in some
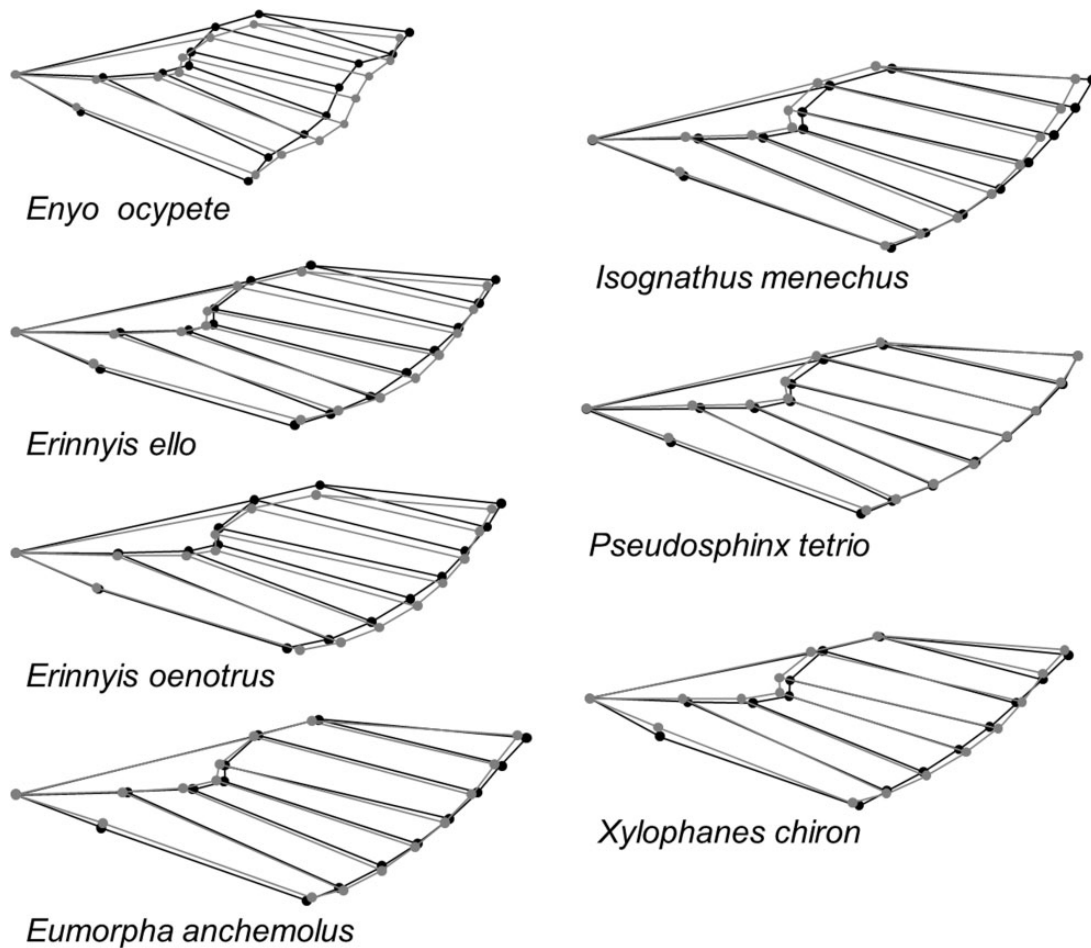
independent variables (see Benítez et al. 2013). In this analysis, we also calculated the slopes of the regressions (*b*) and whether these slopes statistically differed from 1. A calculated $b = 1$ would indicate isometry, thus, a lack of allometry (Pélabon et al. 2014). The normalized residuals of these regressions (normalized difference between the *Y* value predicted for the straight line equation and the actual *Y* value; Zar 2010) were used for assessing the nonallometric variation components in shape variation. For this, deformations in wing shape between sexes were accessed, by performing another set of multiple regressions (i.e., for each species) between the uniform components and partial warps and the normalized residuals, obtained in the first set of regressions, using the software TPSREGR v. 1.31 (Rohlf 2005). Changes in shape, after the effects of size are removed, are deviations from allometry. Dimorphism unrelated to allometry could be explained by adaptation for differences in foraging and breeding activities. Therefore, to verify whether after the effect of size was removed there were significant differences between the wing shapes of males and females, a *t*-test for each species was performed separately.

Fig. 5. Comparison of forewing shapes between males and females of seven Sphingidae species. Black represents males' wings, and gray represents females' wings. Deformations represent the regression between allometric residuals and shape variables in the covariance matrix.

species. Moreover, when the size effects are eliminated from dimorphism, the wing shape of males and females differs significantly in all seven species. There are several hypotheses to explain sexual dimorphism in insects (Wiklund and Forsberg 1991, Fairbairn 1997, Walker and Rypstra 2001, Esperk et al. 2007, Benítez et al. 2010). Most commonly, it is suggested that factors such as fecundity advantages, intersexual resource partitioning, and sexual selection would explain such dimorphic differences (Dale et al. 2007).

Our results comparing centroid size between males and females confirmed the information on the literature regarding sexual dimorphism as a whole (e.g., Janzen 1984). Although size sexual dimorphism is present on the family, such dimorphism exists in a very discreet manner, with female wings slightly larger than males' in all analyzed species. Sexual size dimorphism reflects the adaptation of each sex to their different reproductive role (Fairbairn 1997). Size is a trait directly related to reproductive success (fitness) because larger females produce more eggs and, therefore, are naturally selected (Reeve and Fairbairn 1999, Berger et al. 2008, Allen et al. 2010, Tobler and Nijhout 2010). Although females suffer pressure toward increased size, they suffer pressure in the opposite direction (smaller sizes) by a more efficient flight for migration, hovering for feeding and oviposition and to high predation risk suffered by larger individuals (Acharya 1995, Allen et al. 2010). Hence, it is our suggestion that the allometry effects found in this study are important to maintain flight function. The consideration of allometry as distinct from divergent adaptive patterns finds support in the principle of functional similarity (i.e., function preservation; Peters 1983)

Forewings in males tend to be more triangular on their extremities and possess straighter edges, which suggests friction reduction with air (Lockwood et al. 1998, Bowlin and Wikelski 2008) and may result in a faster flight, with less maneuver capability than the females (Norberg 1990, Lockwood et al. 1998, Bowlin and Wikelski 2008). On the other hand, forewings of females have rounder extremities and larger surfaces, characteristics that suggest a flight with greater maneuverability. The triangular wingtip in insects, birds, and bats represents an evolutionary outcome that increases energy efficiency during the migratory flight (Lockwood et al. 1998, Bowlin and Wikelski 2008, Marinello and Bernard 2014). However, we observed the opposite pattern in the hindwings in both sexes. Although males tend to present shorter and wider wings resulting in rounded shapes, females preset longer and narrower wings resulting in more triangular shapes. Therefore, there seems to be compensation on the hindwing shape, which may suggest a speed gain for females and more maneuverability for males. Additionally, our results showed that the differences found on the hindwings are more acute in relation to the forewings. This pattern of a crescent variability gradient from fore to hindwing also suggests that there are aerodynamic constrictions and greater importance of forewings to flight performance (Strauss 1990).

The adaptive variation not explained by size differences could be explained by the different behaviors associated with each sex, specifically in trade-offs between hovering flight and long distances and high-speed flight. Each sex presents unique activities. Although females forage for host plants and hover for oviposition, males must constantly seek mating partners (Janzen 1984). These activities entail differentiated selection on specific characteristics associated with flight speed and efficiency, such as the size and shape of the wings to reduce the costs involved (Wiklund 2003). Therefore, the morphological compensation
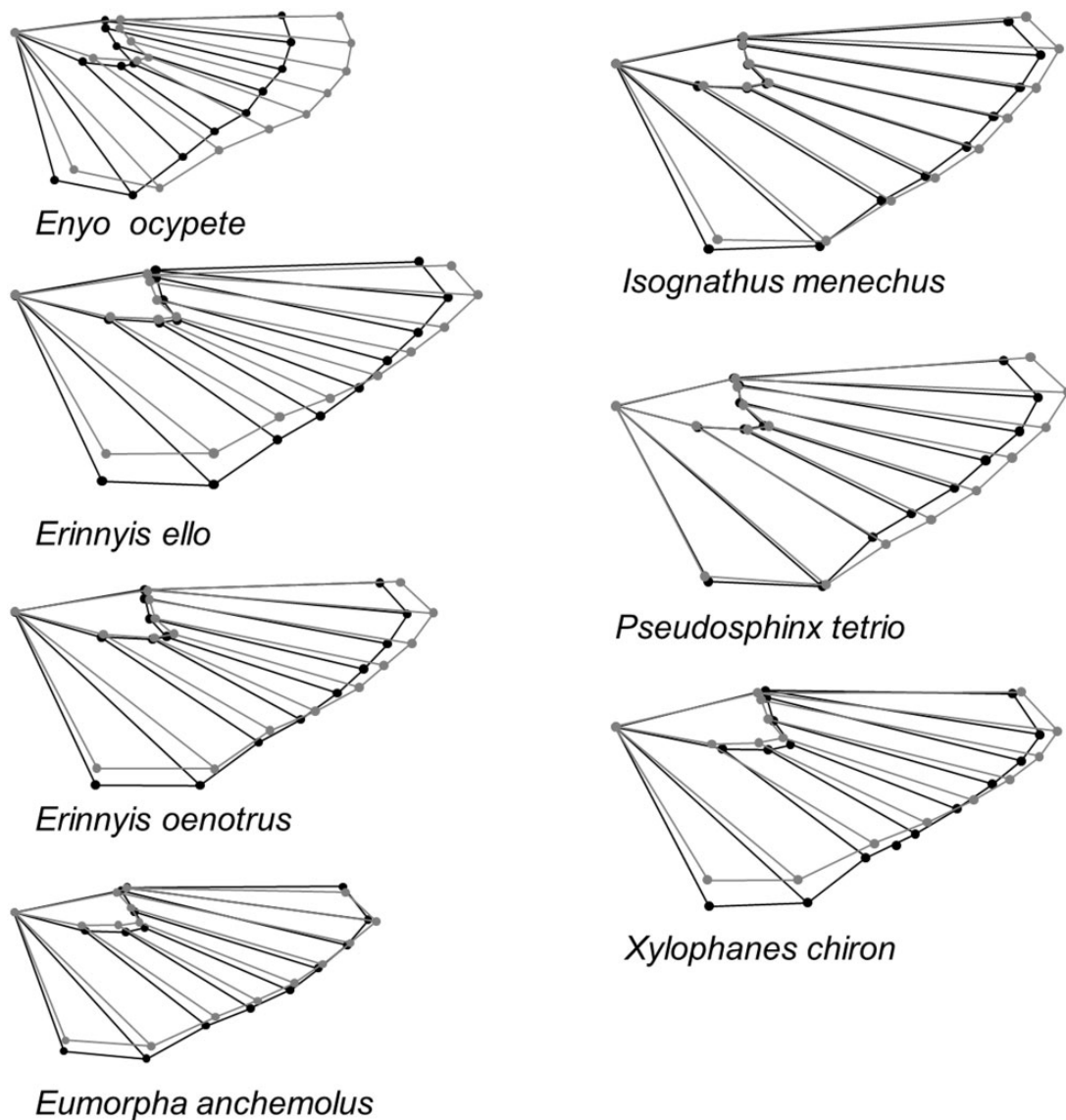
Fig. 6. Comparison of hindwing shapes between males and females of seven Sphingidae species. Black represents males' wings, and gray represents females' wings. Deformations represent the regression between allometric residuals and shape variables in the covariance matrix.

found between the fore and hindwings could be a result of the need to off-set loss of speed in females and hovering capability in males.

Conclusion

This study showed that differences in the wing shape of the Sphingidae species arise from allometry, as a consequence of sexual size dimorphism and possibly from adaptive differences regarding reproductive flight behavior. The forewing shape found in males suggests more efficiency during faster flights that would guarantee better fitness in finding females. On the other hand, females presented wings that may favor slower flight for patrolling and selecting host plants for oviposition and hovering over plants. However, there might be some sort of compensation in the hindwings that increase flight speed for females, and hovering for males. The variation found between sexes could affect, for example, dispersion, migration, nuptial flight, territoriality, search for host plants, and feeding (e.g., Benson et al. 1989, Srygley 1994, Dudley 2000, Breuker et al. 2007, Dockx 2007, Johansson et al. 2009, Benítez et al. 2011). Therefore, selection could possibly act on wing shape to optimize flight characteristics (DeVries et al. 2010). Although our results lead to these interpretation regarding flight dynamics and adaptations, specific tests on flight performances need to be conducted to confirm

whether these hypotheses or some others can explain the patterns found in this study.

Acknowledgments

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