

## Sexual dimorphism and allometric relationships in the wings of two underwing moths (Lep., Erebiidae, *Catocala*)

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**Abstract.** Sexual dimorphism has been observed in various Lepidoptera species, with the majority exhibiting female-biased sexual size dimorphism. As the first geometric morphometric study on *Catocala* wings, we sought to determine the sexual dimorphism in the wing size and shape of *Catocala abacta* and *C. brandti*, as two sympatric congeneric species, and their associated allometric patterns. These two species frequently coexist in western Iran's oak forests. On the fore- and hindwings of males and females of the studied species captured in southwest Iran, 19 and 14 landmarks were digitized, respectively. The patterns of variation in the shape of wings were investigated using relative warp analysis. The results indicated an apparent sexual dimorphism in the shape of the forewings but not the shape of the hindwings. Females of *C. abacta* had larger centroid sizes than males, whereas males of *C. brandti* had larger centroid sizes than females in both wings. Additionally, we observed a distinct allometric pattern on both species' fore- and hindwings. Our finding corroborates previous research demonstrating sexual dimorphism in the wings of Lepidoptera as a proxy character, implying that selection may affect wing shape to improve flight behavior and efficiency.

**Keywords:** *Catocala abacta*, *Catocala brandti*, geometric morphometrics, wing shape.

### Introduction

Sexual dimorphism is a common type of intraspecific variation in Lepidoptera and manifests itself in differences in sexual or nonsexual behavioral, morphological, physiological, and life-history traits between the sexes. There has been a tendency to treat natural selection primarily as a constraint on the degree of sexual dimorphism that evolves due to sexual selection (Allen et al. 2011). Organisms adapt to new conditions through natural selection, whereby individuals can cope with the new conditions, survive, and reproduce. Sexual selection, as a part of natural selection, drives the evolution of traits that increase success in the competition for mating (Andersson 1994). Because mate competition is frequently costly, sexual selection may favor traits that impose high fitness costs, affecting population viability at the individual level (Rundle et al. 2006). However, once sexually selected traits start to evolve, sexual selection can accelerate adaptation (Candolin & Heuschele 2008). Research to determine if a correlation exists between habitat and life-history characters indicates that species with flightless or wingless females (dimorphic sexes) occur in three subfamilies of the Geometridae; in each case, flightlessness is mainly associated with the forest habitat compared to non-forested habitats. However, many species of geometrids occur in forests and are capable of flight. These life-history traits contribute to these species' ability to reach high population densities during years favorable for larval growth and survival, resulting in the species' economic importance (Barbosa et al. 1989).

A typical pattern of sexual dimorphism in insects is a difference in the size of the overall body between the sexes, frequently favoring females over males (e.g., Karlsson et al. 1997, Stillwell et al. 2014). In general, fecundity selection is the primary factor underlying this pattern. According to this theory, selection favors larger females of a species because body size and fecundity frequently correlate positively, implying that larger females exhibit greater suitability than

smaller females (Reeve & Fairbairn 1999). Although sexual selection is the primary driving force in the evolution of sexual dimorphism in insects, particularly Lepidoptera, natural selection alone can drive dimorphism, and the two forces often interact in complex ways to affect the evolution of sexually dimorphic traits (Allen et al. 2011).

Sexual dimorphism has been reported in different Lepidoptera species in life-history traits (e.g., age & size at hatching, size, and the number of offspring), morphology (e.g., size & shape of the wing, genitalia & sensory structures, size & color of pigment patches, and body size & body composition) and behavior (e.g., increased male flight height) (Allen et al. 2011). The study of Lepidoptera's higher taxonomy has benefited from understanding wing morphology (e.g., size, shape, venation, and others) (Strauss 1990). Mozaffarian et al. (2007) demonstrated the existence of sexual dimorphism in the wing shape and size of the carob moth, *Ectomyelois ceratoniae* (Zeller) (Lepidoptera: Pyralidae), which was collected from and reared on four hostplants in Iran: pomegranate, fig, pistachio, and walnut. Benítez et al. (2011) revealed a significant difference in wing shape between the sexes of the moth *Synneuria* sp. (Lepidoptera: Geometridae). Shi et al. (2015) examined the wings of 821 gypsy moths from eight geographic strains and showed sexual dimorphism in the wings of *Lymantria dispar* (L.) (Lepidoptera: Erebiidae) populations with varying female flight capabilities. Wing loads of females were also lower in flight-capable strains. According to Benitez & Vargas (2017), the wings of the moth *Macaria mirthae* Vargas et al. (Lepidoptera: Geometridae) exhibit an apparent sexual shape dimorphism. Male wings are more contracted than female wings in this species.

*Catocala* Schrank (Erebiidae, Erebiinae, Catocalini) is a genus of attractive moths commonly referred to as underwing moths. It is a Holarctic genus that contains approximately 300 species worldwide, including twenty species and four subspecies recorded in Iran (Goater et al. 2003, Alavi et al. 2019). Typically, these moths have

enormous bodies with cryptic forewings that mimic random patterns of tree bark and bright orange, red, yellow, or pink colors on the hindwings with bold dark bands. Underwing moths are solitary species that hibernate as eggs. Larvae are highly cryptic and frequently mimic host plant twigs, branches, and bark crevices. Generally, larval foodplants are *Quercus*, *Salix*, or *Populus*, abundant in Western Iran's Zagros mountains (Goater et al. 2003, Müller et al. 2008, Alavi et al. 2019).

*Catocala abacta* Staudinger and *C. brandti* Hacker & Kautt are on the wing, particularly in the spring, with relatively large populations in the oak forests of Khuzestan province, southwest Iran. While studying these underwing moths in southwest Iran's oak forests (Alavi et al. 2019), we noticed that some *C. brandti* males are unusually larger than females, despite most Lepidoptera exhibiting female-biased sexual size dimorphism (Stillwell et al. 2010). This was the motivation for our study of the sexual dimorphism in the size and shape of the wings of *Catocala abacta* and *C. brandti*, as two sympatric congeneric species. Additionally, the allometric shape changes in the wings of males and females of both species were examined and compared.

## Material and Methods

### Specimen preparation and data acquisition

Moths were captured in May 2017 using a light trap in Mal-aqa village (31° 35' N 50° 00' E, 1100 m.) in Baghmalek, southwest Iran. The specimens' right wings were discolored and mounted on microscopic slides. Wings were photographed using a digital camera

(Canon Powershot SX40) mounted on a stereomicroscope (Olympus SZX12) with 70x magnification. Only the right wings of specimens were used in this study to avoid asymmetry bias between the two wings (Rohlf & Slice 1990). The examined specimens were deposited at the Insect and Mite Collection of Ahvaz (IMCA), Shahid Chamran University of Ahvaz's Department of Plant Protection. The present study examined the *C. abacta* (forewings: 38 males, 39 females; hindwings: 38 males, 38 females) and *C. brandti* (forewings: 38 males, 38 females; hindwings: 39 males, 40 females) using a landmark-based geometric morphometric method (Bookstein 1991, Zelditch et al. 2004).

Nineteen and fourteen landmarks were selected and digitized on forewing and hindwing pictures, respectively, using tpsDig software (ver. 2.31) at vein-vein and vein-edge intersections (Fig. 1) (Rohlf 2015).

### Geometric morphometrics and statistical analyses

To investigate variation in wing shape, digitized landmark data were subjected to a Generalized Procrustes Analysis (GPA) to standardize the raw landmarking data configurations and eliminate variations unrelated to shape (variation by location, scale, and orientation). The shape variables, relative warp scores (RWs), were used to determine the shape variation (tpsRelw software ver. 1.69), performing interpolation to project the data into the Euclidean plane. The results were visualized graphically using a wireframe graph to illustrate the patterns of shape variation (Bookstein 1991, Rohlf 2015).

Procrustes Analysis of Variance (Procrustes ANOVA) is identical to nonparametric permutational MANOVA and is especially useful for shape data (Anderson 2001, Sherratt 2016). To determine the significance of observed differences in graphical shape variations, we conducted a two-way multivariate Procrustes ANOVA with 10000 permutations using the geomorph (R package, v. 3.0.4) under procD.lm function (Adams & Otárola-Castillo 2013, Sherratt 2016).

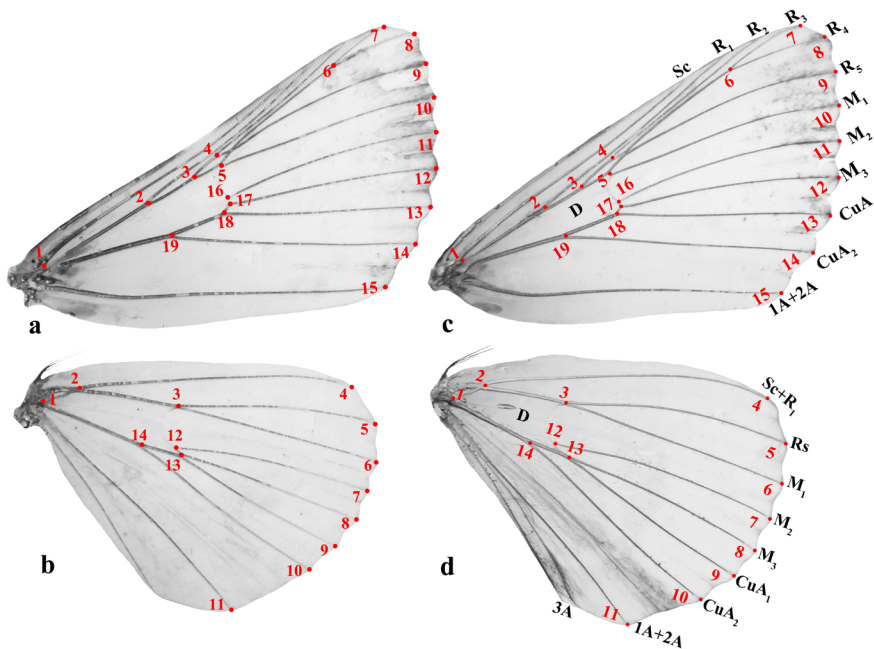


Figure 1. Female *Catocala brandti* wing venation (a-b) and *Catocala abacta* wing venation (c-d) and location of landmarks used in this study: forewings (a, c) and hindwings (b, d), D=discal cell.

As a wing size estimator, the centroid size was calculated as the square root of the sum of squared distances of a set of landmarks from their centroid (Bookstein 1991, Zelditch et al. 2004). Two-way ANOVA was used to analyze sexual size dimorphism based on centroid size, and boxplots were used to visualize the results. SPSS software (v. 24.0, IBM Corp. 2016) was used to conduct statistical analyses.

Static allometry was analyzed using multivariate regression of partial warps and uniform components onto the centroid size of the studied groups. The significance of regression was determined using Goodall's F-test on the percentage of allometric shape changes in the wings of each species when separated and mixed sexes were present. To this end, parametric and nonparametric permutation tests were carried out using tpsRegr (v. 1.45) (Goodall 1991, Rohlf 2016). The

significance of regressions would reject the null hypothesis (absence of allometry) and establish a relationship between wing shape changes and size.

Size (allometry), species, sex, and their interactions were used to express shape variation. A multivariate analysis of covariance (MANCOVA) was used to determine whether there are differences in the patterns of allometric shape variation between the studied groups. Shape variables were used as dependent variables, centroid size was used as a covariate, and groups were used as a fixed factor. The R package geomorph (v. 3.0.4) was used to perform a Multivariate Procrustes ANOVA with 10000 permutations using *procD.lm* (Adams & Otárola-Castillo 2013, Sherratt 2016, Tamagnini et al. 2018).

## Results

### Relative warps analysis

The first two relative warp components explained 71.63% (RW1: 58.97, RW2: 12.66) of the forewing landmark shape variation (Fig. 2) and 72.78% (RW1: 60.34, RW2: 12.44) of the

hindwing landmark shape variation (Fig. 3). The predicted shape deformations of wings associated with different positions were graphically depicted and visualized using thin-plate spline deformation grids in the coordinate system's four quadrants. The relative warp components of the two studied species indicated sexual differences in the forewing but not in the hindwing (Fig. 2, 3).

The forewing differences between males and females of *C. abacta* were most noticeable in the outer angle (apex), which was longer in males than females (landmarks 7, 8, and 9), the outer margin (termen), which was contracted in males compared to females (landmarks 11, 12, 13, and 14), as well as the inner margin (dorsum) and discal cell, which was more expanded toward termen in males than females (Fig. 2). *C. brandti* forewing shape variation was similar to *C. abacta*, but male wingtip (apex) elongation was less than in *C. abacta*. There was no evidence of sexual shape dimorphism in visualized shape changes of the hindwing (Fig. 3).

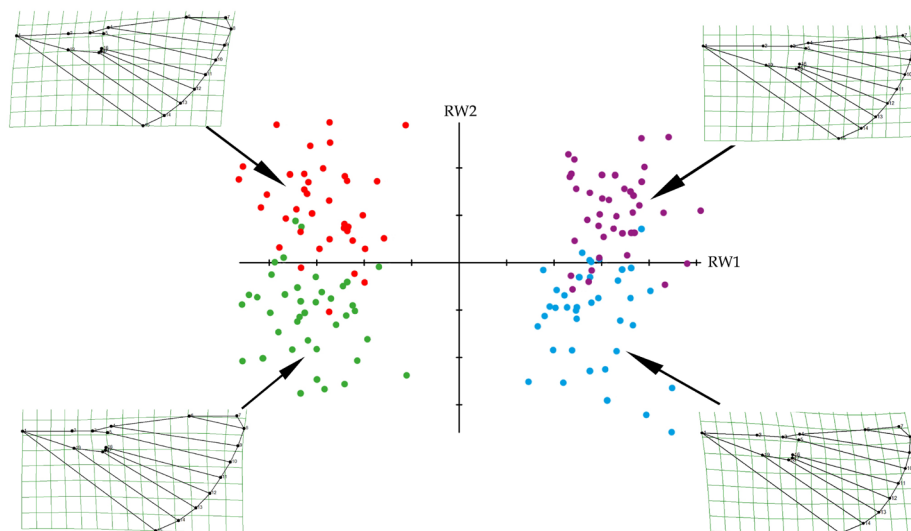


Figure 2. The scatterplot of the first and second relative warp scores for the forewings of *Catocala abacta* and *Catocala brandti*. Red: *C. abacta* male; Green: *C. abacta* female; Purple: *C. brandti* male; Blue: *C. brandti* female. Deformation grids represent shape changes in males and females of the two species.

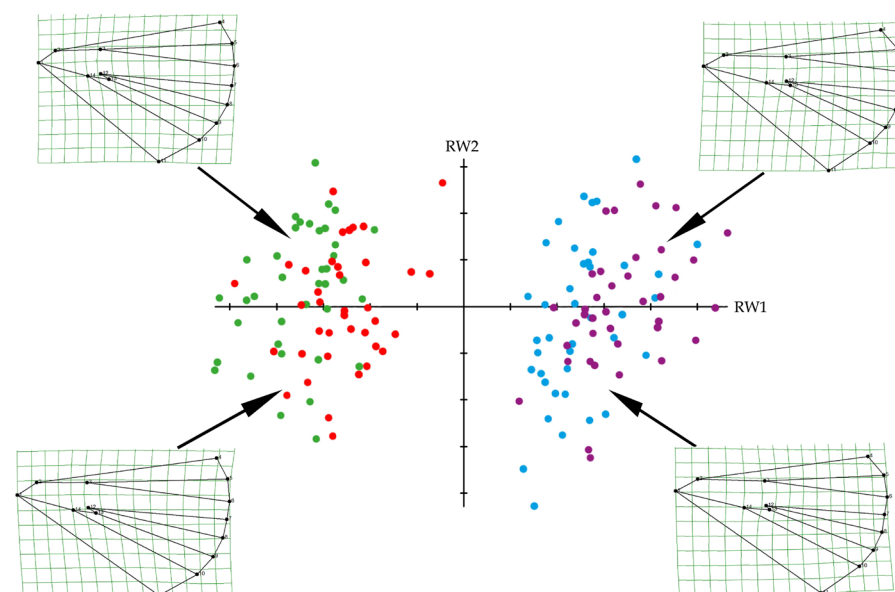


Figure 3. The scatterplot of the first and second relative warp scores for the hindwings of *Catocala abacta* and *Catocala brandti*. Red: *C. abacta* male; Green: *C. abacta* female; Purple: *C. brandti* male; Blue: *C. brandti* female. Deformation grids represent shape changes in males and females of the two species.

### Multivariate analysis of shape variables

The results indicated that species, sex, and their interaction were significant in fore- and hindwing shape variables (Figs 1, 2, Tables 1, 2). Results of interaction indicated that sexual dimorphism of shape variables was not identical in the two studied species. Additionally, we conducted a similar analysis on each species separately. Sexual dimorphism was observed in at least one shape variable of *C. abacta* forewing ( $F=20.43$ ,  $p=1*10^{-4}$ ) and hindwing ( $F=4.47$ ,  $p=1*10^{-4}$ ) as well as *C. brandti* forewing ( $F=17.22$ ,  $p=1*10^{-4}$ ) and hindwing ( $F=3.68$ ,  $p=0.0035$ ).

### Wing centroid size variation

A two-way ANOVA revealed significant centroid size differences between species (forewings:  $F=921.89$ ,  $p<0.0001$ ; hindwings:  $F=670.940$ ,  $p<0.0001$ ) but not between sexes (forewings:  $F=1.32$ ,  $p=0.253$ ; hindwings  $F=1.107$ ,  $p=0.294$ ). There was also a significant interaction between species and sex (forewings:  $F=44.93$ ,  $p<0.0001$ ; hindwings:  $F=35.70$ ,  $p<0.0001$ ), implying the degrees of sexual size dimorphism in the fore- and hindwings of two *Catocala* species were

generally different. Boxplots revealed that *C. abacta* had larger centroid size values than *C. brandti* in both wings (Fig. 4); additionally, the wing size of the females was larger than the males in *C. abacta*, but it was smaller in the females of *C. brandti*.

### Static allometry and covariation between size and shape variables

The null hypothesis (isometry) was rejected, and all multivariate regressions of shape variables on centroid size were significant, except for mixed sexes in the hindwing of *C. brandti* (Table 3).

Variation in shape was significantly related to variation in centroid size. Allometry explained 2.1% of shape changes in the forewing of *C. brandti* (mixed sexes) to 17.6% of shape changes in the hindwing of *C. brandti* males. The permutation method consistently produced results corresponding to the parametric results in all cases (Table 3). The significance of the mixed sexes regressions was consistent with the sexes being separated, except for *C. brandti* hindwing.

Table 1. Two-way multivariate Procrustes ANOVA on forewing shape variables in *Catocala abacta* and *Catocala brandti*. The asterisk represents a significant difference.

	df	SS	MS	r <sup>2</sup>	F	Z	p-value
Species	1	0.140901	0.14090	0.55306	231.0496	7.6603	1*10 <sup>-4*</sup>
Sex	1	0.021000	0.02100	0.08243	34.4350	8.7097	1*10 <sup>-4*</sup>
Species: Sex	1	0.002000	0.00200	0.00785	3.2803	4.8559	1*10 <sup>-4*</sup>
Error	149	0.090865	0.00061	0.35666			
Total	152	0.254766					

Table 2. Two-way multivariate Procrustes ANOVA on hindwing shape variables in *Catocala abacta* and *Catocala brandti*. The asterisk represents a significant difference.

	df	SS	MS	r <sup>2</sup>	F	Z	p-value
Species	1	0.139466	0.139466	0.54521	190.7376	7.2940	1*10 <sup>-4*</sup>
Sex	1	0.004643	0.004643	0.01815	6.3504	5.3790	1*10 <sup>-4*</sup>
Species: Sex	1	0.001284	0.001284	0.00502	1.7565	2.9807	0.0012*
Error	151	0.110410	0.000731	0.43162			
Total	154	0.255804					

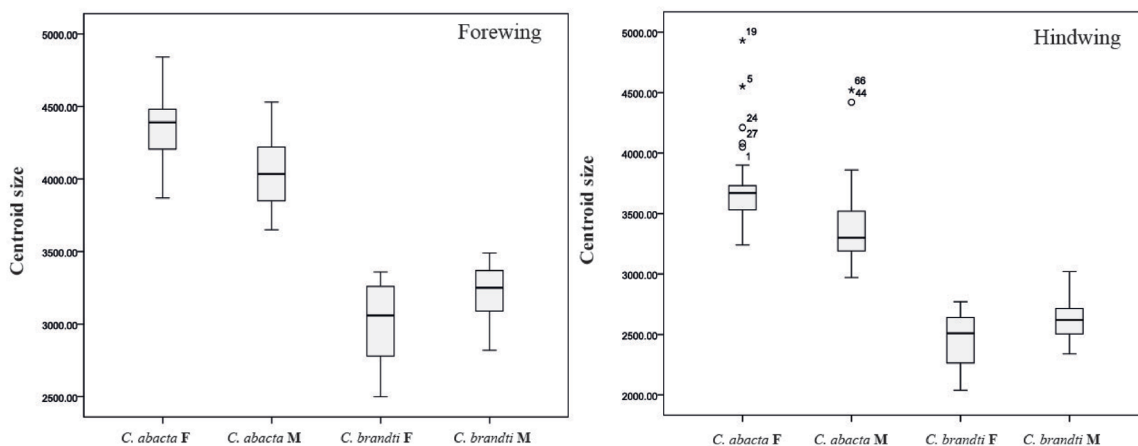


Figure 4. Box-and-whisker plots showing variation in forewing and hindwing of male (M) and female (F) centroid size of *Catocala abacta* and *Catocala brandti*. Boxes show the median, 25th, and 75th percentiles, whiskers show minimum and maximum values, and circles represent outliers.



Table 3. Allometry and the percentage of shape explained by size in *Catocala abacta* and *Catocala brandti* wings.

Species/Sex	Forewing				Hindwing			
	% Explained variance	Goodall's <i>F</i> -test			% Explained variance	Goodall's <i>F</i> -test		
		<i>F</i>	<i>df</i>	<i>P</i> -value		<i>F</i>	<i>df</i>	<i>P</i> -value
<i>C. abacta</i> (Female)	9.7	3.99	34	0.000	13.4	5.56	24	0.000
<i>C. abacta</i> (Male)	13.8	5.75	34	0.000	8.1	3.19	24	0.000
<i>C. abacta</i> (Mixed)	8.1	6.66	34	0.000	2.5	1.91	24	0.005
<i>C. brandti</i> (Female)	13.8	5.77	34	0.000	5.8	2.35	24	0.000
<i>C. brandti</i> (Male)	11.5	4.70	34	0.000	17.6	7.89	24	0.000
<i>C. brandti</i> (Mixed)	2.1	1.59	34	0.016	1.3	0.99	24	0.481

### Visualizing shape allometry

Figures 5 and 6 illustrate patterns of allometric shape change in the fore- and hindwings of two *Catocala* species. In mixed sexes, the costa and termen landmarks of *C. abacta* forewings were elongated to the apex in smaller than larger specimens. In contrast, larger specimens of *C. brandti* had such elongated forewings. In *C. abacta*, larger specimens had slightly elongated hindwings to termen and contracted discal cell landmarks on the inside. The hindwings of *C. brandti* mixed sexes lacked allometry. Female *C. abacta* forewing variation was comparable to that of mixed sexes. Male *C. abacta* specimens exhibited the same pattern, but larger specimens demonstrated further elongation. In larger specimens, the coastal area of the forewings of *C. brandti* females bent toward the post-discal area. The bending is slight in larger males, and the forewings were slightly elongated anteriorly from the discal cell and costa. The variation in the hindwings of males and females of *C. abacta* was similar to that of mixed sexes. As in males, the discal cell landmarks were elongated to termen on the hindwings of larger *C. brandti* females.

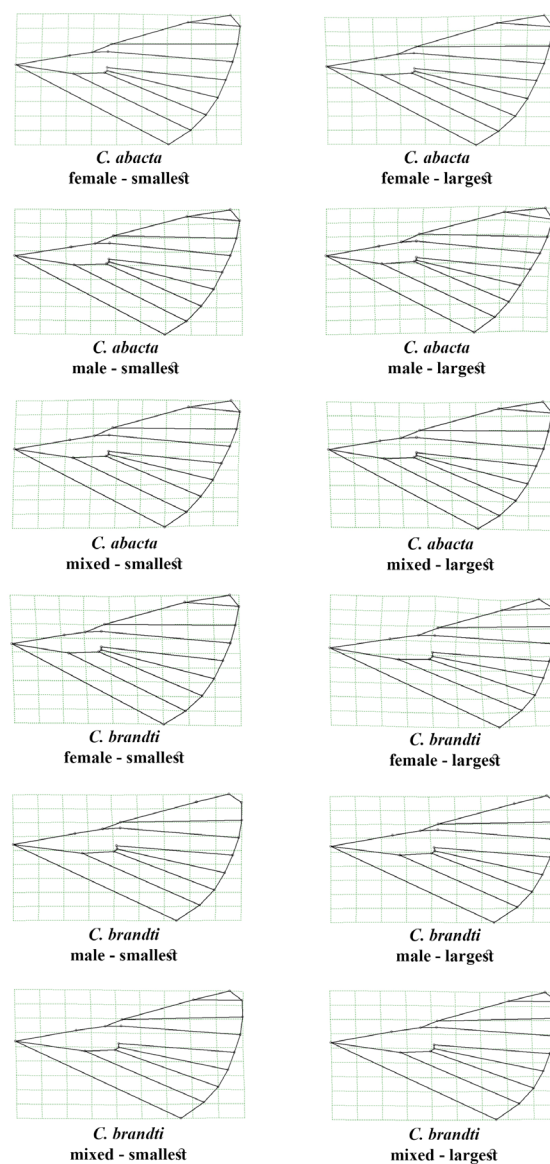
### Allometric patterns in two species

Differences in allometric trajectories between species and sexes were significant in both fore- and hindwings (Tables 4, 5). Centroid size and species were insignificant in forewing interactions ( $p=0.1410$ ), but centroid size and sex were significant ( $p=1 \times 10^{-4}$ ). This indicated that species-level allometric trajectories were similar but varied between sexes. In the hindwings, there was a significant interaction between centroid size, species ( $p=0.0082$ ), and sex ( $p=0.0030$ ). This demonstrated that allometric trajectories vary among species and sexes.

### Discussion

This is the first study to use geometric morphometrics to investigate the sexual dimorphism of wings in the genus *Catocala*. Numerous studies have revealed sexual dimorphism in the shape and size of Lepidoptera's wings (e.g., Mozaffarian et al. 2007, Benitez et al. 2011, Jeratthitikul et al. 2014, Camargo et al. 2015, Benitez & Vargas 2017, Vargas-Ortiz et al. 2018, Moreno & Vilorio 2020). They primarily demonstrated that females had significantly larger wings than males, a common characteristic in Lepidoptera. Based on our findings, we detected shape and size dimorphism in the wings of *C. abacta* and *C. brandti*. This

confirms previous findings that used Lepidoptera wings to study sexual dimorphism. Despite the statistically significant shape dimorphism in both species' hindwings (Table 2), the relative warp analysis revealed no discernible shape dimorphism (Fig. 3).

Figure 5. Visualization of allometric patterns in forewings of *Catocala abacta* and *Catocala brandti* using thin-plate splines.

We conclude that the magnitude of dimorphism in hindwings is insufficient to be biologically meaningful and significant.

Fitness in insects is directly proportional to body size. Individuals with larger bodies live longer and produce more fertile offspring than those with smaller bodies. Evidence indicated that selection on body size might be influenced by environmental factors such as resource availability and competition and genetic variations in growth patterns (Allen et al. 2011, Beukeboom 2018). Sexual size dimorphism is a difference in body size between sexes within a species population. This phenomenon, demonstrated in numerous species of animals, particularly insects, manifests itself in various morphological characteristics, including wing size and shape (Stillwell et al. 2010, Allen et al. 2011). In Lepidoptera, dimorphic traits may play a role in reproductive activities; for example, wing size and shape can be chosen to minimize mate pursuing costs, resulting in improved performance in flight-based mating tactics (Wiklund 2003).

*Catocala abacta* and *C. brandti* occur in oak forest habitats (Alavi et al. 2019). As previously stated, Barbosa et al. (1989) suggest ecological factors such as habitat stability, resource persistence, convergence in plant chemical defenses, and phenological variability in bud-break are shaping the evolution of life-history traits such as flightlessness (a dimorphic state), overwintering larvae or eggs, larval dispersal by ballooning, polyphagy, and univoltinism in some species of forests-inhabiting Lepidoptera. Larval dispersal by ballooning and the ability of larvae to discriminate among leaves in search of high-quality resources must be associated with female flightlessness. However, while larval dispersal may result in higher mortality, female body size can increase to allocate much of females' larval energy and nutrients to eggs rather than wings and flight muscles. Such large-bodied short-lived females would be advantageous (Dixon 1972, Leather 1982), and some of them are significant defoliators of trees and are economically important (Barbosa et al. 1989).

According to a literature review by Stillwell et al. (2010), female-biased sexual size dimorphism was detected in 73% of 48 surveyed species, whereas only 6% of Lepidoptera species studied exhibited male-biased sexual size dimorphism (Stillwell et al. 2010). Female-biased sexual size dimorphism is a natural selection process that occurs due to resource allocation during the larval stage for future reproduction, though it may increase predation risk and decrease flight efficiency (Allen et al. 2011). The advantages of a large male size include an increased chance of success in the competition for mate access. However, it increases costs due to the large juvenile size and increased predation risk (Allen et al. 2011). *Catocala brandti* males exhibited larger fore- and hindwings than females, according to our findings (Fig. 4).

Besides mate competition, male-biased sexual size dimorphism may result from the high cost of producing offspring that requires adequate food during the larval period. However, male-biased sexual size dimorphism could also result from males having a longer larval period than females (Allen et al. 2011). Given that *C. abacta* and *C. brandti* coexist sympatrically in Iranian oak forests under similar

environmental conditions, males may consume different larval food plants or have longer larval periods (e.g., number of larval instars, as stated by Fischer & Fiedler 2001) than females, accounting for the male-biased sexual size dimorphism in *C. brandti*. Although these species' immature stages and feeding habits have not been described, they should feed on the leaves and twigs of *Quercus* plants (Fagaceae) with varying degrees of growth.

Males and females of *C. abacta* and *C. brandti* exhibited allometry on their fore- and hindwings (Table 3).

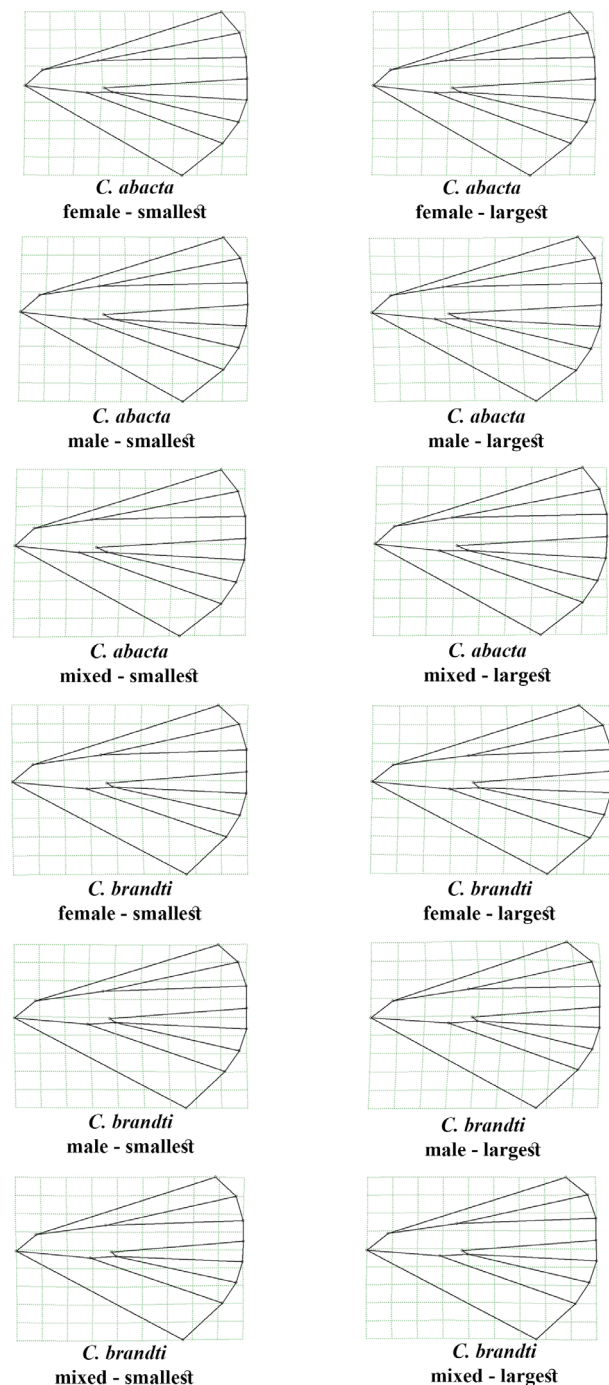


Figure 6. Visualization of allometric patterns in hindwings of *Catocala abacta* and *Catocala brandti* (non-significant in *C. brandti*, mixed sexes) using thin-plate splines.

Table 4. The effect of centroid size, species, and sex (and their interaction) on forewing shape in *Catocala abacta* and *Catocala brandti* was investigated using a three-way multivariate Procrustes ANOVA. The asterisk represents a significant difference.

	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>r</i> <sup>2</sup>	<i>F</i>	<i>Z</i>	<i>p</i> -value
Size	1	0.121309	0.121309	0.47616	199.7698	7.5235	1*10 <sup>-4*</sup>
Species	1	0.021810	0.021810	0.08561	35.9158	8.3147	1*10 <sup>-4*</sup>
Sex	1	0.020353	0.020353	0.07989	33.5171	8.6971	1*10 <sup>-4*</sup>
Size: Species	1	0.000326	0.000326	0.00128	0.5366	1.0798	0.1410
Size:Sex	1	0.001566	0.001566	0.00615	2.5787	4.3953	1*10 <sup>-4*</sup>
Species:Sex	1	0.000686	0.000686	0.00269	1.1295	2.6729	0.0027*
Size:Species:Sex	1	0.000667	0.000667	0.00262	1.0991	2.6200	0.0026*
Residuals	145	0.088050	0.000607	0.34561			
Total	152	0.254766					

Table 5. The effect of centroid size, species, and sex (and their interaction) on hindwing shape in *Catocala abacta* and *Catocala brandti* was investigated using a three-way multivariate Procrustes ANOVA. The asterisk represents a significant difference.

	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>r</i> <sup>2</sup>	<i>F</i>	<i>Z</i>	<i>p</i> -value
Size	1	0.112808	0.112808	0.44099	154.2759	7.0091	1*10 <sup>-4*</sup>
Species	1	0.027888	0.027888	0.10902	38.1398	7.9989	1*10 <sup>-4*</sup>
Sex	1	0.004246	0.004246	0.01660	5.8066	5.2241	1*10 <sup>-4*</sup>
Size: Species	1	0.000941	0.000941	0.00368	1.2864	2.3964	0.0082*
Size:Sex	1	0.001081	0.001081	0.00423	1.4789	2.6454	0.0030*
Species:Sex	1	0.000714	0.000714	0.00279	0.9771	1.8584	0.0319*
Size:Species:Sex	1	0.000638	0.000638	0.00249	0.8722	1.6257	0.0525
Residuals	147	0.107488	0.000731	0.42020			
Total	154	0.255804					

Geometric morphometrics was also used to visualize allometric relationship patterns (Figs. 5, 6). Additionally, shape differences persisted after the allometric effects of size variation were eliminated. This is consistent with previous research on sexual dimorphism in *Chilo suppressalis* Walker (Lep.: Crambidae), *Ectomyelois ceratoniae* (Zeller) (Lep.: Pyralidae), and *Cydia pomonella* (L.) (Lep.: Tortricidae), which indicates that significant shape differences between males and females persist even after size effects are removed (Zahiri et al. 2006, Mozaffarian et al. 2007, Khaghaninia et al. 2008).

Allometry had a small significant effect (2.1-17.6%) on shape changes in our study (Table 3), but it explained up to 60% of wing shape changes in some Sphingidae species (Camargo et al. 2015). Our findings indicate that the percentage of explained shape changes varied between males and females and did not follow a consistent pattern. According to the literature, sexual shape dimorphism in the wings of two *Catocala* species that was not explained by size could be associated with sexual selection, reproductivity advantages, and intersexual resource allocation (Dale et al. 2007, Camargo et al. 2015). Each sex engages in distinct activities and behaviors, which explains the shape dimorphism mentioned previously. Females search for egg-laying sites and nectar sources, while males search for perching and mating sites (Janzen 1984). These activities select various morphological requirements that affect flight behaviors. The two species studied in our research appear to use the forewings for courtship or some behavioral trait that is sexually dimorphic, putting evolutionary pressure on the forewings but not on the hindwings.

Strauss (1990) advocates for aerodynamic constrictions and the forewing's effect on flight efficiency. Females prefer rounded extremities and larger forewing areas, demonstrating greater maneuverability than males. On the other hand, males prefer more triangular forewings on their terminals with more straight edges to reduce friction with the air (Lockwood et al. 1998, Bowlin & Wikelski 2008). While this may result in a faster flight, males have less maneuverability than females. Evolution was selected for triangular wingtips for hexapods, avians, and bats to maximize energy efficiency during migration flight (Lockwood et al. 1998, Bowlin & Wikelski 2008, Marinello & Bernard 2014). Visualizing wing shape changes revealed that males and females of both *Catocala* species studied demonstrated forewings that followed the shape changes mentioned above (Fig. 2). However, in *C. brandti*, the males' larger wing size was a contrast pattern, implying their larger wing surface compensates for greater maneuverability.

The intersexual variation in morphology may affect dispersal, migration, and sexual selection. Additional male characteristics include nuptial flight, territoriality, and sexual selection, while females seek host plants for oviposition and feeding. (Dockx 2007, Johansson et al. 2009, Benítez et al. 2011). Our finding corroborates previous research demonstrating sexual dimorphism in the wings of Lepidoptera as a proxy character, implying that sexual selection may affect wing shape in ways that improve flight behavior and efficiency (DeVries et al. 2010). Nonetheless, additional research on the flight dynamics and adaptations of *C. abacta* and *C. brandti* is required.

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