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SEASONAL VARIATION AND SEXUAL SHAPE DIMORPHISM IN WINGS OF THE NEOTROPICAL HAIRSTREAK *STRYMON DAVARA* (LYCAENIDAE, THECLINAE, EUMAEINI)

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**ABSTRACT.** The northern valleys of the Atacama Desert in Chile have minimal seasonal variations of temperature, which enable continuous growth of many plants and their associated phytophagous insects. This is the case in the Neotropical hairstreak *Strymon davara* (Lepidoptera, Lycaenidae, Theclinae, Eumaeini), whose larvae are able to develop throughout the year on the inflorescences of their only host plant, *Alternanthera halimifolia* (Amaranthaceae). Although minimal, environmental seasonal variations could have some effect on the development of highly sensitive organisms. The first geometric morphometrics study of the wings of *S. davara* was intended to test for seasonal changes in the morphology. The same tools were used to assess for wing sexual dimorphism in this Neotropical hairstreak. Fifteen and 14 landmarks were selected on the fore and hindwings, respectively, of male and female adults collected in winter and summer in the Azapa Valley, northern Chile. The principal component analysis of wing shape shows that the variation was mainly distinguished by sexual dimorphism at the first dimension (PC1) and mostly by season at the second dimension (PC2). This variation might be a plastic response to subtle seasonal variation in environmental conditions and due to sexual niche divergence and behavior of male and female butterflies.

**Additional keywords:** Atacama Desert, geometric morphometrics, seasonality, shape variation, wing shape

The coastal valleys of northern Chile are very important reservoirs for biodiversity of the Atacama Desert, as suggested by data dealing with plants (Luebert & Pliscoff 2006), birds (Estades et al. 2007), mammals (Ossa et al. 2016) and insects (Vargas et al. 2016). This area has a tropical hyper-desertic bioclimate with mean annual precipitation of about 0 mm (Luebert & Pliscoff 2006), but the valleys harbor perennial or semi-perennial streams as a result of summer rains that occur on the high plateau and on the western slopes of the Andes, enabling the presence of native vegetation and its associated fauna (Vargas & Parra 2009). Seasonal variations of temperature are minimal in these valleys, enabling the continuous vegetative growth and flowering of several plants, which in turn enable the continuous reproduction of some associated insects that complete several generations each year (Storey-Palma et al. 2014). This is the case in *Strymon davara* (Stoll) (Lepidoptera, Lycaenidae, Theclinae, Eumaeini), a Neotropical hairstreak whose Chilean range is restricted to a few coastal valleys of the Atacama Desert (Peña & Ugarte 1996), where it is a monophagous species with larvae feeding only on inflorescences of *Alternanthera halimifolia* (Amaranthaceae) (Vargas & Duarte 2016).

Seasonal polyphenism in wing pattern has been described for many butterflies (Shapiro 1976), including some representatives of Eumaeini (Field 1967). These seasonal changes are mostly a result of

differences in photoperiod and/or temperature during larval or pupal development (Shapiro 1982, Kingsolver & Wiernasz 1991). Seasonal changes in wing pattern have been not described for the Chilean populations of *S. davara*. However, despite the minimal temporal variations in photoperiod and temperature in the coastal valleys of the Atacama Desert, the morphology of highly sensitive organisms could be affected seasonally, in the same way that morphological variations of natural populations have been described at a geographical scale as plastic responses to different



FIG. 1. Dorsal surface of wings of *Strymon davara*. Female (a) without a scent patch on forewing; male (b) with a scent patch on forewing.

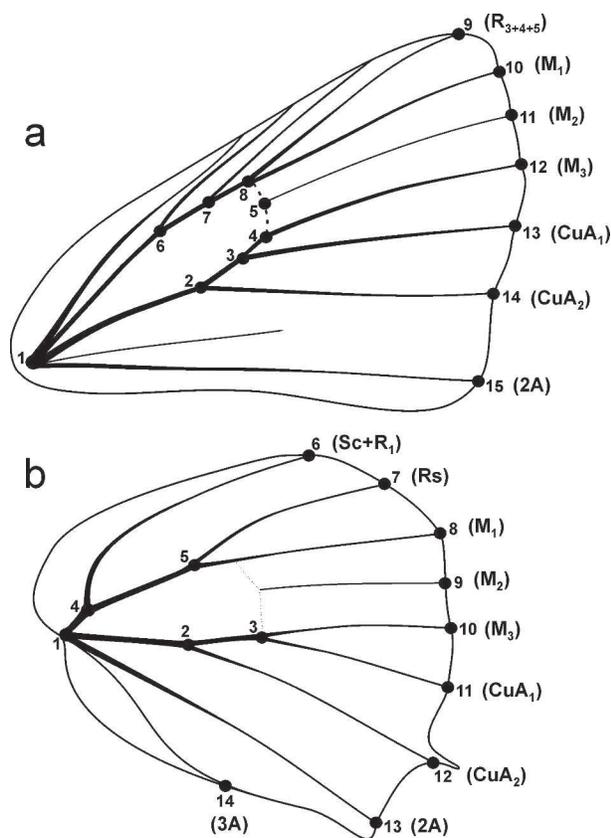


FIG. 2. Forewing (a) and hindwing (b) of *Strymon davara* showing landmarks (black circles) used in this study. In parenthesis the names of the veins of the respective landmarks.

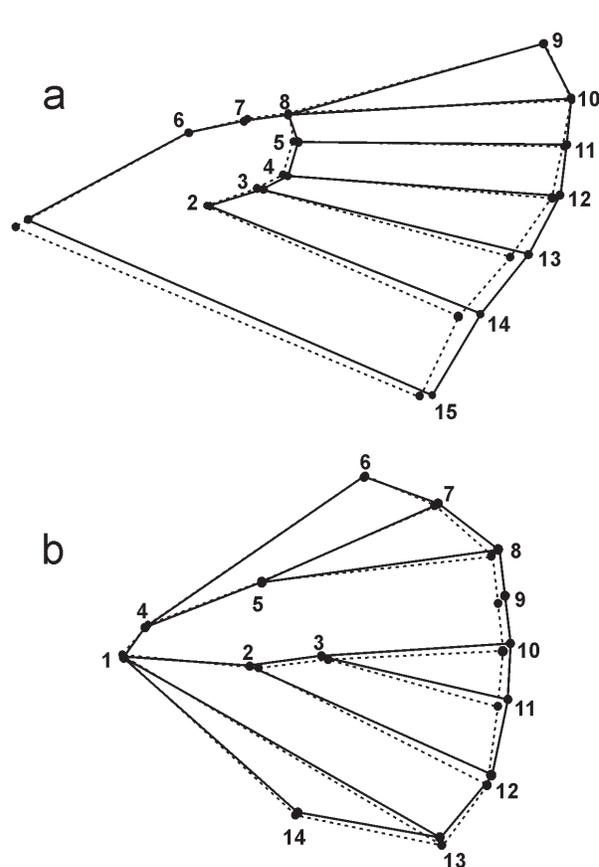


FIG. 3. Forewing (a) and hindwing (b) shape difference between sexes of *Strymon davara*. Female continuous line; male dotted line.

environmental conditions (Benítez et al. 2014, Alves et al. 2016). In the case of *S. davara* it remains unknown if its ability to develop throughout the year has some morphological consequence.

Wing pattern sexual dimorphism is variable between species of Eumaeini, with some extreme cases in which females and males have been described as different species (Robbins & Lamas 2008). Sexual selection and sexual niche divergence are recognized as two not mutually exclusive evolutionary processes underlying dimorphism in animals (Gallesi et al. 2015). In the case of *S. davara*, as described for many species of *Strymon* Hübner, males have a scent patch on the forewings and perch in mating territories (Robbins & Nicolay 2002), while females do not have a scent patch on the forewings and their flight is mostly related to the search for egg-laying sites and nectar sources (Fig. 1). However, despite these sharp morphological and behavioral differences, studies on wing sexual

dimorphism have not been performed for this hairstreak.

During the last few decades geometric morphometric analyses have become recognized as a highly efficient procedure to assess for subtle morphological differentiations between organisms (Jorge et al. 2011, Adams et al. 2013, Jeratthitikul et al. 2014, Costa et al. 2015, Lemic et al. 2016, Mikac et al. 2016, Zhong et al. 2016). In these analyses, shape information is extracted and the other components of variation in size, position and orientation can be removed, while taking care not to alter shape in any step of the procedure (Rohlf & Slice 1990, Goodall 1991, Dryden & Mardia 1998). The extra components of variation can be removed by rescaling the configurations to a standard size, shifting them to a standard position and rotating them to a standard orientation. Moreover, since none of the steps change the shape of the configurations, the variation after the procedure is the complete shape variation.

The aim of this study is to quantify wing shapes in *S. davara* using geometric morphometrics analyses to test whether there is seasonal wing shape variation and wing shape sexual dimorphism.

#### MATERIALS AND METHODS

##### Samples and data acquisition

Adults ( $n = 60$ ) of *S. davara* were collected with an entomological net in the Facultad de Ciencias Agronómicas of the Universidad de Tarapacá, located in the Azapa Valley ( $18^{\circ}31'15''S$ ,  $70^{\circ}10'42''W$ ), Arica Province, northern Chile, in July 2016 (winter) and January 2017 (summer). Thirty individuals (16 males, 14 females) were collected and analyzed in each season. The collected adults were immediately placed in vials with ethanol 95%. In the laboratory, with the aid of an Olympus SZ61 stereomicroscope, the wings were removed from the body of the adults, cleared with commercial NaClO for a few seconds, immersed in a series of increasing concentrations of ethanol until reaching 100%, and then slide mounted with Euparal®. All wings were photographed with a Micropublisher 3.3 RTV-QImaging (Q-imaging, Canada) digital camera attached to an Olympus SZ61 stereomicroscope. As the development of *S. flavaria* from egg to adult emergence is about one month, the maximum and minimum mean air temperatures of the month previous to the sampling were obtained from the Azapa Meteorological Station of the “Dirección General de Aguas”, Arica, in order to associate these values with the results of the morphometric analysis.

##### Geometric morphometric analysis

Fifteen and 14 (Fig. 2) landmarks for the fore and hindwings, respectively, were digitized using TpsDig ver. 2.29. All analyses were conducted with MorphoJ software ver. 1.06d. The landmark coordinates and their shape information were obtained after a Procrustes superimposition (Rohlf & Slice 1990, Dryden & Mardia 1998), which is a procedure that removes the information of size, position and orientation to standardize each specimen according to centroid size. A repetition of the procedure of landmarking and a Procrustes ANOVA was performed for the samples to calculate the measurement error comparing the values of the mean squares (MS) from the ANOVA between the Error 1 and Individuals.

The shape variation between seasonality and sexual dimorphism was analyzed using principal components analysis (PCA) and canonical variate analysis (CVA); the latter is a multivariate statistical method used to find the shape characters distinguishable among groups of specimens. The results were reported as Mahalanobis

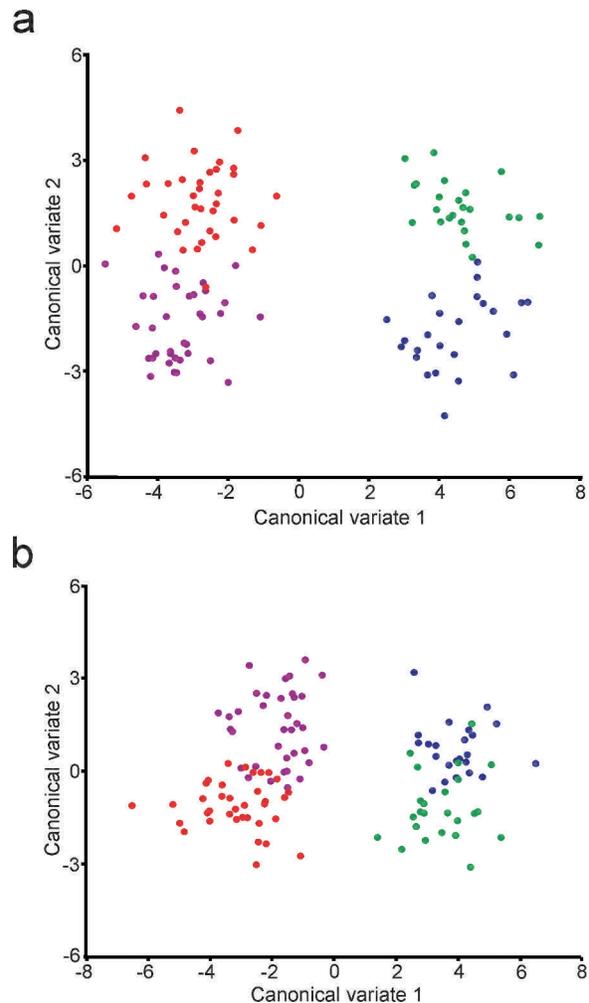


FIG. 4. Canonical Variate Analysis for forewing (a) and hindwing (b) of *Strymon davara*. Red: Female/Summer; Purple: Female/Winter; Green: Male/Summer; Blue: Male/Winter.

and Procrustes distances with their respective P values after permutation tests (10000 runs).

#### RESULTS

Procrustes ANOVA for assessing the measurement error showed that the mean square for individual variation exceeded the measurement error (MSerror: 0.0000026706 < MSindivxside: 0.0002135860).

The PCA showed that the first three PCs accounted for 68.04% (PC1: 44.84, PC2: 15.37, PC3: 7.83) of the shape variation of the forewings and 66.73% (PC1: 43.57, PC2: 14.04, PC3: 9.12) of the hindwings. Forewing differences between sexes were mainly found in veins  $CuA_1$ ,  $CuA_2$  and 2A (landmarks 13, 14 and 15, respectively) (Fig. 3a). It seems that veins  $CuA_1$  and  $CuA_2$  are shorter in males than in females. Vein 2A

TABLE 1. Mahalanobis and Procrustes distances between seasons and sexes in *Strymon davara*.

	Mahalanobis distances						Procrustes distances					
	Forewing groups			Hindwing groups			Forewing groups			Hindwing groups		
	F,S	F,W	M,S	F,S	F,W	M,S	F,S	F,W	M,S	F,S	F,W	M,S
<b>F,W</b>	<b>3.8750°</b>			<b>3,0009°</b>			<b>0.0170°</b>			<b>0.0220°</b>		
<b>M,S</b>	7.6687**	8.6675**		6.7576**	5.9214**		0.0347**	0.0414**		0.0509**	0.0389**	
<b>M,W</b>	8.1672**	8.0290**	<b>4.2118°</b>	7.3761**	6.0625**	<b>2.7499°</b>	0.0347**	0.0363**	<b>0.0152°</b>	0.0493**	0.0354**	<b>0.0158°</b>

\*\*\* =  $p < 0.0001$ ; \*\* =  $p : 0.0001$ ; ° =  $p : 0.0126$ . F: female; M: male; S: summer; W: winter.

apparently does not change in length, although it does in position, since in males it is slightly displaced to the posterior margin. The differences in hindwings between sexes were mainly in  $M_1$ ,  $M_2$ ,  $M_3$ ,  $CuA_1$ ,  $CuA_2$  and 2A (landmarks 8, 9, 10, 11, 12 and 13, respectively) (Fig. 3b). In male hindwings, the ends of veins  $M_1$ ,  $M_2$ ,  $M_3$  and  $CuA_1$  are slightly shorter than in female hindwings. Vein 2A is longer in males, and the origins of veins  $CuA_1$  and  $CuA_2$  are slightly displaced towards the distal margin of the wing, causing a slight modification in the discal cell margin.

The canonical variate analysis (Fig. 4) showed sexual dimorphism and seasonal changes for the fore and hindwings of *S. davara*. Fore and hindwing differences between sexual dimorphism and seasons were also clearly distinguished using Mahalanobis and Procrustes distances (Table 1).

The Procrustes ANOVA for centroid size did not show significant differences by seasonality and sexual dimorphism, opposed to the shape where the differences were clearly significant between sex and season (Table 2).

For forewings, the discriminant function analysis between means of seasons (Fig. 5a) showed that the Procrustes distance was 0.0154 ( $p < 0.0001$ ) and the Mahalanobis distance was 3.5815 ( $p < 0.0001$ ); between means of sexes the Procrustes distance was 0.0351 ( $p < 0.0001$ ) and the Mahalanobis distance was 7.6484 ( $p < 0.0001$ ). For hindwings, the discriminant function analysis between means of seasons (Fig. 5b)

showed that the Procrustes distance was 0.0154 ( $p = 0.001$ ) and the Mahalanobis distance was 2.3530 ( $p < 0.0001$ ); and between means of sexes the Procrustes distance was 0.0419 ( $p < 0.0001$ ) and the Mahalanobis distance was 6.0127 ( $p < 0.0001$ ).

#### DISCUSSION

Although variation in wing pattern and genitalia are sometimes quantified in eumaeine butterflies (Robbins 1990), wing shape variation has not been quantified in any lycaenid species anywhere. This is the first study of a tropical lycaenid (*S. davara*) analyzing the wing shape correlated with ecological patterns using geometric morphometrics. Our results enabled us to detect sexual dimorphism and seasonal plasticity in the wings of this hairstreak.

Wing sexual shape dimorphism has been recently studied using geometric morphometrics in Lepidoptera (Hernández et al. 2010, Benítez et al. 2011, Sanzana et al. 2013), Diptera (Bonduriansky 2006, Gidaszewski et al. 2009) and Hymenoptera (Pretorius et al. 2005, Bonduriansky 2006, Gidaszewski et al. 2009, Hernández et al. 2010). The shape analyses were valuable to detect the sexual shape dimorphism in the wings of *S. davara*, giving support to previous studies using Lepidoptera wings as a proxy of sexual dimorphism (Benítez et al. 2011, Sanzana et al. 2013, Hernández et al. 2010, de Camargo et al. 2015). Sexual dimorphism in insect wings has been mostly associated with sexual selection and sexual niche divergence, these

TABLE 2. Procrustes ANOVA for centroid size (Size) and shape in *Strymon davara*.

	Forewing size		Hindwing size		Forewing shape		Hindwing shape	
	F	P(param.)	F	P(param.)	F	P(param.)	F	P(param.)
<b>Sex</b>	0.31	0.5770	0	0.9623	40.60	< 0.0001	29.73	< 0.0001
<b>Season</b>	0.01	0.9129	0.11	0.7387	8.01	< 0.0001	4.17	< 0.0001
<b>Individual</b>	119.7	< 0.0001	205.54	< 0.0001	3.54	< 0.0001	5.67	< 0.0001

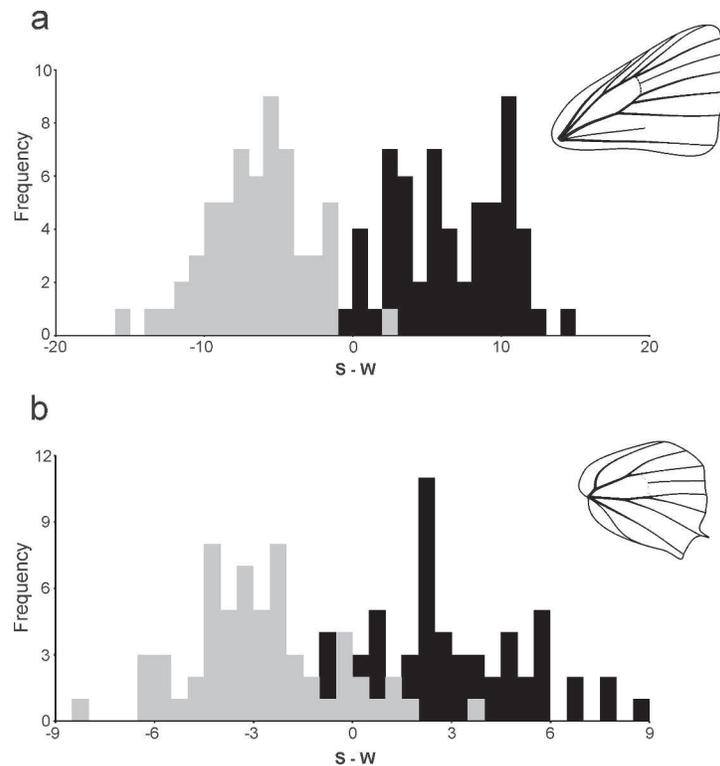


FIG. 5. Discriminant function analysis between means of seasons for forewing (a) and hindwing (b) of *Strymon davara*. S: summer; W: winter.

not being mutually exclusive evolutionary processes (Galesi et al. 2015). Based on our still insufficient knowledge of the natural history of *S. davara*, it appears that sexual niche divergence can be suggested as an underlying cause of the wing sexual dimorphism in this hairstreak, because the flight of males is mostly related to the search for perching sites and females for mating, while the flight of females is mostly related to the search for egg-laying sites and nectar sources (Robbins & Nicolay 2002, Vargas & Duarte 2016).

It is well known that larval development is regularly influenced by stress imposed by seasonality and several other environmental stressors simultaneously (Stoks et al. 2008, Galesi et al. 2016), and that environmental changes could activate morphological adaptations, generating polymorphism or seasonal polyphenism, in which different phenotypes predominate at different times of the season (Shapiro 1976, Nijhout 2003, Galesi et al. 2016). Interestingly, it is known that the wing morphology of butterflies and moths can be affected by host plant use (Jorge et al. 2011, Benítez et al. 2015). However, as mentioned above, *S. davara* is a monophagous butterfly in the study site, with larvae feeding exclusively on inflorescences of *A. halimifolia*, which produces inflorescences throughout the year (Vargas & Duarte 2016). Accordingly, the use of an

alternate host as the underlying cause of the difference in shape between seasons can be ruled out for this hairstreak. In the month previous to the winter sampling the maximum and minimum mean temperatures were 20.2 and 14.8 °C, respectively, while these were 28.0 and 16.6 °C in the month previous to the summer sampling. It is thus probable that the seasonal wing shape change could be associated with the changes in maximum and minimum mean temperatures between winter and summer, in the same way that climatic differences produce different morphological patterns in isolated populations of several insects (Sanzana et al. 2013, Benítez et al. 2014, Alves et al. 2016, Benítez & Vargas 2017). However, this statement must be assessed in further studies under controlled laboratory conditions, ideally including rearing at different temperatures and variations in other environmental conditions, such as photoperiod.

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