



Contents lists available at ScienceDirect

Arthropod Structure & Development

journal homepage: www.elsevier.com/locate/asd

Head shape variation in cerambycid saproxylic beetles as a function of host plant selection

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ARTICLE INFO

Article history:

Received 22 May 2017
 Received in revised form
 7 November 2017
 Accepted 16 November 2017
 Available online xxx

Keywords:

Head shape
 Saproxylic beetles
 Host plant species
 Geometric morphometrics

ABSTRACT

Saproxylic insects depend on deadwood for larval development, and a certain degree of specialization may be involved in their choice of host plants and/or wood in a particular stage of degradation. The plant species chosen for oviposition in turn act as an environmental pressure on the head morphology of larvae and it is expected that head shape plasticity varies directly with the number of woody plant species used for larval development in each insect species. We analyzed head shape variation in saproxylic beetles with respect to host plant species, maximum time of larval emergence and season of the year when insects colonized branches. Generalist species in the use of host plants showed significant variation in head shape and size. Time of emergence and season did not appear to affect head shape, although season was a determinant factor of abundance and possibly head size variation.

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1. Introduction

Insect specialization in the use of plant resources for larval development or for food has been interpreted as one strategy for reducing competition (Janzen, 1980). Many insect orders are dependent on dead wood during larval development (Grove, 2002), and some of these xylophagous species show a degree of specialization in their choice of host plants, wood decay conditions or oviposition season (Jaenike, 1990, 1978; Saint-Germain et al., 2007). The preference-performance hypothesis proposes that ovipositing females select host plants that maximize larval performance and survival in order to minimize the effect of density-dependent competition (Jaenike, 1990). The probability of encountering a mate could be higher when adult individuals choose the same host plants, where encounters with conspecifics are most likely, but larval competition could also be higher if different couples use the same resources for their larvae (Colwell, 1986). In this context, broad diets decrease larval density on a given host plant and thereby increase offspring survival and performance. Even so, mating probabilities could be lower if females search for mates and oviposit on underutilized hosts (Rauscher, 1984).

Among xylophagous insects, most cerambycid insects present different specialization strategies, occupying different host plant species and snag ages or colonizing branches in different seasons (Berkov and Tavakilian, 1999). The highest adult abundances in tropical dry forest occur during the rainy season (Noguera et al., 2002; Toledo et al., 2002), when the most abundant species are generalist in the use of host plants, whereas more specialist species could be present during the dry season (Paro et al., 2012; Noguera et al., 2002). Also, cerambycid larvae were found to have a low occurrence in the first stages of wood degradation but a high occurrence in the mid to late stages when nitrogen levels and the water holding capacity of wood increase (Saint-Germain et al., 2007).

Insect preference for woody host plants can be accompanied by morphological specializations for the exploitation of sapwood (Jarman and Reyes-Castillo, 1985; Lobo and Castillo, 1997; Moreno-Fonseca and Amat-García, 2016). For example, among some species of Passalid beetles, differences in body shape and tibiae are related to their exploitation of different tissues inside dead branches (Lobo and Castillo, 1997; Moreno-Fonseca and Amat-García, 2016). In larvae of cerambycid species and other xylophagous beetles, mandibles are appendages used to break down wood and are usually short and heavily sclerotized, especially along the medial margin where the strength of the jaws seems to be due to the presence of zinc and manganese (Morgan et al., 2003). Larvae

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generally attack sapwood and have chisel-shaped mandibles, allowing them to dig more than what they ingest and to produce a fine frass mixed with feces. Also, larvae possess corporal modifications for living in galleries within wood, for example, a nearly prognathous head immersed into the prothorax cavity and integumental, corrugated and thickened plates on the surfaces of the thorax and the abdomen (Chiappini and Aldini, 2011).

The diversity in resources supplies during the development of insects had an effect on the larval morphology inside species and this capacity determines the presence of species in changing environments and communities (Berg and Ellers, 2010; Lunardi et al., 2017). Also, the phenotypic plasticity in larval morphology has been suggested as a necessary condition for the inclusion of different host plants during the development of insects (Leclaire and Brandl, 1994). In this sense changing environments represent a good scenario to describe the plasticity in functional morphology in generalist versus specialist in the use of a particular resource, as the host plants in saproxylic beetles.

Changes in the composition of woody plants in tropical dry forest (Pennington et al., 2009) could represent a selective pressure for saproxylic beetles, especially if these changes reduce the abundance of their most suitable woody plants. Seasonal changes in beetle abundances and preferences for a range of host plants suggest that a single species can differentially exploit available branches and, therefore, that head morphology is variable enough to allow different substrates to be exploited. We analyze the morphological head variation of four species of saproxylic beetles (Cerambycidae) according to their maximum time of larval development within five different species of host plants that were experimentally provided for oviposition during the dry and the rainy seasons.

We test the hypothesis that two plastic traits (head shape and size variation) within species is related to the number of host plants used by insects, season (rainy/dry) in which insects colonize plants and time spent in branches. We expect that 1) head shape variation among species is directly correlated with the range of utilized host plants and that 2) maximum time of larval growth and season of branch colonization have significant effects on head shape variation. To test these hypotheses, we compare head shape in four saproxylic cerambycid species, three Acanthocinini species (*Eutrichillus comus*, *Lagocheirus obsoletus* and *Mecotetartus antennatus*) and one Elaphidiini species (*Sphaenothecus trilineatus*) in relation to their host plants. Also, we evaluate covariation in head shape and size with respect to the maximum time of emergence of insects, which is used as an indicator of larval growth in branches, in addition to the number of utilized host plants and the season of the year during which branches were colonized.

2. Materials and methods

2.1. Study area

The present study was performed in the tropical dry forest of San Andrés de la Cal, Tepoztlán, Morelos, Mexico (18°57'22.2"W, 99°06'50.2"N, 1495 m a.s.l.). This forest is located in the lowest-lying area of the protected area "corredor biológico Chichinautzin" (Chichinautzin Biological Corridor). At the study site, mean temperature ranges from 12 °C to 18 °C, and annual mean precipitation is 1098 mm (Ruíz-Rivera, 2001). The tropical dry forest of the study area is composed of at least 42 tree species, including the following dominant species: *Sapium macrocarpum* Müll. Arg. (18.4% of individual trees), *Bursera fagaroides* (Kunth) Engl. (14.8%), *Bursera glabrifolia* (Kunth) Engl. (11.0%), *Ipomoea pauciflora* M. Martens & Galeotti (9.8%), *Conzattia multiflora* (B.L. Rob.) Standl. (6.5%), *Ipomoea murucoides* Roem. & Schult. (5.7%),

Bursera copallifera (DC.) Bullock (2.6%) and *Lysiloma acapulcense* (Kunth) Benth. (2.4%) (Vergara-Torres et al., 2010). We studied specimens of the four most abundant saproxylic beetle species (Cerambycidae) that emerged from deadwood in a field experiment on Cerambycidae plant preferences (Table 1). In this experiment, branches of *B. fagaroides*, *S. macrocarpum*, *C. multiflora*, *I. murucoides*, *L. acapulcense* and *B. copallifera* were cut every 2 months (from December 2016 to December 2017) and exposed during two months to environmental conditions on the forest floor to allow beetle colonization. Then, these branches were collected and isolated with mesh barriers, and the insects that emerged from branches in the laboratory were recorded. This procedure was performed on branches cut during the rainy (May–November) and the dry seasons (December–April).

2.2. Morphometric data

Morphometric data were measured for a sample of 120 individuals (Table 1) collected from the previously described material. Digital photographs of the frontal view of insects' heads were taken using a Leica Z16 APO A stereo microscope in the installations of the Entomological Collection of the Autonomous University of Morelos (Universidad Autónoma del Estado de Morelos; Cuernavaca, Mexico). Images were saved in high-resolution (150 dpi) TIF format.

Two-dimensional landmark configurations were established for the images of individual specimens in order to subsequently describe the head shape variation for each species (Table 1). Landmarks were placed at the right side of the head (based on 293 photographs) using the software TpsDig 2.12 (Rohlf, 2008). To select the number and position of landmarks (landmark configurations), we performed a repeatability test, digitalizing the same set of landmarks on a sample of 5 specimens (8 times per individual) per species. A landmark configuration was only accepted if the variance ratio among specimens and the total sample was less than or equal to 0.05 (Pizzo et al., 2006a,b). We selected a configuration with 12 landmarks (variance ratio = 0.033) to describe head shape and 20 semilandmarks to describe eye contour (Fig. 1). Semilandmarks were set using guides drawn in the software Make Fan 8 (Sheets, 2008) and were then digitized in TpsDig2.12 (Rohlf, 2008).

A protocol for the analysis of geometric morphometric data was implemented to study head shape variation using routines in the Geomorph library (Adams et al., 2016) of the statistical platform R 3.3.1 (R Development Core Team, 2016). First, individual differences in landmark configurations resulting from orientation, position and size of specimens were removed by superimposing the configurations using a generalized Procrustes analysis (Adams et al., 2016).

Table 1

Number of individuals of the four beetle species used for morphometric analysis. For each beetle species, the plant species where their larvae grew and the season when they emerged are shown.

Beetle species	Plants species	Season		Total sample
		Rainy (n)	Dry (n)	
<i>Eutrichillus comus</i>	<i>Bursera fagaroides</i>	3	1	4
	<i>Sapium macrocarpum</i>	–	14	14
	<i>Conzattia multiflora</i>	1	14	15
	<i>Ipomoea murucoides</i>	–	6	6
<i>Lagocheirus obsoletus</i>	<i>Bursera fagaroides</i>	10	13	26
	<i>Sapium macrocarpum</i>	5	8	13
<i>Mecotetartus antennatus</i>	<i>Bursera fagaroides</i>	–	11	11
	<i>Bursera copallifera</i>	4	24	28
<i>Sphaenothecus trilineatus</i>	<i>Lysiloma acapulcense</i>	1	23	24
	<i>Conzattia multiflora</i>	14	1	15

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