A revised classification scheme for larval hesperiid shelters, with comments on shelter diversity in the Pyrginae.

Harold F. Greeney
Yanayacu Biological Station & Center for Creative Studies, Cosanga, Ecuador c/o Foch 721 y Amazonas, Quito, Ecuador.
revmmoss@yahoo.com

Abstract. The construction of larval leaf-shelters is a ubiquitous yet poorly understood behavior within the Hesperiidae. Most life history papers treating this family fail to describe this aspect of larval behavior in detail, despite its potential usefulness for comparative ecological and phylogenetic studies. Here, using 15 years of experience rearing Neotropical skippers, I present a means of describing the five basic types of shelters built by hesperiids. In addition, I provide a preliminary look at the distribution of these types within the subfamily Pyrginae and discuss ideas for informative areas of future research.

Key words: behavior, Hesperiidae, larval shelter, leaf-shelter, shelter architecture, shelter construction

Introduction

The construction of leaf shelters by exophytic lepidopteran larvae is a widespread phenomenon within the order (DeVries, 1987, 1997; Frost, 1959; Scoble, 1992; Stehr, 1987). A few studies have examined the process of shelter construction (Fitzgerald *et al.*, 1991; Fitzgerald & Clark, 1994; Fraenkel & Fallil, 1981; Rensch, 1965), while others have investigated the ecological forces which shape the evolution of this remarkable life history trait and its associated behaviors (but see Eubanks *et al.*, 1997; Henson, 1958; Jones, 1999; Jones *et al.*, 2002; Loeffler, 1996; Ruehlmann *et al.*, 1988; Sagers, 1992; Sandberg & Berenbaum, 1989; Weiss, 2003). The construction of most lepidopteran larval shelters is accomplished primarily by harnessing the forces generated by axial retraction of stretched and wetted silk (Fitzgerald *et al.*, 1991) and frequently, particularly in the Hesperiidae, the substrate is further modified during the process by cutting (e.g., Fitzgerald & Clark, 1994; Greeney & Chicaiza, 2008; Greeney & Jones, 2003; Ide, 2004; Weiss *et al.*, 2003).

The globally distributed (with the exception of New Zealand and Antartica) family Hesperiidae includes species whose larvae roll, cut, fold, and tie portions of their foodplant into a diverse array of shelter types (Greeney and Jones 2003). In fact, the remarkable radiation of shelter architectures found within this family, ranging from simple leaf rolls to complex, origami-like tents, rivals the architectural diversity of the entire rest of the Lepidoptera. Despite this, and though natural historians have remarked upon these incredible structures for more than 100 years (e.g., Moss, 1949; Scudder, 1889; Young, 1985), only recently have they received more detailed attention (e.g., Greeney & Warren, 2003, 2004, 2008a, 2008b; Lind *et al.*, 2001; Weiss *et al.*, 2003).

Within the Hesperiidae, shelter architecture varies greatly between genera and even between larval instars (e.g., Greeney & Warren, 2004; Lind *et al.*, 2001), yet within a species the process is stereotyped (e.g., Weiss *et al.*, 2003), and various aspects of basic shelter form and ontogenetic changes in shelter style, in combination with foodplant use, vary predictably between genera, and are often useful characters for identifying larvae in the field (Greeney & Jones, 2003; Moss, 1949). While the key to hesperiid larval shelter types provided by Greeney and Jones (2003) provides us with a useful beginning, our understanding of evolutionary patterns of shelter architecture remains in its infancy. In particular, we lack a detailed understanding of which characters may prove to be phylogenetically informative. Here I supplement the observations of Greeney and Jones (2003) with further observations from throughout the Americas, as well as published descriptions in the literature.

Materials and methods

In addition to reviewing published literature for hesperiid shelter descriptions, I made observations on the larval shelter building behavior of hesperiids in a variety of habitats, in various localities, in the United States, Mexico, Costa Rica, and Ecuador. In order to

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avoid potential laboratory artifacts affecting shelter construction, I include only observations made in the field or from photographs taken *in situ*. Whenever possible, I reared examples of all species observed through adult eclosion and identified them with the help of G. T. Austin and A. D. Warren. For many species, however, I was unable to attain an adult. For these, using 15 years of experience rearing hesperiid larvae, plus online photographs provided by sites such as Dyer and Gentry (2002), Dyer *et al.* (2005), and Janzen and Hallwachs (2006), I identified all larvae to subfamily, and many to genus. For discussions of shelter construction and form I have used terminology presented by Greeney and Jones (2003).

Results

Modifications to Greeney and Jones (2003). After careful consideration of the characters used to construct the dichotomous key to basic shelter types (Greeney & Jones, 2003), and extensive observations on the process of shelter construction, I have modified the existing key in the following ways (see Appendix A).

First, the three final shelter types given by Greeney and Jones (2003) (Types 8-10) are lumped as one shelter type, unified by the use of two major cuts (Greeney & Jones, 2003) in their basic construction. After watching numerous species construct two-cut shelters, it appears that the location of cut initiation (either on the same or opposite sides of the leaf mid-vein) depends, to a great extent, on the morphology of the leaf. For example, a larva on a thin grass blade, which is scarcely broader than the larva itself, has little choice but to initiate cuts on opposite sides of the leaf blade. For this reason I have chosen to lump "Type 8, two-cut folds" under a general two-cut shelter type (Appendix A). Second, the degree to which the distal portions of the two major cuts converge alters the shape of the shelter lid (the resulting folded-over flap). With some experience, the shape of the lid may be a useful character for separating species or genera in the field, but is variable and generally does not include quantifiable parameters. For this reason I have eliminated the "Type 9, unstemmed fold" and "Type 10, stemmed fold" shelter types from the classification of Greeney and Jones (2003), placing them under the broader heading of two-cut shelters (Appendix A).

The third change to the classification of Greeney and Jones (2003), recently discussed by Greeney and Sheldon (2008), is the unification of "Type 3, multi-leaf shelters" and "Type 4, two-leaf shelters." During construction of a shelter involving more than one leaf, in all species that I have observed, the larva rears back onto its prolegs, waving its thorax and head about until it comes in contact with another usable object. Silk is then spun between this object and the leaf on which the larva is resting. In the field this object is most often another leaf or leaflet of the food plant, but is occasionally another part of the same plant (ie. stem, flower), parts of an adjacent non-food plant, or even nearby detritus. Similar observations by other authors, in the field and in the lab, suggest this is a widespread method of shelter construction (eg., Atkins, 1987; Clark, 1936; Jones, 1999; Scudder, 1889; Williams & Atkins, 1997; Young, 1993). As silk is deposited, and portions of the plant are drawn together, other foliage is often incidentally brought closer as well. As the larva flails its head about it subsequently comes in contact with this newly-reachable foliage and incorporates it into the shelter. Similarly, due to the morphology of certain food plants, one cannot move a single leaf or leaflet without displacing several. Thus, what may have been initiated as a two-leaf pocket, often incidentally or superficially involves several leaves. For most species that I have observed that build shelters involving more than one leaf, even the same individual, forced to build several shelters in a row, may switch between the previously defined "Type 3" and "Type 4" shelters. Thus, if they include two or more leaves, it is prudent to lump both "two-leaf pockets" and "multi-leaf pockets" under a single category of multi-leaf shelters.

The fourth major change to the previous classification is to include "Type 7, one-cut slide" with "Type 6, one-cut fold" shelters. I have not seen a second example of a one-cut slide shelter, even within the same species (unknown Pyrginae), and separation of the two types is unwarranted. The penultimate alteration is to eliminate "Type 1, rudimentary shelter" from the classification scheme. Few authors have mentioned species which apparently do not build shelters (e.g., Scudder, 1889; Moss, 1949), and my own observations suggest that even these may have been in error: the observed larvae were simply in-between shelters or feeding away from their shelters at the time of observation. In any case, if non-shelter building species are rigorously documented in the future, there seems little reason to call them anything other than "non-shelter builders!"

Lastly, Greeney and Jones (2003) divided all shelter types into three "groups" based on the number of cuts involved. This is a superfluous division and should be eliminated.

Diversity of shelter types in the Pyrginae. The pyrgines show by far the greatest diversity both in basic shelter form as well as types and combinations of post-construction modifications. In fact, even in my limited sampling, I have found that all major proposed shelter types are built by species of Pyrginae. Here, though there are still many groups un-sampled, I discuss the pyrgine genera which I have observed to build each shelter type, and briefly comment on their behaviors and modifications.

Type 1, no-cut shelters. This is perhaps the least common shelter type built by pyrgines. In a single species of *Aguna* feeding on *Bauhinia* (Leguminaceae), which I have worked with in eastern Ecuador, later instars fold an entire leaf in half along the midvein, slowly eating their shelter away from the edges as they grow. Early instars simply move into the middle of the two halves of new leaves, while they are still folded, thus avoiding the difficulty of having to manipulate large portions of the leaf. Generally only a few lines of securing silk are needed to maintain the young leaves in their folded position. With the exception of this species, however, most pyrgine Type 1 shelters I have observed are built during later instars. Examples include *Astraptes, Epargyreus, Polygonus, Proteides, Carrhenes,* and several species included in or related to the genus *Mylon.* Middle instars of *Epargyreus clarus* (Jones, 1999; Lind *et al.*, 2001) often roll the margin of the leaf into a tube without making any cuts. This type of cut often ontogenetically precedes Type 2 multi-leafed shelters in the final instars of the genera mentioned above. These tube-like shelters are sometimes modified with secondary cuts that allow the larva to seal one end of the tube.

Type 2, multi-leaf shelters. This shelter type is commonly seen in later instars of a variety of pyrgine genera including *Achlyodes, Antigonus, Astraptes, Bolla, Capila, Dyscophellus, Eantis, Epargyreus, Eracon, Erynnis, Gesta, Grais, Narcosius, Ocyba, Phocides, Polygonus, Polythrix, Ridens, Tagiades, Theagenes,* and *Urbanus.* It is perhaps the most commonly observed shelter type within the group, but seems confined to later instars. Often, as was the case for an unknown pyrgine feeding on a bipinnate legume in Amazonian Ecuador, the leaves of the host plant are too small to build a shelter of any other type. The larva is forced to draw multiple leaves or leaflets together until there is sufficient vegetation to hide it from view. As I have observed in *Epargyreus clarus* feeding on *Robinia* (Leguminaceae) and in an unknown *Urbanus* feeding on *Desmodium* (Leguminaceae) the small leaflets of the host are quickly outgrown by later instar larvae, and more than one must be used to cover the larva.

Type 3, center-cut shelters. Unlike the ubiquitous use of this shelter by early instars of the Pyrrhopyginae (e.g., Burns & Janzen, 2001), there are relatively few genera of pyrgines which build this shelter type. They include *Atarnes, Bolla, Capila,* and *Noctuana,* as well as several genera which I have been unable identify. The use of this type of shelter may reveal a great deal about the ecology and evolution of these taxa, as it appears to have arisen multiple times within the subfamily, and is built by species feeding on a wide variety of plants.

Type 4, one-cut shelters. One-cut shelters are seen in a small number of pyrgines including *Quadrus, Pythonides,* and *Systasea.* They are also built occasionally by middle instars of *Astraptes* and by several species related to (or members of) *Carrhenes, Pyrgus,* and *Mylon.*

Type 5, two-cut shelters. This is one of the most common and variable shelter types seen in both early and late instar pyrgines, and often includes post-construction modifications along with a wide diversity of primary cut patterns. Type 5 shelters are built by species of *Achlyodes, Astraptes, Atarnes, Bibasis, Bolla, Bungalotis, Capila, Celaenorhinnus, Cephise, Chrysoplectrum, Coladenia, Drephalys, Dyscophellus, Eantis, Entheus, Epargyreus, Eracon, Hesperopsis, Morvina, Mylon, Nascus, Phocides, Plumbago, Polythrix, Sostrata, Tagiades, Telemiades, Theagenes, Udranomia, Urbanus,* and *Xenophanes.* The shelter lids, or excised portions of the leaf, created during construction of this shelter type vary considerably in shape. They range from nearly round to square, rectangular, or triangular. Subsequently, most are modified in some way by scoring, notching, or perforating, giving the interested natural historian a rich array of characters to choose from when comparing shelters built by various species.

Discussion

While the details of shelter architecture and the plethora of subsequent modifications to the basic form would allow for a great expansion of the shelter key provided by Greeney and Jones (2003), its utility is best enhanced by reducing it down to the most basic types. These can be applied to describing ontogenetic changes in shelter type between instars (e.g., Greeney & Warren, 2004; Lind *et al.*, 2001) as well as describing broader patterns between taxa. Modifications to these few basic types, such as perforations, channels, and notching (e.g., Greeney & Jones, 2003; Greeney & Young, 2006; Young, 1991), as well as ontogenetic changes in basic shelter types (e.g., Graham, 1988; Greeney & Warren, 2004; Lind *et al.*, 2001; Miller, 1990), can then be used as additional phylogenetic characters. As recently pointed out by Greeney and Sheldon (2008), the "devil is in the details," and even superficially similar shelters may prove to be formed by different architectural innovations which are only obvious when the detailed behaviors of shelter construction are described (e.g., Weiss *et al.*, 2003).

Behavioral and natural history characters are

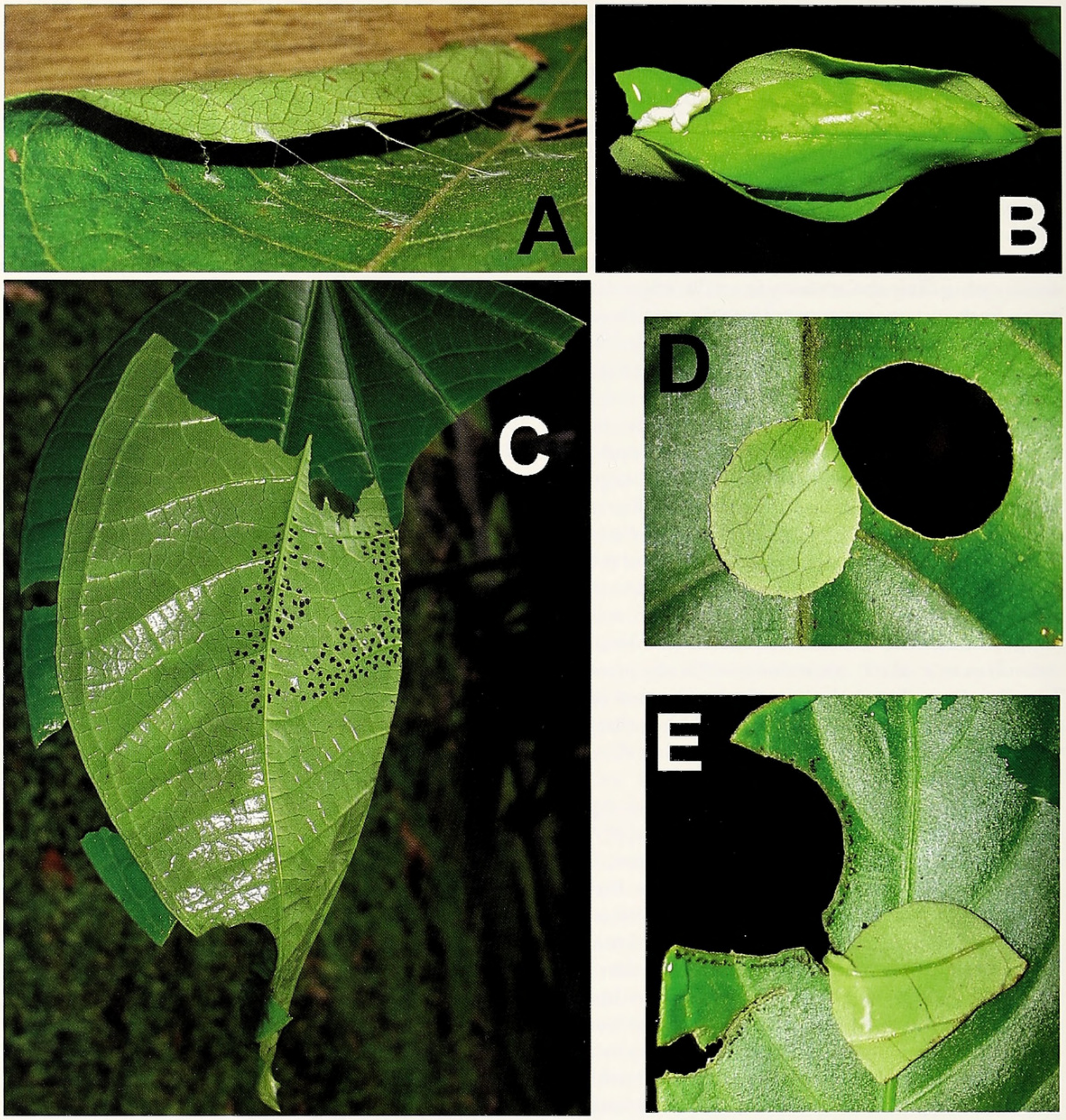

Figure 1. Photographs of the five proposed basic shelter architectures built by hesperiid larvae. **a)** Type 1 shelter built by late instar *Astraptes sp.* **b)** Type 2 shelter built by late instar *Polygonus sp.* **c)** Type 4 shelter built by late instar *Quadrus sp.* **d)** Type 3 shelter built by early instar pyrrhopygine **e)** Type 5 shelter built by early instar *Celaenorhinnus sp.*

frequently used to create and test phylogenetic hypotheses in a variety of taxa (e.g., Hennig, 1966; Lanyon, 1988; Zyskowski & Prum, 1999). Perhaps one of the most useful phylogenetic characters that can be derived from larval shelters is the ontogenetic change in shelter types. The sequence of shelter types built during larval development can be ascertained from most thorough life history papers which take the time to describe shelter ontogeny (e.g., Greeney & Warren, 2008a, 2008b). As an example, the character state for *Noctuana haematospila* would be 3,3,5 according to Greeney and Warren (2004). This, however, provides us only with a single, unordered character. More useful would be five characters derived from the type of shelter built by each instar. As various instars of many species often remain in the shelter built during the previous instar (e.g., Atkins, 1975, 1987, 1988; Greeney & Warren, 2008a, 2008b), these characters are unavailable for the majority of species. From my own experience with several species, procuring these data can be time consuming and frustrating. When removed from their shelter, larvae often wander a great deal before building another. In addition they may take several hours to construct a new home. In the field then, if one does not follow each larva until they at least begin construction, they may be difficult to relocate once you have released them. Anyone with the means to carry out such studies can greatly advance our understanding of shelter building for even the most common species.

In a few species for which I have made careful observations, the ontogenetic switch between shelter types may occur sometime during the middle of the instar. For example, a recently molted fourth instar *Pyrrhopyge papius* will build a Type 5 shelter. When removed from its shelter late in fourth instar, however, it will build a Type 2 shelter (unpublished data). Thus it is important to carefully note the exact stage of development before performing experiments. This type of mid-stadia switch in shelter construction, however, would be an informative line of research.

Except for the age-related variation just mentioned, all species I have observed are consistent in the basic shelter type they construct during each instar (see also Weiss *et al.*, 2003). Modifications to the basic structure, however, can be variable, even within an individual. For example an early fourth instar *Bolla tetra* building a shelter on a mature leaf may use a scoring cut to weaken the shelter bridge before folding the lid. The same individual on a younger leaf may skip the scoring cut, presumably because the softer tissue is easier to manipulate. In the case of recording shelter modifications, therefore, it may be necessary to observe several individuals to get a good measure of behavior for a species or instar. An additional important point is that often modifications occur hours or days after the basic shelter is completed. For example a fifth instar *Telemiades antiope*, which fed while constructing its Type 5 shelter, did not begin making channels in the shelter lid until a few hours after completion of the basic structure (unpublished data). Similarly, the number and extent of shelter perforations made by *Quadrus cerialis* and *Eracon paulinus* larvae slowly increase as the shelter is occupied longer (unpublished data).

An additional area of investigation, which was first observed and described for *Epargyreus clarus* (Weiss *et al.*, 2003), is the form and function of the silk "template" pad which all larvae I have observed spin before beginning to create a shelter. Through observations of multiple species in the field, I have noticed that the shape of this pad, which larvae use to position their bodies during cutting (Weiss *et al.* 2003), may vary greatly between species, but is highly conserved between individuals or species building the same basic shelter type. This study should encourage others to take the time to investigate the details of shelter construction behavior and architecture in other species, even those which are common and apparently "well studied" (see Greeney & Sheldon, 2008).

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APPENDIX A

Dichotomous key to larval shelter types (modified from Greeney & Jones, 2003).

1a. Shelter construction involving one or more cuts in the leaf **3**
1b. Shelter construction not involving cutting of leaf (with the exception of post-construction feeding damage or modifications) **2**
2a. Only one leaf involved in shelter construction, typically a rolled leaf, one folded in half along the mid-vein, or simply the margin

curled over or under slighly .... (**Type 1**; **no-cut shelter**; Figure 1a)

2b. More than one leaf, leaflet, leaf-lobe, or plant part involved in the shelter construction .... (**Type 2**; **multi-leaf shelter**; Figure 1b)

3a. At least one cut begins from the leaf margin **4**

3b. No cuts are initiated from the leaf margin, shelter usually rounded and folded over a narrow section forming a man-hole-cover-like lid .... (**Type 3**; **center-cut shelter**; Figure 1d)

4a. Shelter construction involving only one major cut, cut begins at leaf margin, resulting flap curled, folded or slid over away from its original position .... (**Type 4**; **one-cut shelter**; Figure 1c)

4b. Shelter with two major cuts, cuts originating from leaf margin, resulting shelter may be flattened, tubular, or hang from the apex of the leaf .... (**Type 5**; **two-cut shelter**; Figure 1e)