Shelter building in the Hesperiidae: A classification scheme for larval shelters

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Abstract: The majority of larvae in the family Hesperiidae build and inhabit shelters on or near the host plant. A review of hesperiid natural history publications from all regions, in combination with extensive field observations on New World skippers shows that larval shelters fall into at least ten separate categories. The functions, plasticity, and ontogenetic variation of skipper shelters are discussed. Terms useful in shelter description are defined and a classification system for shelter types is suggested. A dichotomous key to these types is provided.

Key words: life history, larva, skipper, shelter terminology, leaf roll

Introduction

The exophytic larvae of numerous lepidopteran families construct and inhabit shelters made, at least in part, from host plant leaves. Caterpillars roll, fold, tie, or web leaves to make a diverse array of structural retreats (DeVries 1987, Scoble 1992, Stehr 1987). Many of these (ie. Thyrididae, Gelechiidae, Pyralidae, Tortricidae, Lasiocampidae, Oecophoridae, Nymphalidae, Hesperiidae) can be separated into families by their shelters alone (L. A. Dyer pers. com.). The family Hesperiidae comprises over 3,000 species of butterflies (Munroe 1982) and likely contains the greatest diversity of larval shelters within any lepidopteran family. The diversity of shelter types built, however, has remained largely ignored. While natural history studies on immature skipper stages devote much attention to physical characteristics of the larvae, they often fail to accurately describe larval shelters. Not surprisingly, there is no clear method or vocabulary for describing these shelters. Our current under-standing of the pattern and process of shelter building by skipper larvae remains weak, despite detailed observations from

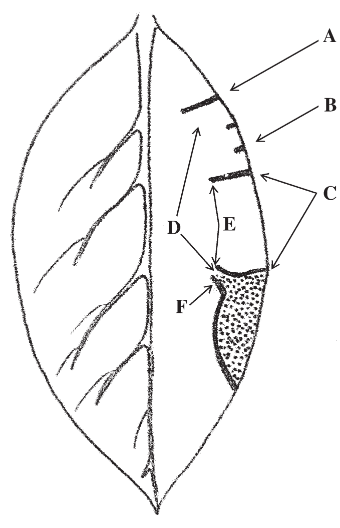

Fig.1. Shelter parts and terminology: Examples of shelter cut patterns for Type 9 (top) and Type 10 (bottom) shelters; stippled area = shelter lid; a) Major cut b) Minor cut c) Proximal portion of major cut d) Shelter bridge e) Distal portion of major cut f) Shelter stem.

early natural historians (e.g. Scudder 1889; Moss 1949).

While a few skippers are reported to live and feed exposed during at least one larval instar (Moss 1949, Scudder 1889, J. Brock pers. comm.), the vast majority construct leaf shelters and spend the majority of their time inside them (eg. Atkins 1975, Atkins & Miller 1977; Moss 1949, Scudder 1889; Young 1991). Despite the time spent inside shelters, frass rarely accumulates within (Greeney & Jones pers. obs.). Using a scoleritized anal comb (Scoble 1992), most skippers forcefully eject frass away from the shelter (Greeney & Jones pers. obs.). A single exception from the literature is described by Scudder (1889) as 'soiling its nest considerably.' Despite the apparent uniformity in larval shelter use, however, shelter architecture can vary greatly across species and between larval instars.

The majority of species described in the literature or observed in the field make at least two separate shelter types during their larval life (eg. Atkins 1988, Williams & Atkins 1996, 1997; Atkins et al. 1991, Graham 1988; Miller 1990; Young 1993), but this ontogenetic change is rarely documented in detail.

Natural history characters can provide useful data for creating phylogenetic hypotheses (DeVries 1987; Hennig 1966). However, the lack of detailed information on shelters makes them unavailable for use in phylogenetic analyses. A review of skipper natural history literature in combination with field observations indicates that some shelters may be diagnostic at species or higher taxanomic levels (Greeney pers. obs.), suggesting they may be important, yet unexplored, phylogenetic characters. By synthesizing field observations and published literature, this study proposes a standardized terminology for describing shelters and presents a dichotomous key for classifying known shelter types.

Materials and Methods

During the past 10 years, observations on skipper natural history and shelter construction were conducted on over 200 species at the following locations: Yanayacu Biological Station and Center for Creative Studies, Cosanga, Napo, Ecuador (YBS); Sacha Lodge Research Station, Sucumbios, Ecuador (SLRS); La Selva Lodge Biological Station, Sucumbios, Ecuador (LS); El Monte Biological Station, Pichincha, Ecuador (EM); Rio Palenque Biological Station, Santo Domingo, Ecuador (RPBS); Tinalandia Lodge, Santo Domingo, Ecuador (TL); Jatun Sacha Biological Station, Napo, Ecuador (JSBS); Celica, Loja, Ecuador (CE); Las Alturas Biological Station, San Vito, Costa Rica (LABS); La Selva Biological Station, Costa Rica (LSBS); Alamos, Sonora, Mexico (AM); Mt. Lemmon, Pima County, Arizona, USA (ML); Tucson, Pima County, Arizona, USA (TA); Oasis State Park, New Mexico, USA (OSP); Springield, Hampshire County, West Virginia, USA (SWV); Georgetown University, Washington DC, USA (GU).

For all hesperiid larvae found in the field we carefully described the form and structure of each shelter and made detailed drawings in nature. Larvae were then brought to the lab for further observations or left *in situ* and observed over the lifetime of the larva. To avoid potential laboratory artifacts affecting shelter construction behavior, only those shelters made by larvae living in the field were considered as legitimate shelter types. Whenever possible, behavior associated with shelter construction was observed and recorded.

To further assess the diversity of shelters we thoroughly examined and compared desriptions and illustrations in the natural history literature. Particular attention was given to those publications with graphic illustrations of shelters (ie. Comstock & Comstock 1943; Fox et al. 1965, Holland 1898; Janzen & Hallwachs 2000; Johnston & Johnston 1980; Larsen 1991; Morris 1980; Riley 1975; Smith et al. 1994; Weed 1917), and these figures were compared with shelters studied in the field. We then used literature and field observations to build a dichotomous key to distinct shelter types. The Megathyminae, whose larvae tunnel inside plant tissues (Scoble 1992), were not included in this study.

Results

Skipper shelters range from a simple resting spot at the base of a leaf secured by a few strands of silk (Fig. 2f), to the elaborately peaked and perforated structures of others (eg. Figs. 2d, 3g, 3h, 4b, 4c). All known shelters, however, may be easily classified into 10 different types using the dichotomous key provided in Appendix A. These types then fall into

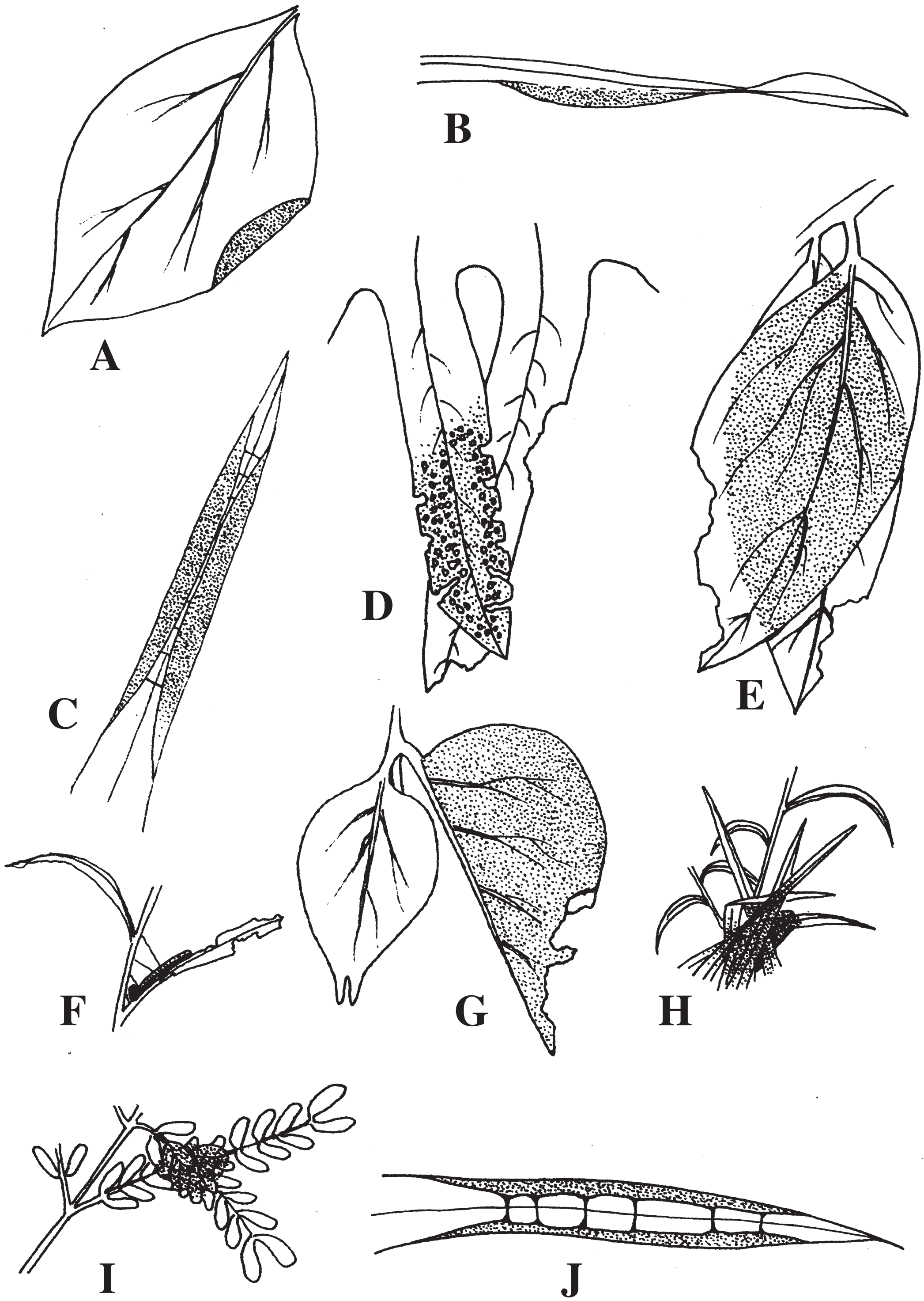

Fig. 2. Group I Shelters: Shelters not always drawn on actual host plant leaf and not drawn to scale; stippled areas indicate the portion of the leaf or leaves which have been manipulated to hide the larva; a) Type 2 folded to ABS, ABV, *Aroma aroma* Hew. (Pyrg), fifth instar, *Cyclanthus* Poit. (Cyclanthaceae), LS; b) Type 2 folded to ABS, LV, *Aroma aroma* Hew. (Pyrg), fifth instar, *Cyclanthus* (Cyclanthaceae), LS; c) Type 2, ADV, unknown Hesp, fifth instar, unknown Poaceae, LS; d) Type 4 with perforations and channels, ADV, *Eracon paulinus* Stoll (Pyrg), fifth instar, unknown hosplant, LS; e) Type 4, ADV, *Eantis thraso* Hübner (Pyrg), fifth instar, Citrus L., LS; f) Type 1, LV showing position of larva, *Atalopedes campestris* Boisduval, first instar, *Digitaria sanguinalis* L. (Poaceae), GU; g) Type 2, LV, unknown Pyrg, fifth instar, *Bauhinia* L., LS; h) Type 3, unknown Hesp, fifth instar, unknown Poaceae, LS; i) Type 3, ADV, unknown Pyrg, third instar, unknown Leguminoidea, LS; j) Type 2, ADV, *Atalopedes campestris* (Boisduval), second instar, *Digitaria sanguinalis* (Poaceae), GU; Abbreviations: : For locality abbreviations see Material and Methods, ABS=abaxial surface, ABV=abaxial view, ADV=adaxial view, LV=lateral view, Hesp=Hesperiinae, Pyrg=Pyrginae.

three major groups; no-cut, one-cut, and two-cut shelters.

Group I Shelters (no-cut shelters, Types 1-4). Group I shelters are formed without any initial cuts made in the leaf. The simplest, Type 1 shelters (rudimentary shelter, Fig. 2f), consist simply of a loosely silked area where the larvae return between feeding bouts. They are defined as areas where resting occurs and silk is deposited, but where the position of the foodplant is not necessarily modified. Often Type 1 shelters consist of merely a small mat of silk about a body length long, and those species reported to lack shelters should be observed carefully to determine if they in fact create such mat of resting silk.

Type 2 shelters (no-cut fold, Figs. 2a, b, c, g j) encompass a diversity of forms dictated in part by leaf shape, size, and thickness. They are formed using only one leaf or leaflet. Often they are more tubular in shape than most shelters (Figs. 2c, j), but can be flattened as well (Fig. 2g). They vary from a leaf edge slightly curled over or under the leaf blade (Figs. 2a, b) to shelters where opposite leaf margins are drawn together to form a tube. This latter type is common among grass feeding hesperiines. Another Type 2 shelter seen in many late instar pyrgines and also formed by drawing opposite leaf margins together, creates a shallow pocket when the leaf is folded along the midvein (Fig. 2g).

Type 3 shelters (multi-leaf shelters, Figs. 2h, i) are typically a disorganized cluster of may plant parts. All Type 3 shelters are composed of more than two leaves, leaflets, or leaf lobes, and are most commonly found on plant species where the size of the leaves or leaflets is too small to accommodate larger larvae. This is a common type, and is often constructed by late instar larvae feeding on grasses (Fig. 2h) or pinnate legumes (Fig. 2i).

Type 4 shelters (two-leaf shelter, Figs. 2d, e, 3g) are formed using only two leaves (Fig. 2e), leaflets (Fig. 3g), or leaf lobes (Fig. 2d). The two blades are most often slid over so that the pocket formed by the overlap is composed of an adaxial leaf surface opposing an abaxial surface. They may, however, be flipped such that one surface opposes the same surface on the other leaf.

Group II Shelters (one-cut shelters, Types 5-7). Group II shelters are constructed using only one major cut. The most easily recognized of this shelter group are Type 5 (center-cut fold, Fig. 3b). In these unique shelters, the major cut is initiated from the center of the leaf and does not begin at the leaf margin as in all other shelter types. Cuts range from circular to oval and the shelter lid may be flipped on to the adaxial or abaxial surface of the leaf.

Type 6 shelters (one-cut fold, Figs. 3a, d, e, f) are the most common type of Group II shelters. They vary from being tightly silked and flattened (Figs. 3a, d) to more loosely silked and conical or tubular in overall form (Figs. 3e, f). In the latter cases, the larvae are often visible from at least one angle. They may be formed on the adaxial (Figs. 3a, f) or abaxial (Figs. 3d, e) surface.

Type 7 shelters (one-cut slide, Fig. 3c) have been observed only once, and it is unknown how commonly they occur. They are formed by one major cut, which allows the portions of the leaf on opposite sides of the cut to be slid over top one another. In Type 7 shelters the abaxial surface of the leaf opposes the adaxial surface.

Group III Shelters (two-cut shelters,Types 8-10). All Group III shelters are constructed using only two major cuts. The three types are separated by the relative position of these two cuts to one another. Type 8 shelters (two-cut fold, Figs. 4d, e, f) differ from other Group III shelters by having the major cuts beginning on opposite sides of the leaf midvein. They typically take on two forms, but both are created by drawing together opposite leaf margins. This results in a tube-shaped (Figs. 4d, e) or flattened pocket (Fig. 4f). In many grass feeding Hesperiines these shelters are often further modified using a positioning cut along the midvein. Frequently the mid vein, at the site of the positioning cut, is subsequently silked so as to firmly hold the shelter out of the plane of the rest of the leaf blade. This often results in the leaf looking diseased or dead (Fig. 4e).

Type 9 shelters (two-cut unstemmed fold, Figs. 3i, 4g, i, j) are similar to Type 10 (two-cut stemmed fold, Figs. 3h, 4a, b, c, h) shelters but are separated by the relative positions of the distal portions of the respective major cuts. Type 9 shelters have the distal ends of the major cuts separated by more than one half the distance between the proximal ends and are folded along a broad shelter bridge. They are often square, or nearly so, in overall shape. In contrast, Type 10 shelters, the distal ends of the two major cuts are separated by no more than one half the distance that separates the proximal ends. This

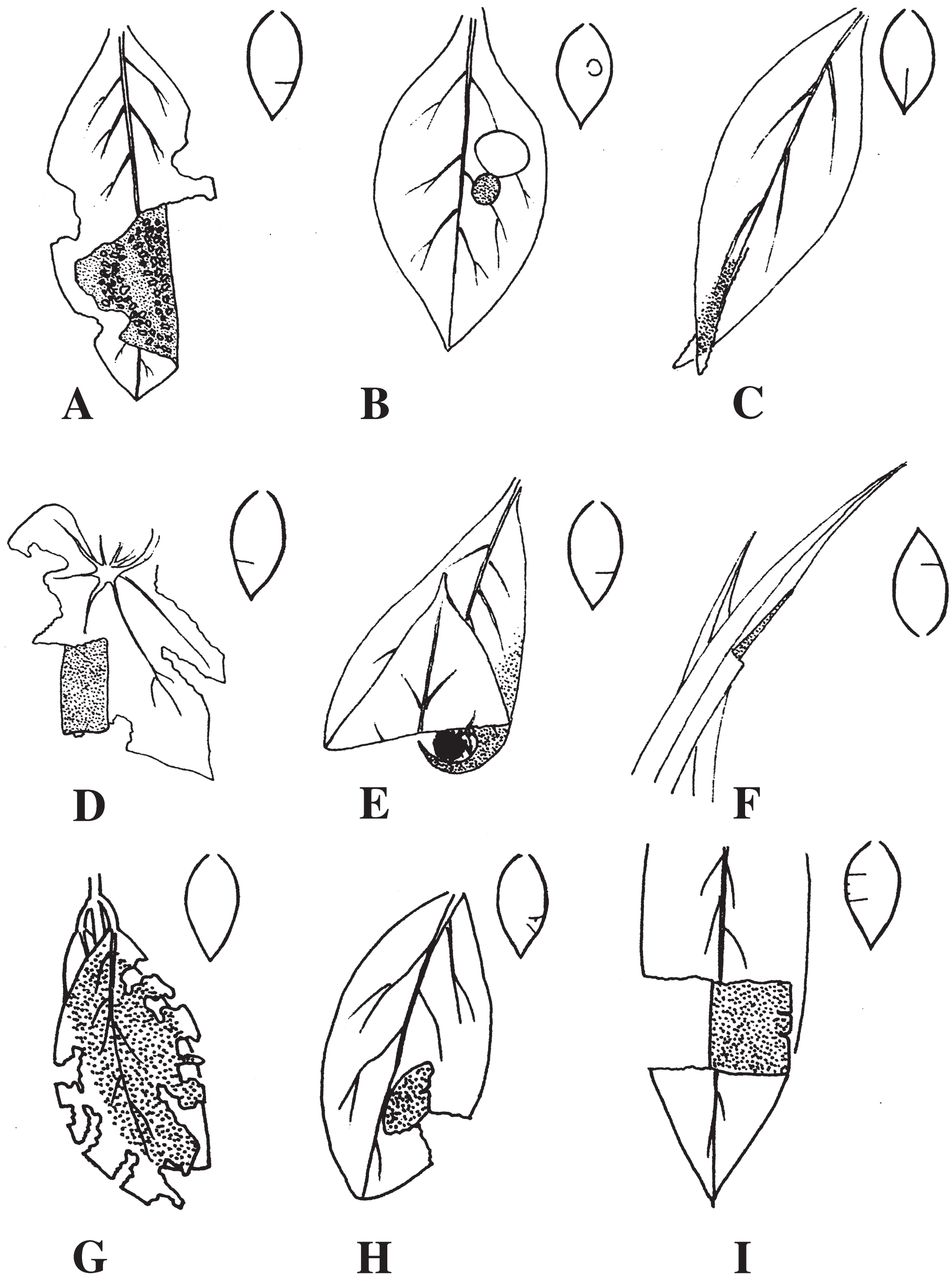

Fig. 3. Group II, Group I, and Group III Shelters: Stylized leaf-outline insets show the positions of major and minor cuts; shelters not always drawn on actual host plant leaf and not drawn to scale; stippled areas indicate the portion of the leaf or leaves which have been manipulated to hide the larva; a) flattened Type 5 (Group II) with perforations, ADV, *Quadrus cerialis* Stoll (Pyrg), fifth instar, *Piper* L. (Piperaceae), LS; b) Type 6 (Group II), ADV, unknown Phyrropyginae, first instar, *Vismia* Vand. (Gutifferaceae), YBS; c) Type 7 (Group II), ADV, unknown Pyrg, fifth instar, *Deffembachia* Schott (Araceae), LS; d) Type 5 (Group II) folded to ABS, ABV, *Systasea zampa* W. H. Edwards (Pyrg), fifth instar, *Abutilon sonorae* Gray (Malvaceae), TA; e) Type 5 (Group II) folded to ABS, anterior view showing position of larva, unknown Pyrg, fifth instar, unknown foodplant, LS; f) Type 5 (Group II), ADV, *Turesis basta* Evans (Hesp), first instar, unknown Poaceae, LS; g) Type 4 (Group I) with channels, ADV, *Erynnis* Schrank, fifth instar, *Robinia* L. (Leguminoidea), SWV; h) Type 10 Group III with one-secondary-cut tent, ADV, *Epargyreus clarus* Cramer (Pyrg), second instar, *Robinia* L. (Leguminoidea), ML; i) Type 9 (Group III) with two-secondary-cut tent, ADV, *Entheus latebrosus* Austin, fourth instar, *Grias* L. (Lethycidaceae), LS. Abbreviations: For locality abbreviations see Material and Methods, ABS=abaxial surface, ABV=abaxial view, ADV=adaxial view, Hesp=Hesperiinae, Pyrg=Pyrginae.

results in a shelter that is folded over along a narrowed shelter bridge and often gives them a stemmed appearance. Often this shelter stem is nothing more than a single, secondary leaf vein.

Terminology. During attempts to adequately describe skipper shelters it became obvious that a unique set of terms was needed for standardization. Below we provide terms useful in describing and differentiating larval shelters.

Cuts. Major cut (Fig. 1a). Any cut essential to the formation of the basic shelter type and which is also more than twice the length of the larval head capsule width (at the time of shelter construction). Positioning cut. Defined as a cut, usually away from the shelter itself, that enables alteration of the shelter's position in relation to the rest of the plant. Generally it functions like (or with) positioning silk. Proximal portion of a cut (Fig. 1c). This is the section of the cut where cutting begins and, with the exception of Type 5 shelters (Fig. 3b), is the portion where the cut meets the leaf margin. Distal portion of a cut (Fig. 1e). This is the opposite end of the major cut from the proximal portion and, in all described shelters, is located away from the leaf margin. Unless shelter construction is observed, distal and proximal portions are generally not identifiable in Type 5 shelters or in positioning cuts.

Shelter parts. Shelter lid (Fig. 1). This is the portion of the shelter (in Group II and III, except Type 8) which has been cut away and manipulated into position to oppose the rest of the leaf blade and hide the larva. Shelter lids may be on the abaxial or adaxial surface of the leaf. Group I and Type 8 shelters, as they are often too disorganized or rudimentary to describe in detail, do not have a shelter lid. Shelter bridge (Fig. 1d). The portion of the shelter (in Group II and III, except Type 7), near the distal portions of the major cuts, along which it is folded. Shelter stem (Fig. 1f). The part of Type 9 shelters, where the distal portions of the major cuts are parallel, or nearly so. This is often a single, secondary leaf vein and is the portion of the shelter between the bridge and the lid.

Shelter modifications. *Perforations.* Perforations are modifications made by feeding damage that do not alter the overall shape of the shelter (Fig. 3a). They differ from channels by never beginning from a leaf margin or cut edge, and are usually circular or oval in form. Channels. Channels are similar to perforations, but begin from a leaf margin or cut edge (Figs. 3g, 4b). Like perforations, they do not alter the overall form of the shelter. Shelters may be modified with both perforations and channels (Fig. 2d). Tented shelters. These are shelters which often, but not always, include minor cuts that allow the shelter to take on a domed or peaked shape. This is created by silking together the opposite sides of a minor cut, or sometimes a pinched together section of the leaf, which draws that portion of the shelter into a peak or crease. Tented shelters may be formed without, or with one (Fig. 3h) or multiple (Figs. 3i, 4c) minor cuts. Multiple lidded shelters. These shelters may be of any type in overall construction but, due to additional feeding damage near the shelter, are partially or completely obscured by one or several flaps of leaf (Fig. 4g). It is not known if this is intentional, but in those species observed to live in multiple lidded shelters this was seen in over 90% of the shelters created (Greeney, unpubl. data).

Shelter silk. The following terms refer to the location or function of silk laid down by the shelter builder and do not necessarily reflect any differences in chemical composition. Silk laying patterns alone can be useful in differentiating shelters built by different species (Greeney unpubl. data). Positioning silk. Positioning silk is that used to alter the overall position of the shelter in relation to the host plant. It does not alter the basic form of the shelter, but simply moves the entire shelter out of its natural position. Positioning silk is commonly used in grass feeding hesperines (Fig. 4e), but has also been observed in at least one species of pyrgine (Greeney & Warren in prep.). It is frequently located at the site of a positioning cut. Sealing silk. This refers to any silk laid in the process of creating the basic shelter shape, moving the shelter lid, or sealing various pieces together. In shelter Types 9 and 10, sealing silk is generally laid at or near the shelter bridge to begin flipping the shelter lid. As the lid approaches the leaf surface, often more sealing silk is then spun between the lid edge and the leaf to draw it into its final position (H. Greeney unpubl. data). In Type 3 shelters, sealing silk is used to draw and anchor the various parts of the leaf or plant together (Figs. 2h, i). Often, many strands of sealing silk form easily visible ties that hold the shelter together (Fig. 2j). Resting silk. This is defined as silk spun inside the shelter which does little or nothing to contribute to the shape or

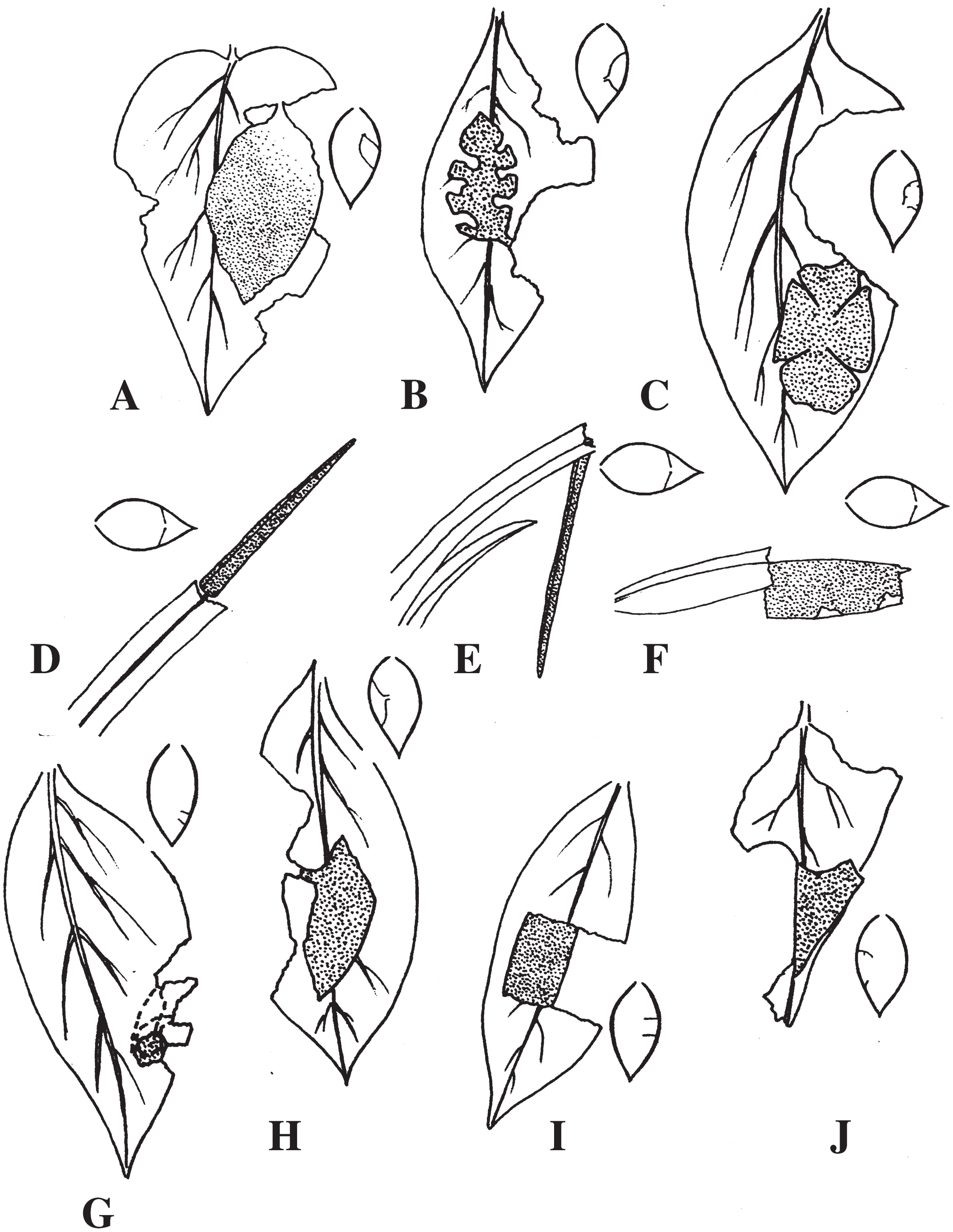

Fig. 4. Group III Shelters: Stylized leaf-outline insets show the positions of major and minor cuts; shelters not always drawn on actual host plant leaf and not drawn to scale; stippled areas indicate the portion of the leaf or leaves which have been manipulated to hide the larva; dashed lines indicate portions of the leaf not involved in shelter construction, but which obscure the shelter in some fashion; a) Type 10 slid rather than folded, ADV, unknown Pyrg, fifth instar, *Inga* Mill. (Mimosaceae), LS; b) Type 10 with channels, ADV, unknown Pyrg, fourth instar, *Inga* (Mimosaceae), LS; c) Type 10 with Four-minor-cut tent folded to ABS, perforations present but not illustrated for clarity of minor cuts, ABV, unknown Pyrg, fifth instar, unknown foodplant, LS; d) Type 8 tubular form, ADV, unknown Hesp, fourth instar, unknown Poaceae, LS; e) Type 8 tubular form in hanging position, LV, *Turesis* Godman (Hesp), fifth instar, unknown Poaceae, LS; f) Type 8 flattened form, LV, *Saliana* Evans (Hesp), fifth instar, *Calathea* G. Mey. (Marantaceae), LS; g) Type 9 with multiple lids, ADV, *Entheus latebrosus* Austin, first instar, *Grias* (Lethycidaceae), LS; h) Type 10, ADV, *Celaenorhinnus jao* Mabille (Pyrg), fourth instar, unknown Acanthaceae, SLRS; i) Type 9 folded to ABS, ABV, *Astraptes talus* Cramer (Pyrg), fifth instar, unknown foodplant, LS; j) Type 9, ADV, *Hesperopsis* Edwards (Pyrg), third instar, *Atriplex* L. (Chenopodiaceae), TA. Abbreviations: For locality abbreviations see Material and Methods, ABS=abaxial surface, ABV=abaxial view, ADV=adaxial view, LV=lateral view, Hesp=Hesperiinae, Pyrg=Pyrginae.

position of the shelter. Resting silk is generally used by larvae for attaching their crochets while inside the shelter (Greeney & Jones pers. obs.).

Discussion

That larval shelters serve important functions is evidenced by the numbers and diversity of lepidopteran families known to create shelters (DeVries 1987, 1997; Scoble 1992; Steh 1987). Leaf shelters may reduce predation (Damman 1987; Eubanks et al. 1997; Jones 1999; Loeffler 1996), alter the interior microclimate by providing shade and/or increasing humidity (Henson 1958), or prevent desiccation (Jones pers. obs.). Rolling or tying leaves may also increase leaf nutritional quality (Sagers 1992), allow larvae to feed on phototoxic plants (Sandberg & Berenbaum 1989), and protect caterpillars from dislodgment (Loeffler 1996). Additional modifications to the basic structure, such as channels or perforations (Figs. 2d, 3a, 3g, 4b), may also serve various functions such as draining the shelter of rainwater or enhancing air circulation inside the shelter and preventing the buildup of pathogenetic bacteria and fungi (Scudder 1889; Young 1991).

In contrast to the uniformity that skipper species or larval instars show in nature, various authors have recorded larvae in the lab using portions of their rearing container in shelter construction (Jones 1999; Scudder 1889; Young 1993). In the field, larvae have been recorded to include adjacent leaves, other parts of non-foodplants, and even nearby detritus (Clark 1936; Jones 1999; Atkins 1987; Williams & Atkins 1997). Manipulative experiments will be of key importance in elucidating the cues used for choosing building materials and constructing shelters.

Despite the extensive number of papers reviewed and the copious field observations used to define these ten shelter types, the unexplored diversity of larval hesperiids and the lack of detailed descriptions in the literature all but guarantee the discovery of further shelter types or groups. The intent of this paper is not to show that all larval shelters will easily fall into one of these ten types, but rather to create a standardized method for describing shelters and discussing shelter construction. It is the hope of the authors that this manuscript will encourage future studies to more thoroughly describe hesperiid shelters and allow for easier comparison and discussion of these ecologically interesting structures. Using this organization of shelter types, we encourage the careful examination and categorization of others in the hopes that shelter construction may prove useful in resolving hesperiid phylogenies.

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Appendix A

Dichotomous key to larval shelter types

1a. Shelter mostly or entirely hiding larvae from view (2)

1b. Shelter rudimentary, barely concealing larvae, usually consists of a naturally formed pocket or crevice on plant or an area where resting silk has been laid that begins to curl leaf blade, shelter area mostly unmodified by larvae (**Type 1 shelter; rudimentary shelter**; Fig. 2f)

2a. Shelter construction involving one or more cuts in the leaf (5)

2b. Shelter construction not involving cutting of leaf (excluding feeding damage modifications such as perforations or channels eaten from shelter structure) (3)

3a. More than one leaf, leaflet, leaf-lobe, or plant part involved in the shelter construction (4)

3b. Only one leaf involved in shelter construction, typically a rolled leaf, one folded in half along the mid-vein, or simply the edge curled over or under the blade (**Type 2 shelter; no-cut fold**; Figs. 2a, b, c, g, j)

4a. More than two leaves, leaflets, leaf-lobes, or plant parts involved, typically a disorganized appearing cluster of small leaves or leaflets silked together, common among grass feeding larvae (**Type 3 shelter; multi-leaf shelter**; Figs. 2h, i)

4b. Only two leaves, leaflets, or leaf lobes involved in shelter design, many be slid over and silked ventral surface to dorsal surface or flipped over with dorsal surface to dorsal surface or ventral surface to ventral surface (**Type 4 shelter; two-leaf shelter**; Figs. 2d, e, 3g)

5a. At least one cut begins from the leaf margin (6)

5b. No cuts are initiated from leaf margin, shelter usually rounded and folded over along a narrow or stemmed section of leaf (**Type 5 shelter; center-cut fold**; Fig. 3b)

6a. Shelter construction involving only one major cut (7)

6b. Shelter involving more than one major cut (8)

7a. Major cut begins at leaf margin, leaf flap curled or folded onto abaxial or adaxial surface of leaf, shelter formed so that abaxial leaf surface opposes abaxial surface or adaxial surface to adaxial surface (**Type 6 shelter; one-cut fold**; Fig. 3a, d, e, f)

7b. Shelter as in 7a, but one section of leaf slid over or under another part, shelter formed so that an abaxial leaf surface opposes an adaxial surface (**Type 7 shelter; one-cut slide**; Fig. 3c)

8a. Shelter with two major cuts, usually both beginning on same side of leaf mid-vein, if on opposite sides of mid-vein then shelter is at apex of leaf and has a definite top and bottom, shelter lid may be folded over along a narrow or broad leaf section (9)

8b. Shelter not as above, two major cuts involved in construction, major cuts always beginning on opposite sides of the mid-vein and typically reach to mid-vein, shelter may be flattened (Fig. 4f) or tubular (Fig. 4d), may hang from end of leaf (Fig. 4e) (**Type 8 shelter; two-cut fold**; Figs. 4d, e, f)

9a. Shelter folded or curled; portion of leaf along which shelter is folded or rolled is more than half the length of the leaf margin portion of the shelter lid; shelter usually square or rectangular; may be folded or curled onto abaxial or adaxial surface of the leaf (**Type 9 shelter; two-cut, unstemmed fold**; Figs. 3i, 4i, j)

9b. Shelter folded, curled, or slid; portion of leaf along which shelter is hinged is less than half the width of the leaf margin portion of the shelter lid; often stemmed in appearance; shelter usually triangular, trapezoidal, or rounded; may be folded or slid onto abaxial or adaxial surface of leaf (**Type 10 shelter; two-cut, stemmed fold**; Figs. 3h, 4a, b, c, g, h)