JOURNAL OF
THE LEPIDOPTERISTS' SOCIETY

Volume 54 2001 Number 3

Journal of the Lepidopterists' Society
54(3), 2001, 77–82

ONTOGENETIC CHANGES IN LEAF SHELTER CONSTRUCTION BY LARVAE OF *EPARGYREUS CLARUS* (HESPERIIDAE), THE SILVER-SPOTTED SKIPPER

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ABSTRACT. In this paper we examine patterns of shelter construction by larvae of the Silver-spotted Skipper, *Epargyreus clarus* Cramer (Hesperiidae). Through observations of field and laboratory populations we characterize 1) the types of shelters constructed over larval ontogeny and their relationship to larval size and instar, and 2) the location of shelters on the host plant. We also describe various aspects of larval feeding behavior. Each larva builds and inhabits its own shelter, successively abandoning shelters and constructing new ones approximately five times across five instars. On kudzu (*Pueraria lobata*; Fabaceae), larvae produce shelters in four distinct styles that change predictably as the insects grow. Ontogenetic changes in style of shelter construction are likely to be related to larval size, needs, and physical capability.

Additional key words: leaf folder, caterpillar behavior.

Lepidopteran larvae in at least 18 families construct shelters from leaves that are rolled, folded, or tied and sealed with silk (Scoble 1992). These shelters are thought to provide a variety of advantages to the larvae, including protection from natural enemies (Damman 1987; Ruehlmann et al. 1988), creation of a favorable microhabitat (Henson 1958), increased leaf nutritional quality (Sagers 1992), or protection from phytotoxicity (Sandberg and Berenbaum 1989). Very little is known, however, about the pattern or process of leaf shelter construction (Clark 1936, Fraenkel and Fallil 1981, Ruehlman et al. 1988, Fitzgerald and Clark 1994).

The vast majority of skippers (Hesperiidae) live singly in a shelter constructed of host leaf material and silk (Moss 1949, Scoble 1992). Shelter styles vary among species, and also across larval ontogeny within a single species (Scudder 1889, Clark 1936, Moss 1949). The diversity of shelter styles includes leaf rolls, folds, peaked tents and perforated pockets (Scudder 1889, Moss 1949). Shelter construction may be initiated at the leaf margin or in the center of the leaf, and may involve a small portion of a leaflet, an entire leaf, or multiple leaves. For certain species on a given host plant, shelter size, style, and placement on the leaf can be diagnostic (H. Greeney pers. comm., J. Brock pers. comm.).

In this paper we describe the pattern of shelter construction by larvae of the Silver-spotted Skipper, *Epargyreus clarus* Cramer (Hesperiidae). Through observations of field and laboratory populations we characterize 1) the types of shelters constructed over larval ontogeny and their relationship to larval size and instar, and 2) the location of shelters on the host plant.

MATERIALS AND METHODS

Study organism. The Silver-spotted Skipper, *Epargyreus clarus*, ranges throughout North America from Saskatchewan in the north through Baja California, Texas, and Florida in the south (Scott, 1986). In the Washington, D.C. area these large skippers fly from mid-April through October, and commonly use black locust trees (*Robinia pseudoacacia*) and kudzu (*Pueraria lobata*) (both Fabaceae) as hosts (Clark & Clark 1951). In this study we used kudzu as our host plant because of its abundance, accessible vining growth form, and the longevity of cut leaves in the laboratory.

Caterpillars inhabit leaf shelters throughout their larval lives, leaving only to feed or to build a new shel-

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TABLE 1. Summary of *Epargyreus clarus* larval and shelter characteristics across 5 instars. Values are given as the mean (SE (sample size).

	Instar				
	1	2	3	4	5
Larval length, mm[a]	5.5 ± 0.1 (29)	8.4 ± 0.1 (25)	14.3 ± 0.4 (20)	26.4 ± 0.5 (21)	36.2 ± 1.2 (20)
Shelter length x width, mm (shelter type)[b]	7.1 ± 0.1 x 8.1 ± 0.2 {1} (69)	13.1 ± 0.4 x 14.7 ± 0.5 {1} (31)	18.8 ± 1.1 x 15.9 ± 0.8 {1} (15)	36.7 ± 1.6 x 18.4 ± 1.2 {2, 3, 4} (25)	46.5 ± 1.6 x 26.3 ± 2.2 {2, 3, 4} (15)
Shelter size / Larval length[c]	1.4	1.7	1.2	1.0	1.0
Distance to subsequent shelter, cm	5.4 ± 0.5 (55)	8.9 ± 0.8 (47)	11.4 ± 1.3 (20)	24.6 ± 11.2 (5)	--
Duration of feeding bout, minutes	3.4 ± 0.18 (97)	5.2 ± 1.2 (8)	5.1 ± 1.4 (3)	2.7 ± 0.2 (73)	4 ± 0.6 (11)
% daytime spent feeding	4.3 ± 0.4 (61)	3.7 ± 1.7 (14)	1.3 ± 0.7 (13)	2.1 ± 0.6 (11)	1.9 ± 1.1 (16)
Maximum feeding distance, cm	1.1 ± 0.2 (50)	1.9 ± 0.1 (20)	2.1 ± 0.2 (20)	7.0 ± 0.6 (15)	18.3 ± 1.9 (15)
Location of feeding site relative to shelter[d]	100% sll (40)	100% sll (37)	100% sll (45)	78% sll, 14% all, 8% alf (36)	4% sll, 20% all, 76% alf (25)

[a] Measurements taken of mid-instar larvae
[b] Measurements taken of only those shelter types indicated
[c] Ratio of (mean shelter width + length)/2 to mean larval length
[d] sll = same leaflet; all = adjacent leaflet, same leaf; alf = adjacent leaf

ter. Larvae do not feed within the shelter, although early instars feed close by (Table 1). Based on observations of many larvae in the field, we determined that during the day, caterpillars spend approximately 3% of their time feeding, and that the average feeding bout (time elapsed between a caterpillar's departure from and return to its shelter) lasts about 4 minutes (Table 1). Young larvae feed on the same leaflet that their shelter occupies, while older larvae may venture to an adjacent leaflet or leaf (Table 1).

Collection and care of larvae

Larvae were obtained from eggs of adults caught on the Georgetown University campus and from meadow habitats on the Eastern Shore of Maryland from June through October 1997 and 1998. After the first generation, the colony contained both lab-reared and field-collected adults. Butterflies were kept outdoors in 2 m^3 mesh cages, and were fed flowers of *Trifolium pratense* (Fabaceae), *Buddleja davidii* (Buddlejaceae), and *Lantana camara* (Verbenaceae), supplemented with 10% sucrose solution. Freshly cut kudzu leaves were provided for oviposition. Kudzu leaves containing eggs were collected from the outdoor cage each morning, brought into the lab, and placed in 13″ × 7.5″ × 4.25″ clear plastic boxes with opaque lids. Larvae were housed in these boxes and were given fresh cut kudzu leaves as needed until pupation.

1) Types of shelters constructed over larval ontogeny

To characterize patterns of shelter construction, we collected and examined over 600 leaf shelters constructed by larvae in field and lab populations, and identified the instar of the inhabitant. Based on our observations of shelter characteristics, we developed a classification of shelter types. We also measured the dimensions of a subset of shelters of each type, and determined the length of their larval inhabitants, using a Mitutoyo Absolute Digimatic caliper (±0.01 mm).

To determine how patterns in the size and shape of shelters relate to the timing of a molt to a later instar, fifteen newly hatched larvae were placed on fresh kudzu leaves in individual plastic boxes in the laboratory. Every other day, the boxes were opened and the larval instar and house type recorded. Care was taken not to touch or manipulate the larvae themselves.

2) Location of shelters on the host plant

In the field, we measured the height above ground of the shelter-bearing leaf for 36 first instar shelters. Height of first instar shelters is a good indication of height at which eggs are laid, because empty egg shells and first shelters are generally found on same leaflet (pers. obs.). We also divided the leaflet into four quadrants (quadrant 1 = right apex; 2 = left apex; 3 = left base; 4 = right base) and noted in which one a shelter was located, for 356

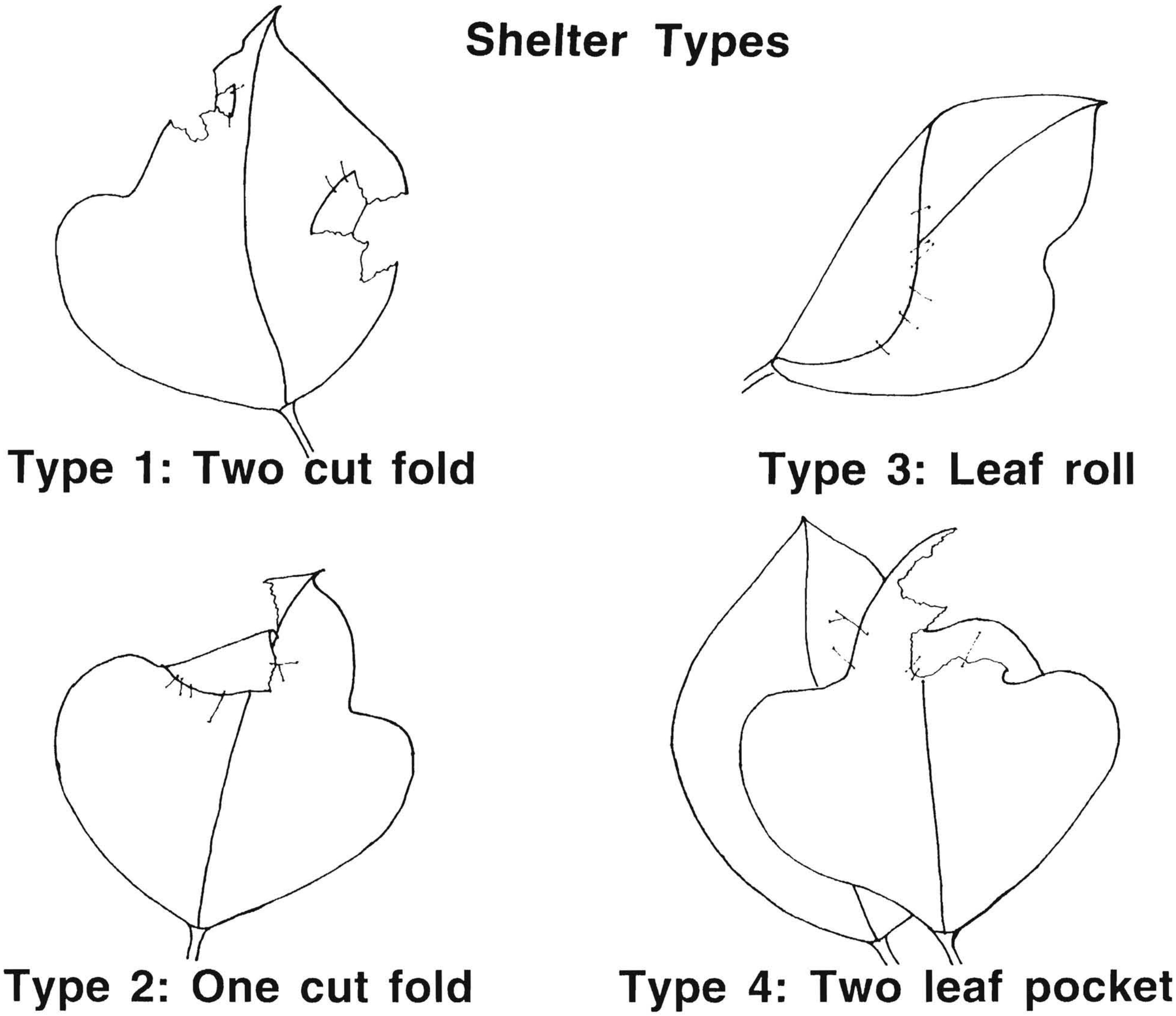

FIG. 1. *E. clarus* larvae construct 4 types of shelters over larval ontogeny. Lines connected to shelters represent silk guy wires.

shelters made by first, second and third instar larvae. We often encountered leaflets or leaves that contained three or four shelters which we inferred were constructed by a single larva, based on the predictable progression of shelter size and style. We used a ruler to measure the shortest linear distance between sequential shelters.

RESULTS

1) Types of shelters constructed over larval ontogeny

We found that *Epargyreus clarus* larvae construct shelters in four distinct styles (Fig. 1), designated types 1, 2, 3, and 4 for the approximate order in which they appear in larval life. For shelter type 1 ('two-cut folds'), the larva makes two cuts of precise length and orientation in from the margin of the leaflet, applies multiple strands of silk at corner 'hinges' to pull the triangular to rectangular flap over towards the center of the leaflet, and secures it to the leaf surface with silken 'guy-wires'. A peaked roof is formed by the tight silking of a small cut perpendicular to one of the main cuts. Type 2 shelters ('one-cut folds') are similar, but entail only one cut in from the leaflet margin. Type 3 shelters ('leaf folds') have no cuts; caterpillars fold the margin of some or all of a leaflet towards the center and secure it to the surface with long guy wires. Type 4 shelters ('two-leaf pockets') consist of two leaflets pulled together by silk strands to form a pocket.

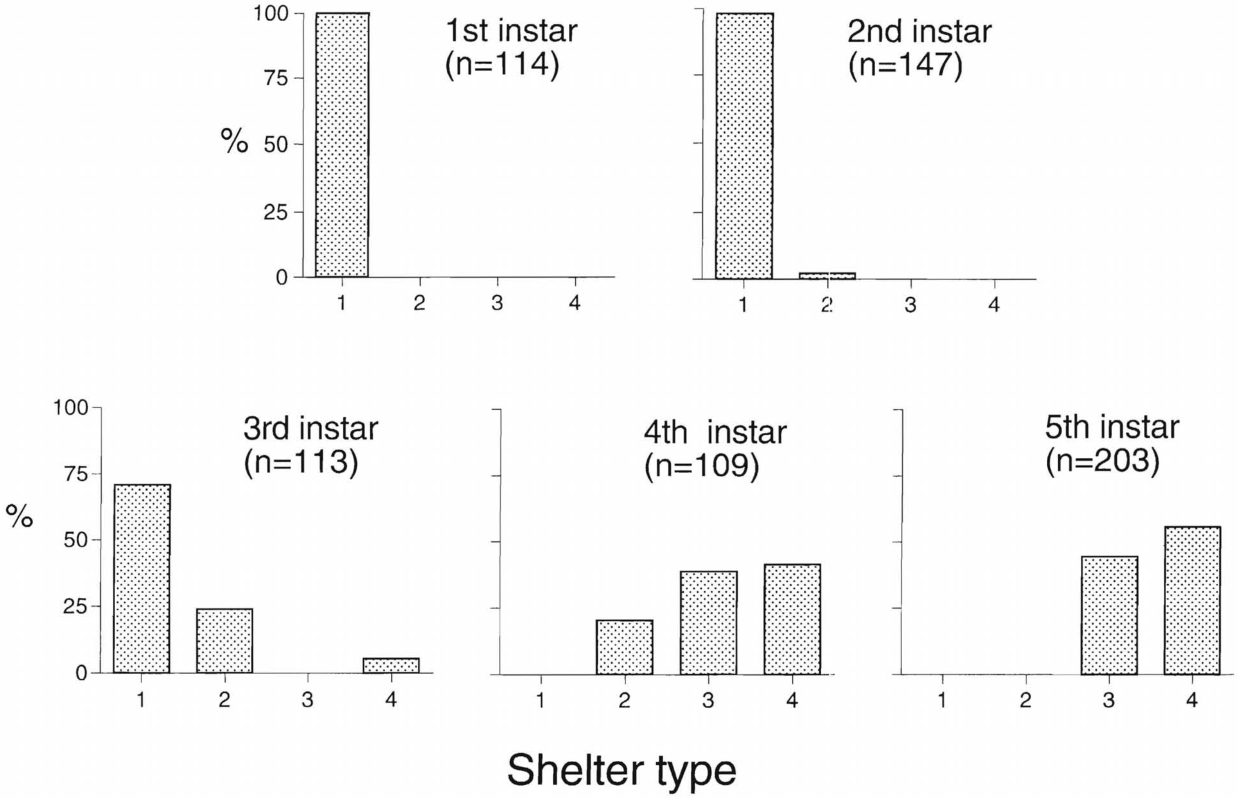

FIG. 2. Distribution of shelter types varies predictably across larval instars.

The style of shelter constructed varies predictably over larval ontogeny (Fig. 2). First and second instar caterpillars build type 1 shelters almost exclusively, while third instar larvae construct mostly type 1, some type 2, and rarely type 4 shelters. Fourth and fifth instars never build type 1 shelters; instead, they construct mostly shelter types 3 and 4.

Larger larvae build larger shelters, both across and within shelter types. That is, each successive shelter type is generally larger than the previous, and for a given shelter type, shelter size is positively correlated with larval size (Table 1). The relationship between larval length and shelter size is relatively constant across all five instars: the size of the shelter (approximated as (length + width)/2) ranges between 1.0 and 1.7 times the length of the larva (Table 1).

Laboratory-reared larvae allowed to change shelters at will built a mean 5.1 shelters (±0.24 SE; N = 15) over five instars. Larvae generally constructed a new shelter one to several days after molting within the previous shelter (mean ± SE = 1.7 ± 0.2 days after first molt; 1.6 ± 0.2 days after second molt; 2.8 ± 0.3 days after third molt; 4.0 ± 0.8 days after fourth molt). Only three out of 60 observed molts took place outside of a shelter.

2) Location of shelters on the host plant

The height above the ground of leaves bearing first instar shelters ranged from 0.25–1.25 m, with a mean ± SE of 0.65 ± 0.03 m. The distribution of shelters across the 4 quadrants differed significantly from random ($X^2 = 109.86$, 3 df, $p < 0.001$). Almost 50% of the shelters were located in quadrant 2, and together quadrants 1 and 2 (the apical half of the leaf) contained three-quarters of all shelters. As larvae grow, the distance between shelters increases. First, second, and third instar shelters are generally located on the same leaflet, while shelters constructed by fourth and fifth instar larvae are often constructed on an adjacent leaflet or leaf (Table 1).

DISCUSSION

Although larvae of many lepidopteran species fold, roll or tie leaves into shelters, it is not uncommon for these taxa to begin their larval lives with a radically different feeding habit, such as leaf-mining or boring (Gaston et al. 1991). Presumably, this is related to the small size of early-instar larvae. For example, *Caloptilia serotinella* (Gracillariidae), the cherry leaf-roller, is a leaf-miner in its early stages, while fourth and fifth instar larvae are leaf-rollers (Fitzgerald & Clark 1994). In a range of other taxa, hatchling and early instar larvae use a shelter made by another species, construct a communal shelter or silk canopy, or hide in a cranny, while late instar larvae build their own shelters (Doerksen & Neunzig 1976, Damman 1987, Cappuccino 1993, Loeffler 1994).

Like *E. clarus*, larvae in several other diverse taxa construct leaf shelters throughout larval life, and exhibit ontogenetic changes in style of shelter construction. The golden-banded skipper, *Rhabdoides* (=*Autochton*) *cellus*, builds shelters in a progression of styles very similar to that of *E. clarus* (Clark 1936). Shelters made by larvae of the skipper *Staphylus hayhurstii* are also similar to those of *E. clarus*, although the shelters lack a notch in the second cut and thus do not have a peaked roof (pers. obs). Larvae of the pyralid moth *Herpetogramma aeglealis* sequentially construct and inhabit shelters of three distinct types on fronds of Christmas fern (Ruehlmann et al. 1988). Early-stage *Nephopterix celtidella* (Pyralidae) larvae web two leaves flatly together, while last-stage larvae web a dead, curled leaf to the surface of a living leaf (Doerksen & Neunzig 1976).

Ontogenetic changes in shelter size and style may be due to the biological needs and/or physical capabilities of the larva. Certainly, to be fully enclosed and hidden from predators, larger larvae require larger shelters, so that while a small folded section of leaflet is sufficient to cover a first instar caterpillar, larger larvae need the increased area that a folded leaflet or two leaves silked together can provide. Perhaps, in addition, a fixed relationship between larval size and shelter size is necessary to maintain a particular internal microclimate, or to restrict access to predators.

Changes in shelter size and style may also reflect changes in the physical abilities of the larvae. A 3-mm-long *E. clarus* hatchling may not be able, even utilizing the axial retraction forces of stretched silk (Fitzgerald et al. 1991) to fold a large flap over itself or pull two leaflets together. It can, however, cut a small flap of leaf tissue and fashion it into a shelter. As the larva increases in size, it is able to manipulate larger pieces of leaves, and cutting eventually becomes unnecessary. Indeed, by the time larvae reach the fifth instar, they rarely cut leaves prior to constructing their shelters, and either fold over the entire edge of a leaflet or join two leaflets together with silk. Cuts made in leaves by late instar larvae might be counter-productive as well as unnecessary, as the weight of a fifth instar larva (~700 mg) could pull down or tear a leaf flap. Cutting leaf tissue may also cause the release of volatile compounds that could attract parasitoids (Turlings et al. 1995).

The types of shelters built by each larval instar may also reflect selection for speed and efficiency of construction, as leaf-rolling or leaf-tying insects are generally palatable to natural enemies (Bernays & Cornelius 1989), and exposed larvae are much more likely to be eaten than are sheltered ones (Damman 1987, Cappuccino 1993).

Little is known about the ontogenetic patterns of shelter construction for most taxa that fold, tie, or roll leaves to make a shelter. Some species, like *E. clarus* and *Herpetogramma aeglealis* (Pyralidae) (Ruehlmann et al. 1988), build very regular structures that change predictably in size and style over larval ontogeny, while others produce more variable shelters (pers. obs.). The relationship between insect size and shelter size is also likely to vary across taxa. Larvae that feed inside the shelter may make relatively larger shelters than those that venture out to eat, and those that retain frass in the shelter may also make larger shelters than those that eject their frass. Comparative studies of shelter-building taxa will help to elucidate the relative importance of various factors, including larval physical ability, feeding and defecation behavior, vulnerability to predators, leaf toughness, and internal microclimate, that may be involved in determining patterns of shelter construction.

The innate behavior patterns underlying the construction of different shelter styles are also worthy of further study. We have determined that the almost invariant size and shape of first instar shelters results from a prescribed pattern of larval movements and behaviors, in which larvae use their body length as a 'ruler', and lay down a silk 'blueprint' on the leaf surface prior to initiating cuts (Weiss et al. in prep.). We are currently investigating the behavior of *E. clarus* on leaves of different sizes and morphologies to determine the degree of plasticity in these seemingly hard-wired behaviors.

ACKNOWLEDGMENTS

We thank Mike Singer and Liz Bernays of the University of Arizona, Tucson, Deane Bowers of the University of Colorado, Boulder, Jennifer Maupin of Georgetown University, and an anonymous reviewer for helpful comments on the manuscript. We are grateful to Stephanie Brooks, Sharon Komarow, and Dhara Levers for capable help in the field. This work was supported in part by USDA NRI grant # 97-35311-5151 to MRW.

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Received for publication 7 September 1999; revised and accepted 2 October 2000.