Journal of Insect Behavior, Vol. 16, No. 4, July 2003 (© 2003)

Uniformity of Leaf Shelter Construction by Larvae of *Epargyreus clarus* (Hesperiidae), the Silver-Spotted Skipper

Martha R. Weiss,[1,2] Eric M. Lind,[1,3] Meg T. Jones,[1,4] Jeremy D. Long,[1,5] and Jennifer L. Maupin[1]

Accepted November 4, 2002; revised May 2, 2003

Larvae of the silver-spotted skipper, Epargyreus clarus *(Hesperiidae), construct shelters from leaves of their leguminous host plants, making four distinct shelter types that change predictably over larval ontogeny. Shelters built by first-instar larvae are located on the apical half of the leaflet and are almost invariant in size, shape, and orientation, suggesting a stereotypical process of shelter location and construction. We have determined that the regularity of these shelters results from a prescribed pattern of larval movements and behaviors, in which larvae use their body length as a "ruler" and employ silk not only as a building material but also as a template to guide the location of cuts in the leaf. Though lepidopteran larvae lack the sensitive antennae, long jointed appendages, and other measurement devices used by structure-building bees, wasps, and caddis flies, they can nonetheless use simple tools and behavioral patterns to produce characteristic and regular shelters.*

KEY WORDS: Lepidoptera; caterpillar; leaf-roller; leaf-tier; leaf-folder.

[1]Biology Department, 406 Reiss Science Building, Georgetown University, Washington, DC 20057.
[2]To whom correspondence should be addressed. Fax: (202) 687-5662. e-mail: weissm@georgetown.edu.
[3]Current address: The Nature Conservancy, 4225 North Fairfax Drive, Arlington, Virginia 22203.
[4]Current address: The National Geographic Society, 1145 17th St. NW, Washington D.C. 20036.
[5]Current address: School of Biology, Georgia Institute of Technology, 310 Ferst Drive Atlanta, Georgia 30332.

0892-7553/03/0700-0465/0 © 2003 Plenum Publishing Corporation

INTRODUCTION

Bird nests, spider webs, and termite mounds are just three of the best-known examples of structures constructed by animals from materials that they obtain from the environment and/or produce themselves. Among the insects, structure-building behavior is particularly well represented in the Orders Isoptera, Hymenoptera, Trichoptera, and Lepidoptera (Hansell, 1984).

Within Hymenoptera, some bees and wasps build structures that are remarkable in their precise geometry (Martin and Lindauer, 1966; Winston, 1987). Such exactitude is achieved using sensitive antennae and jointed appendages for measuring and assessing cell diameter and thickness (Winston, 1987). Other hymenopteran builders, including leaf-cutter bees and ants, similarly use their jointed legs to guide the trajectory of their leaf cuts and to assess the size and shape of the leaf panels (Lutz, 1929; Hasenkamp, 1974; Wetterer, 1990, 1991). The soft-bodied aquatic larvae of some caddis flies (Trichoptera) guide the cutting of leaf segments to be used in shelter construction with a pair of hooks and associated hairs on the posterior of the abdomen (Merrill, 1965; Hansell, 1984).

Many larval lepidopterans construct simple structures externally on a host plant by covering, tying, folding, or rolling plant structures with silk (Gaston *et al.*, 1991). While leaf structures built by some species may be rather variable in appearance, others are remarkably uniform. The process by which lepidopteran shelters are constructed has been little studied (Rensch, 1965, cited by Hansell, 1984; Fraenkel and Fallil, 1981; Fitzgerald *et al.*, 1991; Fitzgerald and Clark, 1994), and it is not known how these soft-bodied larvae, which lack the measuring devices of hymenopterans and trichopterans, produce such regular structures. With respect to the mechanics of shelter construction, Fitzgerald *et al.* (1991) demonstrated that leaf-rolling larvae utilize the axial retractive forces of stretched silk to generate the force required to pull leaf surfaces together.

All larval instars of the silver-spotted skipper (*Epargyreus clarus*; Hesperiidae) are obligate shelter-builders on their leguminous hosts. Larvae construct approximately five shelters, in four distinct styles, over the course of ontogeny (Lind *et al.*, 2001). First-, second-, and some third-instar larvae make what we call a Type 1 shelter, in which the animal cuts two incisions in the leaf and uses silk “hinges” to fold over the resulting flap, producing a tent-like structure. A peaked roof is formed in the tent by the tight silking of a small notch made perpendicular to one of the main cuts. For a given instar, Type 1 shelters appear to be almost invariant in size and shape, suggesting a stereotypical process of shelter construction. Shelter location and orientation on the leaflet also appear to be quite regular: three-quarters of shelters made by first- through third-instar larvae are located on the apical half of the leaflet (Lind *et al.*, 2001), and the orientation of the cuts relative to the axis of the leaflet is consistent from one shelter to the next.

In this paper we address two main questions: (1) How do *E. clarus* larvae build such regular shelters in the absence of specialized appendages for measuring? and (2) How do the larvae determine the location and orientation of larval shelters on the leaf? To understand better the processes of both shelter construction and site location, we videotaped *E. clarus* larvae from the time they were placed on fresh leaflets until both cuts were completed. To examine how larvae construct such apparently regular shelters, we first quantified the uniformity of shelters built by first-instar larvae and then assessed the relationship between larval size and shelter size both across and within stadia. To investigate the cues used by larvae to orient shelters on the leaflet, we manipulated leaf size and shape, and evaluated the effect, if any, on shelter orientation.

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, DC, area these large skippers fly from mid-April through October and commonly use black locust trees (*Robinia pseudoacacia*), kudzu vine (*Pueraria lobata*), or other legumes as hosts (Clark and Clark, 1951; Allen, 1997).

Collection and Care of Larvae

Larvae were obtained from eggs of adults captured on the Georgetown University campus and from meadow habitats on the Eastern Shore of Maryland from June through October 1997—1999. New adults were added to the colony at least weekly; thus the larvae were not inbred and were representative of wild populations in these areas. Adult butterflies were kept outdoors in 2-m^3 mesh cages, and were provided with fresh flowers as nectar sources; a sugar water feeder was also kept in the cage. Freshly cut kudzu leaves were provided for oviposition. Leaves bearing eggs were collected from the outdoor cage each morning, brought into the lab, and placed in $10 \times 14.5 \times 28$-cm clear plastic boxes with opaque lids. Larvae were housed in these boxes and were given fresh cut kudzu leaves as needed until pupation; boxes were cleaned daily.

Process of Site Location and Type 1 Shelter Construction

To determine the process by which first-instar shelters were located and constructed, we placed 10 hatchling larvae on kudzu leaflets under a stereoscope with a video camera and recorder attached and filmed them from their initial wanderings until at least the completion of the cuts. The resulting videotapes were then analyzed frame by frame, and caterpillar positions throughout shelter construction were traced off the screen. We made complete tracings from four individuals and used a number of additional videos to develop a better understanding of the shelter-building process. We also placed approximately 35 first-instar caterpillars on kudzu leaves in the field and observed their behavior in order to confirm the shelter-building patterns seen in the laboratory and to estimate the time required for site selection and shelter-building.

Uniformity of First-Instar Shelters

To assess the apparent uniformity of first-instar shelters, we unfolded and measured the first shelters constructed by 100 hatchling larvae. The dimensions measured were (1) top distance between cuts (TDBC), (2) bottom distance between cuts (BDBC), (3) Cut 1 (made first, generally closest to the apex of the leaflet), and (4) Cut 2 (made second, generally closest to the base of the leaflet) (Fig. 1b). For a subset of the larvae, we also noted the presence or absence of a notch, location of the notch, and height of the completed shelter above the leaf surface. Measurements were made with a Mitutoyo Absolute Digimatic caliper and were recorded to the nearest tenth of a millimeter.

Relationship Between Larval Size and Shelter Size Within and Across Instars

To establish whether Type 1 shelter size correlates with larval size within and across instars, we used a digital caliper to measure both larval length and shelter dimensions for 32 first-instar caterpillars that were removed from their shelters, placed on fresh leaves, and allowed to build new shelters every other day through the third instar. Because larvae generally construct shelters soon after they are placed on a leaf, the larval length recorded on a given day was associated with the dimensions of the next shelter built, rather than with the previously inhabited shelter.

To examine the relationship between shelter size and larval size, we performed a weighted least squares regression of top distance between cuts

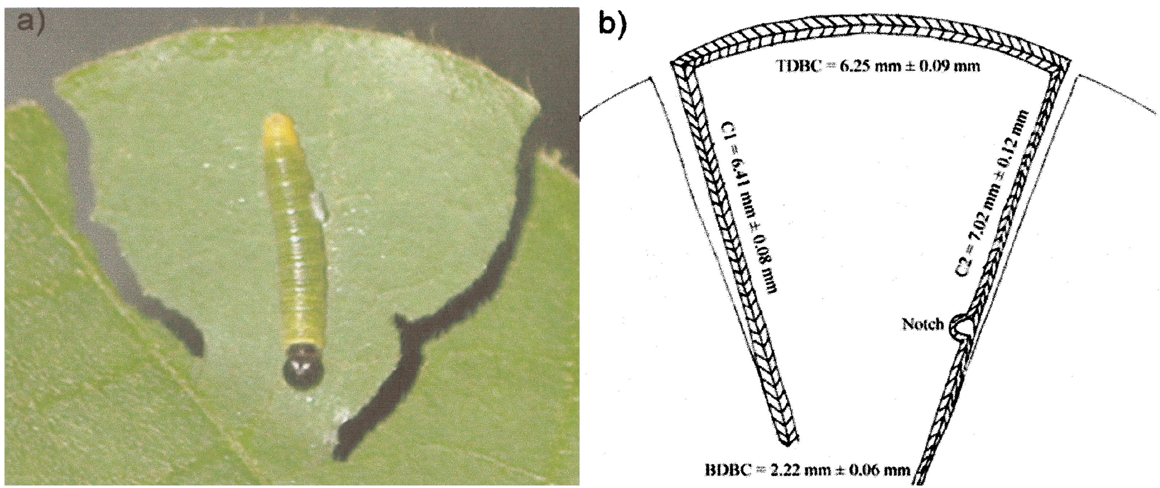

Fig. 1. (a) A second-instar larva has completed its cuts but has not yet folded the shelter. (b) The first shelters built by *E. clarus* larvae are extremely uniform in size and shape. Schematic diagram shows the mean dimensions (central line) ± standard error (hatching) of 100 shelters built by first-instar larvae soon after hatching. TDBC is the distance between the two cuts at the leaflet margin; BDBC is the distance between the bases of the two cuts; Cut 1 is made first and is usually closest to the leaflet apex; Cut 2 is made second, has a notch, and is closest to the leaflet base.

(TDBC) on larval length, using the number of shelters built by each individual larva as the weight (JMP; SAS Institute, Inc., 1999). To determine how shelter size changed within and across larval instars, we plotted mean TDBC against mean larval length for the first and last shelters built by larvae within each of the first three instars.

Orientation of the Shelter on the Leaflet

To investigate the cues used by the larvae to establish the orientation of the two cuts with respect to the orientation of the leaflet, we placed 30 hatchling larvae individually on intact kudzu leaves and another 30 larvae individually on 5.3-cm-diameter circles cut out of the center of kudzu leaflets. The larvae on intact leaves were placed inside clear plastic boxes ($10 \times 14.5 \times 28$ cm) with opaque lids, one leaf to a box, and the larvae on leaf circles were placed on a piece of slightly damp filter paper inside a lidded petri dish (8.5-cm diameter). Both sets of treatments were arranged on a laboratory bench under fluorescent illumination. Larvae were left to build sheters, and the orientation of the cuts on the intact leaflets and circles was later determined.

RESULTS

Process of Site Location and Type 1 Shelter Construction

Epargyreus clarus larvae construct their first shelters following a plan that is stereotypical in the order and content of its major steps. These are (1) selecting the site, (2) laying down an initial silk “template”, (3) making the first cut, (4) making the second cut and notch, and (5) folding and securing the shelter.

Wandering and Site Selection

Immediately after hatching, larvae begin wandering on the upper surface of the kudzu leaf (eggs are generally laid on that surface). Caterpillars cover much of the leaf surface, sometimes traveling on major veins, but spend most of the time walking around the leaf margin. They swing their heads from side to side over the leaf surface, laying down a single strand of silk as they travel. Eventually they stop wandering and settle on a location; once shelter-building is initiated, the larvae do not leave the “construction site” until the shelter is completed.

Laying-Down of the Initial Silk "Template"

Once a site has been selected, the larva begins to lay down a silk template, a mat of silk in a defined pattern, that will guide the location of the two cuts (Figs. 2a–c). This silked region occupies the area that will ultimately become the "ceiling" of the leaf shelter, and the cuts are made along its outer edges. In its center of the mat the caterpillar lays down a thicker, crescent-shaped silk pad, visible to the naked eye; the larva keeps its posterior end on or near this pad throughout the entire shelter-building process (Figs. 2 and 3).

The First Cut

The first cut is made along the edge of the silk template closest to the leaf apex. With its head at the leaflet margin and its anal segment resting on the center of the silk pad, the larva begins to chew an incision along the outside edge of the silk template (Fig. 2a). At various intervals the larva interrupts its cutting and moves around on the mat, depositing silk first in the eventual terminus of Cut 1, and later in the area that will define the location of Cut 2, before returning to the cut in progress (Fig. 2b). Six or seven cutting bouts are required to complete the crescent-shaped incision. In moving around on the mat, the larva frequently executes a distinctive "U-turn" motion, whereby it switches the location of its head and anal segment, so that it faces the opposite direction without changing its relative location on the leaf surface (Fig. 4).

The Second Cut and Notch

After completing Cut 1, the larva turns and moves toward the leaflet margin, where Cut 2 will begin. This cut follows the edge of the recently deposited silk template closest to the leaflet base and is completed in two to four cutting bouts. The first segment of Cut 2, which curves inward toward Cut 1, is often made in a single bout that results in an incision about 75% of the length of the completed Cut 1. The subsequent cutting bout begins adjacent to the end of the first incision, and continues down past the end of the first cut. The juncture of the two cutting bouts produces the characteristic "notch" in Cut 2 (Figs. 1b and 2d), and the ends of the two cuts define what we call the "hinge" area.

Silking, Folding, and Securing

After both cuts are completed, the larva begins laying short strands of silk across the notch and along the hinge area, parallel to the orientation of

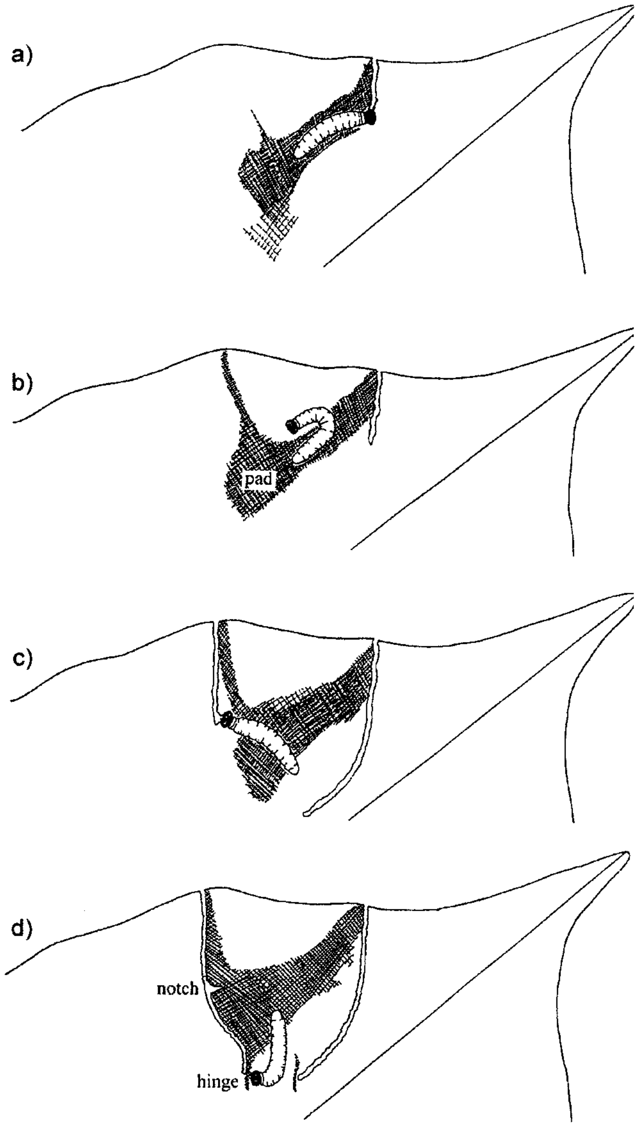

Fig. 2. Schematic overview of the silking and cutting process. (a) The larva makes the first cut along the edge of the silk nearest the leaflet apex. (b) The larva keeps its posterior region on a heavily silked central "pad"; it makes a U-turn to switch direction. (c) The larva makes the second cut, with notch, along the edge of the silk nearest the leaflet base. (d) When the larva silks the "hinge" region the leaf flap rises above horizontal.

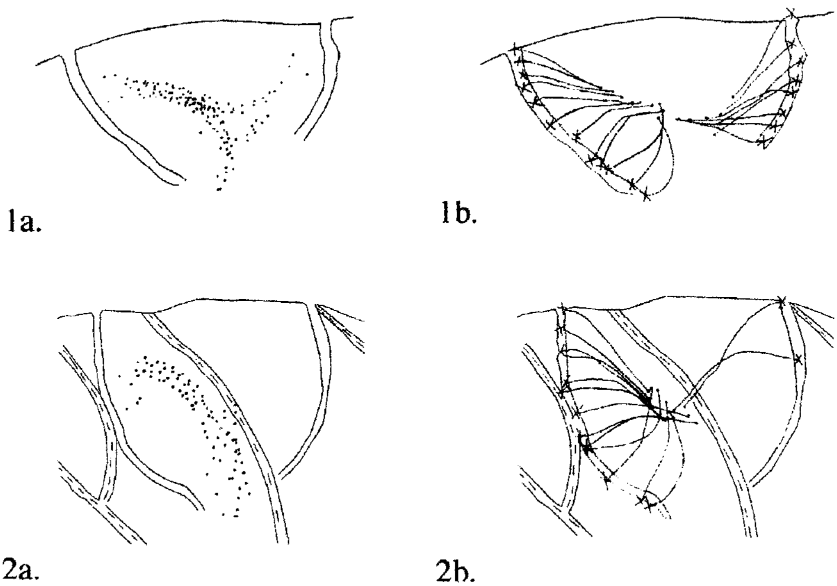

Fig. 3. Larval placement on the leaflet during the silking and cutting stages of shelter construction. Drawings show tracings of location of larval anal segment throughout silking and cutting (1a, 2a), and larval position during cutting (1b, 2b) (X, head location; dot, anal segment location) for two first-instar larvae.

the bases of the cuts (Fig. 2d). Multiple passes back and forth in both regions result in the deposition of heavy bands of silk; as the strands contract, a "pinch" is produced in the notch region, and the leaf flap is pulled up above the plane of the leaflet. Continued deposition of silk in the hinge area pulls the flap over until its margin touches the upper surface of the leaflet. Larvae continue to lay silk across the notch area continues even as the leaf flap is pulled up past vertical. Once the flap is folded over, the pinch at the notch becomes a peak in the roof of the shelter, and the larva begins to make silk "guy-wires" that will attach the edge of the flap to the leaflet surface. With its body resting on the ceiling of the shelter, the larva attaches a strand of silk to the edge of the flap and then affixes the other end to the leaf surface. Many passes back and forth along the strand produce a thick guy-wire. A first-instar shelter is generally fastened to the leaf surface by two to four guy-wires.

Throughout the shelter-building process, the larva periodically stops its activity and rests for several minutes (and up to 30 min) at a time. Periods of inactivity may occur after each cut is completed, after the leaf flap has been raised to about 90°, and after the shelter is inverted, but prior to construction

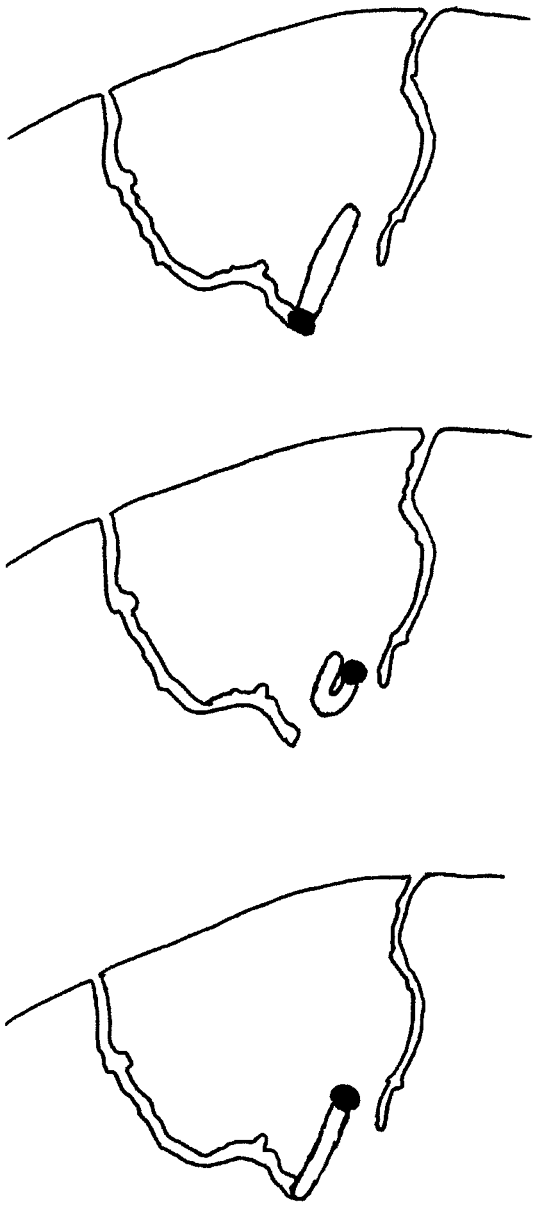

Fig. 4. Larval "U-turn". In a characteristic movement, the larva switches the position of its head and anal segment, without changing its relative location on the silk pad.

of the guy-wires. Once the shelter is finally completed, the larva spends about 95% of its time resting inside on the ceiling, with its head located in the peak of the roof (Lind *et al.*, 2001).

Field Observations

First-instar larvae placed on kudzu leaves in the field constructed their shelters using the same behaviors, in the same order, as did larvae observed in the laboratory. Field larvae wandered for a median time of 32 min (range = 11 min–1 h 55 min; $N = 33$ larvae) before they began the first cut. Median time to completion of a shelter by a first-instar larva, defined as the point at which the edge of the leaf flap contracted the leaflet surface, was 2 h 23 min ($N = 21$) after initiation of cutting. Larvae continued to add additional guy-wires between the leaf flap and the leaflet surface even after the shelter was considered complete.

Uniformity of First-Instar Shelters

Shelters constructed by hatchling first-instar caterpillars are highly regular in shape and size (Fig. 1b). For the hundred shelters measured, the standard error was less than 3% of the mean for each of the four dimensions; for TDBC, the standard error was less than 0.1 mm, or 1.4% of the mean TDBC. Larvae cut a notch on 52 of 53 shelters examined; all notches were made on Cut 2 and were located 64.8 ± 2.1% (mean ± SE) of the distance from the leaf margin to the base of the cut ($N = 15$). Shelter peaks were a mean 2.6 ± 0.05 mm above the leaf surface ($N = 22$).

Relationship Between Larval Size and Shelter Size Within and Across Instars

TDBC and larval length show a strong positive correlation (weighted least-squares regression, $R^2 = 0.814$, $F = 525.8$, $P < 0.0001$; mean weight = 3.8 ± 1.45 measurements/larva) (Fig. 5). The mean TDBC of the last shelters built by larvae of a given instar was noticeably greater than that of the first shelters within the instar, whereas there was little difference between TDBC of shelters built just before and just after the molt (Fig. 6).

Orientation of the Shelter on the Leaflet

Twenty-eight of the 30 larvae placed on an intact leaf completed shelters, and in all cases, Cut 2 (with the notch) was located on the edge of the shelter

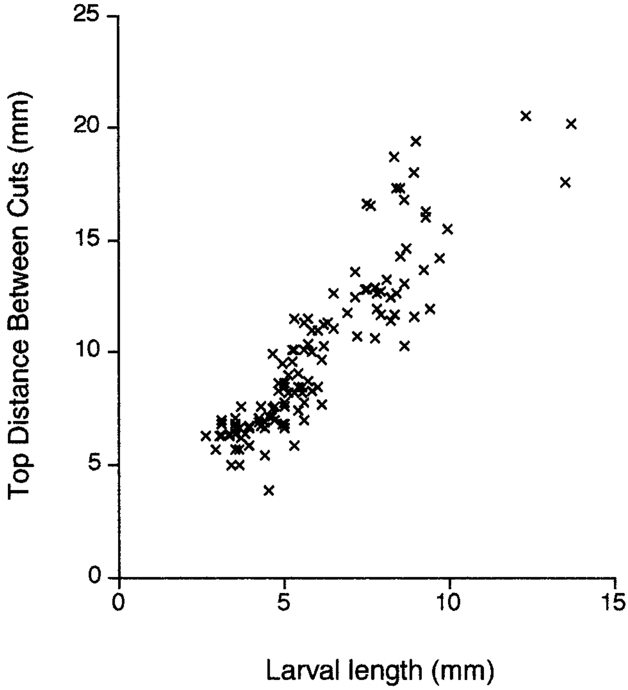

Fig. 5. Top distance between cuts (TDBC) is highly correlated with larval length. Thirty-two first-instar caterpillars were removed from their shelters, placed on fresh leaves, and allowed to build new shelters every other day through the third instar; weighted least-squares regression, $R^2 = 0.814$, $F = 525.8$, $P < 0.0001$. The number of shelters built by each individual larva was used as the weight; mean weight $= 3.8 \pm 1.45$ measurements per larva.

closest to the base of the leaflet. Twenty-five of the 30 “circle” treatment caterpillars completed shelters, and of those, Cut 2 was located closest to the leaflet base in 20 shelters. A chi-square test of independence demonstrated that larvae in the intact and circle treatments differed in the orientation of their shelters ($\chi^2 = 6.17$, 1 df, $P < 0.05$). Within the circle treatment, however, a chi-square goodness-of-fit test showed that the second cut was more likely to be oriented toward the base of the leaf than expected by chance ($\chi^2 = 9.0$, 1 df, $P < 0.01$).

DISCUSSION

Lepidopteran larvae, though lacking many of the tools employed by hymenopteran and trichopteran builders, are nonetheless able to construct

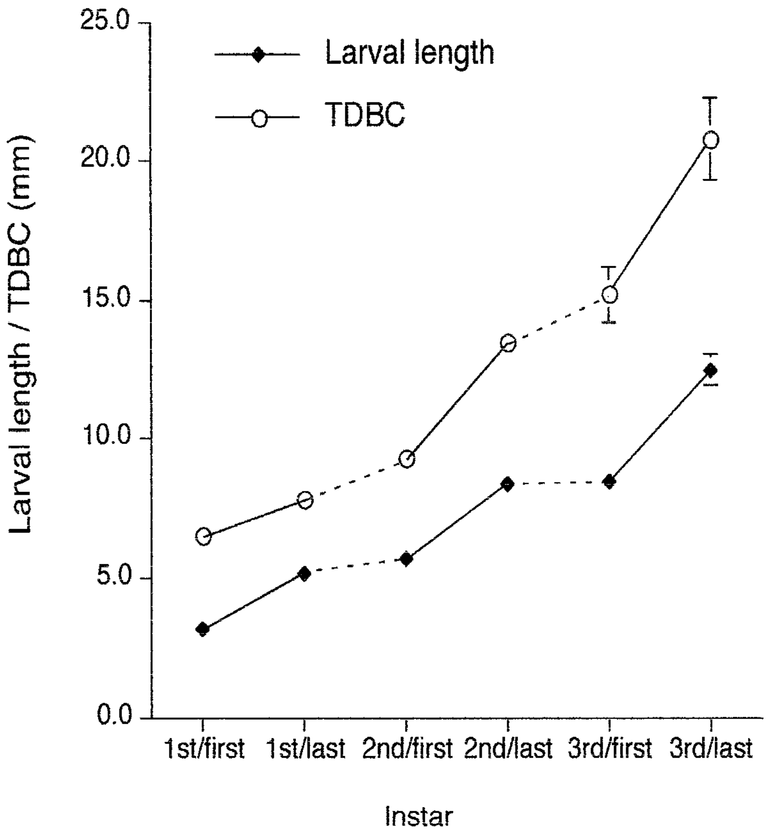

Fig. 6. Mean TDBC increases as mean larval length increses within a given larval instar; both measurements change little across the molt. Each point represents the mean values (±SE) for caterpillars forced to build a new shelter every other day; larval *N*s decrease over ontogeny (first instar, mean $N = 30$; second instar = 26; third instar = 9). Solid lines connect first and last shelters (and associated larval measurements) within an instar; dashed lines connect points across a molt.

characteristic and regular structures (Hansell, 1984). When 100 hatchling *E. clarus* larvae built 100 shelters, the standard error of their TDBCs was less than 0.1 mm (1.4% of the mean), a degree of precision rivaling that achieved by some bees and wasps. Our results suggest that *E. clarus* larvae are able to produce such regular shelters by laying down a stereotypical pattern of silk and maintaining a fixed location relative to the central silk pad when making cuts. While silking and cutting, the posterior end of the larva generally remains on the central crescent-shaped silk pad; "U-turn" movements allow the larva to reverse direction while maintaining its position relative to the margins of the template. Larval length then determines the location of the cuts, such that a larva of a given length produces a shelter of predictable dimensions.

The increase in TDBC within an instar appears to be correlated with the increase in larval length that occurs over the same period. Larvae do not increase significantly in length across the molt, nor does TDBC increase markedly between the last shelter built in one instar and the first shelter built in the next. Though larvae undergo a threefold increase in body length across three instars, the ratio of TDBC to larval length remains relatively constant (range, 1.6–2.1) over the same period. These results strongly suggest that cut location, and hence TDBC, is dependent on larval body length.

It is not clear what process guides initial site selection by an *E. clarus* larva or how larvae establish the orientation of the shelter with respect to the orientation of the leaflet. Prior to initiation of silking and cutting, larvae wander extensively on the leaf, in particular, around its periphery; field larvae wandered for a median of 32 min before settling on a site. Such wandering behavior is seen in other shelter-constructing taxa. Several species of weevils that cut and roll leaves to form a "cradle" for their eggs determine the site at which to initiate cutting through stereotyped walking behaviors around the circumference of the leaf (Sakurai 1988a, b).

With respect to shelter orientation, *E. clarus* larvae placed on intact leaflets oriented the notches of their shelters toward the leaflet base 100% of the time, while those placed on the leaf circles did so 80% of the time, despite the absence of petioles and of normal leaflet curvature. These results suggest that, while features of the intact leaflet play a role, larvae are able to use other cues (e.g., venation pattern or orientation of leaf hairs) to determine shelter orientation.

Shelter-building behaviors in the few lepidopteran species for which the process has been investigated share some features with those of *E. clarus*. A thyridid caterpillar that rolls a leaf into a tube first makes a cut of a fixed orientation and length on the leaf, positions its body with respect to the location of the cut, and stretches out from that position to deposit silk strands and make additional cuts (Rensch, 1965, cited by Hansell, 1984). Larvae of the rice leaf roller, a pyralid, orient their bodies parallel to the long axis of the leaf, and reach from this position to lay down strands of silk between the leaf margins. Behaviors used by some lepidopterans in building their cocoons also resemble those employed by larvae in constructing their shelters. The cecropia silkworm, for example, makes a cocoon that is pointed at the top and rounded at the bottom by repeating two basic movements that involve stretching its body out and attaching silk strands, while keeping its posterior end in a fixed location (Van der Kloot and Williams, 1953). In one set of movements the head is oriented upward; in the other, downward.

The cocoon-lining behavior of the silkworm also involves a simple repeated pattern of movement (Lounibos, 1975).

Despite the regularity of first-instar shelters, *E. clarus* larvae show some plasticity in their shelter-building behavior, both over larval ontogeny and in response to different leaf substrates. As described above, a given larva may construct houses in four distinct styles prior to pupation; the change in shelter styles is presumably innate and seems to be linked to larval size (Lind *et al.*, 2001). *E. clarus* larvae can also adjust their building behavior to some extent in response to the materials available. They use as hosts plants in the pea family, the leaves of which vary in size and degree of dissection. Leaves of kudzu are once-pinnately compound, with only three relatively large leaflets per leaf, while leaves of *Robinia*, another common host of *E. clarus*, are twice-pinnately compound and are composed of many smaller, more dissected leaflets. While first-, second-, and third-instar larvae build shelters that are small enough to fit on a single leaflet of either kudzu or *Robinia*, fourth and fifth instars build shelters that are considerably larger. On kudzu they join two leaflets into a roomy pocket, but on *Robinia* they must silk and pull together from two up to four or five leaflets to make a shelter of sufficient size. Larvae placed on a single kudzu leaflet that has been cut so that it resembles a dissected *Robinia* leaf will pull together several flaps to make a shelter.

The remarkable uniformity of shelters built by *E. clarus* and other lepidopteran larvae illustrates the potential for precise measurement and construction through use of simple tools and behavior patterns. Further studies of shelter-building lepidopterans are likely to reveal interesting variations on the themes of silk as template and body as a ruler. Comparison of the behaviors of larvae that make relatively haphazard leaf ties or folds with those that make highly stereotypical structures would be particularly interesting.

ACKNOWLEDGMENTS

We are grateful to Sharon Komarow for capable assistance in the field and lab and to John McClure for assistance with preparation of the figures. Mike Singer, Elizabeth Bernays, John McClure, Megan Brooks, Erin Wilson, Eliza Beardslee, and two anonymous reviewers provided useful comments on the manuscript. USDA NRI Grant 97-35311-5151 and the Washington Biologists' Field Club provided financial support.

REFERENCES

Allen, T. J. (1997). *The Butterflies of West Virginia and Their Caterpillars*, University of Pittsburgh Press, Pittsburgh.

Clark, A. H., and Clark, L. F. (1951). *The Butterflies of Virginia*, Vol. 116, Smithsonian Institution, Washington, DC.

Fitzgerald, T. D., and Clark, K. L. (1994). Analysis of leaf-rolling behavior of *Caloptilia serotinella* (Lepidoptera: Gracillariidae). *J. Insect Behav.* **7:** 859–872.

Fitzgerald, T. D., Clark, K. L., Vanderpool, R., and Phillips, C. (1991). Leaf shelter-building caterpillars harness forces generated by axial retraction of stretched and wetted silk. *J. Insect Behav*. **4:** 21–32.

Fraenkel, G., and Fallil, F. (1981). The spinning (stitching) behaviour of the rice leaf folder, *Cnaphalocrocis medinalis. Entomol. Exp. Appl*. **29:** 138–146.

Gaston, K. J., Reavey, D., and Valladares, G. R. (1991). Changes in feeding habit as caterpillars grow. *Ecol. Entomol*. **16:** 339–334.

Hansell, M. H. (1984). *Animal Architecture and Building Behavior*, Longman, London and New York.

Hasenkamp, K. R. (1974). Studies on the ecology, physiology and behaviour of leaf-cutting bees (*Megachile). Forma Functio*. **7:** 139–78.

Lind, E. M., Jones, M. T., Long, J. D., and Weiss, M. R. (2001). Ontogenetic changes in leaf shelter construction by larvae of *Epargyreus clarus* (Hesperiidae), the silver-spotted skipper. *J Lepidop. Soc*. **54:** 77–82.

Lounibos, L. P. (1975). The cocoon spinning behavior of the Chinese oak silkworm, *Antheraea pernyi. Anim. Behav*. **23:** 843–53.

Lutz, F. E. (1929). Observation on leaf-cutting ants. *Am. Mus. Novit*. **388:** 1–21.

Martin, H., and Lindauer, M. (1966). Sinnesphysiologische Leistungen bein Wabendau der Hongibeine. *Z. vergl. Physiol*. **53:** 372–404.

Merrill, D. (1965). The stimulus for case building behavior in caddis worms. (Trichoptera). *J. Exp. Zool*. **158:** 123–32.

Rensch, B. (1965). Die Blattrolltatigkeit der Raupe von *Striglina scitaria* (Thyrididae) und eines anderen tropischen Schmetterlings. *Z. Tierpsychol*. **22:** 6–14.

Sakurai, K. (1988a). Leaf size recognition and evaluation of some attelabid weevils. (1) *Chonostropheus chujoi. Behaviour* **106:** 279–298.

Sakurai, K. (1988b). Leaf size recognition and evaluation of some attelabid weevils. (2) *Apoderus balteatus. Behaviour* **106:** 301–316.

Scott, J. A. (1986). *The Butterflies of North America; A Natural History and Field Guide*, Stanford University Press, Stanford, CA.

Van der Kloot, W. G., and Williams, C. M. (1953). Cocoon construction by the *Cecropia* silkworm. I. The role of the external environment. *Behaviour* **5:** 141–156.

Wetterer, J. K. (1990). Load-size determination in the leaf-cutting ant, *Atta cephalotes. Behav. Ecol*. **1:** 95–101.

Wetterer, J. K. (1991). Allometry and the geometry of leaf-cutting in *Atta cephalotes. Behav. Ecol. Sociobiol*. **29:** 347–351.

Winston, M. L. (1987). *The Biology of the Honey Bee*, Harvard University Press, Cambridge, MA.