

Life history and ecological role of the xylophagous aquatic beetle, *Lara avara* LeConte (Dryopoidea: Elmidae)

R. J. STEEDMAN and N. H. ANDERSON Entomology Department,
Oregon State University, Corvallis, Oregon

SUMMARY. 1. This study documents the life history of the xylophagous elmid beetle, *Lara avara*, and estimates its contribution to wood degradation in Oregon streams. The life cycle was found to be 4 to 6 or more years long, with all but 2–3 months of that spent in the larval stage.

2. Larvae grow through seven instars, taking about 1 year for instars 1–3, and from 3 to 5 or more years for instars 4–7.

3. Last-instar larvae leave the water to pupate. Adults live approximately 3 weeks and occur from May to August. The eggs are deposited on submerged wood.

4. Larvae probably obtain their nutrition by absorbing substances liberated into decaying wood by microbial activity. They do not produce their own cellulase, nor do they have a symbiotic gut flora similar to that of xylophagous crane-fly (Tipulidae) larvae.

5. Faecal production by *L. avara* larvae averaged 13% dry body wt d^{-1} . This yields an estimate of faecal production of $1.6 \text{ g m}^{-2} \text{ y}^{-1}$ in Oregon Coast Range streams (about 0.3% y^{-1} of wood standing crop).

Introduction

Lara avara LeConte is a riffle beetle that exploits wood debris for food and habitat. The larvae feed on the surface of submerged, decaying wood, whereas adults are found on damp wood just above the water line. *L. avara* is distributed in montane streams of western North America from British Columbia to California and eastward to Wyoming and Colorado (Brown, 1975). *Lara* is the only Nearctic genus in the subfamily Larinae, which contains 107 species in twenty genera (Brown, 1981). Another species, *L. gehringi* Darlington, has

been described, but may be a synonym (H. P. Brown, personal communication).

In previous studies we have demonstrated that *Lara* is one of the major taxa of insects involved in degradation of wood debris in Oregon streams (Anderson *et al.*, 1978; Anderson & Sedell, 1979; Dudley & Anderson, 1982; Anderson, Steedman & Dudley, 1985). However, its quantitative role in wood decomposition is poorly understood and, therefore, the objectives of the present study were to describe the life cycle of *Lara avara* and to measure its population densities and feeding rates. The life span is at least 3 years (Anderson *et al.*, 1978), so it was impractical to rear *L. avara* through the larval stage. Thus our approach was to determine the number of

Correspondence: Dr N. H. Anderson, Entomology Department, Oregon State University, Corvallis, Oregon 97331, U.S.A.

larval instars and then to develop indirect methods to estimate the duration of each instar.

Methods

Collections were taken in several small streams in the Coast Range of western Oregon, U.S.A., from 1980 to 1982. Most of the study was conducted at Berry Creek, Benton Co., 15 km north of Corvallis. This is a second-order stream draining the foothills on the eastern side of the Coast Range. Samples were taken from a 460 m controlled-flow section where the riparian vegetation is primarily red alder (*Alnus rubra* Bong.) and bigleaf maple (*Acer macrophyllum* Pursh). This section of Berry Creek provides excellent *L. avara* habitat because a diversion dam at the upstream end has prevented freshets since 1961, allowing branch wood to accumulate in the channel. Warren *et al.* (1964) provide a more complete description of Berry Creek.

Because *L. avara* larvae occur almost exclusively on pieces of submerged, decaying wood, they are not readily collected with conventional benthic sampling devices. For general collecting we lifted sticks from the water and examined them for larvae. This method was approximately 50% efficient when compared with slowly drying the sticks in the laboratory (Steedman, 1983a). Thus, for more accurate population estimates, we wrapped the sticks in plastic bags and transported them to the laboratory. The sticks were placed on end in separate buckets, and allowed to dry 1–2 weeks. As the sticks dried, *L. avara* larvae of all instars left their feeding grooves and followed the increasing moisture gradient to the bottom of the stick, where they eventually died and fell to the bottom of the bucket. Close scrutiny of dried sticks usually failed to yield additional larvae. For studies requiring live larvae (mark–recapture, laboratory rearing, etc.), general collections of 50–150 individuals were made monthly at Berry Creek from October 1980 to October 1981. A smaller series of larvae was collected from Yew Creek, a second-order stream 20 km south-west of Corvallis.

We used an ocular micrometer at 25× to measure larval head-capsule widths for instar

analysis. Size–frequency histograms were prepared from measurements of 1200 larvae. The number of instars and their approximate size range were determined by inspecting peaks in the frequency distribution.

Estimation of instar duration by mark–recapture

A mark–recapture study was started in March 1981 with about 100 *L. avara* larvae from Berry Creek. The head-capsule width of each larva was measured and then the thorax was marked with red nail polish in a positional code for date of capture. The larvae were returned to Berry Creek and placed on an isolated group of five flagged sticks that had been cleared of all visible *L. avara*. The basis of this approach was that a larva would retain a mark only until its next moult. That is, after it moults it cannot be ‘recaptured’ as a marked larva. The interval between initial marking and the last date of recapture is a minimum estimate of instar duration.

At monthly intervals for 10 months we repeated the above procedure, collecting all the marked and unmarked individuals from the flagged sticks and measuring their head capsules. The marking date of previously captured larvae was recorded, and unmarked larvae were coded according to the current date. *L. avara* larvae may feed for many months on a suitable stick, but are capable of colonizing new sticks. For this reason there was a gradual loss of larvae from the flagged sticks. To compensate, a sample size of about 100 was maintained on the flagged sticks by marking additional larvae, as necessary, at each collection date. Over the course of the study, 723 larvae in instars 4–7 were marked. Because the ‘field picking’ method was used throughout, few early-instar larvae were collected and marked.

During the first 10 months of the mark–recapture study, unmarked larvae could occur on the flagged sticks because of moulting, accidental mark loss, undetected previous presence, or because of immigration by drifting from upstream. There were no sticks downstream in close enough proximity to provide a likely source of colonizing larvae. Just prior to the January 1982 sample, we placed a net upstream from the flagged sticks to prevent

immigration as a source of unmarked larvae. Commencing with the January sample, no new larvae were placed on the flagged sticks. This allowed us to estimate moulting and drifting rates of an isolated population, in subsequent months.

Field density estimates

We collected fifty sticks from Coast Range streams and obtained total counts of larvae by drying the sticks. Larval biomass was calculated from a regression equation that related dry weight (mg) to head-capsule width (mm): $\ln \text{ dry weight} = 1.304 + 3.629 \ln \text{ head-capsule width}$ ($n=189$, $r^2=0.95$). The sticks included hardwood and conifer wood in various stages of decay, ranging in size from 2 to 10 cm in diameter, and 25–200 cm long. Stick volume was estimated by displacement, after soaking to reduce water absorption during the measurement. Surface areas were approximated by assuming that the sticks were cylindrical. The sticks were weighed to the nearest gram after oven drying at 60°C.

Laboratory studies

Field-collected adults and larvae were maintained in a cool room at 12–13°C with a photoperiod of 16 h light and 8 h dark. Adults were placed in a screened cage, and partially submerged sticks were provided for use as a food source and oviposition site. The larvae were kept on stream-conditioned wood in shallow trays or dishes of aerated water.

To estimate the feeding rate of larvae we measured faecal production in trays supplied with filtered stream water, in an unheated building with a natural photoperiod. Twenty plastic trays, 15×38 cm, were arranged in a four-tiered dripper (Anderson, 1973). Ten large or twenty small larvae were placed in each tray and allowed to feed on a single piece of stream-conditioned alder or conifer wood for 1–3 weeks. Trays containing sticks without larvae were used to control for non-feeding particle production. A mean water temperature for each run was estimated from max–min thermometer readings taken at 1–3 day intervals. Feeding trials were run in spring, summer and late autumn to encompass most of the seasonal temperature range.

Groups of larvae used in the faecal production study were blotted dry and weighed on an analytical balance before and after each run. A regression equation was used to convert live weights to dry weights: $\text{dry weight (mg)} = -0.178 + 0.379 \text{ wet weight (mg)}$ ($n=100$, $r^2=0.98$). Daily instantaneous growth rates were calculated from initial and final mean individual weights for groups of larvae that had fed for 30–40 days:

$$G = [\ln (W_t/W_0)]/t \quad (1)$$

from the logarithmic transformation of $W_t = W_0 e^{Gt}$, where G = daily instantaneous growth rate; W_0 = initial dry weight (g); W_t = dry weight (g) at time t (days); and e = base of natural logarithms. G is the slope of the line resulting when \ln (dry weight) of an organism showing exponential growth is plotted against time in days.

At the end of each run the sticks were removed from the trays, and all particulate material collected by filtering the water through glass fibre filters (effective pore size 2.7 μm) on a Millipore apparatus. The number of exuviae resulting from moults during the run was recorded for each tray. Dry (48 h at 60°C) and ashed (12 h at 450°C) weights of the particulate material were determined on an analytical balance, and corrected for control weights.

We measured oxygen uptake of fourth and sixth instar larvae in a differential respirometer, at 10°C. 5 ml of dechlorinated water and a 1×1×3 cm piece of conditioned wood were placed in a 15 ml reaction flask. Oxygen uptake by the wood was measured for 3–4 h, then seven or eight larvae were added, and O_2 uptake was measured again for 3–4 h. Two replicates of instar 4 and three replicates of instar 6 were used.

Life stages of *Lara avara*

Adults were found in the spring and summer above the water surface on sticks and logs. The dates of collection for specimens in the Oregon State University collection span 26 May to 27 August. Peak adult abundance is probably in June. Females are larger and heavier than males. Dry weight of two gravid females was 5.3 and 5.5 mg, while four males ranged from 2.7 to 4.3 mg.

Adults feed by sweeping the surface of moist wood with their mouthparts. Their mandibles are thinner and more blade-like than those of the larvae and appear to be used for scraping rather than gouging. Adult guts contained diatoms, fungal spores and hyphae, but little wood tissue.

Laboratory-reared females had no ovarian development at emergence. Two field-collected females that were dissected contained 100–150 eggs, which were white, ovoid (0.54×0.42 mm) and had a mean dry weight of 0.013 mg. Both field-collected and reared adults lived for 2–3 weeks in the laboratory. Although the adults copulated frequently, no eggs were obtained during the present study. In earlier trials, N. H. Anderson (unpublished data) obtained about twenty eggs from captive adults. These were loosely attached to sticks near the water line, and hatched after 3–4 weeks of incubation.

The size–frequency histograms for head-capsule width suggest that there are seven larval instars (Fig. 1). In the Yew Creek series

the final instar had two peaks, which is consistent with the sexual dimorphism observed in adults. Head-capsule width of reared instar 1 larvae was 0.28 mm, which corresponds to the smallest size of field-collected larvae (Fig. 1). Larval exuviae associated with reared pupae had head-capsule widths of 1.30–1.40 mm, which is in the upper range of instar 7.

In the monthly samples from Coast Range streams all instars were present in all seasons and in most months (Fig. 2). Instars 1–3 were absent from some samples, especially in the spring. Their under-representation is at least partially due to our missing them with the ‘field picking’ technique. In all collections when larvae were collected by drying the sticks, some early-instar larvae were obtained. Evidence for annual cohort recruitment is provided by the peak in relative abundance of instar 2 in August and September, when larvae from eggs laid in early- or mid-summer would have completed one instar. The duration of the larval stage is considered in detail in the next section.

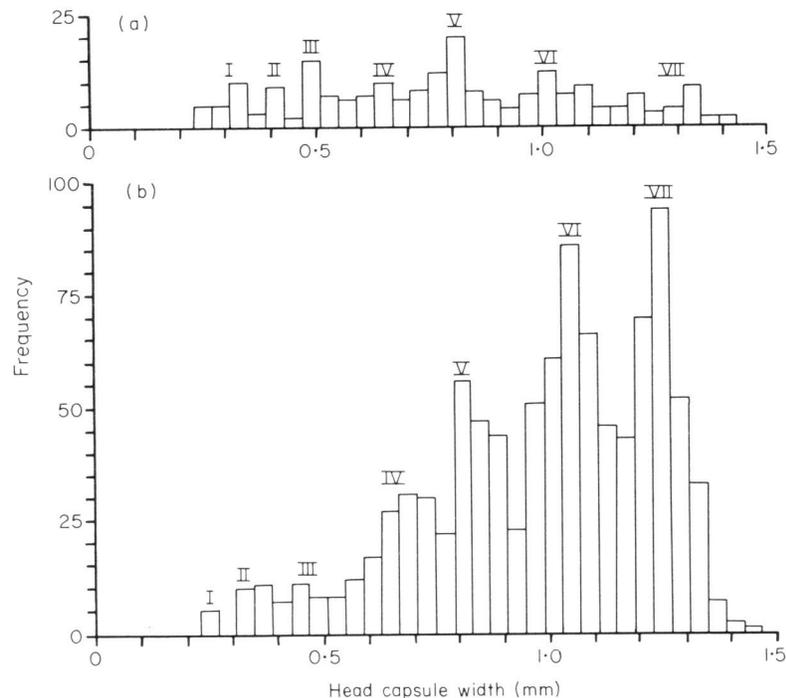


FIG. 1. Frequency distributions of head capsule measurements of *Lara avara* larvae from (a) Yew Creek ($n=213$) and (b) Berry Creek ($n=981$). Roman numerals indicate instars, as represented by peaks in the distribution.

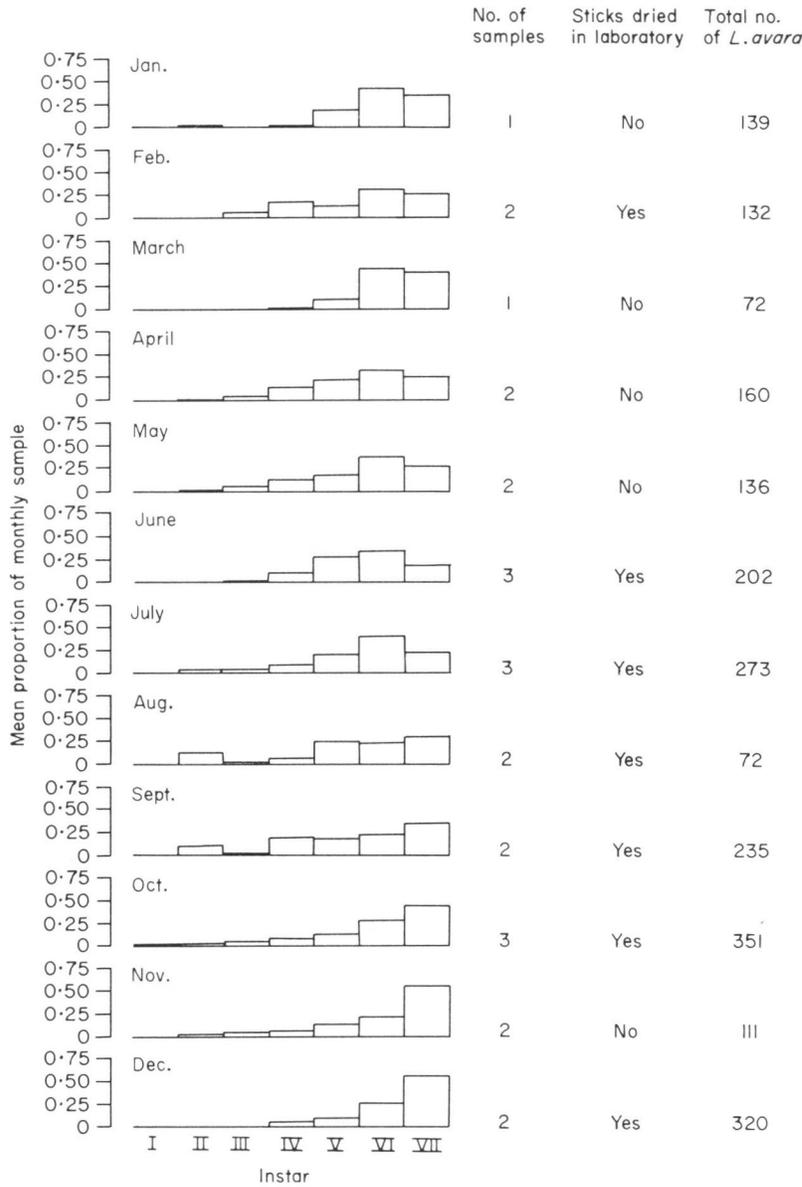


FIG. 2. Relative abundance of *Lara avara* larval instars in monthly collections of sticks from Coast Range streams, 1981-83.

Pupae of *L. avara* were first discovered on 25 June 1981 at Berry Creek. They were buried in small cells under moss on the upper surface of a partially submerged log. The pupa is described by Steedman (1983b).

The final-instar larvae leave the water for pupation. Transport to shore or projecting surfaces may be facilitated by buoyant tracheal air sacs that develop during the last instar.

These sacs occupy much of the abdomen, and their volume is controlled by the tergo-sternal muscles. The larvae are able to float when the tergo-sternal muscles are relaxed, allowing the sacs to expand to their full volume.

L. avara larvae probably require a period of drying to trigger pupation. Many attempts were made to induce pupation in the laboratory by providing larvae with partially sub-

merged sticks, and by manipulating temperature and light regimes. One group of last-instar larvae was maintained for almost 2 years, until they finally died without pupating. In 1982, eight larvae transformed to pupae when the contents of their rearing containers were allowed to dry to the point where no surface moisture was present. We propose that in the field, dry weather in early summer triggers pupation of larvae that have been out of the stream for some time. Some larvae do not leave the stream in the first year of their final instar. Several last-instar larvae that we marked in the winter or spring were recaptured at intervals throughout the next year.

Duration of larval instars

To determine the length of the full life cycle, we had to resort to indirect approaches in estimating duration of the larval instars. We reasoned that if different data sets or several methods of analysis were used, a 'best estimate' of instar duration could be obtained. Instars 1–3 were under-represented in most

field collections, so the estimates are only for instars 4–7. Laboratory rearing provided some data for the early instars.

Estimates of instar duration from mark-recapture information

The oldest mark recovered in each instar provides an under-estimate of maximum instar duration, since the mark was applied after the start of the instar, and recovered before the end of the instar. The age of the oldest mark recovered was 2, 11, 15 and 15 months for instars 4, 5, 6 and 7, respectively.

We assumed that while the net was in place at the head of the riffle, moults would be the major source of unmarked larvae on the flagged sticks, and that the appearance of an unmarked larva indicated a moult since the last collection. The inverse of frequency of moulting per individual per month yields estimates of instar duration of 4, 5 and 18 months for instars 4, 5 and 6, respectively (Table 1). Data from collections of exuviae in the drippery trays, analysed in the same manner, gave estimates of 6 months for instar 4 and 4 months for instar 5 (Table 1).

TABLE 1. Instar duration of *Lara avara* larvae, calculated from the frequency of moults estimated either in the field (by the accumulation of unmarked individuals in a marked group) or in the laboratory (by the collection of exuviae). Instar duration was estimated by dividing '*L. avara* months' (the number of individuals times the period observed) by the number of moults inferred.

Moult	No. of moults inferred	<i>L. avara</i> months	Instar duration (months)
Field			
4th to 5th	3	12	4
5th to 6th	13	67	5
6th to 7th	11	203	18
Laboratory			
4th to 5th	17	94	6
5th to 6th	21	88	4

TABLE 2. Dry weights, in mg, of instars 4–7 *Lara avara* larvae and their exuviae. Total change in weight from one instar to the next, including exuviae, is shown.

Instar (I)	Larval wt			Exuviae wt		Total wt change (I to I+1)
	\bar{x}	SE	<i>n</i>	\bar{x}	<i>n</i>	
4	0.81	(0.058)	39	0.14	2	1.63
5	2.30	(0.164)	40	0.29	16	1.68
6	3.69	(0.250)	24	0.58	17	6.58
7	9.69	(0.593)	30			

TABLE 3. Mean growth rates of instars 4-7 *Lara avara* larvae in drippery trays.

Instar	No. of larvae	Mean temp. (°C)	Daily instantaneous growth rate
4+5	20	7	0.0034
6	16	11	0.0020
7	12	11	0.0012

TABLE 4. Summary of instar duration estimates (months) for instar 4-7 *Lara avara* larvae. N.D.=no data.

Method	Instar			
	4	5	6	7
Field (1) Oldest mark	2	11	15	15
(2) Accumulation of unmarked larvae	4	5	18	N.D.
Laboratory (3) Frequency of moulting	6	4	N.D.	N.D.
(4) Weight gain in drippery	10	5	16	N.D.
Range of estimates	2-10	4-11	15-18	15-?

Estimates of instar duration from larval weight gain

If estimates of the mean weight of successive instars (W_i, W_{i+1}) (Table 2), and daily instantaneous growth rate (G) (Table 3) are known, then instar duration (t) (days) can be calculated for instar i :

$$t = \ln(W_{i+1}/W_i)/G \quad (2)$$

These estimates of instar duration were 10, 5 and 16 months for instars 4-6, respectively.

Total duration of the larval stage

The summed duration of instars 4-7, based on estimates from the mark-recapture study, collections of exuviae in the drippery and from growth rates, ranged from 3 to 5 years (Table 4). The different methods give a wide range of estimates for instars 4 and 5, but the data still conform to the expected trend of the later instars (6 and 7) being of longer duration than the middle instars. Because the larval/pupal moult occurs out of water, methods 2 and 3 in Table 4 were not applicable to determining the duration of the final instar.

We estimate that *L. avara* larvae require a year to grow through the first three instars (>3 months for instars 1 and 2; >4 months for instar 3). This is based on observations of fifteen small larvae reared in the laboratory for 4 months on stream-conditioned wood at 12°C. During this period, two each of instar 1 and 2,

and eight instar 3 larvae were observed to moult.

In summary, based on data from laboratory rearing and the field study, we conclude that *L. avara* has a long and variable life span, with the larval stage lasting 4 to 6 or more years.

Feeding and digestion

The larvae have robust, scoop-shaped mandibles that slice off thin (about $20 \times 100 \times 200 \mu\text{m}$) pieces of wood. The proventriculus is weakly developed, and does not reduce the size of ingested wood particles. The mid- and hind-gut form a straight tube, with no diverticula or 'fermentation chamber', to maintain a symbiotic gut flora.

Permanent microscopic mounts were made of fore-, mid- and hindgut contents of eight *L. avara* larvae from laboratory stocks. When wood particles from the different regions of the gut were compared under a compound microscope, no differences in particle size, texture, or general appearance were observed. Further, the microscopic appearance of wood in faecal particles produced by these larvae was similar to that in scrapings taken from the conditioned layer of the sticks that had been fed upon.

Temporary microscopic mounts were made of fresh fore-, mid- and hindgut contents from larvae of ten *L. avara*, three *Heteroplectron californicum* McLachlan (Trichoptera: Cala-

moceratidae), a facultative wood-gouging cad-disfly, four *Lipsothrix nigrilinea* (Doane) (Diptera: Tipulidae) and one *Austrolimnophila badia* Alexander (Diptera: Tipulidae), both xylophagous craneflies, and examined under a compound microscope. We did not see a gut flora in samples from *L. avara* or *H. californicum*, although we found such a flora, consisting of motile, rod-shaped bacteria 2–3 µm in length, in the hindguts of both craneflies.

The simple structure of *L. avara*'s gut also limits the residence time of ingested wood particles. Gut residence time was 8 h at 12°C ($n=23$, SE=0.5 h), measured with safranin-stained wood as a marker.

We were unable to demonstrate the existence of cellulase activity in the gut tissue or the gut contents of *L. avara* larvae. The assay was based on the measurement of glucose released from hydrolysed cellulose, in *in vitro* mixtures of homogenized tissue, fine particulate cellulose, and citrate buffer. From this negative

TABLE 5. Calculation of approximate assimilation efficiency for instar 4 and instar 6 *Lara avara* larvae. All values in mg per 24 h (dry weights). For this calculation, instar 4 larvae were assumed to weigh 0.81 mg, and instar 6 larvae were assumed to weigh 3.69 mg.

	Instar	
	4	6
Respiration*	0.003	0.011
+Growth	0.007	0.007
=Assimilation (A)	0.010	0.018
+Faecal production	0.130	0.517
=Ingestion (I)	0.140	0.535
Assimilation efficiency (=100×A/I)	7%	4%

* Assuming 0.9 litres O₂ required to metabolize 1 g of carbohydrate/protein food (Schmidt-Nielsen, 1979).

result we conclude that *L. avara* does not produce its own cellulase in significant amounts.

The proportion of ash (3–4%) contained in faeces produced by *L. avara* larvae was similar to that of the conditioned wood eaten. As sound wood contained <1% ash, *L. avara*'s contribution to the mineralization of wood is small compared to that already accomplished by fungi and bacteria. An indirect estimate of assimilation efficiency, based on measurements of respiration, growth and faecal production, was 7% for instar 4 and 4% for instar 6 (Table 5).

Faecal production in laboratory culture

Measurements of faecal production by instar 4–7 *L. avara* larvae in drippy trays ranged from 0% to 41% of dry body weight per day (24 h). Mean estimates of faecal production (% of dry body weight per day) for instars 4+5 and 6+7, respectively, were 15.3 (SE=1.86, $n=11$) and 7.1 (SE=0.87, $n=44$) feeding on conifer wood, and 16.0 (SE=3.59, $n=5$) and 14.0 (SE=1.94, $n=20$) feeding on alder wood (' n ' refers to the number of drippy trays). As a representative faecal production rate for populations of *L. avara* larvae, we chose 13% d⁻¹, the unweighted mean of the data summarized above. During these measurements the water temperature varied between 4 and 18°C, which spans the typical range of temperature experienced by larvae under natural conditions.

Larval growth rates

Using equation (2) and Table 2, we calculated indirect estimates of growth rates of

TABLE 6. Summary of growth rate estimates (% d⁻¹) for instar 4–7 *Lara avara* larvae. Results for methods 1–3 were calculated from instar duration estimates and mean weights of successive instars (see text). N.D.=no data.

Method		Instar			
		4	5	6	7
Field	(1) Oldest mark	1.74	0.14	0.21	N.D.
	(2) Accumulation of unmarked larvae	0.87	0.32	0.17	N.D.
Laboratory	(3) Frequency of moulting	0.58	0.39	N.D.	N.D.
	(4) Weight gain in drippy	0.34	0.34	0.20	0.12
	'Mean' growth rate	0.88	0.30	0.19	0.12

instar 4–7 *L. avara* larvae, from the instar duration estimates (methods 1–3) in Table 4. In these calculations the three instar duration estimates provided the values for 't' in equation (2). Growth rates were also estimated directly from measurements of larval weight gain in the drippery, where 't' was the number of days between weight measurements. The results can be expressed as relative growth rate (% d⁻¹), which is very nearly equivalent to instantaneous growth rate ×100, at the low rate of growth exhibited by *L. avara*.

The growth rate estimates (% d⁻¹) from the various calculations spanned 0.34–1.74 for instar 4, 0.14–0.39 for instar 5, 0.17–0.21 for instar 6, and 0.12 for instar 7 (Table 6).

Feeding impact of natural populations of *Lara* larvae

Population estimates

The abundance of *L. avara* larvae in stick collections varied considerably, depending on the location of collection, and wood type (Table 7). Larval biomass was 2–10 times higher on Berry Creek sticks (258 mg kg⁻¹ wood) than on sticks from other Coast Range streams. Larval biomass on hardwood sticks

(165 mg kg⁻¹ wood) was almost 5 times as high as on conifer sticks (35 mg kg⁻¹ wood). Larval biomass was not strongly related to the size or decay state (measured as density, g cm⁻³) of the sticks. One hardwood stick from Berry Creek and a conifer stick from a Coast Range site had unusually high densities of *L. avara* larvae, 1729 mg kg⁻¹ wood and 371 mg kg⁻¹ wood, respectively. These sticks were relatively small and had a complex surface texture with many feeding grooves, but did not appear to be unusual in any other way.

Feeding impact

Using estimates from Anderson *et al.* (1978) of wood abundance in Oregon streams (kg m⁻²) and our estimates of laboratory faecal production (mg mg⁻¹ d⁻¹) (see above) and field abundance of *L. avara* larvae on wood (mg kg⁻¹) (Table 7), we estimated larval faecal production in Oregon streams. In Berry Creek, faecal production by *L. avara* was 3.7 g m⁻² y⁻¹, or 1.2% of the standing crop of wood debris (<10 cm diam.) per year. The average estimate for Coast Range streams was 1.6 g m⁻² y⁻¹, or 0.3% of wood standing crop per year (Table 8).

TABLE 7. Density (no. kg⁻¹ wood) and biomass (mg kg⁻¹ wood) of *Lara avara* larvae on sticks from Oregon Coast Range streams (dry weights).

	No. of sticks	No. larvae		Biomass	
		\bar{x}	SE	\bar{x}	SE
All sites	50	29	6.9	113	36.0
Berry Creek	14	60	18.3	258	116.2
Sites other than Berry Creek	36	17	5.3	57	15.7
Hardwood sticks	30	41	9.8	165	57.1
Conifer sticks	20	12	7.3	35	18.8

TABLE 8. Estimated faecal production and feeding impact of *Lara avara* larvae in Oregon Coast range streams (dry weights).

	Kg wood m ⁻² streambed*	Mg <i>L. avara</i> m ⁻² streambed	Faecal production:† g m ⁻² streambed y ⁻¹	Feeding impact: % of wood standing crop y ⁻¹
Berry Creek	0.30	77	3.7	1.2
Flynn Creek	0.86	20	0.9	0.1
Coast Range streams (mean)	0.59	34	1.6	0.3

*Data from Anderson *et al.* (1978), for wood <10 cm diam.

† Assuming faecal production of 13% body wt per 24 h.

Discussion

As a xylophagous insect, *L. avara* faces such problems as poor food quality and patchy habitat distribution. However, wood decays slowly and is likely to provide habitat for a long time. Compared with benthic habitats that may be scoured several times a year, wood provides a protected, stable habitat where larvae can continue to feed and grow for several years.

The most obvious results of feeding by *L. avara* larvae are changes to the surface texture of wood debris, and the conversion of wood debris to fine faecal particles. Feeding by *L. avara* larvae also exposes new, unconditioned wood to fungal attack, speeding its decomposition.

Wood that has been fed upon by *L. avara* larvae is often highly grooved and sculptured, allowing us to recognize 'Lara sticks' on the basis of their surface texture and evidence of gouging activity. The creation of feeding grooves may be an important aspect of *L. avara*'s ecological role, as a stick with a spatially complex surface is likely to support a more diverse invertebrate community than is a smooth stick.

Anderson *et al.* (1978) estimated that *L. avara*, *Heteroplectron californicum* and *Juga silicula* (Lea) (Mollusca: Pleuroceridae), the three most important wood processors in Oregon streams, consumed 1.8% of the standing crop of small stream wood debris per year. Their estimates of *L. avara* abundance, which were based on field-picked samples, were lower than the present estimates (22 mg kg⁻¹ wood *v.* 57 mg kg⁻¹ wood for Coast Range streams). Substituting our value for *L. avara*'s contribution to wood degradation (0.3% of wood standing crop per year) into their calculation, the total impact of *L. avara*, *H. californicum* and *J. silicula* is 2.0% of wood standing crop per year, similar to the previous estimate. *L. avara* is responsible for only about 14% of that impact.

Adaptations for xylophagy

Wood debris in streams offers an abundant supply of carbon to organisms capable of digesting cellulose or lignin, but it is a poor source of nitrogen. Wood typically contains

only 0.03–0.10% N (dry weight) as both protein and non-protein compounds (Cowling & Merrill, 1966), while insects contain 1–14% N, mainly as protein (DeFoliart, 1975). The protein content of wood increases with microbial conditioning, because the amount of microbial biomass relative to the amount of wood increases over time. Wood-rotting fungi are able to concentrate N obtained from wood into their mycelia (Merrill & Cowling, 1966), and some bacteria associated with decaying wood in streams are able to fix gaseous N (Buckley & Triska, 1978). Fungal spores, protozoans and microinvertebrates are also present in the wood that is gouged by *L. avara* larvae. By consuming the soft surface layers that contain this community the larvae obtain more protein, and presumably more vitamins and sterols as well, than would be available in unconditioned wood. Baker *et al.* (1983) reported greater microbial activity and N content in decaying alder than in decaying conifer wood. This nutritional difference may help explain the high abundance of *L. avara* on hardwood relative to conifer wood.

Mattson (1980) discussed adaptive syndromes that may allow herbivores feeding on poor quality food, such as wood, to obtain sufficient N to complete their life cycle. These included considerations of life cycle length, body size, feeding activity, gut morphology, microbial endo- and ectosymbionts, and food selection. Some are relevant to our discussion of *L. avara*.

The life cycle is certainly long for an aquatic insect, a phenomenon that can be attributed to slow growth and to the relatively large size (up to 12 mg dry wt and 16 mm length) attained. The growth rates (0.1–0.9% d⁻¹ for the larger instars) are lower than those for other aquatic insects from the same region: 0.9% d⁻¹ for *Heteroplectron californicum*, a facultative wood gouger with a 2-year life cycle (Anderson & Cummins, 1979), 2–3% d⁻¹ for *Lepidostoma* spp., univoltine leaf-shredding caddisflies (Grafius & Anderson, 1980), and 2–5% d⁻¹ for univoltine mayflies of the family Ephemerellidae that consume both detritus and algae (Hawkins, 1982). Life cycle estimates for other species of North American elm mid beetles range from 1 to 4 years (LeSage & Harper, 1976; White, 1978).

Feeding rate, estimated from faecal produc-

tion (13% d⁻¹) is low compared to other xylophagous insects such as *Heteroplectron californicum* (20–95% d⁻¹) or *Lipsothrix* spp. (90–200% d⁻¹ [Dudley, 1982]). *L. avara* is a sluggish insect, with a low metabolic rate (Table 5); slow feeding may be just another manifestation of this, or it may be related to gut retention time and digestion efficiency.

L. avara could assimilate nutrients from ingested wood in the following ways: (1) Absorb molecules previously liberated from the wood by fungal or bacterial enzymes. (2) Use its own enzymes to digest the contents of fungal, bacterial, or animal cells that were mechanically disrupted by feeding. (3) Use sequestered fungal enzymes (Martin, 1979) to digest the wood. (4) Use symbiotic bacteria or protozoans in its gut to digest the wood. (5) Use its own cellulose to digest the wood.

Our observations of gut structure and function in *L. avara* larvae suggest a digestive process based on limited mechanical and biochemical disruption of wood particles. This would place a premium on readily assimilable nutrients derived from microbial activity, rather than from the more refractory structural polysaccharides of the wood.

As insects generally include proteases and lipases in their repertoire of digestive enzymes, *L. avara* is almost certainly able to digest the microbial component of decaying wood. On the basis of the gut morphology (a simple tube), a low assimilation efficiency (4–7%), and the absence of cellulase and a gut flora, it is likely that *L. avara* uses a 'passive' sort of digestive process based primarily on (1) and (2) above. There is no indication that *L. avara* is capable of switching to high-quality foods, such as algae or animal tissue.

This study has indicated some of the constraints imposed by specialization on stream wood debris for food and habitat. Study of other xylophagous aquatic insects, especially in the order Diptera, may show that a short life cycle and xylophagy are not irreconcilable.

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