Freshwater Biology (1987) **17**, 437–451

The biology and life cycles of *Lipsothrix* spp. (Diptera: Tipulidae) inhabiting wood in Western Oregon streams

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SUMMARY. 1. The immature stages of the craneflies *Lipsothrix nigrilinea* and *L. fenderi* are spent in galleries within decayed red alder (*Alnus rubra*), in low order streams of the Pacific Northwest. *L. fenderi* also occurs in some coniferous wood and wood in semi-terrestrial sites at stream margins. Larvae of both species feed on the wood and are important degraders of this material.

2. The immature stages are briefly described and behaviour of the two species is compared.

3. *L. nigrilinea* has a predominantly biennial life cycle. It emerges from April to August in response to receding water level. The absence of this cue results in an extension of the life span to 3 or more years. The non-deterministic life cycle results in high variability of juvenile and adult weights.

4. *L. fenderi* is basically a biennial species, with a more synchronized autumn emergence. A portion of the population may emerge after 1 year if oviposition occurs early enough to allow autumnal growth of larvae or if growth is relatively rapid.

5. The extended life cycle of *Lipsothrix* spp. and the broad emergence of *L. nigrilinea* are concluded to be adaptations to a habitat/resource which is relatively stable and allows long-term association.

Introduction

A diverse group of insects is associated with wood in forested ecosytems. Diptera are particularly important degraders of this substrate and Teskey (1976) recorded larvae of forty-five families in living and dead wood. Dudley & Anderson (1982) considered dipteran larvae the dominant borers, both in abundance and diversity, within aquatic and semi-aquatic wood habitats in headwater streams. Although the Chironomidae is the most numerous and diverse xylophilous family, the large size of cranefly larvae makes the Tipulidae the most conspicuous dipteran wood borers. Alexander (1931) listed nineteen genera and forty-eight species of craneflies worldwide associated with dead trees.

The life cycles of wood-associated aquatic Diptera are poorly known (but see Kaufman, 1983) because this habitat is relatively uncommon in most streams and is difficult to sample. Life cycles of tipulids in general were reviewed

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by Pritchard (1983), but because of the unique characteristics of wood as a resource (low nutrient content, resistance to disturbance), specializations in life histories of xylophagous species might be expected.

In 1977 we began a study of the distribution and biology of North American *Lipsothrix* spp., as part of a long-term investigation of the role of wood in aquatic habitats and the relation of invertebrates to the degradation of wood debris (see Anderson *et al.*, 1978). Five species of *Lipsothrix* are known from America north of Mexico (Hynes, 1965), and all burrow in decayed wood as larvae. *L. sylvia* (Alexander) is found throughout the Appalachian highlands (Rogers & Byers, 1956), whereas the other species occur in the Pacific Northwest (Fig. 1; Dudley, 1982; Dudley & Anderson, 1982). In southern Oregon and northern California *L. hynesiana* Alex. inhabits the coastal redwood (*Sequoia sempervirens*) zone and *L. shasta* Alex. occurs inland in the Klamath, Cascade and Sierra Nevada Mountains. *L. nigrilinea* (Doane) and *L. fenderi* Alex. are sympatric in much of the western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*) zones (defined by Franklin & Dyrness, 1973) of western Oregon and Washington. In addition, *L. fenderi* was collected from the Olympic Peninsula of Washington and the Coast Range in southern British Columbia, and *L. nigrilinea* from isolated locations in the Douglas fir (*Pseudotsuga menziesii*) zone of eastern Oregon.

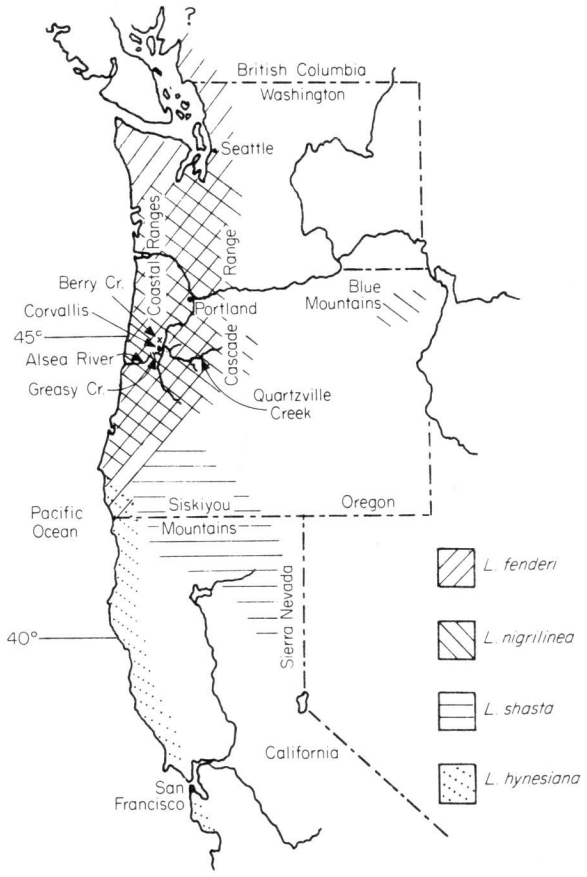

FIG. 1. Map showing ranges of western species of *Lipsothrix*. The northern extensions of *L. fenderi* and *L. nigrilinea* are not known. The streams sampled as part of the transect through the Coast and the Cascade Ranges are all tributaries to three streams (Alsea River, Greasy Creek, Quartzville Creek) in the vicinity of Corvallis, Oregon, and additional data were collected from Berry Creek.

This paper considers *L. nigrilinea* and *L. fenderi* where they coexist in western Oregon. We describe the life histories, and document the habits, habitat associations and the life cycles of these two craneflies.

Methods

Field survey and life cycles

Habitat associations of *Lipsothrix* spp. were established as part of an extensive survey of aquatic invertebrates associated with wood in the western U.S. (Dudley & Anderson, 1982). At each site, pieces of wood were probed with knife and forceps, and organisms removed to alcohol. Wood was characterized, categorized into decay classes (Table 1) and identified if possible.

To document *Lipsothrix* life cycles, an intensive sampling programme was conducted in Oregon along a transect from the Pacific coast eastward to the Cascade Range (Fig. 1). Sites were selected at approximately 15 km intervals to represent a range of elevations and habitat types; eight streams from the Alsea River and Greasy Creek watersheds in the Coast Range, and five from the Quartzville Creek watershed in the Cascade Range. The mid-Willamette Valley was not sampled due to the lack of suitable habitats.

One to three logs were sampled monthly at each site from February 1977 to March 1979. If possible, the same log was sampled on each date by removing a piece (*c.* 100 cm^2 surface area × 3 cm deep) of wood. Samples were broken apart under a dissecting microscope to remove animals. Sorting unavoidably resulted in some bias towards larger larvae. Larval and pupal dry weights (dried >48 h at 60°C, weighed on a Cahn Model 4100 electrobalance) were used to interpret growth and developmental patterns. Densities and pupal sex ratios were estimated from samples, but sex of larvae could not be determined.

Rearing

Larvae were reared in field-collected logs in the laboratory (13°C, 16:8 h light:dark) and in

TABLE 1. Decay classes for alder wood (*Alnus rubra*) (modified from Triska & Cromack, 1980; Dudley, 1982; K. Cromack, unpublished data)

	Decay class					
	1	2	3	4-F	4-M	5
Bark	Intact	Intact	Detached, but firm	Absent or detached	Absent or detached	Absent
Structural integrity	Sound, firm	Sound, firm	Interior sound, outer 1 cm soft but firm	Firm, tissue fibrous	Interior firm, outer 1–2 cm mealy, easily removed	Tissue easily sloughed
Density (mg cm^{-3})	50	30	–	20	10–15	5–12
Colour	Original	Surface darkened	Outer stained, inner original	Grey-brown stain throughout	Same as 3	Dark throughout
Microbial associates	Minimal	Surface bacteria and fungi	Shallow mycelia, possibly internal dry-rot (*Fomes*, etc.)	Extensive internal mycelia	Extensive internal mycelia (*Fomes*, etc.)	Same as 4-M
Total nitrogen (%)		0.15–0.32		0.32–0.33	0.39–0.50	0.45
Lignin (%)		17.5–18.5		21.5–52.0	17.0–23.0	>23.0
Cellulose (%)		47.0–50.0		24.0–39.0	44.5–51.0	44.5

shaded glasshouse stream troughs to substantiate developmental trends and to examine larval behaviour. Wood was kept saturated but exposed to air. Emerging adults were collected in cages over the logs.

Removing larvae from wood destroyed the habitat so we also used an artificial medium for rearing and observation. Soft wood was homogenized in a Waring blender for 5–10 s and placed wet into petri dishes. The blended material retained some structure so that mastication by larvae was necessary.

Colonization

Oviposition behaviour was examined by providing five females in cages with a choice of wood pieces (*c.* 15×10 cm) and wet paper towels. Substrates were set slanting into a dish of water, and in artificial stream troughs. After 1 week, half of each piece was examined for eggs. The remaining wood was set into aerated water to determine if eggs would hatch.

Field colonization by tipulids was examined by distributing uninhabited, decayed alder logs (*Alnus rubra* Bong., dimensions 15×15×40 cm) to thirty-five streams. Elevations ranged from 10 to 1800 m, and vegetation types included old-growth and second growth Douglas fir stands, alder groves and clearcuts. Logs were set out in April 1977 and retrieved in October 1977, when density and biomass of cranefly larvae were determined. In addition, sound alder logs (6 cm diam.×50 cm) were placed in Berry Creek near Corvallis in November 1980, and examined in October 1982 (see Anderson, Steedman & Dudley, 1984).

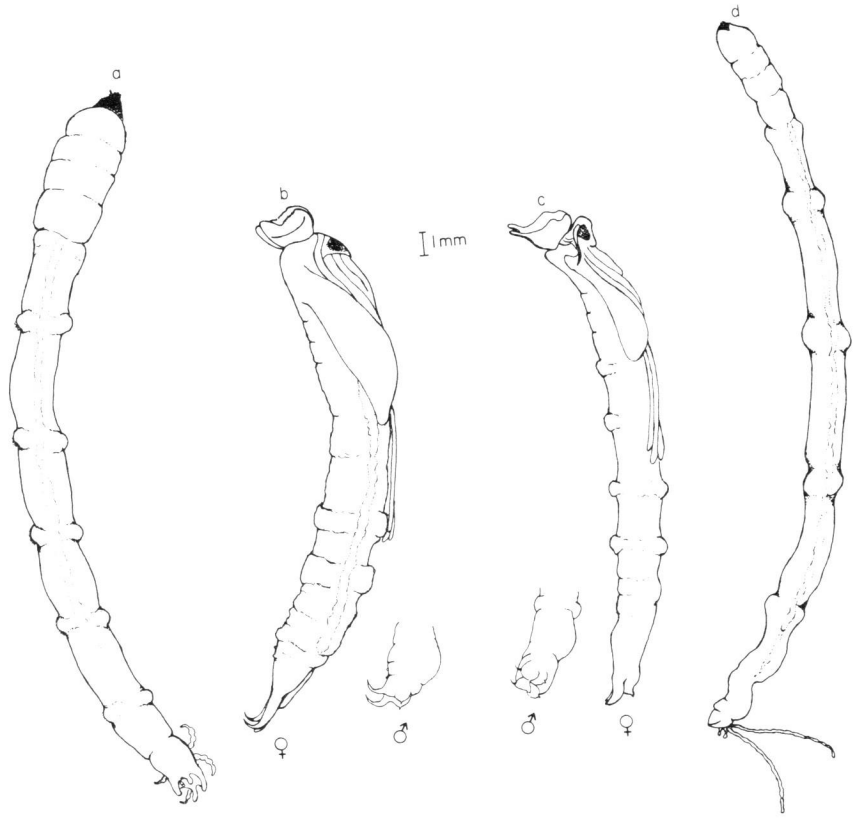

FIG. 2. Immature stages of *Lipsothrix* spp. A and B, *L. nigrilinea* larva and pupa; C and D, *L. fenderi* larva and pupa.

Results

Description of Lipsothrix larvae and pupae

Lipsothrix larvae are more slender than typical cranefly larvae (Fig. 2). The abdominal creeping welts bear numerous minute spines. The maximum body length of *L. nigrilinea* is about 30 mm with the head capsule about 2 mm wide. *L. fenderi* is more slender and fragile, the head capsule 1 mm wide and maximum body length over 35 mm. Anal papillae of *L. nigrilinea* are compact structures while the upper pair in *L. fenderi* is much elongated.

The pupae of *Lipsothrix* spp. are distinctive in that the respiratory organs, or breathing horns, are large fan-like structures (Fig. 2). Hinton (1955, 1967) demonstrated with a European species that these are spiracular gills which function as plastrons to facilitate oxygen diffusion from air or water. *L. nigrilinea* pupae are somewhat larger and more robust than those of *L. fenderi*. Length may vary by a factor >1.5, even within a sex, but males are almost always smaller than females. Pupae are easily sexed because the ovipositor and male claspers are apparent beneath the pupal cuticle.

Habitat characteristics

Habitat types. Lipsothrix spp. were common in first- and second-order forested streams. About 10% of the third-order streams (n>40 sites) had isolated populations where wood debris accumulated out of the main current. Larvae were found in low gradient streams (< 4%) and steeper seeps, requiring wood that remained saturated year-round yet protected from disturbance. These craneflies were uncommon in meadow and valley bottom streams, probably due to siltation and low oxygen levels, although *L. fenderi* tolerated light silt accumulation.

Both species were recovered from the field colonization logs over the full range of forest types tested (Table 2). *L. nigrilinea* density was highest in dense alder stands and low in old-growth and recently cut sites where alder was sparse. Though occurrence of *L. fenderi* was recorded, a severe freeze in the stream trough building killed the larvae prior to enumeration.

Wood characteristics. Alder was the most common wood inhabited by *Lipsothrix* larvae although coniferous wood comprised over half of the debris present. Approximately 95% of *L. nigrilinea* collections were from alder logs and branches, with the most of the others from big-leaf maple (*Acer macrophyllum* Pursh.). The only record of *L. nigrilinea* from conifer wood was a small number of very large larvae in western red cedar (*Thuja plicata* Donn) at a site where no hardwood was available. *L. fenderi* was also collected primarily from red alder (> 80% of collections), but it exploited other wood more often than did *L. nigrilinea*. Douglas fir was inhabited primarily at sites where alder was heavily colonized. Alder and other hardwoods are rare or shrub-like above 1000 m, and this probably sets the altitudinal limit for *Lipsothrix* spp.

L. fenderi and *L. nigrilinea* larvae were found commonly in the same logs, but *L. fenderi* inhabited a broader range of habitats (Fig. 3). It occurred in damp wood at stream margins, overlapping with a semi-terrestrial

TABLE 2. Colonization of experimental alder logs by *Lipsothrix* spp. in streams with different types of riparian vegetation. Proportion colonized indicates number of logs colonized over number of logs available. Matched letters indicate significantly different pairs for mean larval densities (1 SE in parentheses; Newman-Keuls multiple range comparison, P<0.05). *L. fenderi* densities were not available due to mortality (see text).

	L. nigrilinea		*L. fenderi*
Vegetation type	Proportion colonized	Larval density (no. cm^{-2})	Proportion colonized
Old-growth conifer	9/10	0.22^{a} (0.05)	5/8
Clear cut, 5–15 yr (young alder)	3/4	0.16^{bc} (0.03)	4/4
Clear cut, >15 yr (mature alder)	7/8	0.36^{b} (0.04)	4/5
Second-growth conifer	4/4	0.52^{ac} (0.15)	4/4

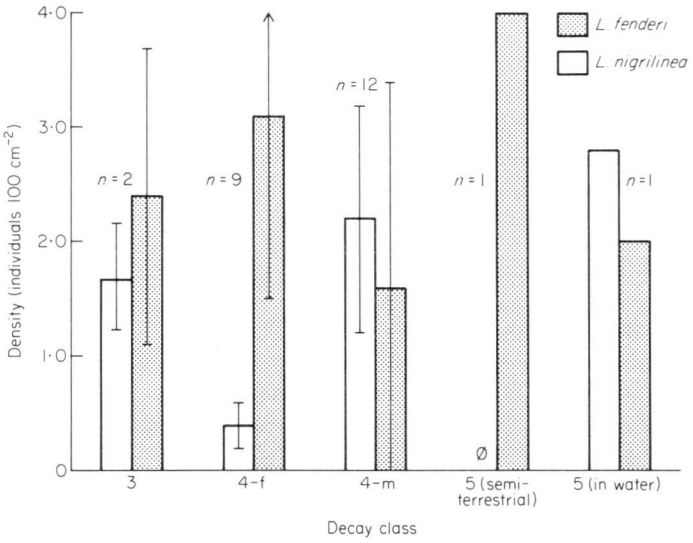

FIG. 3. Density of *Lipsothrix nigrilinea* and *L. fenderi* larvae in alder wood of various decay classes. Each replicate represented mean density within a given log over the 2-year sampling period; data expressed as mean densities (±1 SD) of these pooled observations.

tipulid, *Austrolimnophila badia* (Anderson *et al.*, 1984), and was more abundant than *L. nigrilinea* in wood of decay class 4-F (*t*-test, $P<0.001$).

The time required for microbial conditioning of alder before it was suitable for cranefly colonization depended on the history of the log. Oviposition and larval development took place in dry-rotted wood (Class 4-M or 5) as soon as it was saturated. Class 2 and 3 logs were colonized after about 1 year. Pupae of *L. fenderi* and large larvae of *L. nigrilinea* were collected from the sound alder (Class 1, became Class 3) after 2 years. To reach these stages of development, the logs would have been colonized within a year of being placed in the stream (Anderson *et al.*, 1984).

Biology and behaviour

Larvae. Small and medium-sized larvae occurred within 5 mm of the wood surface whereas larger larvae were generally 5–15 mm below the surface. They were deepest in soft wood (Class 4-M or 5; *L. fenderi* max. 15 mm, *L. nigrilinea* max. 30 mm).

The larval gallery is orientated in a plane with the log surface, often in the spring wood between the harder winter layers. Galleries may wind extensively in close proximity, and can be at least 15 cm long. Larvae move within them by slow peristaltic contractions which force the creeping welts against the walls.

An individual probably remains in one log from egg to emergence. However, mature *L. nigrilinea* larvae left experimental logs that were drying or poorly oxygenated whereas *L. fenderi* larvae never escaped from such stressed conditions.

Feeding. Larvae fed by cutting a piece of wood (*c.* 0.5×0.5 mm by fourth instars) with their mandibles, and then retracting the head. Continuous ingestion apparently moved the bolus through the gut, but starved larvae voided the hindgut of contents while food was retained in the fore- and midgut for over 10 days. A pouch connected to the hindgut was packed with filamentous bacteria, which may produce cellulase or provide micro-nutrients not available in the wood (M. Klug, Michigan State University, personal communication). Frass was egested as loosely aggregated pellets at the log surface or packed in the gallery where it may be re-ingested. *L. nigrilinea* fed actively in winter, even at 1°C, but *L. fenderi* was quiescent at low temperatures.

Studies of the role of *Lipsothrix* spp. in processing wood debris (Dudley, 1982; Ander-

son *et al.*, 1984) indicated that ingestion rates (based on egestion rates over several weeks) can be greater than 200% of dry body weight per day. Increasing temperature resulted in a higher feeding rate, but higher nutrient content appeared to reduce rates. Substrate hardness was the most important factor determining feeding rate, however, since Class 3 wood was processed at 88% body weight per day, compared to >200% for Class 4-M and 5 wood. Consequently, the greatest impact on wood debris occurs late in the decomposition process. As an example of this role, a 53 g piece of Class 5 alder was colonized in the laboratory by *L. nigrilinea*; after 12 months only 5 g of sound wood remained. Larvae also inoculate the wood with microbes as stained tissues were commonly found radiating from galleries in deeper undecayed wood.

Larval mortality. *Lipsothrix* larvae (and pupae) are generally protected within a log from physical disturbance. However, *L. fenderi* appeared to suffer greater mortality than did *L. nigrilinea* due to its proximity to the wood surface and use of a wider variety of habitats. Two populations of *L. fenderi* in transect logs were partly eliminated when high flows abraded the surface, while *L. nigrilinea* larvae survived because they were deeper in the wood. Flooding dislodges some logs and probably kills associated larvae, but many logs are well stabilized so are rarely moved. Four populations of *L. fenderi* were lost from stream margin logs due to desiccation during dry periods, but only once was a log with *L. nigrilinea* found drying. Dead *L. fenderi* larvae were collected ten times from frozen logs at stream edges but only once were freeze-killed *L. nigrilinea* found, and most larvae in this log survived in the deeper galleries.

Predation may occur in the field, since *Lipsothrix* larvae were preyed upon by a variety of naturally-occurring aquatic and semi-aquatic insects (e.g. *Dicranota, Xylophagus, Tabanus,* Hydrophilidae) within decayed wood in the laboratory. The marginal zone between aquatic and terrestrial systems shares components of both communities (Merritt & Lawson, 1979), and *L. fenderi,* being more common in these habitats, is exposed to a greater diversity and number of predators. In the transect collections, six predatory taxa co-occurred with *L. nigrilinea,* at a mean density of 0.21 individuals per 100 cm^2, and eight with *L. fenderi* at a mean density of 0.39 predators per 100 cm^2. Ten potential competitors (0.53 100 cm^{-2}) were with *L. nigrilinea* compared to thirteen taxa (2.04 100 cm^{-2}) with *L. fenderi.* Density differences were statistically significant ($P<0.05$; Mann-Whitney U test). *L. nigrilinea* is the more aggressive of the two species, and preyed on small larvae of both species; predation by *L. fenderi* was not observed (Dudley, 1982).

Pupa. Prior to pupation, the larval gallery of *L. nigrilinea* is widened about 20 mm below, and parallel to, the wood surface. This chamber curves upward to terminate in a firm turret-like structure similar to that described for the New Zealand tipulid, *Limonia nigrescens* (Anderson, 1982). *L. fenderi* enlarged a distal portion of the larval gallery as the pupation chamber. A disc of wood resembling a manhole cover was partially cut out at the surface and pushed out at emergence. The pupal stage for both species lasted a minimum of 11 days for males and 16 days for females at 15°C ($n=10$ and 18 respectively).

Adult. Emergence at the log surface took 10–14 min for both species ($n>20$). The pupal exuviae remained extended from the surface. Teneral adults rested near the emergence site and eliminated the fluid used in swelling the body to split the exuviae. The body was hardened for flight within 10 min.

In the field. adults remained in moist areas on streamside vegetation, and adults flew to the riparian zone when released in direct sun. Both sexes exhibited bobbing behaviour which may be related to mate attraction, since activity rates increased upon male contact with the female.

Eggs and oviposition. Eggs were not collected in the field, so observations are based on those dissected from females or deposited in the laboratory. The eggs were cream-coloured, oval-oblong, and flattened on one side. *L. nigrilinea* eggs were larger and heavier than those of *L. fenderi,* but there was a smaller overall investment in reproductive tissues in the former (Table 3).

Females deposited eggs individually into sodden wood. They probed for soft spots or crevices and the ovipositor valves were then forced 1–3 mm into the wood. Both species required a substrate that extended from the

TABLE 3. Eggs and clutch sizes for *L. nigrilinea* and *L. fenderi*. Weights were based on eight and seven clutches, respectively, and counts were from twenty-six *L. nigrilinea* and sixteen *L. fenderi* females. Reproductive allocation (R.A.) is the proportion of female body weight (thirty-six *L. nigrilinea*, twenty-eight *L. fenderi*) allocated to eggs and other reproductive tissues including oviducts and ovipositor; difference between reproductive allocations is significant at $P < 0.01$ (Mann-Whitney U test). R.A. of both species increases with size of females and males (Dudley, 1982).

Species	Size (mm)	Weight (mg)	Clutch ($\bar{x}$, range)	R.A.
L. nigrilinea	0.5×0.25	0.012	185 (106–380)	0.536
L. fenderi	0.45×0.2	0.009	138 (60–198)	0.650

water, as was noted by Rogers & Byers (1956) for *L. sylvia*.

Texture was the primary determinant of wood suitability for oviposition, and wood species was also important for *L. nigrilinea*. Five females given a choice oviposited primarily into soft alder (90% in Class 4-M and 5), but left no eggs in 4-F alder, soft hemlock nor paper towels. The remainder were in Douglas fir, but these did not hatch while eggs in alder hatched successfully, suggesting the presence of toxic compounds in coniferous wood. *L. fenderi* oviposited primarily in soft alder but placed eggs in all substrates (45% of recovered eggs in 4-M alder, 19% in Class 5 alder, 21% in Douglas fir, 6% in hemlock and 9% in paper towels). The results indicate less discrimination by *L. fenderi* for oviposition sites. Both species used any soft wood if given no choice. Females were also introduced into a cage over a laboratory stream containing Class 4-M alder, soft Douglas fir previously inhabited by *L. fenderi*, hemlock and cedar. Larvae of both species were found only in alder the following summer.

Life cycles

Lipsothrix spp. exhibit extreme variability in phenologies, resulting in complex life cycles. All size classes were found throughout the year and field-collected pupae encompassed a wide range of sizes. To explain these patterns, we propose a model for the life cycle of each species. Data from field collections and laboratory rearing are given to support the models.

Life cycle of L. nigrilinea. Model. L. nigrilinea is predominantly a biennial species, but with developmental plasticity allowing a non-deterministic life-span extending to 3 or more years. Variability in size-class composition results from a non-synchronous response to a pupation cue. The proximate cue is a receding water level, which makes terrestrial emergence possible, so individual larvae within a log are stimulated independently. Emergence may occur for several months at a single site. Some larvae continue to grow if they do not receive, or are not sufficiently mature to respond to, the pupation cue. The oviposition period is long, resulting in further variability due to differences in hatching times. Environmentally induced differences in growth rates result in further disparity in final weights.

Duration of life cycle. The difficulty in determining the duration of the life cycle is apparent in Table 4. All sizes classes of larvae were collected at all times of the year. The data indicate that early instars are most abundant in autumn and winter, but other growth patterns are obscure.

Initial evidence of multiple cohorts of *L.*

TABLE 4. Size class distribution of *Lipsothrix nigrilinea* larvae from Cascade Range sites. Data expressed as numbers collected in each time interval and percentage of a given size class occurring in a 2-month period. Many sites were inaccessible in January–February.

	Jan–Feb		Mar–Apr		May–June		July–Aug		Sept–Oct		Nov–Dec	
Site class	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Small (<0.15 mg)	5	(4)	5	(4)	5	(4)	16	(11)	42	(30)	67	(48)
Medium (0.15–0.49 mg)	7	(5)	20	(14)	8	(5)	24	(16)	19	(13)	68	(47)
Large (0.50–1.99 mg)	4	(4)	51	(23)	26	(12)	53	(24)	25	(11)	61	(27)
Very large (> 2.0 mg)	8	(9)	31	(18)	24	(14)	24	(14)	49	(28)	30	(18)

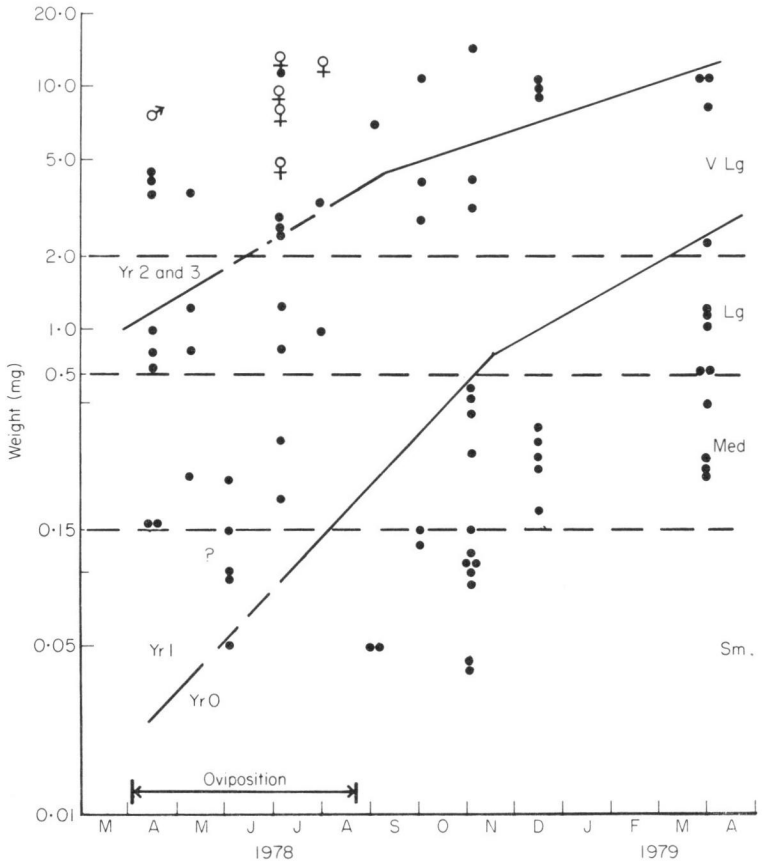

FIG. 4. Apparent cohorts of *Lipsothrix nigrilinea* based on larval and pupal (gender symbols) weights in samples from a single log for 1 year. Collections from a Cascade Range site, elevation 580 m. Horizontal lines indicate size classes; slanted lines separate suggested year classes.

nigrilinea within a single log was derived from a plot of larval weights against collection date (Fig. 4). We subjectively delineated each cohort or year class. With this interpretation, larvae grew to 0.5–1.5 mg (early instar IV) during the year, and fit an exponential growth model (r^2=0.55, P<0.05). Weights of the second year class are too variable to fit a curve. Pupae are produced after at least 2 years; pupal weight is about 50% of larval weight due to loss of gut contents and energy expended in metamorphosis. Fig. 4 illustrates the suggested life cycle but the imprecision in accurately describing the life cycle is apparent from the overlapping cohorts and some anomalously large pupae.

A minimum life cycle of 2 years was demonstrated with the field colonization logs. No adults of *L. nigrilinea* emerged the first year and the larvae at this time averaged 0.38 mg. The maximum size was 1.58 mg, which fits with the range suggested above for the first-year cohort.

Pupation and emergence. The emergence pattern of *L. nigrilinea,* as indicated by pooled collections of pupae and pupal exuviae from both the Coast and Cascade Ranges, was asynchronous with no apparent temporal peak (Table 5). Emergence was also spread on a local scale, with a mean time period per log of 2.8 months in the Cascades and 3.8 months in the the Coast Range. Several logs produced adults over all 5 months. This suggests that emergence is not induced by a thermal or photoperiodic cue.

The induction of pupation by water level decline was hypothesized because the emergence period coincided with the annual decrease

TABLE 5. Emergence pattern of *L. nigrilinea* from the Coast and Cascade Range sites, based on the number of pupae and pupal exuviae collected. (Exuviae were recorded as adults from the previous month; pupae as adults of the current month.)

Sex	March	April	May	June	July*	August
Male	1	14	8	7	13	4
Female	0	2	9	7	6	5
Unknown	0	4	1	3	16	4
Total	1	20	18	17	35	13

* July emergence exaggerated by large number of exuviae collected from one anomalous log.

in stream flow. To test this, an alder log was cut into three sections and placed horizontally in an artificial stream. Sections were 20%, 50% and 80% submerged. Thirteen adults emerged from the most exposed treatment, twenty-two from the intermediate level and only one female came from the 80% submerged log. All were from exposed portions. Many large larvae remained in the most submerged log while very few remained in the exposed logs. Furthermore, induction of pupation and emergence resulting from desiccation was repeatedly observed in the laboratory and field. Development from pupae to adults was also inhibited by water, as eight pupae experimentally submerged for 7 weeks (twice the normal period) successfully emerged when the wood was removed from the water.

Pupal development was also influenced by temperature. The numbers pupating increased and time to emergence decreased at warmer temperatures for mature larvae held in media at 1, 3, 8 and 15°C (Dudley, 1982). Temperature differences associated with altitude and distance inland may explain some differences in larval growth rates at the field transect sites. However, adult emergence periods for high and low altitude sites spanned the same interval, suggesting further that water level decline plays the overriding role in induction of pupation. In fact, the earliest maturation of *L. nigrilinea* occurred, unrelated to temperature, in the five smallest streams where water level receded earliest in the spring.

Extended duration of the life cycle. Use of receding water level (=desiccation) as a proximate cue for pupation can result in a life cycle that is 3 years or longer. If the water level does not drop sufficiently in a given year, or if a log is displaced to deeper water, the larvae continue to grow for at least an additional year. Third-year larvae (weight *c.* 12 mg) were obtained in the laboratory from logs submerged in aerated water for over 2 years.

Extension of the life cycle provides an explanation for the wide range of larval size classes observed at any one time and the extreme differences in pupal weights. The uppermost (oldest) cohort in Fig. 4 included very large larvae occurring after the emergence period; these probably would have required a third year before pupation. Support for this interpretation was also obtained from two sites where larval weights were compared in the

TABLE 6. Distribution of pupae and 'very large' larvae of *L. nigrilinea* in relation to water level at two field sites in the Cascade Range. Pupation was significantly decreased by submergence (Fisher exact test, $P<0.001$).

	Above water line		Below water line	
	Site 1	Site 2	Site 1	Site 2
No. of pupae	16	8	1	0
No. of 'very large' larvae (after emergence period)	1	0	9	4

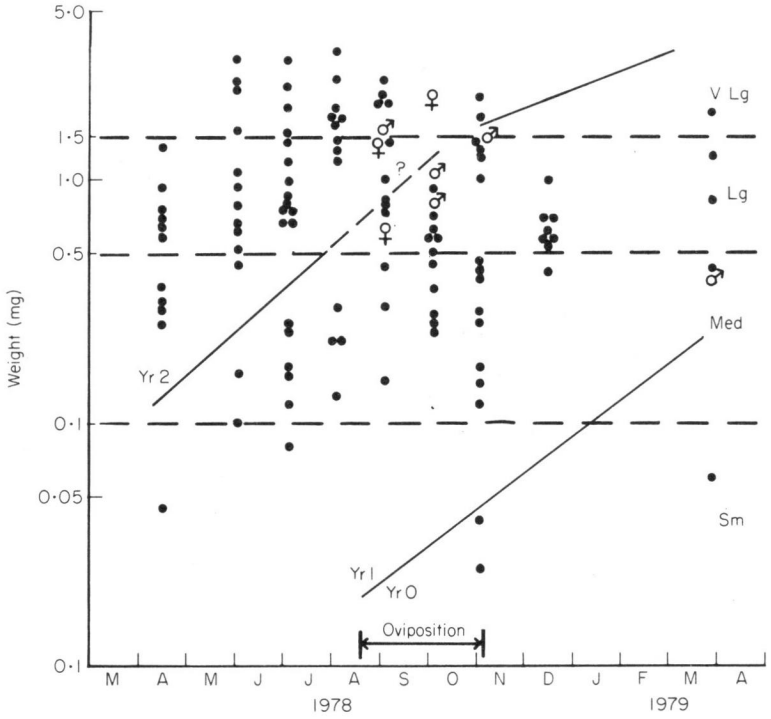

FIG. 5. Apparent cohorts of *Lipsothrix fenderi* based on larval and pupal (gender symbols) weights in samples from a single log for 1 year. Collections from a Coast Range site, elevation 275 m. Horizontal lines indicate size classes; slanted lines separate suggested year classes.

same log sampled above and below the water line. After the summer emergence period, very large larvae were absent above the waterline (and pupal exuviae were present), but they remained in the submerged portion of the wood (Table 6).

Life cycle of L. fenderi. Model. The basic pattern for *L. fenderi* is also a 2-year life cycle, but a portion of the population completes development in 1 year. Emergence occurs in the autumn and is more synchronized than that of *L. nigrilinea*. Despite the relatively greater synchrony, there is enough spread in the oviposition period to affect voltinism. Eggs deposited early hatch before winter, whereas those laid later may remain dormant until spring. Larvae that grow over winter can complete development in 1 year but the spring emergers require 2 years. Size variability in *L. fenderi* may be related partly to voltinism but it is also accentuated by the wide range (relative to its congener) of habitats utilized.

Duration of life cycle. Sequential collections from a single log illustrate the biennial life cycle of *L. fenderi* (Fig. 5). The two cohorts are distinguishable, with the first starting in late autumn and reaching 0.5–1.5 mg within a year (fits an exponential growth curve

TABLE 7. Numbers of *Lipsothrix fenderi* in various size classes in bimonthly intervals. Data are pooled for both Coast and Cascade Range sites.

	Nov–Dec	Jan-Feb	March–April	May–June	July–Aug	Sept–Oct
Small	11	13	58	43	13	3
Medium	28	12	16	53	41	44
Large	92	20	48	52	69	54
Very large	19	11	22	41	122	15
Total	150	56	144	189	245	116

for March–December; $r^2=0.59$, $P<0.05$). Continued growth in the second year leads to emergence the following autumn. The pooled size-class data (Table 7) also support the biennial pattern. The pulse of early instars from March–April attained the large size-class by November; this cohort is present as the very large class in late summer of their second year, just prior to emergence. Considerable variability and overlap are still obvious for this species.

In contrast to *L. nigrilinea,* few *L. fenderi* larvae of the second-year cohort remained after the emergence period (Fig. 5). However, the presence of some very large larvae after this time may indicate that these were triennials. Definitive evidence that a 1-year life cycle is possible was obtained from the alder logs at Berry Creek. These were placed in the stream in November 1980, after the flight period of *L. fenderi,* and some pupal exuviae were present in the autumn of 1982.

Pupation and emergence. Emergence of *L. fenderi* occurred from late August to November with a major peak in September (Table 8). Water level did not appear to be an emergence cue. In three pairs of small logs that were 20% or 80% submerged, there was no significant difference ($P>0.20$, chi-square test) in emergence: forty-five adults in the 20% submerged and thirty-four in the 80% submerged. Some pupae emerged under the water but failed to moult successfully. As photoperiod is unlikely to be detected by larvae within a log, we suspect that temperature is the primary emergence cue. In the field, water temperatures start dropping about the same time that emergence begins. Temperatures within the log mimic the surrounding water, but with less diel fluctuation, so the decline provides a dependable indicator of seasonal change.

TABLE 8. Emergence pattern of *Lipsothrix fenderi* from the Coast and Cascade Range sites, based on the number of pupae and pupal exuviae collected. (Exuviae were recorded as adults from the previous month; pupae as adults of the current month.)

Sex	Aug	Sept	Oct	Nov	Total
Male*	4	23	8	1	36
Female	1	24	8	1	34
Unknown	3	12	9	1	25
Total	8	59	25	3	95

* One pupa also collected in March.

Discussion

Life cycles of Lipsothrix spp.

The low standing crop and species richness of aquatic insects on wood debris compared with leaf detritus indicates that there are barriers to the exploitation of wood in stream systems (Anderson *et al.*, 1978; Anderson & Sedell, 1979). Low nutritional quality (C:N ratio>300:1) and tissue toughness are the most obvious nutritional and physical barriers. The mandibles of *Lipsothrix* larvae are of a strong, gouging type, similar to those of other xylophages such as the elmid beetle, *Lara avara* and the caddisfly, *Heteroplectron californicum* (Dudley, 1982; Steedman & Anderson, 1985). The bacterial gut flora may play a significant role in digestion of wood, but this remains to be investigated.

There are some clear advantages to an internal association with wood. Mortality from drying and freezing is reduced, and the potential for encounter with predators and competitors is much lower than in the rest of the stream channel. In small streams, logs often remain in place for many years (Triska & Cromack, 1980), so the habitat/food resource exhibits long-term stability.

Relaxation of synchrony and extended duration of life cycles may be life-history consequences of wood association. Unlike many aquatic insects, *Lipsothrix* larvae rarely move among microhabitats. Logs and portions of a log vary in quality and larvae experience a single microhabitat rather than averaging the range of microhabitat conditions. Environmental heterogeneity is apparently the primary factor responsible for the variability observed in larval size and timing of life-history phenomena.

Life cycle models of *L. nigrilinea* and *L. fenderi* (Fig. 6) incorporate timing of emergence and oviposition, proportions emerging each year, and the general growth patterns. Other north temperate tipulids have narrower local emergence periods and adult size ranges (Freeman & Adams, 1972); they typically have annual life cycles, and in the subfamily Limo-

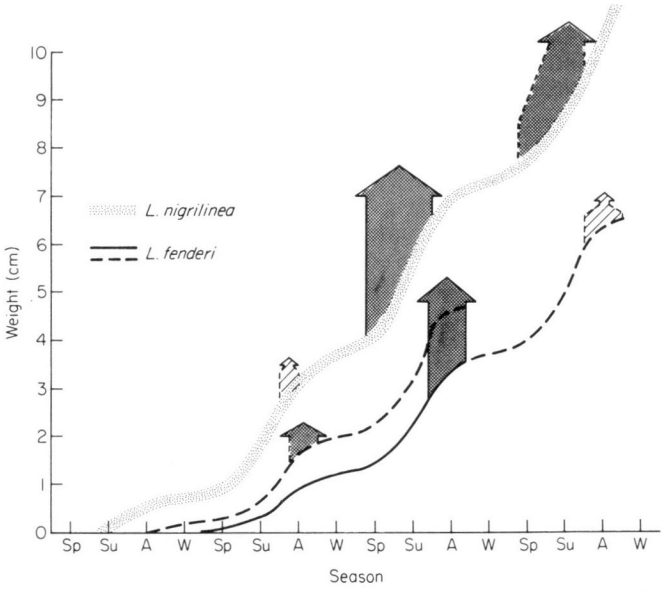

FIG. 6. Comparison of the generalized growth pattern of *Lipsothrix nigrilinea* and *L. fenderi.* Solid line indicates the typical pattern for *L. fenderi* and the dashed line shows the 1-year and 3-year variants. The stippled line for *L. nigrilinea* suggests wider variance in individual sizes. Stippled arrows indicate major emergence periods; slashed arrows are hypothesized variants. Width of arrowheads indicates relative proportion emerging each year.

niinae attain a smaller maximum size. Asynchrony and extension of life cycles observed elsewhere result from growth differences due to cooler temperatures between sites (Coulson, 1959; Hofsvang, 1972; MacLean, 1973). The variability in *Lipsothrix* life cycles exists at any single site, and can be broken into two components: differences in growth rates, and asynchrony associated with timing of emergence, oviposition and hatching. Differences in growth may be due to variation in microhabitat quality and to endogenous variability in individual growth rates (Laughlin, 1960; Meats, 1975; Pritchard, 1980). Differences in wood quality also explain univoltine and bivoltine populations of xylophagous chironomids (Kaufman, 1983). However, for *Lipsothrix,* and especially *L. nigrilinea,* developmental timing overwhelms such growth-related variation when it causes individuals of the same cohort to emerge in different years or to initiate growth in different seasons. The complicating effects of such 'cohort-splitting' on life cycle analysis has also been discussed by Pritchard (1980) for *Tipula sacra* in beaver ponds.

Extension of life cycles beyond 1 year allows individuals to continue growing and eventually to emerge at a larger size, at the cost of longer generation time. Increased size may confer a reproductive and physical advantage to individuals (Calow, 1977), if the habitat is such that life cycle extension is possible. Thus, it may well be that the relatively benign and predictable wood habitat *allows,* rather than causes, the increased size and age of these craneflies, as well as the flexibility in their life cycles.

Differences in the life cycles of the two species are related to their responses to habitat characteristics. Although *L. fenderi* and *L. nigrilinea* co-occur within many logs, the former also extends into margin habitats where risk of mortality is greater. The shorter life cycle, smaller size and greater reproductive allocation of *L. fenderi* are traits associated with occurrence in unpredictable environments with shorter term favourability for survival (Southwood & Comins, 1976). As *L. fenderi* larvae are associated with more kinds of wood in a wider variety of conditions, growth may be more variable within a cohort even though emergence is relatively synchronous.

The use of decreasing water level as a

pupation cue by *L. nigrilinea* is effective for a spring–summer emerger, but not for an autumn species such as *L. fenderi,* because water levels typically recede in spring and summer but rise in the autumn with the onset of the wet season in Oregon. A desiccation-related developmental cue has also been indicated for aquatic dryopoid beetles (Brown, 1973; White, 1978; Steedman & Anderson, 1985).

Ecological role of Lipsothrix spp.

The role of *Lipsothrix* spp. in wood degradation is dependent on wood condition and on stream size. Alder, the predominant wood exploited, is a relatively high quality resource because it decays rapidly and has a high nitrogen content (Baker, Morita & Anderson, 1983). Larval densities and individual processing rates both increase dramatically as decay proceeds and wood tissue becomes softer. In the smallest streams where stream power is low, erosion has the least effect, so wood is most abundant and remains long enough to reach the final stages of decay. Having ample supply of habitat suitable for oviposition and growth, craneflies achieve their highest population sizes here and have the greatest impact. In larger streams the wood remaining within the channel will lose the softer, more suitable portions to abrasion by high water flows.

The distribution and abundance of *Lipsothrix* spp. are related to forest succession. They are most closely associated with alder, an early successional tree species. Thus, these craneflies occur most abundantly where the riparian area has been disturbed, allowing alder to colonize, then to become senescent and fall into the stream. As the forest matures, densities again decline to endemic levels until the cycle is repeated.

Acknowledgments

This paper was derived from a thesis submitted by T. L. Dudley as part of the Master of Science degree at Oregon State University. We thank Ken Cummins, Mary Jo Wevers, Gordon Pritchard and several others for their help in field work or formulation of ideas. Wendy Madar provided biological illustrations. We appreciate the editorial assistance of Carla D'Antonio and Scott Cooper, and an anonymous reviewer who provided many useful suggestions. This work was supported in part by National Science Foundation grant No. DEB 78-10-594.

This is Technical Paper No. 7465 of the Oregon Agricultural Experiment Station.

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(Manuscript accepted 28 August 1986)