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Biology, Ecology, and Control of the
LODGEPOLE NEEDLE MINER

LIBRARY ABSTRACT

Struble, George R.

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The lodgepole needle miner attacks lodgepole pine forests in the Western United States and Canada. Only two insect species—*Coleotechnites milleri* (Busck) and *C. starki* Freeman—have been identified and studied in detail. Infestations by *C. milleri* were studied at Yosemite National Park, California, beginning in 1954. This bulletin summarizes findings on the biology and ecology of this species, natural enemies and pathogens, effects of climate and physiography, and field tests of insecticides.

Keywords: Defoliators, insect, *Coleotechnites milleri* (Busck), natural control, aerial spray, lodgepole pine.

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Cover Photo

Defoliated lodgepole pines stand as mute evidence of a devastating infestation by the lodgepole needle miner. These trees, on the Tenaya Creek drainage, Yosemite National Park, California, were killed between 1910 and 1925.
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ACKNOWLEDGMENTS

SUMMARY

The lodgepole needle miner attacks and kills indigenous lodgepole pine forests in the Western United States and Canada. Only two species—*Coleotechnites milleri* (Busck) and *C. starki* Freeman—have been identified and studied in detail. *C. milleri* is best known for long periods of outbreaks in Yosemite and Sequoia-Kings Canyon National Parks in California. Three periods of infestation have been reported since 1900. Each lasted 10 to 20 years and was followed by a shorter period of light infestation in between. Infestations by *C. starki* are well known in the Banff and Lake Louise National Parks in the Canadian Rocky Mountains. Scattered infestations of unidentified needle miner species have been found in and near Yosemite National Park and on the Inyo National Forest in California; in Yellowstone National Park, Wyoming; and in central Oregon.

This bulletin summarizes findings from studies conducted in Yosemite National Park on the biology and ecology of *C. milleri*, its natural enemies and pathogens, relationship of climatic and physiographic influences to successive generations of needle miners, and field tests of insecticides.

The life cycle of *C. milleri* spans 2 years. Moths oviposit between July 15 and August 20 every odd-numbered year in Yosemite. Mean incubation period of eggs lasts 35 days. Overlapping generations are unknown. Of the five larval instars, the first and fourth overwinter, and the fifth pupates beginning about the third week of June.

After eclosion, larvae enter and remain within the first needle through the third instar; they migrate to and mine two additional needles each in the fourth and fifth instar. A minimum of five needles are mined, and entries are made into many others by time of pupation.

Extreme populations of 75 or more insects per twig tip mark the beginning of new infestations; 30 insects per tip are usual through the third generation. Afterward, the stress of defoliation and growth of shorter and fewer needles result in lower populations. Populations are larger and more uniform in the tops and midcrowns of trees.

Possible insect enemies of the lodgepole needle · miner include 57 species in five orders. None has been found highly effective against outbreak infestations.

Sharp reductions in outbreak infestations followed adverse weather during flight and oviposition.

Control by toxic chemical sprays applied by helicopter has been undertaken in Yosemite National Park as a stopgap measure to save recreational forests from devastation. Malathion proved the most effective. Moths were sprayed by helicopter at the rate of 1 pound malathion in 10 gallons diesel oil per acre. The sprays caused infestations to drop and remain at innocuous levels. Nontarget organisms did not suffer any evident lasting damage.

BIOLOGY, ECOLOGY, AND CONTROL OF THE LODGEPOLE NEEDLE MINER

By George R. Struble [1]

INTRODUCTION

On the upper slopes of California's central Sierra Nevada stand dead forests of lodgepole pine (*Pinus contorta* var. *murrayana* [Grev. & Balf.] Engelm.). The snags contrast vividly with nearby living trees. Many thousands of trees stripped of their foliage foretell a similar fate for others in the years ahead. Some of these "ghost forest" trees have stood for more than 60 years, but many trees have fallen into crisscross entanglements.

The cause of this devastation is the larvae of a tiny moth—the lodgepole needle miner. Several species of the insect attack lodgepole pine foliage. All belong to the genus *Coleotechnites* (Hodges 1965) = *Evagora* (Freeman 1960) = *Recurvaria* (Lepidoptera: Gelechiidae). They are found in parts of California, Oregon, Idaho, Utah, and Wyoming in the Western United States; and in Alberta, Canada.

To date, only two species—*C. milleri* (Busck) and *C. starki* Freeman—have been identified and studied in detail. *C. milleri* is most notorious for long periods of outbreaks in the upper Tuolumne-Merced River watersheds in Yosemite National Park, California (Patterson 1921; Struble 1958; Yuill 1942). Lesser infestations have occurred 125 miles to the south in the upper Kings-Kern watersheds of the Sequoia and Kings Canyon National Parks. Epidemic outbreaks of *C. starki* have been recorded in Banff and Lake Louise National Parks in the Rocky Mountains of Canada (Stark 1959). Though highly destructive, these outbreaks persist for shorter periods than those of *C. milleri*.

Three periods of major infestations by *C. milleri* have been reported since 1900. The first began about 1903 and subsided after 1921; the second extended from 1933 to 1941; and the third lasted from about 1947 to 1963 (fig. 1).

The 2-year life cycle of *C. milleri* begins in the odd-numbered year and that of *C. starki* in the even-numbered year. *C. milleri* causes far more damage to needles initially, in subsequent generations, and for longer periods than does *C. starki*. Sustained higher populations and more

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Figure 1.—*A*, Dead forest, killed about 1906; *B*, infested, pole-size trees among snag remanants in 1953; *C*, dying, mature forest in 1963, heavily infested since 1953; *D*, twig tips with reduced complements of shortened foliage.

feeding per larva contribute to this difference between the two species.

Another species of *Coleotechnites*, closely related to *C. milleri*, has been observed infesting lodgepole pine in the Inyo National Forest, Mono County, California (Struble 1968). This species is similar to *C. milleri* in its biology and 2-year life cycle except that its generations, like *C. starki*, are established every even-numbered year. The effects of its infestations are less severe than those of *C. milleri*.

To gather more data about *C. milleri*, the Pacific Southwest (then California) Forest and Range Experiment Station joined forces with the U.S. National Park Service in cooperative studies at Yosemite National Park, starting in 1954.

This report summarizes findings from these studies on the biology and ecology of *C. milleri*, including natural enemies and pathogens, relationship of climatic and physiographic influences to successive generations of needle miners, and field tests of insecticides.

HOSTS AND DISTRIBUTION

Lodgepole Pine

A subspecies of lodgepole pine (*P. contorta* var. *murrayana*) is the major host tree of the lodgepole needle miner. The tree grows on the Cascade Mountains of Washington and Oregon and on the Sierra Nevada of California (Fowells 1965). Within this range, it ranks as a major timber species. In northern California, lodgepole pine grows on mountainous terrain between 6,500 and 10,000 feet elevation.

Major infestations have been found only in stands at 8,000 to 10,000 feet elevation west of the Sierra Nevada crest along the eastern boundaries of Yosemite National Park. Large blocks of mature lodgepole pine have been the most severely attacked.

Smaller trees have not been spared in needle miner infestations. Highly damaging infestations have also been found in younger, dense lodgepole pine stands, where trees ranged between 4 and 14 inches diameter at breast height. These were growing among scattered, heavily infested, older trees and the gray snags remaining from an earlier outbreak (Struble 1958). Attacks have also been heavy and persistent in the crown tops of saplings taller than 5 feet. Often the smallest seedlings became infested when populations of larvae dropped from the mined-out foliage of overstory trees.

Many of the areas of dead forest in Yosemite National Park have been replaced by nearly pure lodgepole stands. Some stands are dotted with dense, almost impenetrable thickets of saplings. Evidence is strong that, over the course of several hundred to a thousand years, repeated devastating needle miner outbreaks have been followed by successive replacements of lodgepole pine forests.

Outside of Yosemite National Park, several smaller infestations have been known since 1923.

They have occurred in stands growing in similar elevation and terrain, west of the Sierra Nevada crest, in widely separated pockets of less than 1,000 acres in the Kings-Kern watershed south of Yosemite.

Associated Host Trees

Several other forest conifers are distributed throughout the area of needle miner infestations. Some species grow as nearly pure stands covering from a fraction of an acre to several acres; others as single trees broadly dispersed. Mountain hemlock (*Tsuga mertensiana* [Bong.] Carr.), the closest associate, is found in nearly pure stands on north-facing slopes and on other well-drained but moist land. Red fir (*Abies magnifica* A. Murr.) grows often in draws and slopes up to 9,000 feet elevation. More scattered are western white pine (*P. monticola* Dougl.), whitebark pine (*P. albicaulis* Engelm.), and Jeffrey pine (*P. jeffreyi* Grev. & Balf.). Western juniper (*Juniperus occidentalis* Hook.) is found along the most exposed, dry, rocky slopes and occasionally as a single tree within a nearly pure lodgepole pine stand. White fir (*A. concolor* [Gord. & Glend.] Lindl.) is rarely found above 8,000 feet.

All of these conifers except western juniper have been occasional hosts of the lodgepole needle miner when they grow as understory of lodgepole pine. Attacks usually result from larval migration when fresh lodgepole pine foliage is gone before the larvae are fully grown in spring of the flight year. The amount of mining in associated host species varies considerably, but there is no evidence of continuing infestations beyond a single generation.

LIFE CYCLE

In the 2-year life cycle of *C. milleri*, which is established only in odd-numbered years, adults emerge, mate, and oviposit between July 15 and August 15 (fig. 2), with deviations from generation to generation because of slight variations in seasonal weather. No evidence of overlapping generations has been found. The eggs hatch in 30 to 35 days, and each larva then bores into a separate needle. Normally, hatching ends by September 20, and first-instar larvae continue mining until late November, when cold weather forces them into overwinter dormancy. Larvae resume feeding in April and May, continuing until November as development advances through second, third, and fourth instars. Cold weather forces a second overwinter dormancy. The fifth, and final, larval instar occurs after feeding resumes again in April and May, and continues for a month. Pupation, lasting almost 30 days, is completed the last 2 weeks in June.
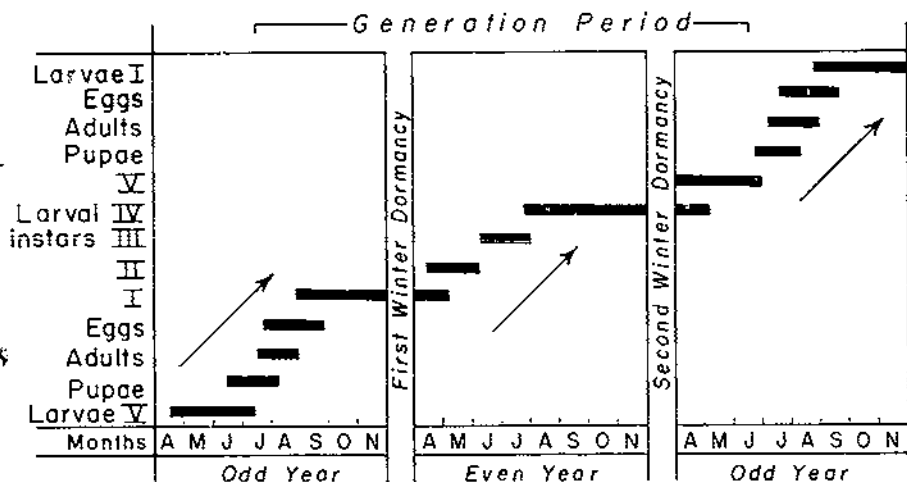
Figure 2.—Life cycle of the lodgepole needle miner (*Coleotechnites milleri* (Busck)) in Yosemite National Park, California.

LIFE STAGES

Adults

The mean width from tip to tip in both male and female moths, wings fully extended, is 12 mm.; it ranges from 8 to 13 mm. Body length from the head to the abdominal tip in both sexes ranges from 4 to 4.5 mm. Except for the white labial palpi and face, the head, thorax, and forewings are all light gray, mottled by irregular darkened areas. The hindwings are light dusky gray. The abdomen of the male is slender, silvery gray, and ends in characteristically pubescent claspers. The abdomen of the freshly emerged female is cigar-shaped and light gray, soon deepening to yellowish as the oocytes develop (fig. 3).

Eggs

The eggs are lemon yellow, typically ovoid, and 0.2 to 0.3 mm. long. The chorion is transparent, iridescent, and hexagonally patterned.

Larvae

Larvae acquire one of several uniform, often dusky colors after they enter lodgepole pine foliage. Lemon yellow predominates, but varying shades of orange, pink, and red occur among each of the five instars before pupation. The significance or cause of color difference is unknown.

All larval instars are naked and black-headed. Paired sclerotic areas appear in the third instar, dorsally on the first thoracic and ninth abdominal segments. Male gonads become increasingly visible dorsally between the fifth and sixth abdominal segments as growth continues beyond the third instar.

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Figure 3.—Development stages of the lodgepole needle miner: *A*, eggs in mined needle; *B*, larva; *C*, pupa in silk-lined cell within mined needle; *D*, adult.

Morgan [2] determined five in-star groupings after measuring

[2] Morgan, Furniss David. Factors in-fluencing the abundance of *Recurvaria milleri* (Busck) (Lepidoptera: Gelechi-idae). 1956. (Unpublished Ph.D. thesis on file at the University of California, Berkeley.)

head capsules of larvae in the 1953 to 1955 generation. I veri-fied this grouping in head meas-urements of 150 larvae each, taken every 2 weeks between July 11 and September 5, 1958, and again in June 1959. En-trance and exit holes in needles
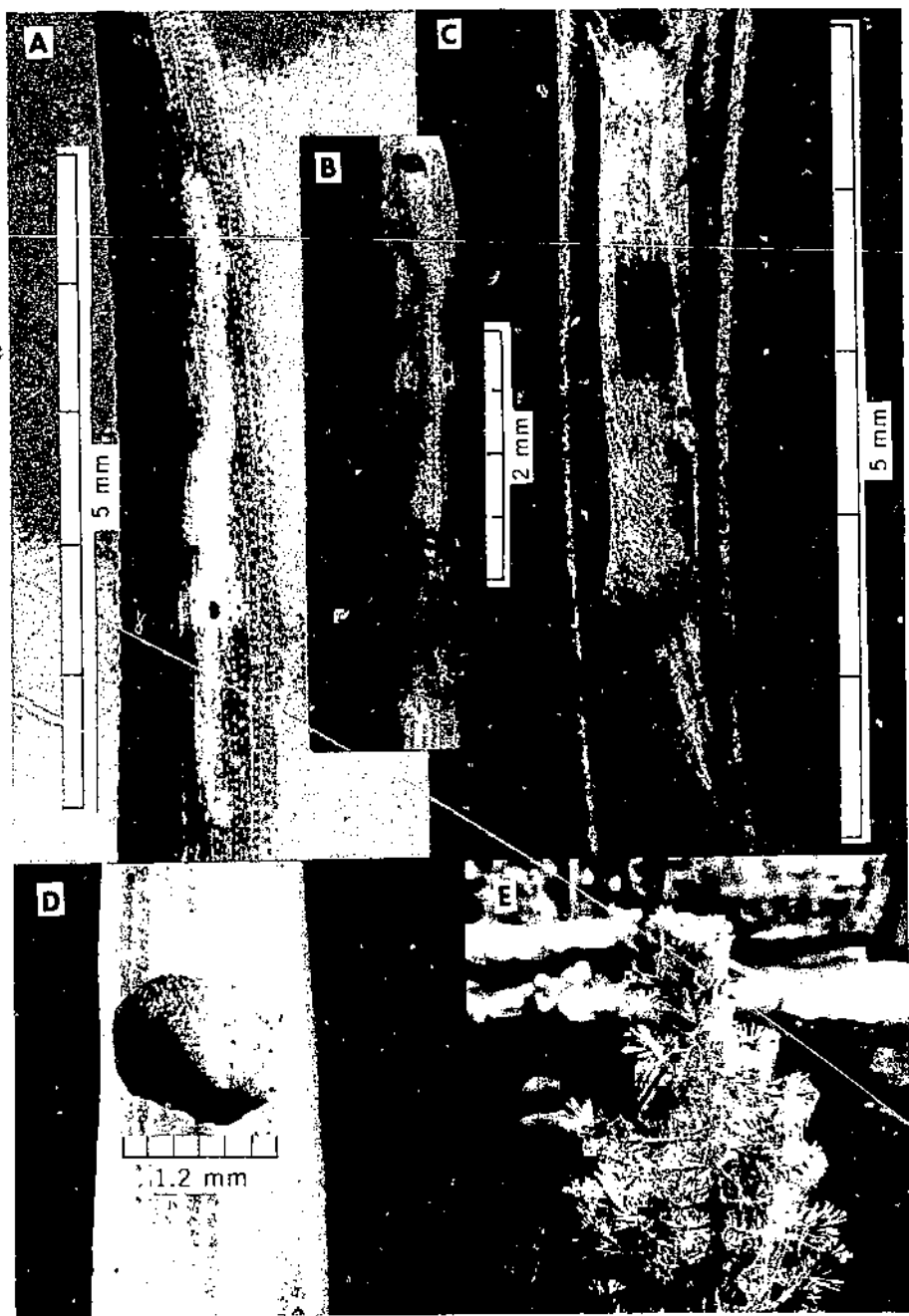
Figure 4.—Needle mining by different larval instars: *A*, first instar *B*, first-instar entrance (lower), second-instar frass exit (middle), third-instar exit (upper); *C*, silk tube leading to fourth-instar entrance at needle apex; *D*, moth exit; *E*, silk tent formed on understory sapling by fourth and fifth instars dropping from defoliated trees.

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bored by the five different instars were also readily identified by measurements across the widest points. The width of hole mined by each instar was as follows: first—0.1 mm.; second—0.3 mm.; third— 0.5 mm.; fourth—0.8 to 0.9 mm.; fifth—0 to 1.2 mm. (fig. 4).

Pupae

The pupa is 1.1 to 1.2 mm. wide and 6.0 to 6.2 mm. long. Newly formed pupae retain the larval coloration for 24 to 48 hours, then darken gradually to velvety, jet black. They are usually oriented with the anterior end toward a silk-lined ramp and exit. The exuvium of each fifth-instar larva is behind and often remains attached (fig. 3C).

BIOLOGY

Emergence and Sex Ratio

Emergence lasts about 3 weeks (table 1). The adult forces a triangular split in the anterior ventral end of the pupa. With head exposed and forelegs extended, the moth crawls forward within the needle, still attached to the pupal case. The moth continues along a silk-lined ramp leading through an exit hole which was bored by the fifth-instar larva before pupating (fig. 4D). The split pupal case becomes lodged against the exit, enabling the moth to gain freedom to the outside.

Males usually begin to emerge at least 10 days before females and continue to emerge 5 days ahead through this period. The number emerging rises rapidly after 10 days, peaks 2 to 3 days later, and is nearly concluded 7 to 8 days later; 95 percent of the emergence occurs within about 14 days.

The sex ratio on emergence is nearly equal. In more than 25,000 moths examined in four generations from 1957 to 1963, the mean male-to-female ratio was 1:0.84, with variations between generations from 1:0.78 to 1:0.91.

Table 1.—*Period of moth emergence during eight generations at Tuolumne Meadows, Yosemite National Park, California*

Year	Beginning date	Number of days to—	
		Peak	End
1953	July 20	16	22
1955	July 15	12	20
1957	July 7	10	20
1959	June 30	15	22
1961	July 6	12	20
1963	July 19	20	32
1965	July 20	25	50
1967	July 20	18	30

Flight

Moths can begin flying as soon as their wings have straightened and dried, but the beginning and end of flight are determined largely by temperature and light. Remaining quiescent and hidden within the tree crowns, few moths are seen during the day for the first week to 10 days, afterward they are seen increasingly in slow moving air above 50°F. during daylight and darkness. Maximum flight occurs on

clear evenings when the air is still or moving lightly, temperature is low, and light intensity is diminishing. Moths remain quiet during thunderstorms and rainfall. During cold mornings and when daytime breezes increase above 5 miles per hour, they cling to tree surfaces, unless disturbed by local vibrations in tree crowns. In still air, they fly without any consistent pattern—air movement determines direction.

Drifting along with slow-moving air, the older moths tend to concentrate in the trees lying along the periphery of an outbreak. The spread of infestations is greatest in the direction of prevailing air movement from southwest to northeast. Infestations move more slowly in other directions, with temporary shifts in evening airflow.

Dead moths are found commonly in still pools within 3 weeks after the beginning of emergence. Masses accumulate in backwashes along streams (fig. 5) 10 days before the flight period ends.

Mating and Oviposition

Reproduction activity begins toward evening as lowering temperatures approach 65° F. Morgan [3] reported that maximum mating occurred at about 55° F. It ends as temperatures drop below 51° F. The mating period was between 6 and 10 p.m., with maximum activity between 7 and 8:30 p.m.

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[3] Morgan, op. cit.

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Figure 5.—Dead moths accumulated along leeward edge of still pool.

Mating occurs most often within the tree crowns among the branch tip foliage. Other locations are on the twigs, branches, and trunk.

Females begin ovipositing within 24 hours after mating. Between twilight and darkness they search for favorable sites. They lay eggs after probing needle surfaces, bud scales, bark depressions, and spaces between closely appressed needles with their ovipositors. Two sites are preferred: (1) Current year's needles which are firmly attached, partially mined apically, emptied of frass and cast skins, and with an open third- to fourth-instar exit hole; (2) older, weathered, gray, cracked needles with a long mine and a green, firmly attached base. Eggs are most frequently deposited as a single group in old mines. They are held together apparently by adhesion between surfaces. Occasional deposits of a single egg and as many as five groups of eggs have been found at a single site.

Needle sites were examined in 1959 and 1961. The data for the respective years are as follows: 623 and 3,500 sites examined; 26 percent and 38 percent of sites with eggs; an average of 11 and 7 eggs per occupied site.

The number of eggs per group varies between generations. This variation was shown by counts made 15 or more days after the peak of emergence was over in three successive generations, 1959 to 1963. The mean number of eggs per group dwindled in each successive generation, from 11 to 7 to 4.

Incubation and Eclosion

Stages of egg development are readily recognized by color and form: (1) Freshly laid, lemon-yellow eggs deepen to orange in about 10 days; (2) darkened eye spots, deepening head color, and the beginning of larval body form appear between the third and fourth weeks; (3) fully formed larvae are evident within the egg sacs in 4 to 7 weeks. Eclosion is then imminent.

The mean period between peak oviposition and peak eclosion was 35.5 days in the first four generations and 60 days in the fifth and sixth generations (table 2). These differences were attributed to seasonal variations in weather.

Larval Development

After eclosion new, first-instar larvae tend to remain relatively immotile for 1 to several hours or longer. Then, each larva searches for and enters a fresh, green needle and passes the first winter. Rarely is there more than one larva in a needle.

The first and second larval instars and the major portion of the third instar are completed in summer within the first needle entered. Migration to another needle begins in the third and is completed in the fourth instar. After overwintering again, the larvae transform into the fifth instar. During this second winter, dormancy begins by mid-November and lasts until May. By mid-June, the insects pupate.

The number, location, and size of entrance or exit holes or those bored for the release of frass help identify the larval stages.

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Table 2.—*Incidence and incubation period of eggs in seven generations in Yosemite National Park, California*

Year	Date of—			Days to peak hatch
	First eggs	Peak production	Last eggs	
1955	July 20	Aug. 5	Aug. 20	35
1957	July 23	Aug. 6	—	35
1959	July 10	Aug. 1	Aug. 10	35
1961	July 12	July 25	Aug. 13	38
1963	July 27	Aug. 15	Aug. 28	60
1965	—	Sept. 5	Sept. 20	60
1967	—	Aug. 20	Sept. 5	38

Those bored by the first three instars are primarily through the curved surface near the apex of the needle; those by the fourth and fifth instars are through the flat surface between the base and apex.

In a lodgepole pine stand long free from an infestation, the first-instar larvae enter the oldest needles—especially those growing from the 6th to 11th internodes. When development reaches the third and fourth instar, the larvae migrate to and enter the elongating youngest needles and those of the most recent internodes.

First-instar larvae enter the needles along the rounded or convex surface, rarely the flattened or concave surface. A normal entry, requiring 8 to 36 hours, is 4 to 8 mm. back of the needle apex (Yuill 1942). The mine, in the mesophyll tissue beneath the epidermis, is seen on the outside as a thin, whitish streak leading from a barely perceptible entrance hole. By mid-October the miner often dips deeper into the needle, then reverses back along the original route. The mine is then widened apically from the entrance and is extended basally about 8 mm. beyond the entrance by mid-November (fig. 4A). The tunnel is widened and deepened the following May.

Infrequently, first-instar entries are made through a silk tube spun on the needle surface. Most entrance holes are left open and serve for frass disposal. Sometimes the entrance is sealed off with silk, but the mines remain largely unlined.

Between late May and July, the change to second instar occurs within the widened area of the mine, which is further widened and deepened in this stage, with extensions through the vascular region to the adaxial epidermis. Light filtering through this hollowed area reveals ample space for the larva to maneuver and reverse its direction. Often an exit is bored through the convex surface of the needle and used for expelling borings and frass. The amount of silk spinning varies considerably among second-instar larvae. Infrequently, the initial entrance and one or more frass exits are sealed off by this stage.

The second ecdysis, resulting in the third instar, begins in late June. Most third-instar larvae remain in the first needle through the third ecdysis. A small number migrate to and enter a second needle.

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Third-instar larvae mine primarily in the adaxial vascular region of the first needle entered, between the widened area and the needle apex. Two channels are hollowed along both sides of the needle, along with much of the central vascular area. This hollowing results in a flattened central core between epidermal layers.

Third-instar larvae also bore an exit hole large enough for the fourth-instar larvae. The dorsally located exit hole is often near the original entrance hole and may obliterate it. Infrequently, the exit hole is bored through the flattened surface just back of the needle apex.

Many fourth-instar larvae remain for variable periods within the needle originally entered. They transfer to a second needle by late September. Many of them are lost within needles prematurely dropped. Before transferring, larvae in this stage may be seen in numbers within the first needles entered between July 23 and September 15. Migrations during four generations, 1956 through 1962, were similar in timing, beginning the third week in August and ending a month later.

Transferring larvae migrate to the new-growth foliage of the terminal internodes of each twig. A larva enters between the opposing flat surfaces of the two needles of a fascicle. It spins a silk tube between these surfaces or on a single surface where needles are apart (fig. 4C). Where the opposed flat surfaces are close, it may enter both needles but fully mine only one. As the terminal foliage becomes fully infested, the larva may enter unmined needles of the older twig internodes.

Newly transferred larvae are visable within fresh needles several hours to a day after entry. They bore continuously and rapidly, and hollowed portions become plainly visible.

Once within the second needle, the larva continues to mine rapidly until cold weather returns in November. A needle 50 to 60 mm. long may be hollowed within 3 weeks. Some new needles, shortened by the effects of preceding generations of needle miners, are hollowed in less than 10 days. In trees previously heavily infested, larvae often shift to four or more short needles.

Heavy populations of fourth-instar larvae spin downward on silk strands in search of fresh needles after completely defoliating the host trees. Large trees are often enveloped within a fragile, short-lasting tent; small understory trees are defoliated and enclosed by heavy webbing (fig. 4E).

The fourth ecdysis, and the beginning of fifth-instar larvae, occur ordinarily about mid-April, with major transformation continuing in May. Fifth-instar larvae mine one or more normal-length needles. The mines are lined heavily with silk, particularly in the last-mined needle, which is the pupal chamber. The pupal cell often has thin, protective barriers of silk. A silk ramp leads from the anterior end of the cell through the heavily lined exit (fig. 4D). The exit is oriented toward the needle apex, usually along the flattened surface, about 16 to 23 mm. from the entrance bored by the

fourth-instar larva. The fifth-instar larva seals the entrance before it pupates.

Pupal Period

The pupal period lasts about 30 days, usually from mid-June to mid-July. In eight successive generations between 1953 and 1967 the period varied between 26 and 36 days. The period was delayed by 1 to 3 weeks in the 1963, 1965, and 1967 generations.

EFFECT ON HOST TREES

Foliage Loss and Regrowth

Individual twigs of noninfested lodgepole pine may keep their needles up to 11 years. The oldest internodes lose their needles naturally, but keep many of them. Almost all needles of the five terminal internodes are usually kept.

When trees first become infested, abscission and dropping intensify loss of the older foliage, since the whole fascicle will fall when only one of the needles is attacked. Intact needles and unmined portions of needles entered turn yellowish to golden within 11 months after larval entry, then drop off—often before many larvae have moved on to a second needle.

Forests quickly show the effect of heavy needle miner infestations. Trees become yellowish after 10 months and appear scorched within a year, as larvae quickly mine the younger foliage. The fading, yellowish-white crowns become thinner and somewhat grayish because of their loss of older needles. By June, as the 2-year life cycle of the needle miner is nearing completion, the forest appears to be dying. This change is offset considerably within a few weeks by elongating shoots, the growth of new needles, and the dropping of mined foliage. But the thinned crowns are evidence of the damage potential of successive needle miner generations.

A recognized but unmeasured amount of needle killing is done by fourth-instar larvae. They often enter the two closely appressed needles of a fascicle and spin a silk tube between them. Only one needle may be hollowed, but both die. Other needles that the larva barely enters and then abandons also die.

Infested trees may lose nearly 90 percent of their needles during the first generation of an outbreak. The loss is distributed about equally among all internodes of needles. The loss of foliage becomes increasingly damaging in successive generations as needle miners continue to attack the vital, younger needles. In the second, third, and often the fourth generations, populations established per twig progressively decline, but the damage impact on the host tree often increases.

Shortened needles of the terminal shoots are conspicuous in fall at the beginning of the third successive outbreak generation, and each year thereafter as infestations continue. Needle length may be reduced to half normal or less after four or more generations, and the numbers of
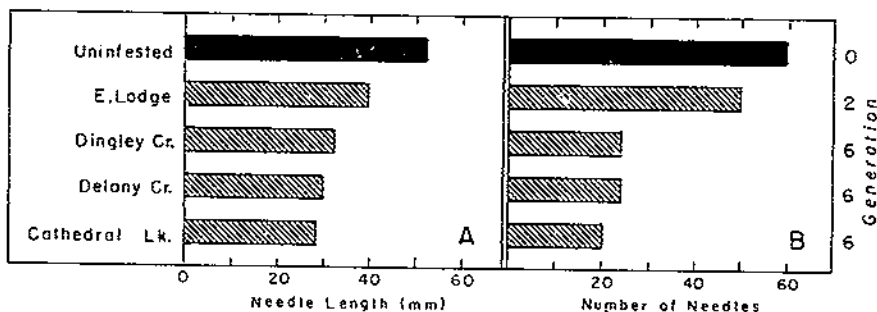
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Figure 6.—Reduced average length (A) and number (B) of midcrown terminal needles per twig in young uninfested and older heavily infested lodgepole pine stands. (Basis: 20 twigs per 10 trees each, 1961.)

new needles are reduced even more (fig. 6).

Stem and Shoot Growth Decline

After a tree loses its needles, growth of lateral wood and terminal shoots is soon reduced. The slowdown, which is variable between trees, is gradual during the first heavy infestation, but continues more intensively in successive generations.

Reduced lateral growth and decadence in lodgepole pine forests were reported by Patterson (1921). In 1957, I found severe reductions in radial growth in 20 living mature lodgepole pine which had survived previous and current periods of outbreak. These reductions, in two periods between 1890 and 1957, contrasted with a regular pattern of radial growth in 30 nearby non-defoliated, mature red fir (fig. 7). Stark and Cook (1957) found reductions in the width of annual rings of mature and young lodgepole pines that had been about 50 percent defoliated by *C. starki.* In Yosemite Park, they found similar reductions in width between 1945 and 1950 in two trees about 30 percent defoliated by *C.*

milleri. In one of the trees the width of annual rings increased to previous levels after 1950; the tree had been sprayed the preceding year.

Terminal shoot growth is severely shortened. In 1958, I compared the lengths of 20 terminal internodes, each dating from 1939, in 10 infested, pole-size lodgepole pine and in 10 noninfested red fir check trees (fig. 8). In lodgepole pine, the severe shortening of internodes was progressive, beginning in 1949 after heavy and sustained needle miner infestations. In red fir, the usual fluctuations in length of
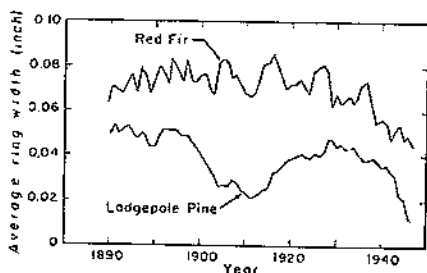

Figure 7.—Reduction in radial wood growth of lodgepole pine by needle miner infestations in Yosemite based on mean radial growth of 30 mature lodgepole pines and 30 mature red fir nearby.
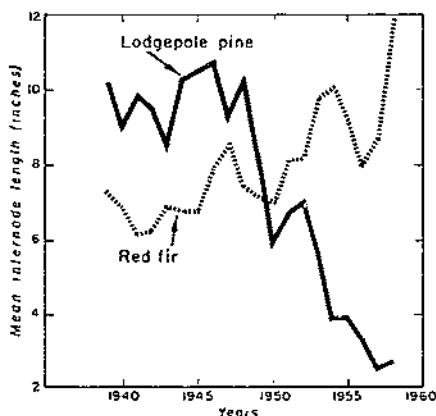
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Figure 8.—Mean internode length of 10 trees each of lodgepole pine and red fir. The effects of infestation can be seen in the reduction in internode length of lodgepole pine, starting about 1947.

terminal internodes continued unchanged in and after 1949.

In the heaviest centers of *C. milleri* infestations between 1947 and 1963, defoliation by each generation was commonly estimated between 90 and 100 percent. Annual rings were less than 0.1 mm. wide—radial wood growth essentially stopped.

Tree Injury and Mortality

Loss of needles, shortened new growth, and decline in stem and shoot growth culminate in the death of a lodgepole pine forest. Mature and overmature stands have been the most severely damaged by *C. milleri* outbreaks. The major damage impact of infestations since 1947 has occurred in older trees.

Between 1953 and 1963, entire forest stands were killed on more than 6,000 acres in the Conness, Dingley, and Delaney drainages and in the Cathedral Lakes basin in Yosemite National Park. In age, 25 trees sampled ranged from 135 to 485 years; mean was 278 years. The trees had been weakened by needle miner infestations and attacked later by the mountain pine beetle. Their diameters varied from 22 to 52 inches d.b.h., and they stood more than 120 feet tall.

During this same period of infestations, young stands of variable ages from 20-year-old saplings more than 5 feet tall to trees more than 100 feet tall were severely damaged. Pole-size and larger trees suffered branch killing and seriously depressed growth. In the Cathedral, Murphy, Budd Creek, and Tenaya Creek drainages, dead and top-killed trees greater than 4 inches d.b.h. were numerous in heavily stocked areas.

STUDIES OF INFESTATIONS

Long periods of damaging infestations followed by sudden collapse have been characteristic of the needle miner. Infestations fluctuate in intensity, showing similarities in numbers of larvae in successive generations in various locations. Infestations may develop at different times in different stands and disperse outwardly as each new generation is established. Bounds have been identified beyond which infestations fail to develop. Spread is determined by weather, the association of an arthropod parasite-predator complex, and diminishing host food.

The sudden collapse of infestations may be associated with

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natural catastrophes. Winter temperatures dropping well below normal were closely associated with the collapse of *C. starki* between 1950 and 1956 (Stark 1959). In Yosemite, temperatures in winter from 1947 to 1963 were never low enough to reduce infestations below damaging levels, but sharply declining populations after 1963 followed cold, wet summer weather at the time of moth flight and eclosion in that year.

The similarity in makeup and variability of infestations was observed at 25 locations between 1953 and 1963. At each site, rapid changes from light to heavy infestations were evident by the second or third generation. Larval populations dropped to lower levels in the next two to three generations as host food diminished (fig. 9).

Sampling Procedures

Dependable population estimates were possible from samples of larvae taken in October of the odd-numbered year, after complete eclosion; in spring and early summer of the even year, before the larvae start to move to the second needle; in the fourth instar after September of the even year; and at the pupal stage in early summer of the next odd year. Data at other periods were not comparable because of larval migrations from needle to needle, the dropping of infested needles, and other natural control factors. The best estimates of emergence were obtained from samples of pupae collected after mid-June.

The five-internode terminal was considered the most reliable
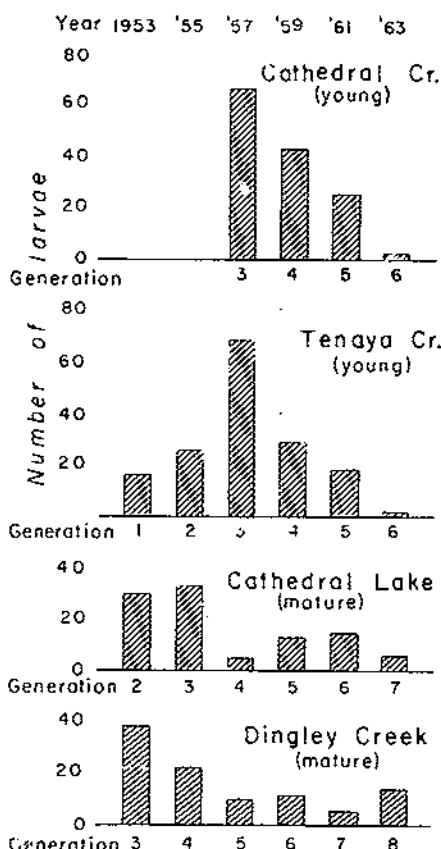
Figure 9.—**Larval populations per tip in six generations of needle miner infestation.**

unit for sampling infestations of *C. starki* (Stark 1952), and was adapted for the sampling of *C. milleri* in the first to second generation. Afterward, as defoliation progressed, the terminal two to three internodes of needles were all that remained as a unit base for population estimates. The shorter tips remained acceptable until the number of infesting larvae fell below that required for the sampling accuracy of a reasonable-sized area sample.

In sampling during the first two generations of an outbreak,

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populations of larvae under 10 in the latest five internodes were rated light; 10 to 30, moderate; 30 to 40, heavy; and over 40, very heavy. After two generations of heavy to very heavy infestations, six to 12 larvae in the remaining internodes of needles were rated moderate, and more than 12, heavy.

Tip samples of four per tree were clipped from midcrown branches of medium-height trees, with pole-pruners reaching 18 or more feet above ground (fig. 10). Midcrown populations were not found to be significantly different from those in the top levels and were acceptable as the crown mean (table 3). The number of trees sampled in a given area was determined from the infestations per tip: 10 trees in heavily infested, and 15 to 25 trees in moderately infested stands.

A sequential sampling system was developed by Stevens and Stark (1962) for population estimates in large blocks of forest. Adapted from the system for *C. starki* (Stark 1952), the system for *C. milleri* used only the latest two infested internodes. Four infestation classes were designated: light, medium, heavy, very heavy. Living insects in samples from the midcrowns of 12 to 15 trees were counted in the field. Counting was discontinued when

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Figure 10.—Collecting twig tips for sampling needle miner population.

the total living infestation of the sample unit fell into one of the infestation classes (Stevens and Stark 1962; fig. 11).

Populations in lightly infested stands were generally below lev-

Table 3.—*Populations in upper- and midcrowns of lodgepole pine in Yosemite National Park, California, 1956 (Basis: 40 tips, 10 trees)*

Date	Top		Midcrown		Significance (t)
	Mean	SE	Mean	SE	
	No.	*No.*	*No.*	*No.*	
July 2	34.9 ±	2.16	32.5 ±	2.76	[1] 0.67
Sept. 15	43.8 ±	1.86	39.0 ±	2.40	[1] 1.57

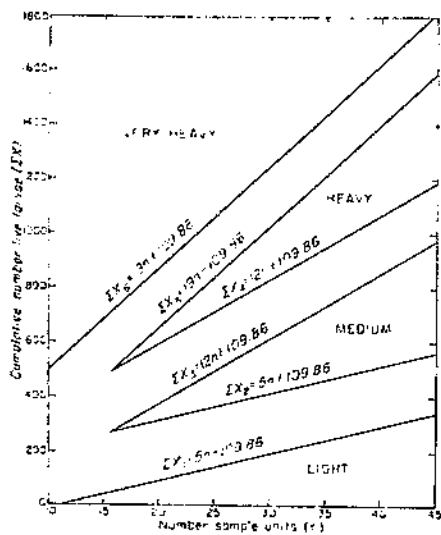[1] Not statistically significant.

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Figure 11.—Sequential sampling lines for *Coleotechnites milleri* (Stevens and Stark 1962).

els that allowed reliable sampling procedures. Estimates in a given area were based on total counts of infested needles. Two categories of light infestation were recognized: (1) between one and four larvae per tip; (2) less than one larvae per tip. The number of larvae accepted as representing the higher level required 100 random tips from 25 to 50 trees. The lowest population level was estimated from all tips in branch samples from 10 to 25 trees; each branch had about 25 tips.

Zone Limitations

Between 1947 and 1963, needle miner infestations in Yosemite National Park spread generally from west to east and remained confined to lodgepole pine forests within an elevation range of 8,000 to 10,000 feet (fig. 12). Spreading south and east from the most northerly infestation centers (Rodgers, Matterhorn, Virginia Canyons), outbreaks developed in the north tributaries of the Tuolumne River (Conness, Dingley, and Delaney Creeks). Spreading north and east at the same time from the most southerly centers (Tenaya Lake, upper Tenaya Creek, Murphy, and Cathedral Creeks), outbreaks developed in the Cathedral Lakes basin and into the south tributaries of the Tuolumne River (Budd, Unicorn, and Rafferty Creeks). Coalescing into the major drainage basin of the upper Tuolumne River, infestations from both the northwest and south continued to spread eastward through Tuolumne Meadows on into the two major forks of the Tuolumne River and toward Mono and Tioga Passes.

Heavy infestations in Tuolumne Meadows began in 1955. By 1963 they had extended east and south into the drainages of Dana and Lyell Forks and north into the basin surrounding and east of Dog Lake.

All previously recorded infestations occurred within the same range in elevation as the 1947 to 1963 outbreak. Many dead and bleached snag remnants from earlier outbreaks were still standing upright within this zone. Below 8,000 feet elevation there was no evidence of previous infestations.

Successive generations of moderate needle miner infestations occurred in stands along north- and west-facing slopes reaching 10,000 feet elevation. Eastward toward Mono and Tioga Passes, infestations remained extremely light for successive generations

in forests above 9,600 feet, but no studies were made to explain why. Also, populations remained light at elevations above 9,000 feet toward the passes (table 4; fig. 12). Strong air currents near the passes may have prevented infestations from developing. Heavy infestation and damage continued in stands at lower and higher elevations elsewhere within the zone.

Table 4.—*Larvae established in successive generations at locations eastward from Tuolumne Meadows near Mono and Tioga Passes (Basis: total count from 100 tips each)*

| Station | Elevation | Larvae per tip | | |
		1959	1961	1963
	Feet	*No.*	*No.*	*No.*
Gaylor	9,300	0.93	0.63	0.11
Upper Mammoth	9,500	.61	.29	.02
Lower Mammoth	9,200	2.00	1.32	.06
East Lyell	9,200	.18	2.70	1.71
West Lyell (N)	9,100	2.63	4.22	3.54
West Lyell (S)	9,100	1.74	1.22	.42

NATURAL CONTROL

Needle miner populations are affected by natural enemies, disease, climate, and available food. But natural factors do not exert their controlling effects soon enough during epidemics to prevent widespread tree mortality, as demonstrated in each of the three known outbreaks since 1900. Needle miner populations that have reached a peak tend to persist for 10 to 20 years before collapsing.

The biological control of needle miner epidemics can help reduce and hold populations below damaging levels. Among many native arthropods which prey upon or parasitize the needle miner, some insect species have demonstrated considerable capacity for control. But no single species, group, or combination of all arthropods could hold down outbreaks of *C. milleri* in five successive generations studied between 1953 and 1963.

Climatic changes, however, could account for the decline of all Yosemite infestations below damaging levels.

Arthropod Enemies

Insects outnumber all other arthropod enemies of the needle miner. Predatory mites and spiders, including two families each, are the major arthropods other than insects (table 5). Most of the insect enemies are parasitic (fig. 13). Best known are hymenopterous species of internal parasites that are biologically synchronized with the host's life cycle. Nearly all complete development and emerge from the host larvae, most of them from the final instar; several species

California Location Map

Redding

Yosemite
National Park

Area of map

Sacramento

San
Francisco

Los
Angeles

MONO COUNTY

0   1   2   3   4   5
M I L E S

- - - - Boundary of infestation

Heavily infested zone 1961

Forests killed 1953-1963

+   Locations (table 3)

Matterhorn Canyon

Virginia Canyon

Rodgers Can

McCabe Lakes

Creek

Return

Mt Conness

Tuolumne

Tioga
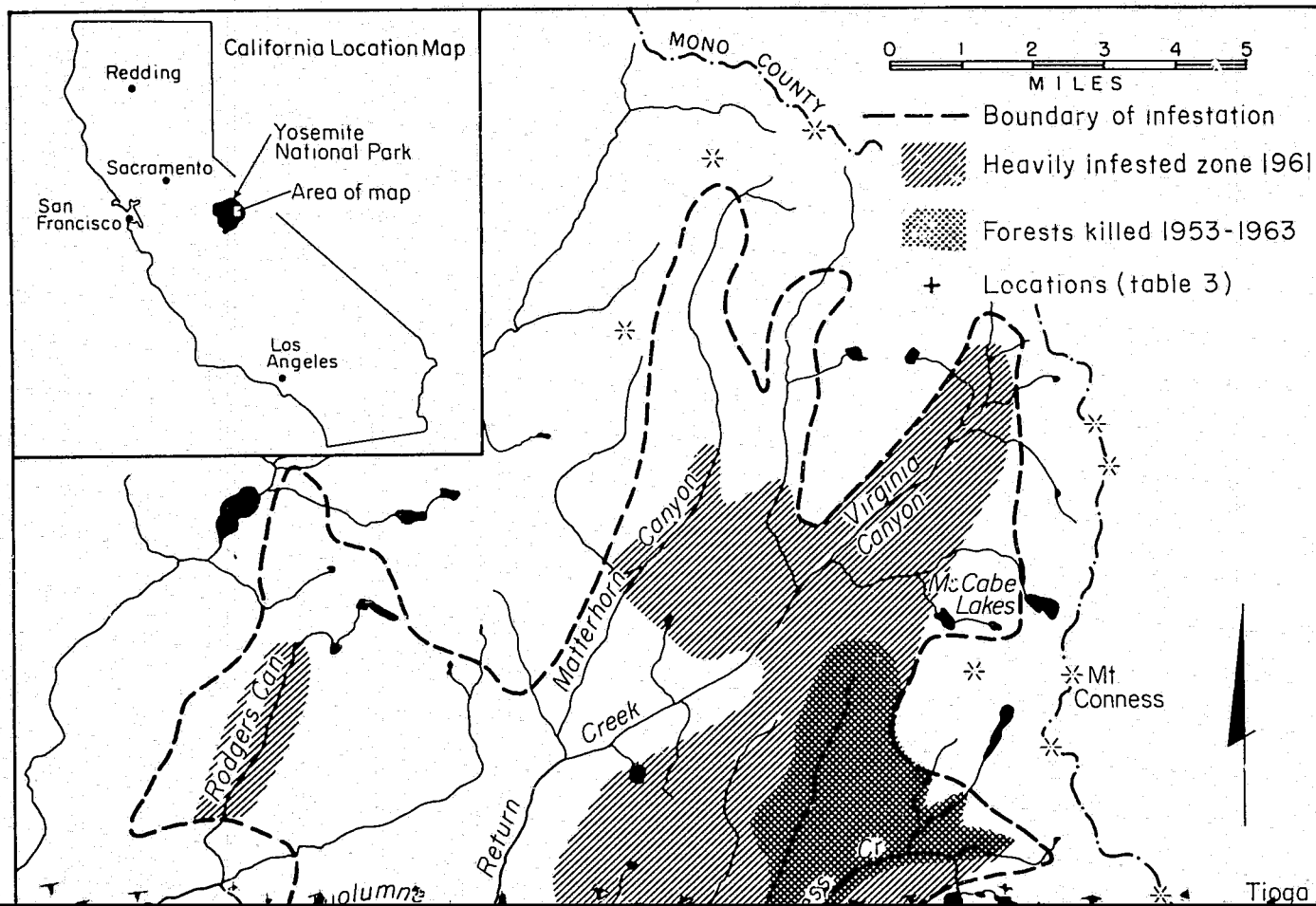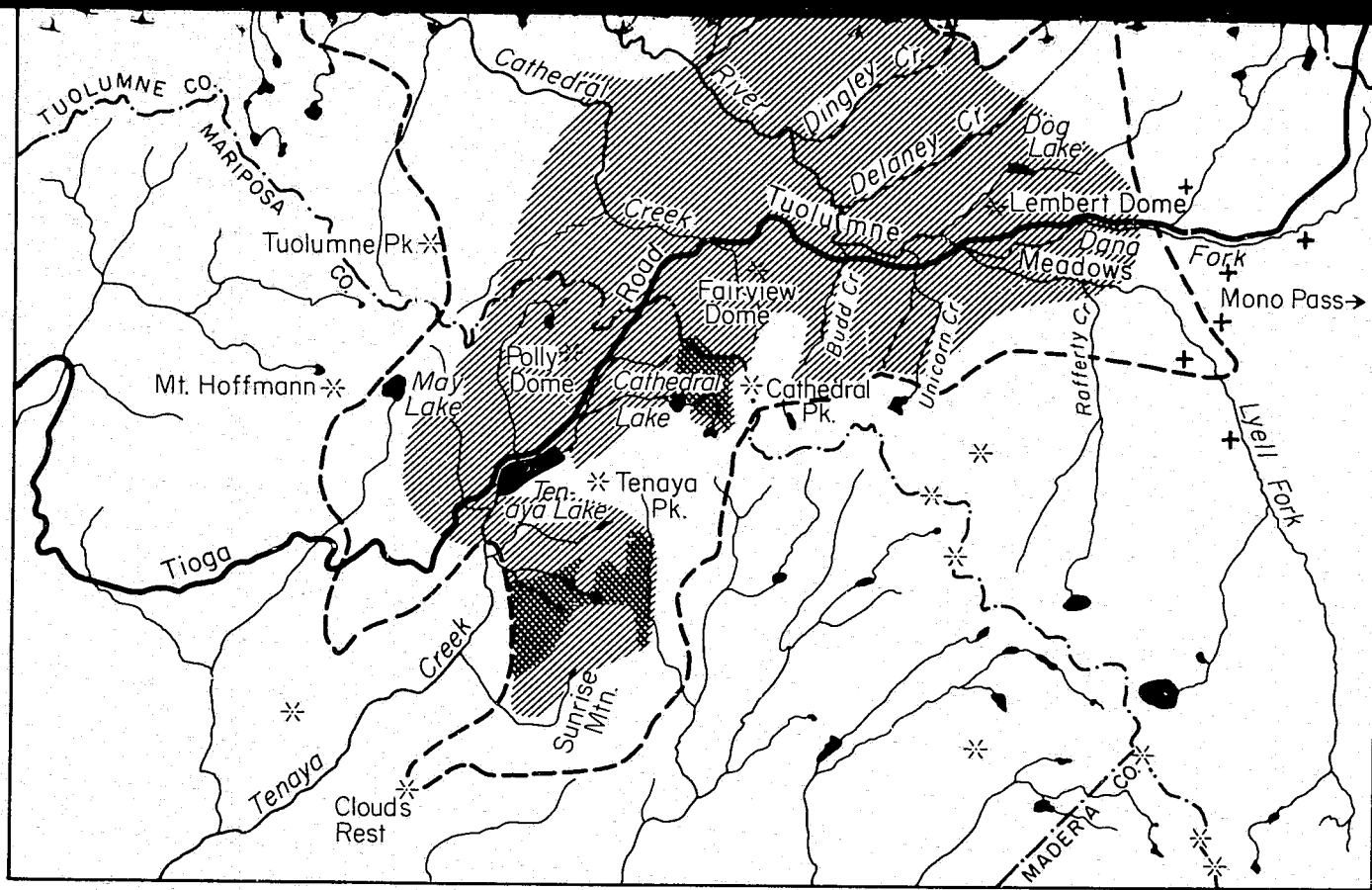
Figure 12.—Needle miner infestation zone and dead forests in Tuolumne-Merced watershed, Yosemite National Park.

emerge from pupae. Several hymenopterous species are parasitic externally, have short life cycles, and also parasitize the larvae of other host insect species.

Identities of insect enemies have been recorded by McLeod (1951), Patterson (1921), Struble (1967), Struble and Bedard (1958), Struble and Martignoni (1959), and Telford (1961a). Determinations by specialists include five orders, 19 families, 46 genera, and 57 species of Class Insecta. Predatory species are represented by six families in four orders. The parasitic species are all in order Hymenoptera.
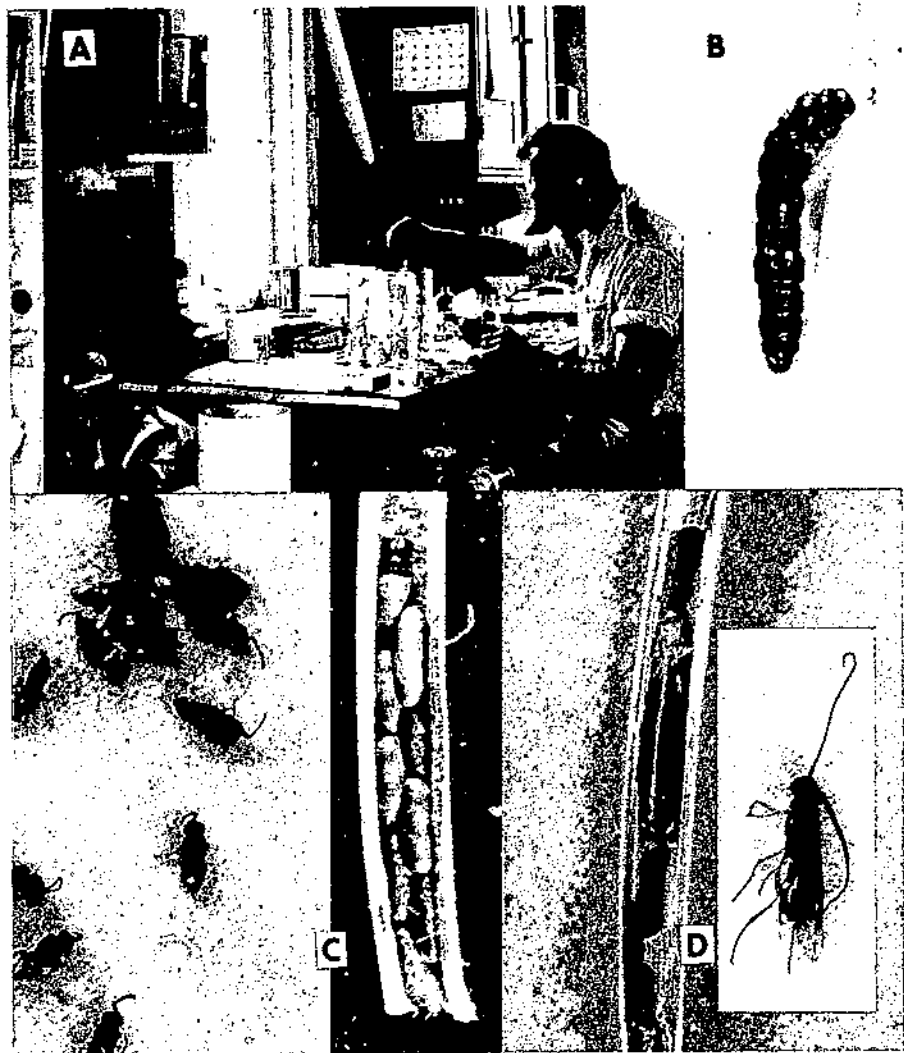
Figure 13.—Needle miner parasites: *A*, separating species; *B*, needle miner larva parasitized by eulophid larva; *C*, needle miner larva compartmented by polyembryonic *Copidosoma* larvae and *C. deceptor* adults; *D*, pupa and adult of *Meteorus pinifoliae*.

Table 5.—*Parasites and predators associated with the lodgepole needle miner*

Class	Order	Family	Genus and species* [1,2]
Arachnida	Acarina	Anystidae	*Anystis* sp. (Ba)
		Erythraeidae	*Balaustium* sp. (BA)
	Araneida	Thomisidae	*Misumenops* sp. (Cr)
		Salticidae	*Sitticus* sp. (Cr)
Insecta	Neuroptera	Hemerobiidae	
	Thysanoptera	Thripidae	
	Hemiptera	Anthecoriidae	
	Diptera	Empididae	*Euthyneura* sp. (A)
			Tachydromia sp. (A)
		Heleidae	*Forcipomyia* sp.
		Chamaemyiidae	*Leucopis* sp. (S)
	Hymenoptera	Trichogrammatidae	*Trichogramma* sp. (G) Eggs
		Braconidae	*Meteorus pinifoliae* Mason (W) pupae
			Apanteles californicus Mues. (M) larvae
			A. alticola (Ashm) (M)
			Aphidius varigatus Smith (M)
			Eubadizon sp. (M)
		Ichneumonidae	*Aethecerus pinifoliae* Mason (W) pupae
			Scambus aplopappi (Ashm) (CU) pupae
			Eriplatys sp. (W) pupae
			Itoplectis behrensii (Cress.) (M) pupae
			I. conquisitor (Say) (W)
			Scambus hispae (Harris) (Cu)
			Cremastus evetriae Cushman (Cu)
			Hemiteles sp. (W)
			Horogenes sp. (W)
			Campoletis sp. (W)
		Mymaridae	*Ooctonus* sp. (Bu)
			Polynema sp. (Bu)
		Eulophidae	*Sympiesis* sp. (Bu) larvae
			Dicladocerus sp.[2] (Bu) larvae, pupae
			Chrysocharis sp.[2] (Bu) larvae, pupae
			Zagrammosoma multilineatum (Ashm.) (Bu) larvae
			Z. nigrolineatum (Crawf.) (Bu) larvae
			Diglyphus sp. (Bu) larvae
			Z. americanum[2] Girault (Bu)
			Tetrastichus sp. (Bu)
			T. silvaticus Gahan (Bu)
			Derostenus sp. (Bu)
			Diaulomorpha sp. (G)
			Cirrospilus flavoviridis Crawford (G)
			Achrysocharoides sp. (G)
			Euderus sp. (G)

Table 5.—*Parasites and predators associated with the lodgepole needle miner*—Continued

Class	Order	Family	Genus and species* [1,2]
		Thysanidae	*Thysanus* sp. (Bu)
		Encyrtidae	*Copidosoma deceptor* Miller (Bu) larvae
			C. bakeri (How.) (Bu) larvae
			Copidosoma sp. (Bu) larvae
			Aphycus sp. (Bu)
			Blastothrix longipennis Howard (Bu)
			Lyka sp. (Bu 1952)
			Syrphophagus sp. (Bu)
		Torymidae	*Torymus* sp. (Bu)
		Pteromalidae	*Amblymerus* spp.[2] (Bu) larvae
			Hypopteromalus sp. (Bu) larvae
			Tridymus sp. (Bu)
			Spintherus sp. (Bu)
		Eurytomidae	*Eurytoma* sp. (Bu)
		Platygasteridae	*Platygaster* sp. (M)
		Sphecidae	*Xylocelia* sp. (K)
			Passaloecus sp. (K)
		Chalcididae	*Spilochalcis albifrons* (Walsh) pupae (Bu 1955)
			S. side (Walker) (Bu) pupae
			S. sanguiniventris (Cress.) (Bu) pupae

*Starred species are parasites found emerging from the needle miner stage specified.

[1] Abbreviation of identification specialists of the U.S. National Museum are in parenthesis as follows: A—Arnaud, P. H., Ba—Baker, E. W., Bu—Burks, B. D., Cr—Crabill, R. E., Cu—Cushman, R. A., G—Gahan, A. B., K—Krombein, K. V., M—Muesebeck, C F. W., S—Sabrosky, C. W., W—Walkley, L. M.

[2] Hyperparasitic; Telford (1961a).

Trichogramma sp. (Trichogrammatidae) was the only parasite I reared from needle miner eggs. The incidence was rare among thousands of eggs examined in five needle miner generations.

No parasites have been reared from host adults, but there is a single instance of adult predation by the empidid, *Tachydromia* sp.

Certain of the parasitic Hymenoptera have shown greater capability than others in biological control. Telford (1961b) rated as best those having host-synchronized life cycles and a great capacity for seeking out needle miners. Studies of encyrtids and braconids were later extended to include some of the asynchronous nonhost-specific eulophids (Struble 1967).

Hyperparasites may limit the effectiveness of primary parasites in serving as natural controls. Telford (1961b) found that *Copidosoma deceptor* and *Apanteles californicus* were parasitized by *Amblymerus* sp. "a," *Zagrammosoma americanum,* and *Chrysocharis* sp. "a." *C. deceptor* was also parasitized by *Tetrastichus* (prob.) *coerulescens* and *Tetrasti-*

chus sp. "a." *Aethecerus pinifoliae* was parasitized by *Amblymerus* sp. "a" and *Chrysocharis* sp. "a." In an earlier study, Telford (1961a) concluded that complementary attacks of the six most consistent primary parasites could — hypothetically — reduce needle miner infestations to non-outbreak status, even though these parasites did not control the outbreak during the generations studied.

Between 1961 and 1965, I studied parasites closely synchronized with the needle miner life cycle and those asynchronous (Struble 1967). The number of both maturing and newly established needle miners was high in 1961. In 1963, maturing populations continued in outbreak proportions, but the newly established ones declined sharply. Host populations begun in 1965 were well below those started in 1963. The causes of declines in populations noted in 1963 and 1965 could not be associated with the parasite complex.

From data gathered between 1959 and 1966, I tentatively concluded that certain primary eulophid parasites were more common than previously recognized (Struble 1967). For example, *Dicladoecerus* sp. was highly consistent in each needle miner generation, in parasitizing among all larval instars and pupae. Parasitism by this genus increased progressively among each of the first four larval instars, but decreased in the fifth instar and pupae. Two other primary eulophids, *Sympiesis* sp. and *Z. multilineatum*, commonly parasitized third- to fifth-instar larvae. Periodically, other less common asynchronous, primary parasites often were numerous in specific locations but absent from others. The ichneumonid *Aethecerus* sp. and chalcid *Spilochalcis* sp. emerged from pupae only in certain generations.

Primary parasites synchronized with the needle miner life cycle occurred most often in the fifth host instar at pupation. In order of most consistent occurrence they were: encyrtid, *C. deceptor*; and braconids, *A. californicus* and *M. pinifoliae* A decline in these parasites proportional to declining host populations was evident after 1963.

Birds

Birds play a variable role in the control of infestations. They may contribute measurably at times, but their effectiveness relative to other biotic factors is not known. Several species feed on maturing needle miner larvae and pupae inside the needles and on adults in flight. Bird predation has not been observed on the minute eggs and on early larval stages the first year. As a food source for birds, needle miners are available only during the final months of a generation.

The known avian association in lodgepole needle miner outbreaks is very limited. Observations during three maturing generations have given little more than clues to the frequency, abundance, and food habits among different bird species identified. The bird species observed associated in needle miner outbreaks and identified from published descriptions (Peterson 1941) are, by categories:

1. Feeding on larvae and pupae:

Mountain chicadee (*Penthestes atricapillus*)
(Western) warbling vireo (*Vireo gilvus swainsoni*)
Audubon's warbler (*Dendroica auduboni*)
Cassin's purple finch (*Carpodacus cassini*)
Oregon junco (*Junco oregonus*)

2. Suspected feeding on larvae and pupae:
   Western tanager (*Piranga ludoviciana*)
   Pine siskin (*Spinus pinus pinus*)

3. Feeding on adults (moths):
   Western wood peewee (*Myochanes richardsoni richardsoni*)
   Hammond's flycatcher (*Empidonax hammondi*)
   Audubon's warbler (*Dendroica auduboni*)
   Calaveras warbler (*Vermivora ruficapilla ridgwayi*)

Evidence is strong that maturing needle miner populations comprise a major portion of a chickadee's diet (Telford and Herman 1963). Other birds associated with the chickadee would benefit similarly if their migration coincided with the period of outbreak. But this food source would be available less than 6 months every 2 years.

Pathogens

A native granulosis virus in needle miner populations has been known since 1951 (Steinhaus 1957). In a single area, mortality in 1953 attributed to infection by this virus was estimated at between 30 and 50 percent.[4] This was the highest incidence found among outbreak populations maturing through 1963. The virus did not become epizootic, though widely distributed within outbreak areas. The infection rate varied, but remained well below an effective level of control (Struble and Martignoni 1959).

Heavy resining of needles containing dead first-instar larvae has followed infections by a needle fungus in certain locations. The needle fungus, identified as *Hypodermella montana* Darker,[5] was found localized in lodgepole pines growing in stream bottoms. Fungus infections identifiable in June were found in resin-saturated needles attacked by the needle miner the previous fall. There were no larvae surviving in numerous needles observed.

Weather

Weather appears to have an important bearing on the epidemiology of needle miner populations. Wellington (1954) proposed that variation in climate just before or at the beginning of an outbreak by an insect species that exhibits large and sudden fluctuations can determine the course of an epidemic. In studies of *C. starki*, Henson et al. (1954) found that periodic winter flows of unusually cold and stagnating air masses were associated with immediate heavy mortality. The possibility of predicting *C. starki*

[4] Thompson, C. G. Semiannual report, Jan. 1 to June 30, 1953. (Unpublished report on file, Dep. Biol. Contr., Univ. Calif., Berkeley.)
[5] Identified by R. S. Smith, Pacific SW. Forest and Range Exp. Sta., Forest Serv., U.S.D.A., Berkeley, Calif. Personal communication, Aug. 8, 1963.

outbreaks based on weather fronts and local climatic disturbances was emphasized by Stark (1959). He based his thesis on the relative roles of biotic and climatic factors. Additional observations of the species have led to the speculation that "weather during the oviposition period regulates the population" (Shepherd 1963).

Cold weather and storms occurring just before and during the period when new needle miner generations are being established may cause an outbreak of *C. milleri* to decline. My observations in Yosemite between 1955 and 1965 showed that (1) pupation and emergence were delayed when late spring and early summer temperatures remained several degrees below normal; and (2) mating and oviposition stopped whenever air temperatures dropped below 50° F., wind speeds were above 5 miles per hour, and rain fell.

Delayed and prolonged emergence and flight of *C. milleri* adults in 1963 and 1965 were unequaled in studies of the previous five generations between 1955 and 1961, (table 1), and not indicated in my observations of earlier generations between 1945 and 1953. A corresponding delay followed in the establishment of the next two generations, as measured by the duration of oviposition and rate of egg hatch. The emergence periods of adults were more prolonged in 1965 than in 1963 (fig. 14).

Compared with previous generations established, larval populations declined progressively in October 1963 and 1965, to 27 percent and 11 percent of the 1961 level, respectively (fig. 14). This was a two-generation drop from epidemic numbers of more than 25 larvae per twig to endemic levels of fewer than 2.5 larvae per twig.

Temperatures in June and July 1963 and 1965 were well below those for the same months in 1961. In addition, there were 8 consecutive rainy days in August 1965. Seasonal temperature differences can be expressed as degree-days above the developmental threshold assumed to be 40° for the needle miner. At the recording location, degree-days from June through August for 1961, 1963, and 1965 were respectively 2,598, 1,873, and 1,600 (table 6).

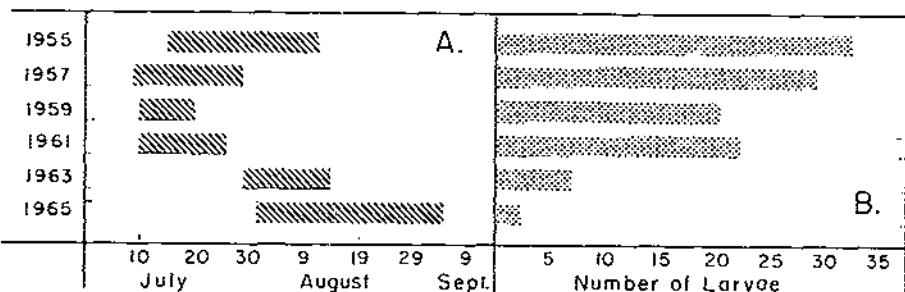A decline in population level in 1963 was suggested by the third

Figure 14.—Adult emergence and brood established in six needle miner generations: A, period of adult emergence; B, number of larvae per twig.

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Table 6.—*Degree-days during needle miner-establishing periods, Yosemite National Park, California*

Year	June	July	August
1961	398	880	1,320
1963	194	598	1,081
1965	200	480	920

to fourth week after oviposition was completed. Eggs did not begin to hatch until late in September, a time when most hatching should have been completed. Counts the following spring showed that 20 percent of the eggs failed to hatch. This trend continued more sharply downward in 1965, when all eggs observed in late September were in the beginning period of incubation, and no signs of hatching

were evident before the middle of October.

Larval populations established in 1963, 1965, and 1967 were progressively smaller in eight out of 15 drainage basins at elevations ranging between 8,000 and 9,600 feet, previously undisturbed by aerial sprays (table 7). Incomplete data from six other drainages suggest a similar downward trend. In the remaining drainage (Murphy), the population dropped sharply in 1963 and 1965 but then increased in 1967. However, survival was much higher than average in certain locations at lower elevations in 1963, 1965, and 1967. Populations of larvae established in 1967 at six of the lower stations were 23 times the number occurring at nine higher stations.

Table 7.—*Larvae established in three generations in Tuolumne-Merced watershed, Yosemite National Park, California (Basis: 100 tips, 10 trees per station)*

| Locality | Elevation | Generation | | |
		1963–65	1965–67	1967–69
	Feet		*Number*	
Lower Tenaya	8,000	..	..	674
Murphy	8,400	220	190	425
Murphy Weather Station	8,400			267
Olmstead #1	8,400	840	286	150
Olmstead #2	8,300		339	74
Bear Pits	8,700	502	290	204
Cathedral Creek West	8,500	110	0	11
Cathedral Creek North	8,500		151	0
Cathedral Creek South	8,500	110	107	10
East Cathedral	8,600		135	23
Dog Lake	9,200	193	62	28
Delaney Creek	9,200	1,572	205	10
Dingley Creek	9,200	1,380	206	4
May Lake	9,600	300	146	24
Cathedral Lake	9,600	788	218	8

The higher rate of survival at the lower elevations of the infestation zone suggested local protection from strong winds, adverse cold, and storm conditions. The lower stations showed similarities of terrain and forest cover: (1) close proximity of high mountains and tall trees to serve as barriers to prevailing air movement; (2) moderate to dense lodgepole pine cover in flats and along slopes often interspersed by varying sized, exposed granitic rock outcroppings and glacial boulders capable of absorbing and radiating heat from exposure to the sun. Slightly higher temperatures were probable in these lower locations, tending to favor earlier and longer establishing periods than those in similarly protected locations at higher elevations.

I have suggested the term "survival refuges" for areas of this kind, which may well serve as epicenters from which epidemics could spread when weather conditions become favorable for flight, oviposition, and incubation. The physical makeup, bounds, and micro climates of refuges remain to be fully identified and described. The identification and surveillance of survival refuges could be of great importance in pest management procedures, particularly during endemic periods. Early corrective measures might be taken on these small areas for possible prevention of future epidemics. The rate of population increase in refuges could forewarn of more widespread increases.

In addition to generalized weather influences, local effects have been observed. There was strong evidence of a localized freeze-killing of *C. milleri* larvae in Tuolumne Meadows, Yosemite National Park, during the winter of 1961–62. This was the first positive instance of potentially catastrophic killing observed in the continuing outbreak populations since the infestations began there in 1947. Freeze-killing ranged from 15.3 to 89.6 percent (table 8), all above snow level on the trees at the lowest meadow elevations; needle miners on lower limbs were protected by the snow. No freeze-killing was found in a site along a slope 150 feet higher than the lowest meadow elevation. A minimum temperature of $-22°$ F. registered there was evidently above temperatures approaching the killing range (not yet determined) of *C. milleri*. This killing was highly localized across Tuolumne Meadows and had little effect on the general level of populations. The winterkilling of *C. starki* in 1949–50 came earlier in the course of the epidemic.

Weather elements other than cold can adversely affect the needle miner. Wind, wind and rain, or hail can kill needle miners indirectly by dislodging infested

Table 8.—*Localized winter freeze mortality in Tuolumne Meadows, Yosemite National Park, California, 1961–62*

Elevation Feet	Stations	Larvae in samples	
		Total number	Percent killed
8,600	7	1,204	89.6
8,625	3	580	70.8
8,650	4	671	48.2
8,700	3	792	28.9
8,750	1	85	15.3

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needles. Severe localized thunderstorms with heavy amounts of hail or rain dislodge the greatest number of needles. Many needles fall during moderate to high gusty winds. Two periods in the life cycle may be subjected to these severe storm effects: (1) August and September, before third- and fourth-instar larvae have moved on to fresh needles; and (2) June and July, before adult moths have emerged. Dropping of needles in August-September is enhanced by abscission layers formed in most of the infested, older needles. Larvae were found in 12.3 percent of the mined needles dropping in 400 square feet of area for 22 days in August 1960 (fig. 15). Pupae totaled 1,450 in an estimated 15,000 needles dropping in 200 square feet for 1 week in June 1959.

Thus, weather appears to act in several ways against the needle miner and could be a factor in determining the course of an epidemic. (1) Adverse weather at the time of the establishment of two successive generations could be the primary agent in reducing the infestation from epidemic to endemic level. (2) Win-
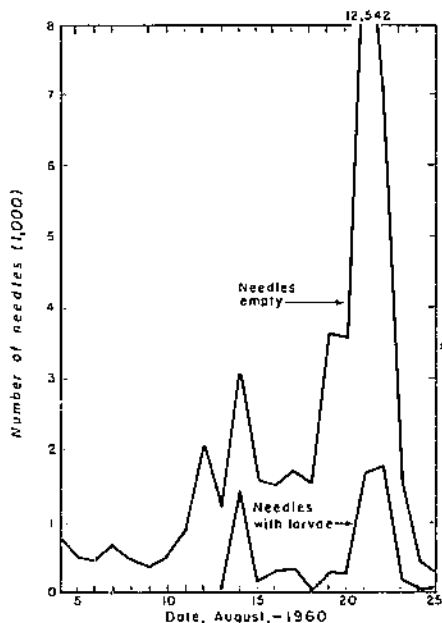

Figure 15.—Larvae in 51,000 storm-dropped needles.

ter freeze-kill can cause heavy, highly localized mortality, but may not have a major effect on the course of the epidemic. (3) Storms at certain periods cause infested needles to drop from the trees; this loss of needle miners may not affect the course of an epidemic.

INSECTICIDAL CONTROL

To control the lodgepole needle miner, a variety of insecticides have been tried. At best, insecticidal sprays are a stopgap measure to prevent excessive needle miner damage in stands affected by continuing epidemic infestations.

Aerial DDT sprays were tried in 1949 and 1953 as control measures, but they did not prove ef-

fective. As newer insecticides became available, they were compared with DDT. These newer toxicants—endrin, dieldrin, malathion, and heptachlor—were used as oil or emulsifiable concentrates diluted in diesel oil or water, respectively. Sprays were applied against the different developmental stages of the insect, beginning in 1954. Some sprays

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were timed to coincide with migration of larvae and emergence of adults. And some were tested as toxic penetrants against larvae and pupae within needles.

Preliminary tests of dosage, coverage, and insecticidal action were made with hand-operated spray equipment. They were followed by larger tests of power mist-blower applications to trees. The aim was to obtain a uniform spray coverage similar to that obtained by aerial sprays. Spray droplet diameters ranged between 150 and 300 microns mass median diameter.

As more powerful helicopters became available, they were used to spray test plots in 1957 and 1958. The dosage volume per acre was determined by measuring droplet patterns on oil-sensitized cards (Isler and Yuill 1956). Applications were timed against the insect stages found most vulnerable in earlier tests: (a) migrating new larvae after eclosion, and (b) newly emerged moths before ovipositing.

In 1959, the National Park Service began insecticidal control operations at Yosemite National Park. The aim of applications between 1959 and 1963 was to conserve specific areas of scenic forest having good prospects for recovery. Some areas were old stands that had been weakened by two successive generations; some were younger forests of poles (6- to 10-in. d.b.h.) and smaller diameter trees weakened by three or more generations. Nine thousand to 10,000 acres were sprayed. Outbreaks in both old and younger stands had developed from the gradual enlargement and coalescence of infestation centers.

The application in 1959 was two pounds of malathion in 20 gallons of diesel oil per acre; this was applied in July for the moth and in August for the first instar larva. In 1961 and 1963, the dosage was reduced to one pound in 10 gallons per acre and was used only for the moths.

Each helicopter spraying of needle miner infestations in 1959, 1961, and 1963 [6] was an extension of the last area to be treated. The total area sprayed was divided between the three operations—each covering about 4,000 acres.

The beginning spray date was predicted 30 days ahead from the mean 30-day pupal period. It was forecast as soon as pupation approached 25 percent in representative periodic samples from the area to be sprayed. A 5-day notice of the spray date followed immediately, as moth emergence averaged 1 percent in daily samples. Experience in 1959 had suggested a reasonable assurance that a minimum 25 percent of all insects would emerge by the beginning spray date in 1961. Five percent of the emerged insects would be females. This timing assured against heavy oviposition before spraying.

Criteria for terminating spray applications depended on continuous daily sampling until mean emergence was 70 percent, or 15 days from the beginning spray

[6] Unpublished reports on file, National Park Service, Yosemite National Park, Calif., by Sharp and Smith (1959), Thompson and Orr (1961), and National Park Service (1963). Unpublished reports on file at Pacific SW. Forest and Range Exp. Sta., U.S.D.A. Forest Serv., Berkeley, Calif., by Stevens and Struble (1959), Stevens (1961), Moore (1963).

date. In 1961, spraying was completed long before the 15-day limit. Because low seasonal temperatures delayed emergence in 1963, the beginning date was 2 weeks later than in 1961.

Effect on Needle Miners

In both preliminary and operational tests, control effectiveness was determined by comparing sprayed and unsprayed infested tips samples before and after spraying. Between 1954 and 1956, the comparison showed that malathion-diesel oil solution sprays caused the highest needle miner mortality: malathion > dieldrin > endrin > heptachlor > DDT.[7]

Of the aerial sprays tested in Yosemite National Park, malathion proved the most effective. It was applied by helicopters at the rates of 1 pound in 10 gallons and 2 pounds in 20 gallons of diesel oil per acre. The amount of control ranged from 68 percent for larvae to 75 percent for moths.

Larvae were eliminated as a target stage in 1961 and 1963 because of superior controls against moths and the inefficiency of separate operations against each of the insect stages.

[7] Struble, G. R. Biology and ecology of the lodgepole needle miner, progress report of research in 1957. 1958.

Struble, G. R., and Stevens, R. E. Tests to control the lodgepole needle miner in Yosemite National Park, season of 1958. 1960.

Trostle, G. C., and Eaton, C. B. Tests with insecticides to control the lodgepole needle miner, 1956 and 1957 seasons. 1958.

(Unpublished reports on file at Pacific SW. Forest and Range Exp. Sta., U.S. Forest Serv., Berkeley, Calif.)

Also, the higher dosage rate was discarded as a result of laboratory research. Of the nine additional chemicals compared in spray chamber tests, only lindane excelled malathion in the highest relative potency estimated in all trials: lindane > malathion > trithion > diazinon > dieldrin > heptachlor > carbaryl > dimethoate > demeton.[8] Malathion was selected over lindane for continued use because of the rapid decline of its residues and its lower hazard to fish and wildlife.

Spraying by helicopter resulted in greater control than was achieved in earlier test applications of malathion. Success was attributed to better timing, improved equipment, tighter controls over insecticidal formulations, and flying conditions. With applications aimed at the moth stage, the amount of control against needle miner populations was 89.9 percent in 1959, 90 in 1961, and 87.5 in 1963. With few exceptions, only one spraying was needed to control infestations.

Control proved long lasting. Before spraying in 1959, maturing needle miner populations were 37.68 ± 4.98 per tip. In 1961, mean populations of the maturing generation were 3.14 ± 0.18 per tip in the sprayed area, while in surrounding unsprayed lodgepole they were more than 18 per tip. Two and four years after spraying, the same relative difference in populations was maintained in

[8] Lyon, Robert L. Insecticides for controlling the lodgepole needle miner. 1962. (Unpublished report on file at Pacific SW. Forest & Range Exp. Sta., U.S. Forest Serv., Berkeley, Calif.)

sprayed and unsprayed forests (Struble 1965). Similar results were achieved from the 1961 and 1963 operations. The long-term Measurements of radial wood growth in 1966 showed immediate recovery after the 1959 spray application (fig. 16).

Table 9.—*Needle miner larvae established in October in sprayed and surrounding unsprayed lodgepole pine*

Locality	Total larvae in 100 tips	
	1965	1967
	No.	*No.*
Trees sprayed, 1959–63		
Lembert	168	48
Campground	46	33
Plot H	65	21
Plot G	14	6
Base	60	39
Plot A	4	0
Plot O	16	0
Mean	53.3	21.0
Unsprayed trees		
Upper Tenaya	230	95
East Cathedral	135	64
Delaney Creek	205	49
Cathedral Lake	87	28
May Lake	146	59
Dog Lake	195	45
Olmstead #2	292	133
Mean	184.3	67.7

effect of treatment was still evident in 1965 and 1967 (table 9), when the number of larvae was found to be more than three times higher in unsprayed than in sprayed sites.

The spray treatment in 1959 produced striking differences in appearance between sprayed and unsprayed young lodgepole pine forests. Such differences were visible in 1961. By 1963, trees in the sprayed area had produced five full noninfested internodes of green needles. Trees sprayed in 1961 had three new internodes of intact needles per twig by 1963.

Effect on Nontarget Organisms

Because of their rapid breakdown to nontoxic substances, malathion-oil sprays were selected as least hazardous to forest life other than the needle miner. Against invertebrates there was considerable killing of exposed species on contact with spray droplets. Some fish in oil-covered, still pools were killed. And there was evidence of considerable killing of embryos in oil-covered incubating eggs. There was no evident damage to large or small mammals.
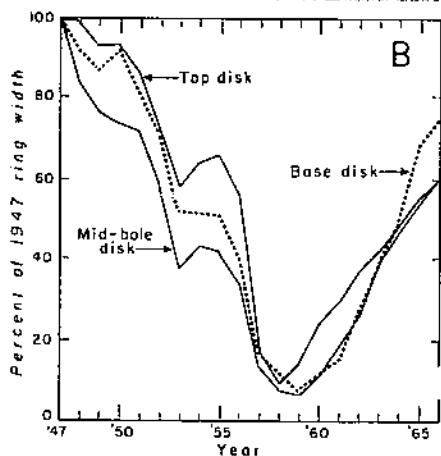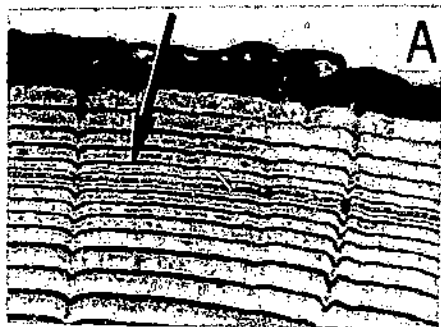
Figure 16.—Recovery of radial wood growth after 1959 spraying: *A*, basal disc section arrow points to period of of depressed ring widths; *B*, annual ring widths expressed in percent of 1947 ring width.

Drop-cloth collections disclosed that massive numbers of adult insects and many spiders were killed. Most of them fell within the first 24 hours, but some continued to fall 14 days after the spray applications. After the 1961 sprays, 60 families in 12 orders of insects and two species of spiders were listed in counts of dead insects. These amounts were somewhat higher than those in counts made after the 1959 and 1963 applications.

Among the arthropods killed by the spray were five key hy-menopterous parasites, two of them host-synchronous, and the predatory arachnids. The possibility of permanent harmful effects against natural enemies of the needle miner was foreseen from bioassay tests made after the 1959 operation (Telford 1961a). But no such effects were found in population samples from sprayed and unsprayed forest 2 and 4 years after spraying (Struble 1965). The proportions of the host insect to its principal parasites remained similar to prespray levels. Also, the species composition of all parasites was relatively unchanged.

Harmful effects on fish were nominal.[9] Because some of the fish killed were downstream, toxic concentrations of malathion were suggested. Other fish were found in stagnating pools covered by oil film. No damage was reported among trapped fish held in full flowing streams exposed to malathion sprays. Considerable numbers of stream invertebrates—an important source of fish food—were killed.

No signs of gross physiological damage to small mammals and songbirds because of exposure to malathion deposits were apparent. Cooperative research studies reported by U.S. Bureau of Sport Fisheries and Wildlife [10] strongly

[9] Unpublished reports of California Division of Fish and Game on file at Pacific SW. Forest and Range Exp. Sta., USDA Forest Serv., Berkeley, Calif.; Bishoff 1961; Hunt 1963.

[10] Keith, James O. Evaluation of local pesticide wildlife problems in the western United States. Work unit D–34. Malathion applications in Yosemite. 1964. (Unpublished report on file at Bureau of Sport Fisheries and Wildlife, Fish & Wildlife Serv., U.S. Dep. Interior, Box C, Davis, Calif.)

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suggested that malathion applications had no immediate measurable harmful effect other than the indirect influence resulting from the killing of insects.

CONCLUSIONS

The number of lodgepole needle miners surviving in successive generations is the basis for appraising, predicting, and planning to forestall damage. The number is determined by properly timed surveys. The timing of *C. milleri* surveys begins in odd-numbered years: (1) October 1 (first instar); (2) September 15 (fourth instar); (3) June 15 (pupae).

In any given area, increasing infestations between generations are indicated by a sharp rise in numbers of larvae in, or adults emerging from, infested needles. When mean emerging populations rise above six per tip, plans to forestall damage should be made. No action is required, however, unless emerging populations rise above 12 per tip. More than 12 moths per tip indicate that progeny populations greater than 20 larvae per tip will reach destructive levels.

Aerial insecticidal sprays have demonstrated good control potential against devastation; but, because complex relationships must be considered, the proper time is not always clearly evident. Aerial sprays should be used only when the risk of injuring life forms other than the target insect is at a minimum. Machines, dispersal equipment, and insecticides are available, but the best combinations for the most effective and safest use remain to be developed, tested, and proved.

Weather appears to be a major cause of fluctuations in needle miner populations. Between 1963 and 1967, *C. milleri* populations declined from epidemic to endemic numbers. This decline began during the periods of establishment in 1963 and 1965 in two successive generations. Below-normal cold weather preceded establishment, and cold, stormy weather followed during flight, oviposition, and incubation.

There is growing evidence that the lodgepole needle miner found in Yosemite National Park develops in refuges within the high-elevation outbreak zone areas that harbor endemic populations many times larger than average. Usually found in drainage basins, these refuges vary in size and have protective features that favor needle miner survival during unfavorable weather. It may be possible to detect and control rising populations in refuges and thereby prevent outbreaks. But to do so, it will be necessary to identify the physical bounds of refuges and the climatic influences on outbreaks. From results obtained so far, early detection of outbreaks by this approach appears to be an attainable goal.

Pesticides Precaution

This publication reports research involving pesticides. It does not contain recommenda-

tions for their use, nor does it imply that the uses discussed here have been registered. All users of pesticides must be registered by appropriate State and/or Federal agencies before they can be recommended.

CAUTION: Pesticides can be injurious to humans, domestic animals, desirable plants, and fish or other wildlife—if they are not handled or applied properly. Use all pesticides selectively and carefully. Follow recommended practices for the disposal of surplus pesticides and pesticide containers.

PROTECT

Use Pesticides Safely

FOLLOW THE LABEL

U.S. DEPARTMENT OF AGRICULTURE

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