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THYMELICUS LINEOLA (LEPIDOPTERA: HESPERIIDAE) AND ITS PARASITES IN EUROPE[1]

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Abstract

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The distribution, ecology, and host-plants of the European skipper, *Thymelicus lineola* (Ochs.), are described, and notes given on its biology and abundance in continental Europe. Agricultural practices are responsible for its virtual absence from hay-fields; however, even in undisturbed wild host-plant communities, it is never abundant, and has never required control measures as in Canada. Parasites of *T. lineola* are listed, with notes on their life-histories, distribution, host spectra, relative abundance, annual fluctuations, and interpopulation variations. Parasites reared were *Phryxe vulgaris* Fall., *Thecocarcelia incedens* Rond. (both attacking larvae, but sometimes emerging after host pupation), *Rogas tristis* Wesm. (larval parasite), *Labrorychus delarvatus* Grav. (larval–pupal parasite), *Stenichneumon scutellator* Grav. and *Brachymeria intermedia* Nees (pupal parasites); an undetermined mermithid was reared from larvae and also once from an adult *S. scutellator*. *Rogas tristis* was attacked by the hyperparasite *Mesochorus macrurus* Thoms., and *S. scutellator* by *Gelis cursitans* F. Potentialities of the more important species for biological control of *T. lineola* in Canada are discussed. *S. scutellator*, which is well synchronized with the host, regularly parasitizes 30–50% of pupae and is the most promising natural enemy for introduction, although in Canada it will compete with the native *Itoplectis conquisitor* (Say). *R. tristis* (3–57% parasitism) and *P. vulgaris* (8–44%), with high constancy in Europe, might be considered for introduction to Canada because of the absence there of effective native larval parasites. *T. incedens*, although probably a specific hesperiid parasite, is uncommon (usually 1–5% parasitism) and has low constancy in central Europe. All other species encountered are rare on *T. lineola*. Comparison of parasite complexes in Europe and Canada, where the host has acquired 22 natural enemies, shows that four genera are represented in both areas; of three holarctic species two have been found associated with *T. lineola* only in Canada, and one only in Europe.

Introduction

The European skipper, *Thymelicus lineola* (Ochs.), is a widely distributed palearctic butterfly (Bergmann 1952). The larvae feed on various economically important hay and pasture grasses. Lepidopterists consider it rare and of no economic importance in Europe, a view confirmed during the present study.

T. lineola was accidentally introduced to Canada in about 1910 (Saunders 1916; Arthur 1962) and has since spread from London, Ont., where it was first recorded, through southern Ontario and the adjoining parts of Ohio and Michigan. Its recent spread in Canada has been recorded by Pengelly (1961) and Arthur (1962, 1966). In contrast to its status in Europe, *T. lineola* has been locally abundant in Canada and has caused extensive damage to hay-fields and pastures. In Europe it occupies a wide range of climates; so it is unlikely that this factor is responsible for its greater abundance in North America.

[1]These investigations were made at the request of the Research Institute, Canada Department of Agriculture, Belleville, Ont., Canada.

It is more likely that, in addition to different agricultural practices, the absence of adapted and effective natural enemies may permit the insect to attain numbers above a subeconomic level. For this species biological control would be especially appropriate, since at present chemical control is too costly and constitutes a hazard to livestock (Arthur 1966).

This paper describes the biology of *T. lineola* in Europe, listing its natural enemies and evaluating their presumed usefulness as biological control agents. The European parasite complex is compared with that recorded for North America by Pengelly (1961) and Arthur (1962).

Materials and Methods

To determine possible differences in the parasite complex in different climates large collections of *T. lineola* were made near Neusiedl Lake in eastern Austria, which has a Pannonic, continental climate; and in the more maritime climate of French Alsace (bordering northeastern Switzerland). Smaller collections were made in the Swiss Alps, which have a boreo-alpine climate; and at other localities in France, Switzerland, and southern Germany.

Host larvae from the second and later instars were collected by sweeping through grass with insect nets. The number collected per unit time gave a value for relative density. Larval parasitism was determined by rearing (in mass, or individually) or dissection. The latter method eliminated possible errors due to the higher mortality that might occur in parasitized hosts during rearing, and made it possible to follow the development of internal parasites and the interactions between them.

Pupal parasitism was difficult to assess. Few pupae were obtained by sweeping, even at the highest densities, because pupation occurred close to the ground. All laboratory-reared pupae exposed to parasitism in field cages were eaten by non-specific predators, such as ants and spiders. Somewhat better results were obtained when host larvae were confined in field cages, and the cages removed for exposure to parasites, after pupation had occurred. However, with this method losses due to predation by mice and other (unknown) factors often reached 90%. It is very unlikely that such high losses occur in nature, and it is thought that overcrowding in the cages (100–500 final instar larvae/sq. m) made the artificial populations vulnerable to predators.

Because collecting pupae was difficult, assessment of parasitism is based on smaller numbers than would otherwise have been considered adequate, but the consistency of the results obtained during several years indicates that no important parasite was overlooked.

Egg parasites of *T. lineola* are still unknown, since, in spite of concentrated efforts, no eggs have been found in the field; moreover all attempts to obtain eggs from field-collected females failed. Eggs of the closely related species, *Thymelicus thaumas* Hufn., which is about as abundant as *T. lineola*, were found in large numbers, and up to 83% were parasitized by *Trichogramma* sp. Apart from the fact that *T. lineola* remains in diapause in the egg from late summer until spring, whereas *T. thaumas* enters diapause as a first-instar larva, the two species have very similar biologies and share certain larval parasites. Thus in *T. lineola*, egg parasitism may also be an important mortality factor.

The Host

Distribution. Bergmann (1952) lists *T. lineola* as eurasiatic; Stokoe (1950) reports it from England "chiefly along the coast" and points out that "farther inland it seems to frequent chalky hillsides and marshes". It is uncommon in the plains of northern Germany, occurs locally in the plains of middle Germany, and more rarely in the mountains (Bergmann 1952). In the German and Austrian Alps it was found by Klimesch and Burmann (pers. comm.) up to an altitude of 1600 m. According to Vorbrodt (1911) and Kauffmann (1951) many local races occur in Switzerland; in the lowlands north of the Alps, as well as in the Swiss Jura and in the Alps up to 2000 m. Kauffmann (1951) recorded it south of the Alps, in the northern Tessin. During the present study *T. lineola* was also collected in France (the southernmost record from near Lyon), throughout Switzerland, Germany, and Austria, and in Slovakia.

Ecology. Bergmann (1952) describes *T. lineola* as characteristic of warm damp meadows at the bottom of valleys, preferring stands of soft grasses. It also occurs on terraces, where it prefers stands of couch grass associated with bushes on damp clay. Although the species has its ecological optimum in these conditions, larvae were also found in very cool localities, e.g. along borders of forests on north-facing slopes, as well as in dry places if some humid area was close by. It seems that humidity is essential for adult survival, whereas larvae can tolerate very dry conditions.

T. lineola causes extensive damage to hay-fields in Canada (Pengelly 1961). In Europe, larvae are virtually absent from such areas and are restricted to headlands, forest borders, river-banks, roadsides, pasture land, etc., i.e. places not used agriculturally or used only sparingly. Intensive cultivation in most parts of central Europe apparently prevents the development of *T. lineola*. The eggs, in diapause from August until April, and the larvae, developing in May and early June, are often eliminated when the crop is harvested. Only in eastern Austria, where the harvest occurs after completion of larval development, were hay-fields found to be infested.

The following food-plants are recorded in Europe: *Holcus lanatus* L., *Agropyron repens* (L.) Beauv., and *Brachypodium sylvaticum* (Huds.) Beauv. from England (Stokoe 1950); Vorbrodt (1911–27) adds *Dactylis glomerata* L. and *Arrhenaterium elatius* (L.) Beauv., and Bergmann (1952) *Festuca* sp. Feeding tests confirmed that all these plants and, in addition, *Lolium perenne* L., recorded by Pengelly (1961) in Canada, and *Holcus* spp. were suitable. I have collected *T. lineola* only on the following food-plants: *Holcus lanatus*, *H. mollis* L., *D. glomerata*, and *A. repens*.

A factor determining whether or not plants were attacked by *T. lineola* was their sociability. Braun Blanquet (1951) defines the sociability of plants as the area covered by a single species and recognizes five categories: (1) plants growing singly; (2) those growing in groups or tussocks (length of sides approximately 10–20 cm); (3) those growing in patches or cushions (20–100 cm); (4) those growing in small colonies or larger patches (1–5 m); (5) those covering areas larger than in (4). Plants in categories (1) and (2) were not attacked by *T. lineola*; and those in (3) only rarely and lightly. In some of these instances no larvae could be found, but the presence of adults indicated the existence of sporadic populations. Wherever *T. lineola* larvae could be collected in appreciable numbers, the grass belonged to category (4) or, more often (5).

Abundance. Numbers of larvae collected according to locality and year are shown in Table I. Allowance must be made for sampling error resulting from differences in the host-plant species and its growing conditions. By repeatedly sweeping the same area it could be shown that the proportion of larvae taken from

TABLE I
Abundance of *Thymelicus lineola* (Ochs.) at Courtetelle, Simplon, and Goeschenen, Switzerland; at Hirzbach, France; and Neusiedl, Austria

Locality	Average no. larvae collected per hour			
	1961	1962	1963	1965
Courtetelle	<1	<1	x†	x
Simplon	9	12	5	3
Goeschenen	2	7	2	x
Hirzbach	21	26	7	0
Neusiedl	10*	84	134	55

*Estimated from collections by collaborators.
†x, no count made.

a population will vary with the density of the vegetation. Thus, in dense stands of couch grass, the proportion collected will be lower than that obtained from sparse stands of *Dactylis* on alpine pastures. This error affects the comparability of data from different localities, but can be ignored in considering the population changes at individual localities in consecutive years.

The localities sampled are described below.

Courtetelle (Swiss Jura, 470 m above sea level). Dry permanent pasture on Jurassic limestone with some wet areas on clay, northwestern exposure, bordered by forest, thin vegetation, food-plant *Holcus mollis*, sociability (1) to (3).

Hirzbach (Alsace, France, 270 m). An abandoned hay-field on diluvial gravels, dry, southwestern exposure, dense grass vegetation being gradually displaced between 1961 and 1964 by weeds, mainly thistles and St. John's-wort. Food-plants *Agropyron repens* (2) to (5), *Holcus mollis* (2) to (4), *Dactylis glomerata* (2) and (3), their sociability decreasing from year to year.

Plancher-Bas (near Belfort, France, 245 m). Waste land on sandy loam, dry, southwestern exposure; dense stands of *Holcus lanatus* (5), intermingled with oak shrubs and *Sarothamnus* sp., small stream at distance of 200 m at the bottom of the valley. This area was surveyed only in 1965 and 1966 for the pupal parasite *Stenichneumon scutellator* Grav., about 60 larvae being collected per hour.

Simplon (near Gabi, Switzerland, 1450 m). Permanent pasture on dry crystalline schist with thin vegetation, food-plant *Dactylis glomerata* (2) to (4), small stream about 50 m away.

Goeschenen (near St. Gothard Pass, Switzerland, 1400 m). Conditions same as at Simplon.

Neusiedl (eastern Austria, 130 m). Belt of meadows along the northern and northwestern edges of Lake Neusiedl, intermingled with barley and wheat fields on heavy loam, food-plant *Agropyron repens* (4) and (5) growing on headland, roadsides, and to some extent in neglected hay-fields.

Although fluctuations in population density occurred in consecutive years, they were relatively small and did not reach outbreak level during the period of investigation (Table I). The 1963 season was preceded by an exceptionally severe winter, which apparently had no adverse effect on the host populations (cf. Neusiedl), but possibly an extended period of unusually heavy rains in 1965 led to high mortality of early larval stages (cf. Neusiedl).

Neither the results obtained from the above localities nor those from 90 additional checkpoints provide evidence that there is a correlation between the climate of individual areas and abundance, e.g. populations at Neusiedl and Plancher-Bas (not shown in the table) were of similar size. Neither is there an apparent correlation between altitude and abundance. Kauffmann (*in litt.*) states that in Switzerland this species is generally more numerous in the Alps than in the lowlands. This is due to a difference in agricultural methods which provide larger undisturbed areas of host-plants in the former area.

While there is no apparent correlation between species of host-plant and population density of *T. lineola* (e.g. Hirzbach and Simplon or Neusiedl and Plancher-Bas with different host-plants, but similar abundance), the close connection between size of host-plant stands and the skipper population is striking. Hirzbach demonstrates this. The progressive displacement of food-plants by weeds caused a gradual reduction of their sociability and a decline of infestation in successive years. In 1966 *T. lineola* had become so scarce that to collect larvae was no longer feasible.

At the two most heavily infested areas, Neusiedl and Plancher-Bas, the number of larvae inhabiting 1 sq. yd was estimated by recording the number of larvae within 3 sq. yd selected at random. Seven larvae per square yard were found at Neusiedl in 1965 and eleven at Plancher-Bas in 1966. Using a similar method, Arthur (1962) found 151 to 224 larvae per square yard at Priceville, Ont. Thus, populations in heavy infestations in Canada can be about 20 times as high as in Europe.

Biology. Pengelly (1961) describes the biology in detail. Only a brief outline is given here as background for the section on parasitism.

T. lineola is univoltine. Mating occurs soon after emergence which commences about 20 June. Adults are found for approximately 6 weeks. The eggs are laid in rows along grass stems, being inserted under the overlapping edges of leaf sheaths. Only a few eggs were obtained when field-collected females were caged with food plants. No eggs were found in the field. The eggs contained fully developed motile larvae about 20 days after oviposition.

Eggs kept under field conditions remain in diapause until late April of the following year (Pengelly 1961). In contrast to this, Koch (1956) and Kauffmann (pers. comm.) state that eggs hatched after an incubation period of 3 weeks, and the first-instar larvae underwent diapause enclosed in silken webs. My own observations, like Pengelly's, showed that *T. thaumas*, but not *T. lineola*, diapaused in silken webs.

The first larval stage was not encountered in the field. Feeding second-instar larvae were usually found during the first half of May. In Europe the species passes through five larval instars, in Canada six (Pengelly 1961). In all instars larvae draw the leaves together in the shape of a "V" by fixing the edges together with silken threads at a distance of a few centimetres. The larvae hide on the upper leaf surface which is covered with a thin, but dense, layer of silk. Feeding usually occurs on one of the margins; sometimes it starts at the tip of the leaf and proceeds towards the base. Final-instar larvae were found about 4 weeks after second-instar larvae had first been encountered, but spells of cold and wet weather during the larval period (e.g. 1965) retarded development for up to 2 weeks.

Final-instar larvae, recognizable by the presence of two pairs of wax cushions on the ventral side of the last two body segments, form a very loose web, often reinforced with bits of grass, and usually pupate close to the ground. The pupal period lasts 10–14 days. In years with normal weather, pupation commences about the beginning of June, but varies in different areas in relation to local climate. Thus, at Neusiedl, pupation usually occurs about 10 days earlier than at Hirzbach and Plancher-Bas and more than 20 days earlier than at Simplon or Goeschenen.

Parasitism

The only parasite of *T. lineola* known from the European literature is the tachinid *Phryxe vulgaris* Fall. recorded by Baer (cited by Thompson 1947).

During the present work the following nine primary and secondary parasites were reared from larvae or pupae of the skipper.

Larval Parasites

TACHINIDAE

Phryxe vulgaris Fall. (sometimes emerges from pupae)

Thecocarcelia incedens Rond. (often emerges from pupae)

BRACONIDAE

Rogas tristis Wesm.

MERMITHIDAE

Mermithid (genus and species not identified)

Larval–Pupal Parasite

ICHNEUMONIDAE

Labrorychus delarvatus Grav.

Pupal Parasites

ICHNEUMONIDAE

Stenichneumon scutellator Grav.

CHALCIDIDAE

Brachymeria intermedia Nees

Hyperparasites

ICHNEUMONIDAE

Mesochorus macrurus Thoms.

Gelis cursitans F.

This list shows that *T. lineola* has a small parasite complex compared with many other Rhophalocera. Only *T. incedens* and probably *S. scutellator* are restricted in their host range to hesperiids. The only known host record for *T. incedens* is *Parnara mathias* F. (Risbec, cited by Herting 1960) from Senegal. *S. scutellator* is mentioned from several hosts (Thompson 1947), but Kerrich (*in litt.*) doubts all records other than *T. lineola* and *T. actaeon* Rott.

In contrast, 22 species of parasites have been recorded from *T. lineola* in Canada where the skipper has only been present for about 60 years (Arthur 1962). But these are all polyphagous species that have occupied, most of them imperfectly, the new vacant "parasitological niche" provided, a process presumably facilitated by the absence of competition.

Notes on Individual Parasites

Phryxe vulgaris Fall.

Distribution and Host Range. This common species occurs throughout Europe. Thompson (1951) listed 74 hosts but Herting (1960) was able to verify only 36. He considers Thompson's larger number of host records to be partly the result of confusion with *P. longicauda* Wainwr. and *P. nemea* Meig. All hosts reported by Herting are Macrolepidoptera. For North America Thompson records 15 hosts of which, according to Mesnil (pers. comm.), all but 1 refer to *P. pecosensis* Tnsd. and the only certain host record of *P. vulgaris* is *Pieris rapae* L.

The lists referred to above suggest a wide host range in Europe, but there is evidence that not all hosts recorded are attacked indiscriminately. For instance, only one specimen has been reared from *Dicranura vinula* L., one from 1200 larvae of *Malacosoma neustria* L., and only a few records are known from well-studied species such as *Euproctis chrysorrhoea* L. (Herting 1960). That 17.5% of *Pieris rapae* larvae in garden populations were parasitized, but only 1.7% of the closely related *P. brassicae* L. (Richards, cited by Herting 1960) indicates that the parasite has a restricted host range, and discriminates fairly well. Mesnil (pers. comm.) suggested the existence of biological races with different host preferences, and the very narrow host spectrum of *P. vulgaris* in Canada would support this view.

Constancy, Abundance, Searching Capacity. The constancy of *P. vulgaris* in *T. lineola* was 100%: it was in all host populations examined. It was also fairly abundant: at high host densities it parasitized 8–44% of the final-instar larvae collected. The rate of parasitism decreased with decreasing host density, but *P. vulgaris* was still present when the number of host larvae per 100 sq. m was less than one. At first sight this suggests very effective searching. Whereas this may be so, the phenomenon may be explained otherwise. Where *P. vulgaris* was recorded from very low populations of *T. lineola* (e.g. Courtetelle), high populations of *T. thaumas* also occurred in which the rate of parasitism was similar to that in *T. lineola*. It is therefore possible that the parasite searching was directed primarily towards the more abundant *T. thaumas*, and that *T. lineola*, as an integrated part of the total host reservoir, was parasitized at the same rate.

Biology. The species is multivoltine and therefore heteroxenous. Larviposition in *T. lineola* occurs in instars IV and V, rarely III. The mode of larviposition, and the point at which the maggot penetrates the host integument, could not be ascertained. Artificial inoculations with parasite larvae obtained from dissected females failed, although larvae, placed on various parts of the host body, tried to penetrate the skin. During instar I the parasite larva lives freely in the body cavity of the host; the instar II larva attaches itself to a main tracheal trunk or to a spiracle when the respiratory funnel is formed. At this stage parasitism becomes visible externally with the formation of a darker zone around the affected spiracle. The host is killed after the parasite has reached instar III. The parasite larva is full-grown 17–22 days after larviposition and leaves the dead host before pupation. Parasite larval development is usually completed in the last-instar host larva, rarely in the early pupal stage of the host. Generally two to four (maximum five) larvae develop in one host. The parasite pupa lasts 8–12 days; males lived 7–9 days and females 8–15 days.

Thecocarcelia incedens Rond.

Distribution and Host Range. This species is considered by Herting (1960) to be a southern form reaching its northern limit of distribution in the Vienna plain. However, Mesnil (pers. comm.) observed it near Versailles.

The only previous host record is that given by Risbec (cited by Herting 1960) who reared it from another hesperiid, *Parnara mathias*, in Senegal. It is probable, therefore, that *T. incedens* is a specific hesperiid parasite.

ABUNDANCE. In eastern Austria parasitism usually fluctuated between less than 1% and 5.5%, but in 1966 it reached 15%. The reason for this fluctuation is not understood. The species probably depends on alternate hosts and, due to its narrow host range, is perhaps limited by lack of a sufficient alternate host reservoir. Thus population fluctuations may be induced by variations in the availability of alternate hosts rather than of *T. lineola*.

BIOLOGY. Instar I and II larvae were usually obtained by dissection of last-instar host larvae, seldom from the penultimate stage. Parasitized larvae and pupae can be distinguished by the presence of a large, conspicuous blackish-brown ring around the respiratory funnel of the parasite, which becomes visible when it reaches instar II. The funnel is attached to a thoracic spiracle of the host. Usually one, rarely two, parasites developed in one host. Last-instar parasite larvae emerged from fully grown host caterpillars or, more often, from pupae. The pupal stage lasts 10–13 days, and adults lived in the laboratory for up to 20 days, although breeding experiments were unsuccessful. The short life of adults in captivity suggests that the generation emerging from *T. lineola* in June does not hibernate, i.e. the species must be multivoltine and therefore heteroxenous.

Rogas tristis Wesm.

DISTRIBUTION AND HOST RANGE. This is a central European species of which Thompson (1943–1958) mentions the following hosts: *Aethes smeathmanniana* F. (Germany; on flowers of Compositae), *Clysia ambiguella* Hb. (Austria, Germany; on grape vine, *Hedera*, *Cornus*, *Ligustrum*, *Acer*, *Viburnum*, *Syringa*), *Eupithecia pimpinellata* Hb. (Britain; on Compositae and Umbelliferae), and *Polychrosis botrana* Schiff. (Austria, Germany; on grape vine and *Clematis*). Dr. Fischer, Vienna (pers. comm.), gave the following: *Lycaena hylas* Esp. (Austria; on Papilionaceae), *Zygaena exulans* Hochenw. (Austria; on low plants), *Epinephele tithonus* L. (Austria; on grasses).

Fischer considers *Rogas bicolor* Spin. a synonym of *R. tristis* since the only differentiating character is the colour of the mesonotum which varies from red to almost black. In this case the six host records for *R. bicolor* must be added to the list of alternate hosts: *Oidaematophorus monodactylus* L. (Russia; on low plants), *O. tephradactylus* Hb. (Britain; on leaves of Compositae), *Polyommatus icarus* Rott. (Russia; on Papilionaceae), *Zygaena filipendula* L. (Britain; on low plants), *Epinephele jurtina* L. (Austria; on grasses), and *Lycaena eros* Ochs. (Austria; on *Oxytropis* and *Astragalus*). During the present study *R. tristis* was also reared from *T. thaumas*. This list suggests a fairly wide host spectrum for the parasite, and that it frequents open land, many of its hosts inhabiting the same biotopes as *T. lineola*.

CONSTANCY AND ABUNDANCE. The constancy of this parasite was 100%. Its abundance fluctuated widely, generally ranging from 10 to 30% parasitism, but with a minimum of 3% and a maximum of 57% in third- to fourth-instar hosts.

BIOLOGY. The species is multivoltine. It passes the first and a partial second generation on *T. lineola*, and this probably accounts for a gradual increase in parasitism towards the end of the host larval period.

R. tristis is an internal parasite which oviposits and completes its larval development usually in the third- but occasionally in the fourth-instar larva of the host. Hosts died 10–13 days after attack. These hosts turned brown and their integument hardened. The parasite pupates inside the mummified host and emerges 8–10 days later. Development takes 19–23 days. Adults lived in captivity for up to 29 days. Mating occurred readily, but oviposition was erratic.

Hyperparasitism. *Rogas tristis* was parasitized by *Mesochorus macrurus* Thoms. The primary parasite develops to a late larval instar and causes the typical change in colour and appearance of its host before being killed by *Mesochorus*. Usually hyperparasitism was 1–5%, but in one instance 10% of the primary parasites were killed (Austria in 1962). The constancy of *Mesochorus* was 30–60% in consecutive years.

Competition. Of 275 second- to fourth-instar host larvae dissected, 32 were parasitized by *P. vulgaris* and 47 by *R. tristis*. In three instances, hosts were attacked by both parasites, and *P. vulgaris* had been killed, as a first-instar larva by *R. tristis*.

Stenichneumon scutellator Grav.

Distribution and Host Range. According to Schmiedeknecht (1929–1930), this rare palearctic species occurs in central and southern Europe: Rasnytsin (1959) reported it from Russia. Thompson (1957) gives host records as *Abraxas grossulariata* L., *Nygmia phaeorrhoea* L. and *Panolis flammea* Schiff., and Kerrich (in litt.) writes: "Old host records are *Liparis chrysorrhoea*, *Zerene grossulariata* and *Trachea piniperda* (given in Schmiedeknecht and Berthomieu) but I strongly suspect all these. It was most probably *St. lineator* F. (*trilineatus* Gmel.) that was reared from *grossulariata* and *piniperda*". Kerrich comments further that the specimens in the British Museum originate "most probably from Essex, the English locality for *T. lineola* and from the Dorset coast, the English locality for *T. actaeon*" which implies that he thinks that *S. scutellator* is a typical hesperiid parasite. Further evidence is needed, but the close synchronization with the biology of the host suggests that they are closely linked.

Constancy and Abundance. Only heavily infested areas such as Neusiedl, Hirzbach, and Plancher-Bas were surveyed for pupal parasites, and *S. scutellator* was the most abundant, always causing a mortality of 30–50%. Adult males were found in all localities, even those lightly infested, such as Simplon and Goeschenen, but assessment of their abundance was not possible.

Biology. This species is very closely synchronized with its host. It is univoltine and mated females hibernate with undeveloped ovaries. Rasnytsin (1959), in a study of ichneumonid hibernation sites, found the species four times, always with several individuals in the same place, under the bark of trees (probably pine and spruce) 2–3 m above the ground and tolerating temperatures down to —40°C. In the spring, active females were first observed at the onset of pupation of *T. lineola* in early June. They were never found flying above the grass, but apparently stay low in the grass searching for hosts. Eggs are laid in young host pupae.

The average number of eggs laid daily in the laboratory by seven field-collected females was 1.1; the average number of hosts stung was 2.4. Stung hosts developed normally. Host pupae are available for 30–40 days; thus, the reproductive potential of the parasite is comparatively low (33–44 eggs), unless the daily oviposition rate is higher in nature than under experimental conditions. Field-collected females lived in captivity until the end of the host pupal period, and died during July. During larval development of the parasite the host pupa becomes pale yellow, turning light brown on pupation of the parasite within. Egg and larval development take 18–23 days, that of the pupa 10–14 days. The adult parasites emerge by breaking off the head of the host pupal skin. There is no significant proterandry.

The flight period of males in the field lasts about one month and ceases about mid-August. During this period males fly actively, hovering just above the vegetation where they encounter females. Neither sex appeared to be attracted to flowers, although presumably females feed before hibernation.

HYPERPARASITISM. In 1963, three and six per cent, respectively, of host pupae from two populations were hyperparasitized by *Gelis cursitans* via *S. scutellator*. This degree of hyperparasitism amounted to a loss of 8.5 and 17% of the *S. scutellator* population. The hyperparasite larva feeds externally on larvae and pupae of the primary. Thompson (1943–1958) cites four other (phytophagous) hosts, but probably in these cases *Gelis* also acts as a hyperparasite.

An adult female once stung a host pupa but failed to oviposit. It was dissected and two mermithids were found in the abdomen. Their attack had led to the sterilization of the female but otherwise it appeared healthy, although the parasites filled virtually the whole abdominal cavity.

Labrorychus delarvatus Grav.

Of this common European ichneumonid Kerrich (*in litt.*) states: "this species is recorded by Schmiedeknecht as the commonest Anomaline in Thuringia in late summer; this suggests it is not at all host specific". Only four specimens were obtained from *T. lineola*. This species probably attacks mature host larvae and emerges from pupae.

Brachymeria intermedia Nees

This very polyphagous holarctic species attacks a large number of Macro- and Micro-lepidoptera, as well as several tachinids (Thompson 1943–1958). Eight specimens were obtained from pupae of *T. lineola* from Neusiedl and Hirzbach.

Mermithid Genus and Species Not Identified

An undetermined mermithid, generally rare, was more abundant during the wet spring of 1965 when it killed up to 6% of final-instar larvae in individual samples. On one occasion two specimens were found in the abdomen of a sterile *Stenichneumon* female.

Larval Parasitism

Table II shows the rates of primary parasitism in different larval stages of the host from different localities, in one year. (Percentages recorded in the table are given as integers if derived from less than 101 observations, to one decimal place if derived from more than 100, and to two decimal places if from more than 1000.) The localities Luxeuil and Lantenot belong to the same general area as Hirzbach. Both are relatively small plots of waste land; the host density was six and nine larvae per collection hour, respectively. The table shows that the main parasites are *P. vulgaris* and *R. tristis*, while *T. incedens* and the mermithid are scarce, and *L. delarvatus* is absent.

R. tristis is absent from samples of larvae older than the fourth-instar (attacks on this instar are rare, most being confined to the third-instar). It is interesting to note the increase in parasitism by *Rogas* towards the end of the host's larval period. This is clearly shown in the two samples from Hirzbach where parasitism rises from 2.6% on 25 May to 56.8% on 20 June. In the Neusiedl sample on 4–9 June *Rogas* is at its peak of activity. These collections were made towards the end of the larval period as shown by the proportion of mid- to final-instar

TABLE II

Percentage of larval parasitism of *Thymelicus lineola* (Ochs.) at Neusiedl, Austria; and at Hirzbach, Luxeuil, and Lantenot, France, in 1962

Locality	Date	*Thymelicus lineola* larvae examined		Larvae parasitized (%)	By *Phryxe vulgaris* (%)	By *Thecocarcelia incedens* (%)	By *Rogas tristis* (%)	By mermithid (%)
		No.	Instar					
Neusiedl	4–9.VI	640	III, IV	26.6	3.3	0	23.2	0
Neusiedl	4–9.VI	2,230	V	8.49	8.25	0.08	0	0.16
Neusiedl	27.VI	65	V	11	8	3	0	0
Hirzbach	25.V	114	II–IV	24.7	21.2	0	2.6	0.9
Hirzbach	20.VI	95	III, IV	62	5	0	57	0
Hirzbach	20.VI	160	V	44.4	44.4	0	0	0
Luxeuil*	4.VI	72	II–IV	12	8	0	4	0
Lantenot*	4.VI	55	II–IV	13	9	0	2	2

*Fifth-instar larvae not yet available.

TABLE III

Percentage parasitism by the more abundant larval parasites of *Thymelicus lineola* (Ochs.) at Neusiedl, Austria*

	Parasitism (%) by		
Year	*Phryxe vulgaris*	*Rogas tristis*	*Thecocarcelia incedens*
1961	20.0	14.5	5.5
1962	8.49	23.3	3
1963	9.93	2.9	1.71
1965	4.0	5.0	5.5
1966	17.5	†	15.0

*In 1961 all percentages are based on the total of third- to fifth-instar host larvae collected, in subsequent years those for *P. vulgaris* and *T. incedens* on the fifth-instar total only, and those for *R. tristis* on the total for the third- and fourth-instars. The true values for 1961 are therefore higher than those in the table.
†No assessment made.

larvae. On the other hand, at Luxeuil and Lantenot parasitism is low, as in that of the early Hirzbach sample.

Phryxe was reared from both size groups of the host. Like *Rogas*, the species is capable of completing a partial second generation on the univoltine host, and parasitism consequently increases towards the end of the host's larval stage, as seen from the sequential samples from Hirzbach. A comparison of parasitism in mid- and final-instar larvae suggests a marked preference of the parasite for full-grown larvae if both size groups are present (e.g. parasitism at Hirzbach was 5.3% in young but 44.5% in final-instar larvae). The table shows remarkable variations in the degree of parasitism in different populations. While parasitism at Luxeuil and Lantenot was probably still increasing, it had reached its maximum at Neusiedl (8.3%) and Hirzbach (44.4%). At Neusiedl the host density was about three times as high as at Hirzbach, and was probably too high to be parasitized as much as the lower populations by a parasite obliged to maintain populations on alternate hosts.

T. incedens was only represented in the samples from Neusiedl and only at a low level. Its absence from other host populations was taken as proof that the northern boundary of this species is in the plain east of Vienna. But in 1966 it was recorded from Plancher-Bas which belongs to the same general area as Hirzbach–Luxeuil–Lantenot. The regular occurrence at Neusiedl (cf. Table IV) and its sporadic appearance elsewhere indicate that it is a true parasite of *T. lineola* and also that it is barely able to maintain itself north of the Pannonic area.

The fluctuations of larval parasitism in a series of years (apart from 1964 when the study was interrupted) at Neusiedl are summarized in Table III. Similar fluctuations in larval parasitism occurred elsewhere.

The causes of considerable fluctuations in parasitism are certainly complex, and to correlate them with single factors would be an over-simplification. However, some factors likely to have contributed substantially to these changes may be mentioned here: (1) The winter in central Europe in 1962–1963 was extremely severe, with January minima 11°C below normal. Although no reduction in host population was observed in 1963, parasitism by *P. vulgaris* and, more particularly, *R. tristis* was low. (2) The abnormally rainy and cold spring in 1965, when the

TABLE IV

Percentage of parasitism of *Thymelicus lineola* (Ochs.) at Neusiedl, Austria; and at Hirzbach and Plancher-Bas, France

		Parasitism (%) by		
Locality	Year	*Stenichneumon scutellator*	*Brachymeria intermedia*	*Gelis cursitans*
Neusiedl	1963	37	5	6
Neusiedl	1965	49	0	0
Neusiedl	1966	34	6	0
Hirzbach	1963	42	3	3
Plancher-Bas	1966	30	0	2

mean precipitation in June was the highest since 1878, almost certainly affected the activity of adult parasites, and may have increased the asynchronization between *R. tristis* and *T. lineola* which exists even in normal years. Evidence of the significance of these particular weather conditions was also obtained in the other areas surveyed, where parasitism was similarly low. (3) Changes in the abundance of alternate hosts of all three parasite species (Table III) certainly play a part in their population fluctuations, although this is not evident from the table. The drop in parasitism by *Phryxe* from 20% in 1961 to 8.3% in 1962 might well be connected with the eightfold increase of the host population which occurred during the same period.

Pupal Parasitism

Far fewer data were accumulated on pupal than on larval parasitism because of the technical difficulties involved; Table IV summarizes the results.

S. scutellator is the only efficient pupal parasite (Table IV) and its parasitism is considerably higher than that of any other parasite, pupal or larval. Figures obtained at Neusiedl during three years suggest that populations of this well-adapted species fluctuate less with changing host density and weather than do those of other parasites. It must be stressed that these data were obtained from relatively high host populations. Parasitism at lower population levels could not be assessed, but male parasites were observed where host densities were low.

While the hyperparasite *G. cursitans* usually occurs at an insignificant level, it may occasionally reduce the efficiency of *S. scutellator*. Hence, if in a biological control programme *S. scutellator* is introduced without it, the latter's efficiency might be increased appreciably.

The polyphagous *B. intermedia* is an unimportant mortality factor in *T. lineola* populations (Table IV).

Comparison of Parasite Complexes in Europe and Canada

Phytophagous insects known to have been introduced into a new area are ideal models for demonstrating the development of parasite associations. An account of some of these has been given by Bartlett and Van den Bosch in DeBach and Schlinger (1964, p. 286). A particularly interesting example is that of the North American parasite *Macrocentrus ancylivorus* Rohw. which attacks the introduced oriental fruit moth more effectively than do the parasites introduced from the native home of the pest species (Allen, Holloway, and Haeussler 1940).

T. lineola also illustrates how quickly an empty parasitological niche may be occupied by endemic parasites.

From several thousand host larvae and several hundred pupae Pengelly (1961) and Arthur (1962) reared 22 parasite species in Canada: 6 tachinids, 8 ichneumonids, 5 braconids, and 3 chalcidids. A comparison of Canadian and European records shows several interesting points.

A much larger number of parasite species was recorded in Canada than in Europe from comparable host numbers (at least as far as larvae are concerned); most species involved are polyphagous. In general the parasitism appears to be incidental: 13 species were obtained only once, 5 species 2 to 10 times, and 3 species parasitized between 1 and 3% of the host. The only exception was *Itoplectis conquisitor* (Say), which parasitized up to 30% of the host pupae, showing how rapidly the adaptation to a new host may proceed. Arthur (1966) has shown that one factor in this process is associative learning. He theorizes that "after finding and parasitizing a few hosts of a particular species, the female learns to associate certain characteristics of the oviposition site with the presence of hosts, and its host-finding ability is thus greatly increased".

The greater number of species in the parasite complex in Canada is noteworthy. This indicates that a parasite complex in the process of development tends to become qualitatively reduced by elimination of unadapted species, and quantitatively richer by progressive specialization of other, biologically adapted species. Support for this assumption is offered by the fact that in Canada but not in Europe *T. lineola* is attacked by two holarctic species: *Compsilura concinnata* Mg., a native of the palearctic introduced into North America in 1906, and the holarctic *Pteromalus puparum* L. There is no plausible explanation for the absence of these species from the European parasite complex unless it is assumed that these and possibly others have been displaced by more efficient and better adapted species. A third species, now holarctic, is the originally palearctic *Phryxe vulgaris*. In contrast to the above two species, *P. vulgaris* is one of the more important parasites in Europe but has not been reared from the skipper in Canada. An explanation offered by Mesnil (pers. comm.) is that *P. vulgaris* is likely to comprise several biological races, each with a restricted host range. The Canadian *P. vulgaris* probably belongs to a race biologically different from that attacking *T. lineola* in Europe.

There is a striking systematic similarity between some of the parasitic species in both associations: five species occurring in Canada have congeneric counterparts in Europe. These are *Phryxe pecosensis* Tnsnd., *Rogas* sp., *Gelis* sp., *Labrorychus* (?) *alpinus* Davis, and *Brachymeria ovata* Say. Zwölfer (1961) compared the parasite complexes of the related palearctic fir budworm (*Choristoneura murinana* Hb.) and the nearctic spruce budworm (*C. fumiferana* Clem.), and found that in spite of a close inter-relationship between several such parasite "pairs", there was no evidence to show that the complexes are the result of parallel evolution of the hosts and their parasites. Parallel evolution has been shown to exist between other entomophagous parasites and their hosts (Pschorn-Walcher 1963). Similarities in the parasite associations, as investigated by Zwölfer, result from the occupation of similar niches by related species. In Europe, parallel evolution of *T. lineola* and its parasites is unlikely (with the possible exception of *T. incedens* and *S. scutellator*), and in Canada is impossible. Yet related pairs of parasites with equal ecological potentialities occur. Thus, Zwölfer's interpretations are supported.

Discussion

In Canada *T. lineola* causes considerable damage to hay-fields, but agricultural practices in most parts of Europe apparently prevent it from invading cultivated land (exception: Neusiedl). Even where undisturbed by cultivation, the species is under natural control and apparently does not reach the limits of its food supply. The highest density recorded during the present study was only 5% of that in outbreaks in Canada (Arthur 1962). Considerable variation in density between different populations was observed (lowest at Courtetelle, highest at Neusiedl, ratio 1:740), and this could be directly linked with factors such as the sociability of the host-plants and exposure. On the other hand, variations in time between individual populations remained within narrow limits during a period of 5 years (ratio between lowest and highest level usually less than 1:10), and in the absence of conflicting literature records it appears unlikely that this amplitude is exceeded over longer periods.

Adverse weather (e.g. in 1963 and 1965) did not significantly affect population levels, nor do climatic factors seem to be responsible for their generally stable levels, since these are similar under very different climatic conditions (the survey included continental, atlantic, boreo–alpine, and mediterranean climates). Exclusion of these factors considerably restricts the number of possible natural controlling agents. Accordingly, it is possible that natural enemies constitute a significant regulating factor, although, in the absence of detailed information on other possible causes of mortality, this conclusion must remain tentative.

Of the larval and pupal parasites *S. scutellator* is certainly the most efficient and most promising species for attempted biological control of the skipper in Canada. Factors in its favour are: (1) Its life-cycle is well synchronized with that of its host, i.e. it does not depend on alternate hosts even though it is not strictly monophagous. This lack of strict monophagy may even be advantageous when *T. lineola* is scarce. (2) It attacks the host at a crucial stage when few or no other factors are likely to cause significant mortality before the host reaches maturity. Thus, a parasitism of 50%, as has been observed in Europe, will greatly reduce the host population in the adult stage, and hence also the initial number of eggs of the following generation. (3) This species seems to have a wide ecological and climatic tolerance, as indicated by its occurrence from Russia to the Atlantic, and from the plains to altitudes of 5000 ft. (4) It does not compete directly with the other important parasites in Europe (*R. tristis* and *P. vulgaris*). (5) In the absence of hyperparasitism its efficiency might well be increased.

If established in Canada, this species would inevitably compete with the native *Itoplectis conquisitor*, which also attacks pupae which it parasitizes up to 30%. Were *S. scutellator* to be the more successful competitor, it should have a better chance of controlling *T. lineola* than has the heteroxenous *I. conquisitor*, and competition might eventually result in displacement of the native species. Such displacement in Canada would in turn offer an explanation for the absence in Europe of ecologically homologous species, such as *Itoplectis maculator* F., which according to Zwölfer (1961) is considered to be the European counterpart of *I. conquisitor*.

The two main larval parasites in Europe, *P. vulgaris* and *R. tristis*, are far less effective than *S. scutellator*, and are both about equally important as mortality factors. Although *R. tristis* is not as well synchronized with the host as is *P. vulgaris*, its parasitism attains approximately the same level. Both suffer from their dependence on alternate hosts, i.e. they can become effective at high host densities of *T. lineola* only if an adequate alternate host reservoir is available during that part of the year when there are no skipper larvae.

Any prediction of the potentialities of these two species if introduced into Canada is impossible since the abundance of potential alternate hosts is unknown. In spite of this, introduction of one or both species appears desirable in view of the negligible parasitism exerted by native larval parasites in Canada. These larval parasites would, unlike *S. scutellator*, find a virtually empty parasitological niche.

The restricted host range of *P. vulgaris* in Canada, and its absence from the parasite complex of *T. lineola*, suggest the existence of races with various host preferences. But other factors, such as lack of coincidence in space and(or) time, may also play a role preventing *P. vulgaris* from attacking the skipper in Canada. It would be worth investigating the factor or factors involved, and considering the introduction of the European *P. vulgaris* if the North American race proves to be unadapted to this host.

Present evidence suggests that *T. incedens* is a southern form which, possibly for this reason, usually remains at a lower level than the parasites mentioned above. Moreover, this species is almost certainly heteroxenous and, being presumably restricted in its host selection to hesperiids, may accordingly have only a limited choice of alternate hosts; and this may be a further reason for its scarcity.

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THE SEASONAL MOVEMENTS OF WIREWORMS (COLEOPTERA: ELATERIDAE) IN RELATION TO SOIL MOISTURE AND TEMPERATURE IN THE ORGANIC SOILS OF SOUTHWESTERN QUEBEC

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Abstract

A 4-year study in the virgin organic soils of southwestern Quebec revealed that most elaterid larvae moved from the subsurface to the top 10 in. of soil in early May, when the soil temperature at a depth of 4 in. was approximately 35°F. This upward movement reached its peak when the topsoil moisture content was 200% and the soil temperature at 4 in., 55°F. In early June, when the soil temperature reached 67°F, the larvae began to move downward and very few larvae were found in the first top layers of soil when the temperature was above 72°F. This downward movement lasted until the end of August and again the larvae moved up to feed near the surface of the soil until the first frost, usually recorded in mid-November. The data indicate that June to early September is generally the most favourable period for growing vegetables.

Résumé

Des recherches, effectuées en sol vierge organique durant quatre années consécutives, ont démontré qu'au début de mai, lorsque la température maximum de sol à quatre pouces de profondeur était d'environ 35°F, la plupart des larves de taupins quittaient le sous-sol pour se diriger vers la zone superficielle. Cette migration ascendante atteint son point culminant lorsque l'humidité du sol est d'environ 200 p. cent et que la température du sol est de 55°F. Au début de juin, les larves commencent à migrer en profondeur lorsque la température du sol est d'environ 67°F et, au-delà de 75°F, on trouve très peu de larves dans la zone superficielle. Les larves demeurent dans le sous-sol jusqu'à la fin d'août puis migrent à nouveau vers la zone superficielle jusqu'aux premières gelées. La période s'étendant de juin à septembre coïncide avec la migration en profondeur et ainsi s'avère la plus propice à la culture des légumes.

Introduction

The elaterid larvae are serious pests in vegetable crops grown in newly cultivated organic soils of southwestern Quebec. A knowledge of their vertical movements seasonally was of prime importance in determining the timing of insecticide applications, and the seasonal period when the topsoil is free of larvae and therefore safe for vegetable growing. Hence, research work was carried out in organic soils of Ste Clotilde, Que., 1963 to 1966 inclusive, to determine their