DEPARTMENT OF AGRICULTURE, SOUTH AUSTRALIA

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THE BIOLOGY OF SITONA SPECIES WITH PARTICULAR REFERENCE TO *S. humeralis*

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Research Officer (Entomology).

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CONTENTS

1. DENSITY OF SITONA

Densities in excess of 46.5 adult sitona weevils (Sitona humeralis Steph.) per 1,000 cm^2 (50 per sq. ft.) are found frequently in lucerne in South Australia (Allen 1969). At Roseworthy in 1972 Moulden (unpublished) estimated a density of 277.7 newly emerged adults per 1,000 cm^2 (247.5 per sq. ft.).

In 1971 Allen reported that highest densities of S. humeralis are found associated with annual medic pastures. Near Cummins, larvae were found in densities approaching 200 larvae per 1,000 cm^2 and probably averaging 100 per 1,000 cm^2 in the paddock, a pasture of Medicago truncatula and M. polymorpha. In sampling at Roseworthy in 1972 Moulden (ubpublished) found a density of 24.7 larvae per 1,000 cm^2 (23.0 per sq. ft) in a paddock of regenerated medic pasture, the first year after cereal cropping.

2. ADULTS

2.1 Longevity

Observation carried out by Melamed-Madjar (1966b) in Israel showed that adults of Sitona lividipes Fahrs., Sitona hispidula I Sitona crinitus Hbst. and Sitona lineata L. survived from 250-300 days after termination of diapause when kept in the laboratory where temperatures fluctuated between 16°C and 24°C.

2.2 Seasonal life history

Refer to Appendix II for a summary of the seasonal life histories.

2.2.1 S. humeralis

In South Australia, adults of S. humeralis emerge during October-November and the females are sexually immature (Allen 1971). In 1972 S. humeralis began to emerge at Roseworthy on 13th October. Maximum rate of emergence occurred on 25th October with 28.3 adults emerging per 1,000 cm^2. By 13th November 97% had emerged, and the remainder emerged by 15th December (Moulden, unpublished). Newly emerged adults feed actively if green legumes (mainly lucerne) are present. Adults diapause from December to March or April and shelter in cracks in the soil, under vegetable debris or at the base of plants.

They resume feeding during autumn and damage may be evident during brief warmer periods of winter. Females become sexually mature with the formation of the first eggs during April and oviposition continues throughout the winter months to mid-November. Most adults are dead by October but a few live till December after living as adults for approximately a year. Refer to Appendix IIA.

This life cycle as described by Allen (1971) is similar to that described by Alimolzhanov (1941) in Tashkent, Uzbekistan. Hibernation of S. humeralis occurs in the adult stage. Adults are present all year since the over-wintered ones survive until the following generation emerges.

The life cycle of four species of Sitona (including S. hispidula and S. lineata) in Israel appears to be similar to that of S. humeralis in South Australia. Melamed-Madjar (1966b) sowed that egg laying begins in December, larvae are found in January-March, pupae in March-April and adults of the new generation in April-May. These adults feed freely but do not oviposit and in June-July they seek shelter and enter diapause which lasts until the close of the year. Then feeding resumes and oviposition begins shortly afterwards. Refer to Appendix IIB.

2.2.2 S. lineata

Jackson (1920) found S. lineata to be dormant during winter and active during summer in Britain.

From January to March or April, adult weevils remain in their winter quarters, sheltering amongst long grass, in stacks of pea straw, amongst the stubble of clover fields or even lying more or less exposed on the earth between plants. In the first warm days of spring, the majority migrate to peas and beans, only a very few remaining on clover. They very soon commence to lay eggs and egg laying continues until shortly before the death of the parent weevil: which occurs at the end of June or the beginning of July in the South of England or in August or the beginning of September in the north of Scotland. Jackson never observed the adults to live through a second winter. The eggs hatch in 20-21 days and the young larvae become mature in about 6 or 7 weeks. The pupal stage lasts about 3 weeks, commencing in England in July and in Scotland in August. All the weevils emerge before winter except in rare cases in the north of Scotland. Newly emerged weevils are sexually immature, the ovary of the female being undeveloped and maturing very slowly so that egg laying does not commence till the following spring. There is only one generation in the year. Refer to Appendix IIC.

Prescott and Reeher (1961) describe the seasonal history of S. lineata in the Pacific North West of North America. Refer to Appendix IID.

The Pacific northwest has milder winters than northern Europe so the development of the weevil's life stages, the activity of the overwintered adults and the host-plant development are from 1-2 months earlier than described in European literature.

S. lineata has a single generation annually. Overwintered adults start flying usually about the middle of March when they are attracted to fields of lucerne and clover. By the end of March flying is greatly accelerated and there is general migration to peas and vetch for oviposition. During the last part of May the overwintered weevil population declines rapidly from normal mortality.

Studies by Prescott and Reeher (1961) show that hibernation is not obligatory in the mild climate of the Pacific Northwest and that in this region sexual maturation and egg-laying begin much earlier than in Great Britain.

Egglaying beings in Mid-February and is greatly increased after the middle of March, reaches a peak in April and declines rapidly after the middle of May. The normal incubation period during the peak of egg-laying in April is about 18 days.

The larvae feed on nodules and are occasionally found damaging small rootlets. Larvae are found as deep as 11 inches but the majority (51%) are found in the top 3 inches of the soil. The larval stage generally lasts about 35 days.

The pupae begin appearing in the soil late in May and reach peak abundance in the middle of June. By the middle of July most of them have transformed to adults.

The new adults fly intensively for several weeks beginning early in July. In this manner, as well as on foot, weevils disperse widely in search of the still succulent perennial legume crops, chiefly lucerne and red clover.

The new adults aestivate from late summer throughout most of the autumn. Aestivation begins with an abrupt cessation of feeding coinciding with the disappearance of the weevils around mid-August. In areas of low winter temperatures such as northern Europe the aestivation period evidently extends without interruption into a period of true winter hibernation lasting until spring. In Oregon those weevils that had aestivate in legume fields end their aestivation and resume a moderate amount of feeding during warmer periods beginning by mid-October and continuing throughout winter.

2.2.3 S. hispidula

Jackson (1920) also described the life cycle of S. hispidula in Britain which differs from S. lineata in having two periods egg-laying, one in autumn and one in spring, the autumn laid eggs not hatching till the following spring.

There is only one generation of S. hispidula in the year. Adults emerge from the pupal stage from July-September and commence egg-laying 6-8 weeks after emergence. A few eggs are laid during the winter and vigorous oviposition recommences in spring. Towards the end of June, egg-laying descreases and during July most of the weevils die. Eggs laid in late autumn do not hatch till the following spring, but a few of the September eggs and all those laid in spring and summer hatch in 25 days. The last few eggs laid by the old females in July produce fully fed larvae and pupae in the end of October, but these perish during the winter. Hence the principal period during which larvae occur is the summer, from the end of April to August. The winter is passed almost entirely in the egg and the imaginal state. Refer to Appendix IID. Bigger (1930) recorded the life history of S. hispidula in Central Illinois which is basically the same as in Britain.

2.2.4 Sitona cylindricollis Fahrs.

Bird (1947) gave an account of the life history of S. cylindricollis in Manitoba, which is similar to that of S. lineata in Britain but S. cylindricollis begins hibernation in early October whereas S. lineata begins hibernation in late November in Britain.

Adults over-winter in the surface trash and soil to a depth of one inch. They start to become active during the latter part of April, the peak being mid-May. Belated individuals continue in hibernation until the end of July. Migration takes place in spring by running and flying and in the autumn only by running. Mating commences shortly after the weevils become active and egg-laying starts in May and continues to August when the weevils die of old age. The eggs are dropped indiscriminately in the soil and hatch after 10 to 21 days.

The larvae burrow into the soil up to a depth of 7". The majority are found in the 2-3" level with a good many in the 3-4" level. The fourth instar larvae migrate upward, and the pupae are found in the upper inch of soil. The new generation begins to emerge in late July with a peak in early August. They feed actively but do not mate. They go into hibernation with the first frosts. Refer to Appendix IIE.

The life history of S. cylindricollis in Tashkent, Uzbekistan described by Alimdzhanov (1941) differs from all life cycles previously mentioned, since the weevil passes through two generations per year. Hibernation only occurs in the adult stage and over-wintered weevils survive until the beginning of June. The egg, larval and pupal stages lasts 9-10, 32-38 and 5-8 days respectively. Larvae are present from April to mid-June and August to mid September. Refer to Appendix IIF.

2.3 Diapause

In Israel and South Australia, diapause occurs only in the adult stage but in Bulgaria winter diapause of S. hispidula occurs in the egg, larval and adult stage (Grigorov, 1956); and in England (Jackson, 1922) and in U.S.A. (Bigger, 1930) it has been found this species may over-winter in the egg-stage.

In Finland, adults of S. hispidula diapause in mid-summer and this interrupts oviposition between the end of June and mid-August; feeding and movement are at a minimum (Rautapaa et al 1966). Oxygen consumption of diapausing adults is about one-third the consumption during the autumn egg-laying period. In earlier studies in Finland, temperature and food supply in spring and summer had no apparent effect on the occurrence of diapause. It appears that diapause is predetermined by conditions prevailing before the spring oviposition period.

In Finland (Markkula et al 1961) and in Israel (Rivnay et al 1959) S. lineata terminates diapause later than in other species. According to Markkula et al (1961) this is due to the fact that pea, its main host, begins to grow later than other leguminous plants. In other words, there seems to be a fixed synchronization between host and dependent. Thus the time of termination of diapause depends upon the species and its particular host.

Climate also affects the date of emergence of adults of Sitona from their diapause quarters. An early rain may hasten their emergence at the beginning of the season (Melamed-Madjar, 1966a).

It has been shown that dormancy is characterized by a drop in oxygen consumption, a cessation of the development in the reproductive organs and a slight rise in fat content; and that termination of dormancy is characterized by a reversal of these conditions, but the water content does not change (see Davey, 1959). The physiology of over-wintering S. cylindricollis was studied (Davey, 1956). Although the total respiration exhibited the characteristic U-shaped curve from entry into dormancy until its cessation, the carbon monoxide - insensitive respiration remained at a low level throughout. Termination of dormancy requires a period of exposure to low temperatures. It was concluded that this dormancy is not essentially different from diapause in immature insects.

2.4 Feeding

2.4.1 Food preferences

Adults of Sitona defoliate legumes; initial feeding causes characteristic "scalloping" of leaf margins and, with heavy infestations, feeding can result in complete defoliation. Early reports suggested that Sitona also attacks non-leguminous plants but Jackson (1920) found these unsubstantiated. Menozzi (1930) and Anon (1970) claimed that sugar beet is attacked in Italy and Victoria, respectively. Apart from this, all damage has been reported on legumes.

S. humeralis in South Australia has a preference for annual medics and lucerne and will eat subterranean clover and strawberry clover (Allen, 1971). Reimers (unpublished) found S. humeralis in South Australia prefers red clover to annual medics and lucerne. Anon (1967) found lucerne is preferred by S. humeralis in N.S.W., but burr and spotted medics, white and red clovers, subterranean clover and various vetches are also attacked. At Kiev (U.S.S.R.), Grossheim (1928) found S. humeralis feeds on a range of both annual and perennial leguminous species. First it attacks lucerne and then migrates to summer vetch and peas.

Feeding preferences for other more common Sitona species are:

S. lineata: peas, beans and vetches (Melamed-Madjar, 1966a).
S. crinitus: various leguminous crops, in particular vetch and peas (Melamed-Madjar, 1966a).
S. hispidula: In America and England clover and lucerne are preferred (Bigger 1930, Jackson 1922). In Israel the main host is clover and it is occasionally found on lucerne, vetch and broad beans (Melamed-Madjar 1966a).
S. cylindricollis: is a pest of sweetclover (Melilotus officinalis) in North America (Bird, 1947).
S. lividipes: In Israel it is abundant on clover (Melamed-Madjar, 1966a).

2.4.2 Feeding rate

Calkins (1969) studied effects of temperature, light and date of collection on the feeding rate of S. cylindricollis. He found that feeding rates are highest for weevils collected in autumn and lowest for those collected in mid summer. Weevils collected in spring and summer eat more when the temperature is between 24 and 32°C. Weevils that have over-wintered feed more when exposed to light than when exposed to complete darkness, but newly emerged adults collected in July feed significantly more in the dark than in the light. These responses correspond with their daily period of activity in the field.

2.4.3 Feeding prior to diapause

In South Australia, the importance of spring feeding for adult survival through summer is not understood. It appears that prolonged feeding prior to aestivation is not necessary because the highest densities of S. humeralis are found in annual medics areas, especially on Yorke and Eyre Peninsulas. Where there is very limited suitable green feed in spring and early summer. (Allen, 1971).

Loan (1963) found adults of Sitona scissifrons (Say) feed after emergence though sustained feeding may not be necessary before diapause.

2.5 Oviposition

In South Australia, eggs of S. humeralis are ready for oviposition in April and oviposition extends throughout the winter months to mid-November (Allen 1971). At any time during winter, field populations contain a wide range of larval instars which would be a consequence of the extended oviposition period.

In Israel, newly emerged adults of Sitona spp. are active and feed freely prior to aestivation, but do not oviposit until after aestivation (Melamed-Madjar, 1966b). Throughout most of Finland Sitona oviposits after hibernation, but in the more southern districts three species, one of them S. hispidula, also oviposits in the autumn before hibernation. In Bulgaria S. hispidula and two other species examined do not oviposit until after hibernation (Grigorov, 1966). According to Markkula et al (1961) oviposition is interrupted in some species of Sitona whereas other lay continuously. For example, females of S. hispidula oviposit during the spring in Finland, cease to do so during the summer and resume oviposition during the autumn. On the other hand females of S. lineata in the same country lay uninterruptedly.

Grossheim (1928) found that in insectaries the oviposition period of S. lineata varied from 1-4 months.

Melamed-Madjar (1966b) found that in the field, eggs are commonly laid on the ground near food plant; some are laid on leaves but these usually fall to the ground later. Grossheim (1928) stated that eggs are laid singly on stems or leaves of the food plant. Anon (1967) observed that eggs of S. humeralis are laid singly on the soil surface. In Russia S. humeralis lays eggs scattered at random (Alimdzhanov, 1941).

Andersen (1933) found that oviposition by females of S. lineata in Germany is affected by temperature; no eggs are laid below 11°C or above 26°C in June-July, the optimum temperature for egg laying being 24.5°C (Andersen 1934a). In Israel, however, peak oviposition is reached in March-April when temperatures are about 18°C and the rate of egg-laying does not increase with further seasonal increases in temperature (Melamed-Madjar, 1966b).

In S. hispidula oviposition may occur at 4.4°C although normally it does not take place until a temperature of 10°C. The maximum temperature for oviposition in this species is 21°C so that egg laying ceases in hot weather in summer (Bigger 1930).

Andersen (1935) investigated the effect of exposure to a low temperature before the commencement of oviposition on oviposition rate and total egg production in S. lineata. The rate of oviposition and the total number of eggs decreases as the females are kept for an increasing length of time at 11-12°C before being tansferred to a temperature favourable to oviposition.

In an experiment in Bavaria on the effect of air humidity on adult feeding and egg production in S. lineata (Andersen 1934b) it was found that in 4 days, females produced averages of 88, 42 and 40 eggs at 100, 70-75 and 32-35% humidity respectively, when they were allowed to feed for about 3-4 hours daily. When the eggs laid on the first day were omitted from the count, the numbers averaged 69, 28 and 29. The amount of food taken was sufficient to maintain life, but was inadequate for egg production. In another experiment weevils were continuously supplied with food. The average number of eggs was 48, 28, 104 and 128 at 100, 75, 50 and 17-20% humidity. The explanation of the discrepancy between the results of these experiments is that more food was eaten as the air became drier, the moisture in the leaves being used to compensate for the loss of body moisture.

Rautapaa _et al_ (1966) demonstrated that there is no influence of daylength on the amount and frequency of oviposition of _S. hispidula_ in Finland.

Marshall (1934) found that eggs of _S. hispidula_ in Kansas are laid within 12 hours of copulation.

2.6 Fecundity

Melamed-Madjar (1966b) working with four species of _Sitona_ found the average number of eggs laid per female varied from 519-1113 depending on the species. The majority of females of _S. lividipes_ and _S. hispidula_ laid 300-1,200 eggs, few laid more, and none laid less than 100. On the other hand females of _S. crinitus_ laid only 100-600 eggs each, though one laid nearly 3,000 (this female lived exceptionally long and had a correspondingly long reproductive period). The greatest number of eggs was laid by two females of _S. lineata_, both of which produced more than 3,000 eggs; in this species fecundity varied more than in others. _S. lineata_ is distinctly more fecund than the other 3 species, mainly because of a high daily rate of oviposition. As a result , large numbers of eggs are laid by females of this species even when their life span is short.

Melamed-Madjar (1966b) also found significant differences in mean numbers of eggs laid by adults feeding on different food, indicating that the four species are to some extent adapted to different food-plants. Females of _S. lividipes_ and _S. hispidula_ produce the greatest number of eggs when fed on clover, whereas those of _S. crinitus_ and _S. lineata_ produce the greatest number when fed on pea. Egg production in _S. lividipes_ is much diminished by a diet of broad-bean, vetch or pea, in _S. hispidula_ by a diet of clover or lucerne. These results can also be used to indicate the suitability of food-plants. If an arbitary level of 300 eggs per female or more is taken to indicate suitability, then clover is a suitable food only for _S. lividipes_ and _S. hispidula_, broad bean only for _S. lineata_, and vetch or pea only for S. crinitus and S. lineata. Ulashkevich (1935) and Markkula (1959) also found the type of food influences fecundity.

2.7 Activity

Andersen (1931a) found S. lineata active between 0.7°C and 42.5°C with an optimum at 25°C. Adults of S. hispidula are most active when temperatures are between 50 and 75°F (10-24°C) (Bigger, 1930).

Calkins et al (1968) studied the seasonal changes in daily activity periods of S. cylindricollis in Nebraska. Light appears to be the major factor influencing activity and temperature is secondary. Activity seems to be highest at night unless low temperatures cause the insects to shift their activity to the warmer daylight hours. This may explain the daylight activity in spring and autumn when night-time temperatures tend to fall below the threshhold for weevil activity.

The reactions of S. cylindricollis to various weather factors in Manitoba were stuedied in the laboratory and field by Heidwig et al (1961). The preferred temperature is dependent on the temperature to which the weevils are conditioned. Weevils emerging from hibernation have a lower temperature preference than weevils collected later from the field during the summer months. High humidity inactivates the weevils at all temperatures. Light does not change the reaction to temperature but high temperature reverses the negative reactions to light.

2.8 Flight activity

S. humeralis in South Australia spreads in two ways; by flight from one paddock to another and by transport in machinery and plant material such as hay. In high density areas in South Australia, flying adults can be seen "swarming" in spring. Reasons for swarming are not understood, but it occurs with higher temperatures on days with little wind. Flight activity of adults in early spring creates special problems from handling grain free of insects to severe nuisance problems in houses in the high Sitona density areas of South Australia (Allen, 1971). Densities of flying adults recorded 3-4 miles east of Maitland on 30th Novermber 1971 were approximately 1 per 5 cubic yards of air, measured by holding a 12 inch diameter net from a travelling vehicle for 1 mile (Birks & Allen, unpublished). Adults have been found landing on ships seven miles out to sea off Yorke Peninsula (Allen, 1971).

The threshhold ambient temperature for flight of S. cylindricollis in the field in bright sunshine is 25°C. This implies a threshhold body temperature of about 35°C which is found to be the threshhold under laboratory conditions. A wind speed of 0.1 m/sec. decreases the flight activity and at 0.6 m/sec. flights cease completely. Feeding and adaptation to high temperature and light intensities increases the threshhold for flight activity. Young weevils normally do not fly. The attraction of colour and odour to flying insects was investigated with baited traps. S. cylindricollis does not show any reaction to colours. Coumarin proves to be a significant olafactory stimulus for terminating flights. (Heidwig et al, 1961).

Prescott et al (1963) studied the flight of S. hispidula in Oregon. They found the dispersion flight is effected by new generation weevils about 2 months after they have emerged from the soil and continues for several weeks immediately preceding sexual maturation and autumn egg laying. Thus, it appears that flight is evoked by the coincidence of an appropriate physiological state with such external stimuli as high temperatures. They suggest flight as the major means of dispersal.

Dispersal flights of S. cylindricollis in Manitoba occur mainly during a short period in May (Heidwig et al 1961). Later in the year the weevils do not often encounter flight - inducing high temperatures in their habitats.

2.9 Mating

Loan (1963) describes in detail thebehaviour of S. scissifrons in Ontario. The behaviour of overwintered weevils is concerned mainly with mating and feeding. The males of S. scissifrons, as with other species of Sitona, are carried about by the females during copulation. Copulating pairs are first seen on the ground in foliage in May and June. The weevils drop to the ground in a cataleptic state if they are approached with caution. The weevils do not drop to the ground when disturbed if the soil surface temperature is high e.g. 138°F. Much time is expended running up and down blades of grass and vetch foliage. Some of this movement is probably the searching of males for females. Often a weevil, when it reaches the tip of a stem, will rear up and wave its forelegs for an instant. Such behaviour is very similar to the preliminary flight attempts of S. cylindricollis but weevils of S. scissifrons cannot fly. Motionless weevils in copula or alone are frequently seen on vetch leaves in bright sunshine, but they are also numerous in vetch during rain or at night.

In Illinois mating of S. hispidula starts about the third week in September and occurs during all active periods until death. (Bigger, 1930). Mating is promiscuous. In several cases the males died during the course of Bigger's experimental work and when new males were supplied mating and oviposition proceeded as before.

2.10 Mortality and Survival

Females of S. lineata live longer at 75% humidity than at 100% but as the humidity decreases below 75 their life becomes suddenly shorter (Andersen, 1934b).

The adults of S. hispidula are able to undergo submergence in water for at least 24 hours and survive. (Bigger, 1930). Several times the insects were frozen in solid ice and resumed activity when thawed out.

3. EGGS

3.1 Incubation Time

Species	Location	Incubation Time	Conditions	Reference
Sitona spp.	Finland	29-32 days	11.5-12°C	Markkula (1959)
	Finland	22-26 days	17-17.5°C	Markkula (1959)
S. crinitus	Ukraine	11-14 days		Ulashkevich (1935)
S.cylindricollis	Central Asia	17-39 days	in shade	Yakhantov (1935)
S. hispidula	Ontario	27-35 days		Hudson (1925)
S. humeralis	S.Australia	14 days	Moist 22°C	Allen (1971
	"	26 days	Moist 15°C	Allen (1971
	"	2 months	Moist 10°C	Allen (1971
	U.S.S.R.	8-10 days	24-28°C	Alimdzhanov (1941)
	N.S.W.,Aust.	10-14 days		Anon (1967)
	U.S.S.R.	10-12 days		Grossheim (1928)
S. lineata	Britain	20-21 days		Jackson (1920)
	Ukraine	11-14 days		Ulashkevicl (1935)

3.2 Hatching

Melamed-Madjar (1966b) working with 4 species of *Sitona* in Israel found a very high percentage of eggs hatching at 90% relative humidity. However, when temperatures were increased above 25°C, hatching was reduced.

Eggs of *S. lineata* kept continuously at temperatures below 7°C or above 33°C fail to hatch (Andersen 1934b). Experiments were made to determine how long eggs could resist exposure to temperatures above or below these critical points. It was found that 60% of the eggs hatched after 4 weeks storage at 6.5°C or after 22 days at 0°C. Some hatched after 4 days at 36°C. The very long periods necessary for determining the length of development at low temperatures may be avoided by exposing the eggs to the low temperature of only $\frac{1}{2}$-$\frac{1}{4}$ the time that development is estimated to take at that temperature and then continuing the experiment at a higher temperature for which the development time is known. A formula for calculating the total period needed at the low temperature is given.

No eggs of *S. hispidula* in Central Illinois have been found to hatch in the autumn, but eggs laid in the autumn, as well as eggs laid in the spring will hatch in the spring (Bigger 1930). Autumn laid eggs require 138-200 days to hatch. Eggs laid in the spring require 17-21 days to hatch early in the season and 15-16 days to hatch late in the season.

4. LARVAE

4.1 Duration of Larval Stages

Species	Location	Duration	Conditions	Reference
S. crinitus	Israel	35 days	field	Melamed (1966b)
	Ukraine	30-42 days		Ulashkevich (1935)
S. cylindricollis	U.S.S.R.	30-40 days	field	Alimdzhanov (1941)
S. hispidula	Illinois	21-27 days	field	Bigger (1930)
	Israel	58 days	field	Melamed (1966b)
	U.S.A.	65 days	18°C	Newton (1958)
S. humeralis	U.S.S.R.	30-40 days	field	Alimdzhanov (1941)
	U.S.S.R.	29-40 days		Grossheim (1928)
S. lineata	Britain	6-7 weeks		Jackson (1920)
	Israel	38 days	field	Melamed (1966b)
	Ukraine	30-42 days		Ulashkevich (1935)
S. lividipes	Israel	52 days	field	Melamed (1966b)

4.2 Damage and feeding

Sitona larvae are subterranean feeders and feed on root nodules, roots or both, depending on the species (Danthanarayana, 1967). Damage to nodules by Sitona larvae is of two types. Young, first instar larvae burrow into nodules without leaving external signs and when the contents of the nodules are devoured and only the cortex remains, larvae exit through small holes. Older larvae feed from the outside of the nodules and leave an empty shell (Manglitz et al, 1963). Danthanarayana (1967) found Sitona regensteinensis Herbst. larvae feeding on broom restricts its feeding to cells in the nodule containing bacteria. He questioned whether host specificity of Sitona to legumes is associated with leghaemoglobin.

Loan (1963) working with S. scissifrons in Ontario found the first two larval instars develop within the nodules of Vicia cracca. No other head capsules were recovered from nodules suggesting third and fourth larval instars move freely in the soil and feed externally on nodules and other parts of the root system.

Grandi (1913) recorded larvae of S. humeralis feeding on the roots of Medicago sativa, M. lupulina and M. minima in Italy.

George (1962) worked with S. lineata in south-central England. In 3 out of 4 comparative tests he found infestation by larvae reduced the number of root nodules produced by pea plants growing in poor and nitrogen-enriched soil, but there was no subsequent reduction in the yield of peas.

S. humeralis larval damage may render plants more susceptible to soil-borne plant pathogens. Isolations from roots of Medicago polymorpha damaged by S. humeralis collected from Cummins, South Australia in September 1971, contained the pathogens Pythium irregulare, Pythium sp. (possibly graminicolum) and Fusarium solani. The rhizoctonia, Ceratobasodium sp., a parasite of roots was also isolated (Allen 1971).

Larval damage by S. hispidula, internal breakdown of crown tissue, and associated and independent root rot are the major factors in the lack of persistence in red clover in U.S.A. (Newton 1960).

Lucerne plants were exposed to larvae of S. hispidula Fusarium oxysporum fsp medicaginis and Corynebacterium insidiosum in factorial combination (Hill et al. 1969). S. hispidula and F. oxysporum significantly reduced the growth of the lucerne plants. A higher level of Fusarium wilt was observed when S. hispidula was present than when it was absent. C. insidiosum did not reduce the growth of lucerne. No relation between effects of S. hispidula and C. insidiosum was detected.

However, in a different experiment (Dickason et al 1968) there was no significant difference in forage yields between control plots and those infected with S. hispidula larvae, fungi and nematodes. The authors concluded that lucerne is an extremely hardy plant capable of withstanding the biotic agents that can cause mortality in alsike clovers under similar conditions.

On white clover, root rot was more severe where soil was heavily infested with *Sitona* spp. larvae (Kilpatrick et al 1961).

S. hispidula larvae increased the incidence of *Fusarium* root rot in Ladino white clover (Graham et al. 1960).

On *Trifolium hybridum* in Oregon there was a direct relation between the occurrence of vascular decay and incidence of injury by *S. hispidula* and a less marked one between insect injury and rootlet rot (Leach et al, 1963).

Experiments with red clover showed a relationship between the incidence of larval damage by *S. hispidula* and an increase in root rot, *Fusarium roseum* (Graham et al, 1959).

4.3 Behaviour

Andersen (1931b) who studied the behaviour of *S. lineata* larvae in Germany found that the eyeless larvae do not respond to light by definitely directed movements, though erratic movements indicate their strong perception of light. They can recognise the presence of moisture and prefer a moist environment but avoid free water. They can detect the nodules of beans at a distance of 2-3 yards, probably through a sense of smell. His results imply that only those larvae survive that hatch during a period of rainy weather or at least in damp ground.

5. PUPAE

5.1 Pupation

In South Australia, pupae of *S. humeralis* can be found in the field as early as September (Allen 1971).

Alimdzhanov (1941) found in Russia that pupation of *S. humeralis* occurs in the upper layer of the soil and that the minimum duration of the pupal stage is 5 days. Pupae develop normally on muslin in the laboratory provided that humidity of the air is suitable, but none produce adults at relative humidities below 70-75%. Young adults remain in the soil for some time after emerging.

The pupal cell of S. hispidula is an oval earthen cell usually found within 3 inches of the surface (Marshall, 1934). The larva shapes the cell by turning its body and by using its mandibles. When the cell is shaped, a liquid is added from the mouth to the soil which aids in preventing the soil from crumbling. Two or three days are required for the construction of such a cell.

5.2 Length of Pupal Period

Species	Location	Length	Reference
S. crinitus	Israel	25 days	Melamed (1966b)
	Ukraine	9-13 days	Ulashkevich (1935)
S. hispidula	Illinois	16-22 days	Bigger (1930)
	Kansas	8-16 days	Marshall (1934)
	Israel	34 days	Melamed (1966b)
S. lineata	U.S.S.R.	8-11 days	Grossheim (1928)
	Britain	3 weeks	Jackson (1920)
	Israel	21 days	Melamed (1966b)
	Ukraine	9-13 days	Ulashkevich (1935)

6. DISCUSSION

6.1 Densities of S. humeralis

Allen's work at Cummins (1969) on densities was purely an estimation. If biological control is to be undertaken it will be necessary to test the effectiveness of this control. The best method would be to estimate population densities of the larvae. There is no reference in the literature to sampling populations to Sitona larvae. It will therefore be necessary to develop such a technique.

6.2 Bionomics

The comparison of life cycles of Sitona spp. will be important when considering the choice of parasites and sites for their collection. One important consideration is that Sitona aesitivates in South Australia and Israel, but hibernates in Northern Europe and North America.

It is also important to understand the bionomics of Sitona when evaluating the success of the biological control programme against S. cylindricollis in North America. McLeod

(1962) reported that the programme had limited success. The braconid wasp Microctonus aethiops (Ness) was initially released to control S. cylindricollis but was not successful. It was subsequently released in eastern and mid-west U.S.A. against Hypera pestica Fabr. which has been more successful (Day et al, 1971). A study of the bionomics of S. cylindricollis and H. postica. (Appendices IIE and IIG) suggests a reason for the differing success. With S. cylindricollis the overwintered adults are beginning to die out in mid-July and the new generation does not begin emergence till late July, with a peak in early August. With H. postica there is a definite overlap of generations. It is suggested that the generation overlap in S. cylindricollis is not sufficient to maintain the parasite, whereas in H. positica it is sufficient.

If biological control of S. humeralis is to be considered, it will be necessary to investigate the absence or extent of this overlap of generations.

6.3 Diapause

A knowledge of diapause in Sitona spp. is important because eggs and larvae cannot be produced all year round which restricts research. If diapause could be terminated prematurely then larvae could be studied continuously.

All that is known about diapause in Sitona is that

(i) Termination of diapause is synchronized with the host plant. (Rivnay et al 1959) This suggest that the presence of food or the presence of young food could have an effect on the maturation of the adult.

(ii) Termination of diapause in S. cylindricollis requires a period of exposure to low temperature (Davey 1956).

(iii) Temperature and food supply in spring and summer had no apparent effect on the occurrence of diapause in S. hispidula in Finland. (Rautapaa et al 1966).

6.4 Oviposition

It is important to know the ideal conditions for oviposition so larvae can be reared in the laboratory.

(i) Oviposition is affected by temperature. Optimum of 24.5°C for *S. lineata* in Germany (Andersen, 1935). Optimum of 18°C for *Sitona* spp. in Israel (Melamed, 1966b). If females are exposed to 11-12°C prior to oviposition then the rate of oviposition is decreased (Andersen, 1935).

(ii) Oviposition is affected by humidity and food with *S. lineata* most eggs are laid at 100% relative humidity when there is limited feeding, but when there is a continuous supply of food, most eggs are laid at 17-20% humidity (Andersen, 1934b).

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APPENDIX 1A - Distribution of various *Sitona* spp.

SPECIES	LOCATION	REFERENCES
S. crinitus	Ukraine	Grossheim (1928)
	England	Jackson (1922)
	Poland	Krasucki (1926)
	Israel	Melamed (1966b)
	Caucasus	"
	Turkestan	"
	Latvia	Ozols (1933)
	Poland	"
	Austria	Ripper (1937)
	U.S.S.R.	Ulashkevich (1935)
S. cylindricollis	Tashkent	Alimdzhanov (1941)
	Massachusetts	Brown (1940)
	New York	"
	New Brunswick	"
	Nova Scotia	"
	Manitoba	"
	Manitoba	Bird (1949)
	Nebraska	Calkins (1969)
	Minnesota	Ellingboe (1969)
	Manitoba	Heidwig et al (1961)
	Kansas	Lilly (1952)
	Iowa	"
	Israel	Melamed (1966b)
	Ontario	Munro (1949)
	Vermont	"
	Vermont	"
	Connecticut	"
	Maryland	"
	Indiana	"
	Ohio	"
	Illinois	"
	Michigan	"
	Wisconisn	"
	Minnesota	"
	Iowa	"
	Missouri	"
	N. Dakota	"
	S. Dakota	"
	Nebraska	"
	Montana	"
	Indiana	Wilson (1951)

SPECIES	LOCATION	REFERENCE
S. flavescens Marsh	Ukraine	Grossheim (1928)
	England	Jackson (1920)
	U.S.A.	Sankaran (1970)
S. hispidula	W. Siberia	Allard (1864)
	Illinois	Bigger (1930)
	New York State	Forsythe et al. (1962)
	Bulgaria	Grigorov (1956)
	Ukraine	Grossheim (1928)
	W. Virginia	Hansen et al. (1957)
	Ontario	Hudson (1925)
	Britain	Jackson (1920)
	Wales	Jenkins (1926)
	New Hampshire	Kilpatrick (1961)
	New Jersey	Lau et al (1960)
	Oregon	Leach et al (1963)
	Sweden	Loan et al (1961a)
	Nebraska	Manglitz et al (1963)
	Kansas	Marshall (1934)
	Finland	Markkula (1959)
	Israel	Melamed (1966b)
	Oregon	Newton (1958)
	Michigan	Pettit (1918)
	Oregon	Rockwood (1926)
	Virginia	Underhill et al (1955)
	California	Van Dyke (1917)
	Denmark	Wagn (1954)
	Idaho	Walters (1964)
	Maryland	Webster (1915)
	Pennsylvania	"
	Caucausus	Winkler (1924-32)
	Syria	"
S. humeralis	Tashkent	Alimdzhanov (1941)
	South Australia	Allen (1971)
	N.S.W., Aust.	Anon (1967)
	Vic., Aust.	Anon (1970)
	Southern England	Edwards et al (1964)
	Italy	Grandi (1918)
	Mleev, Ukraine	Grossheim (1928)
		Hannotiaux (1965)
	Britain	Jackson (1920)
	France	Loan et al (1961a)
	Sweden	Loan et al (1961b)

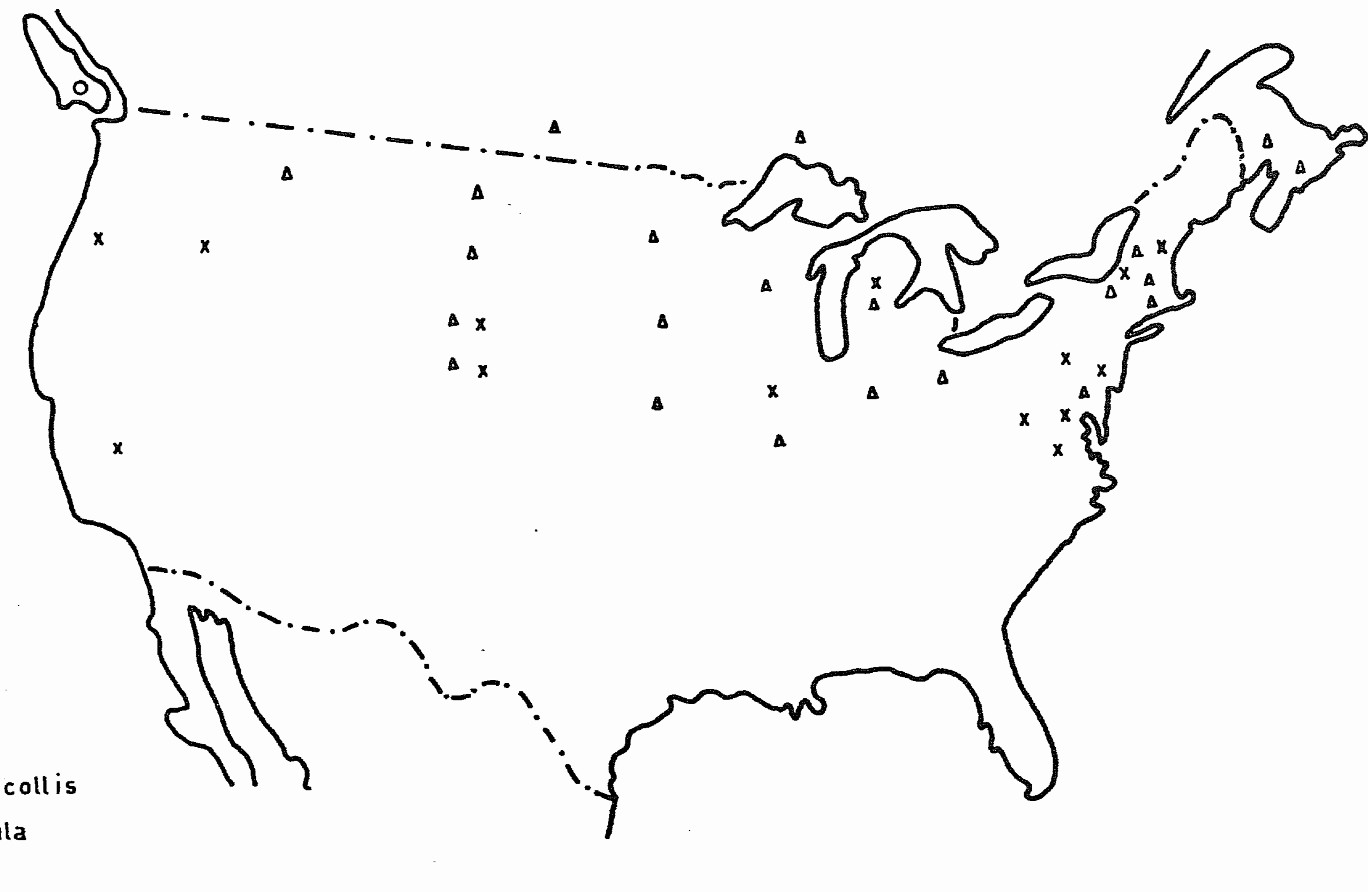
SPECIES	LOCATION	REFERENCE
S. humeralis (Contd.)	Italy	Menozzi (1930)
	Austria	Ripper (1937)
	Yugoslavia	Tansijevic (1959)
	Germany	Urban (1923)
	Stavropal	Uvarov (1914)
	Europe	Van Emden (1939)
	Mediterranean	"
	Central Asia	"
	N. America	"
	Denmark	Wagn (1954)
	Central Asia	Yakhontov (1935)
S. lineata	Tashkent	Alimdzhanov (1941)
	Bavária	Andersen (1931a)
	Latvia	Anon (1924)
	Moscow	Baranov (1914)
	Bulgaria	Chorbadzhiev (1928)
	Leningrad	Dobrodeev (1915)
	Vancouver	Downes (1938)
	Holland	Franssen (1955)
	Central England	George (1962)
	Mleev, Ukraine	Grossheim (1928)
	Britain	Jackson (1920)
	Wales	Jenkins (1926)
	Stokholm	Kemner (1918)
	Yugoslavia	Kovacevic (1929)
	S.E. Poland	Krasucki (1926)
	Sweden	Loan et al (1961a)
	France	Marchal (1920)
	Finland	Markkula et al (1960)
	Switzerland	Meier (1961)
	Israel	Melamed (1966a)
	Orel, U.S.S.R.	Mizerova (1916)
	Czechoslovakia	Obrtel (1962)
	Latvia	Ozols (1933)
	Cyprus	Papachrysostomou (1926)
	Finland	Rautapaa et al (1966)
	Austria	Ripper (1937)
	Norway	Schoyen (1919)
	Tula, U.S.S.R.	Sopotzko (1916)
	Vinnitzia, U.S.S.R.	Ulashkevich (1935)
	Kiev, U.S.S.R.	Vassiliev (1913)

SPECIES	LOCATION	REFERENCE
S. lineata (Contd.)	Denmark	Wagn (1954)
	Stuttgart	Wahl et al (1914)
	San Juan Archiphelago	Winkler (1924-32)
S. lividipes	Sardinia	Anon (1924)
	Corsica	"
	North Africa	"
	Syria	"
	Israel	Melamed (1966b)

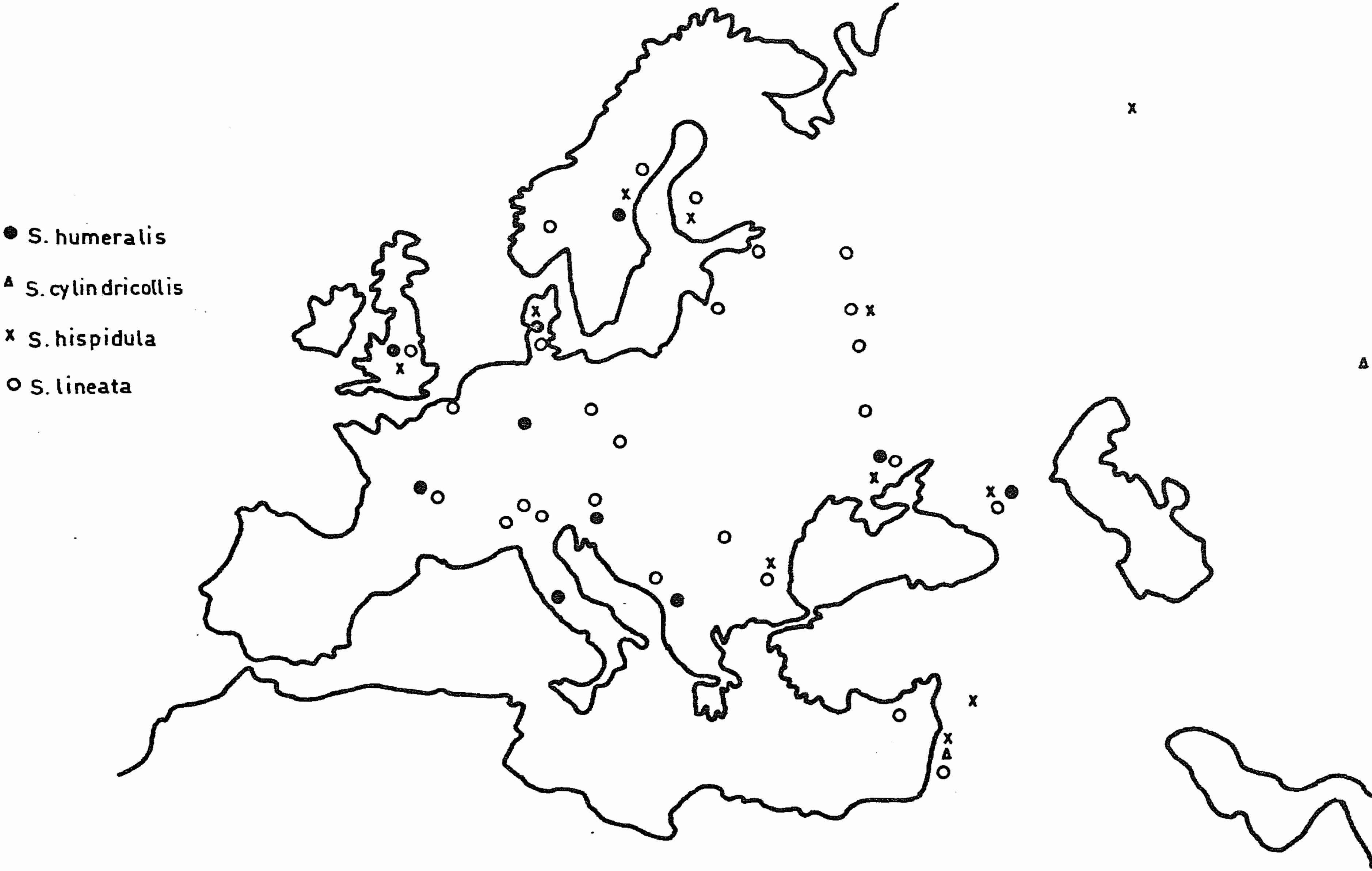
Other species mentioned:

Grossheim (1928):	S. inops Gyll. S. callosa Gyll., S. sulcifrons Thnb S. longula Gyll. (Ukraine)
Jackson (1920):	S. punticollis Steph., S. sulcifrons Thnb. (Britain)
Loan (1963):	S. scissifrons Say (Ontario)
Markkula (1960):	S. sulcifrons Thnb, S. decipiens Lindeberg (Finland)
Malamed-Madjar (1966a):	S. limosus Rossi, S. concavirostris Hch, S. gressorius F, S. ocellatus Kust. S. stierlini Rett S. intermedius Kust. (Israel)
Rockwood (1926):	S. tibualis Herbst (Oregon)
Yakhontov (1935):	S. callosa, S. longula (Central Asia)

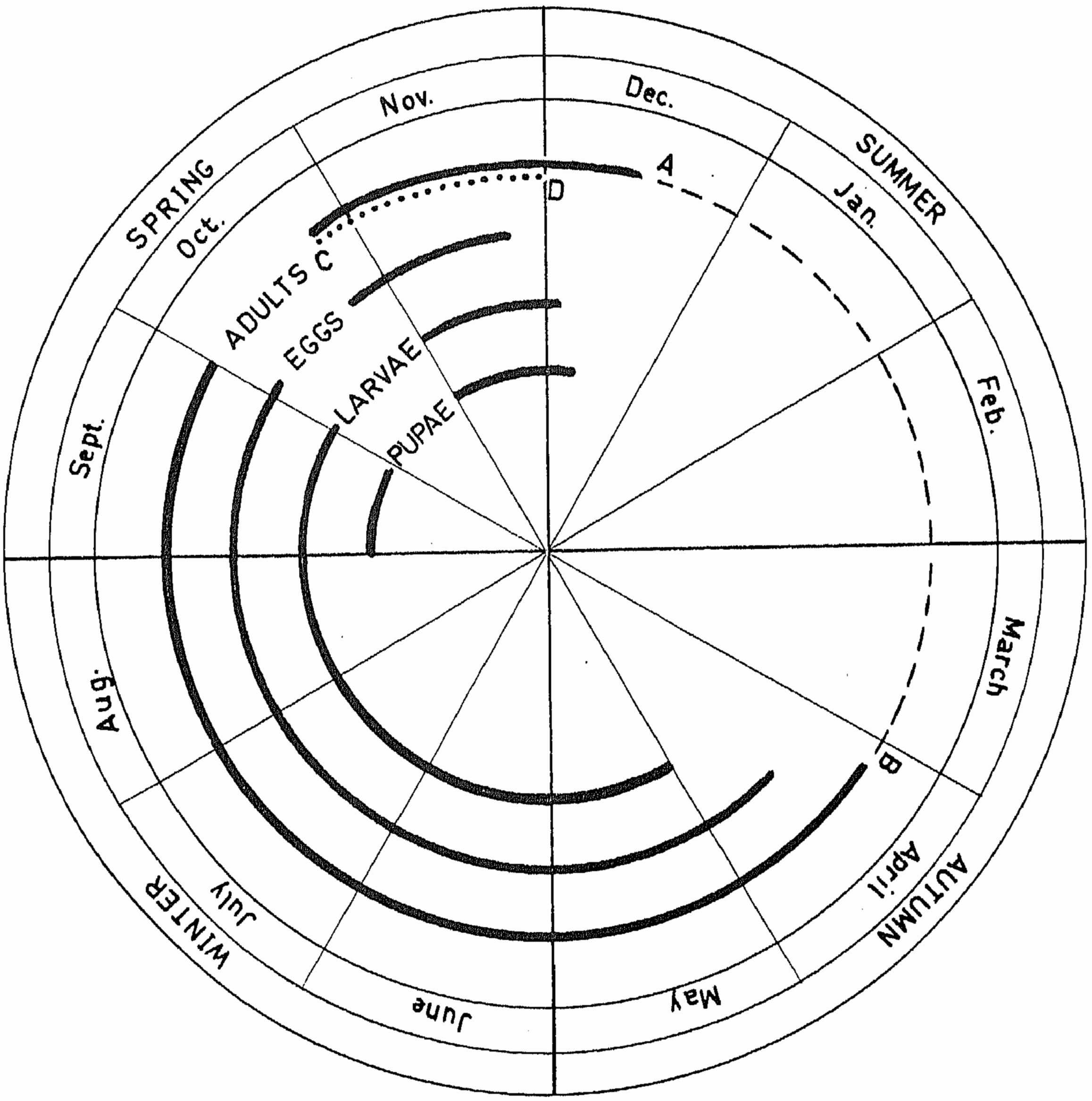
APPENDIX 1B - Distribution of common Sitona spp. in North America



APPENDIX 1C - Distribution of common *Sitona spp.* in Europe.



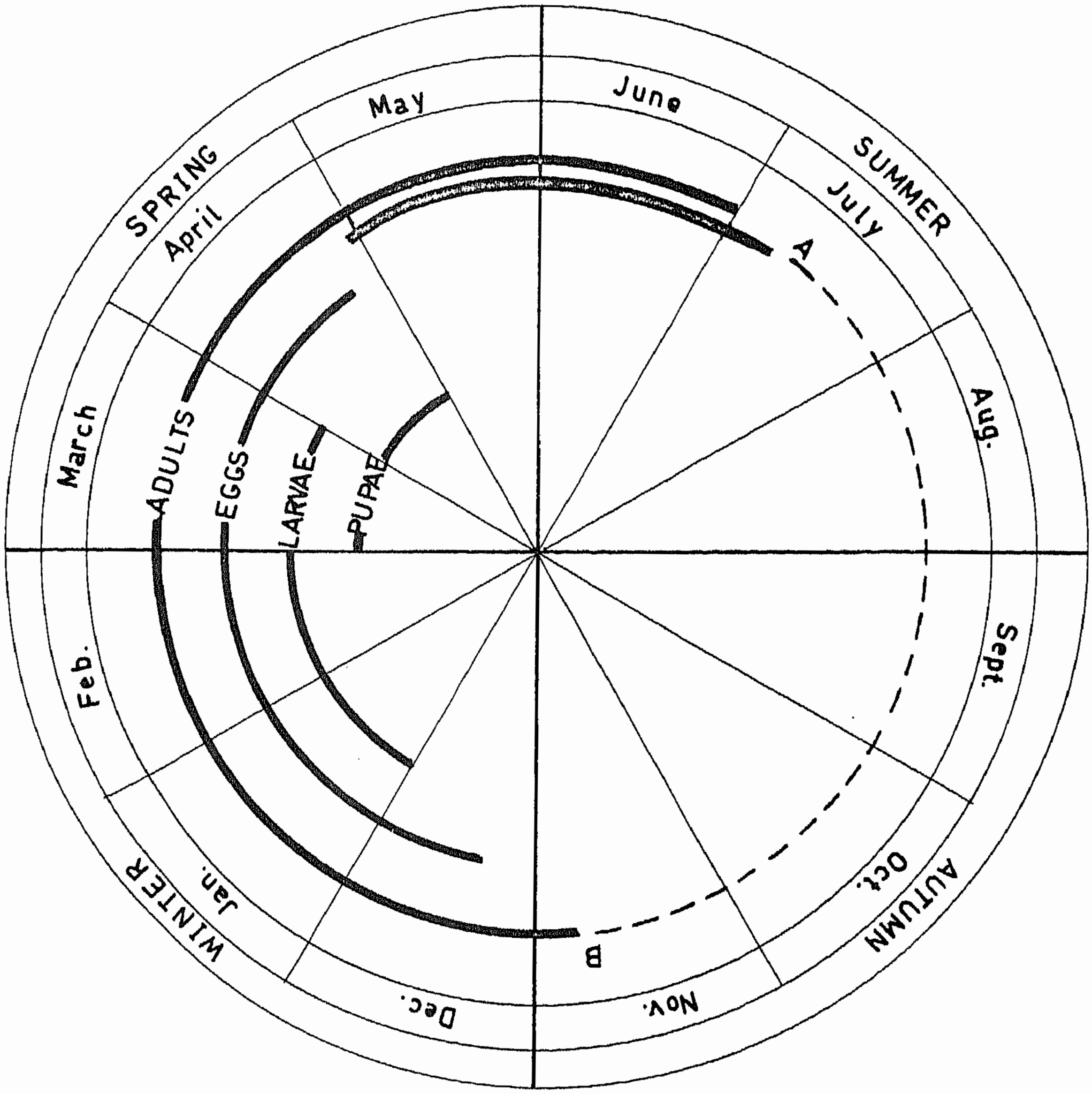
APPENDIX 2A - Seasonal life history of *S. humeralis* in South Australia



A— — —B: Adults in diapause

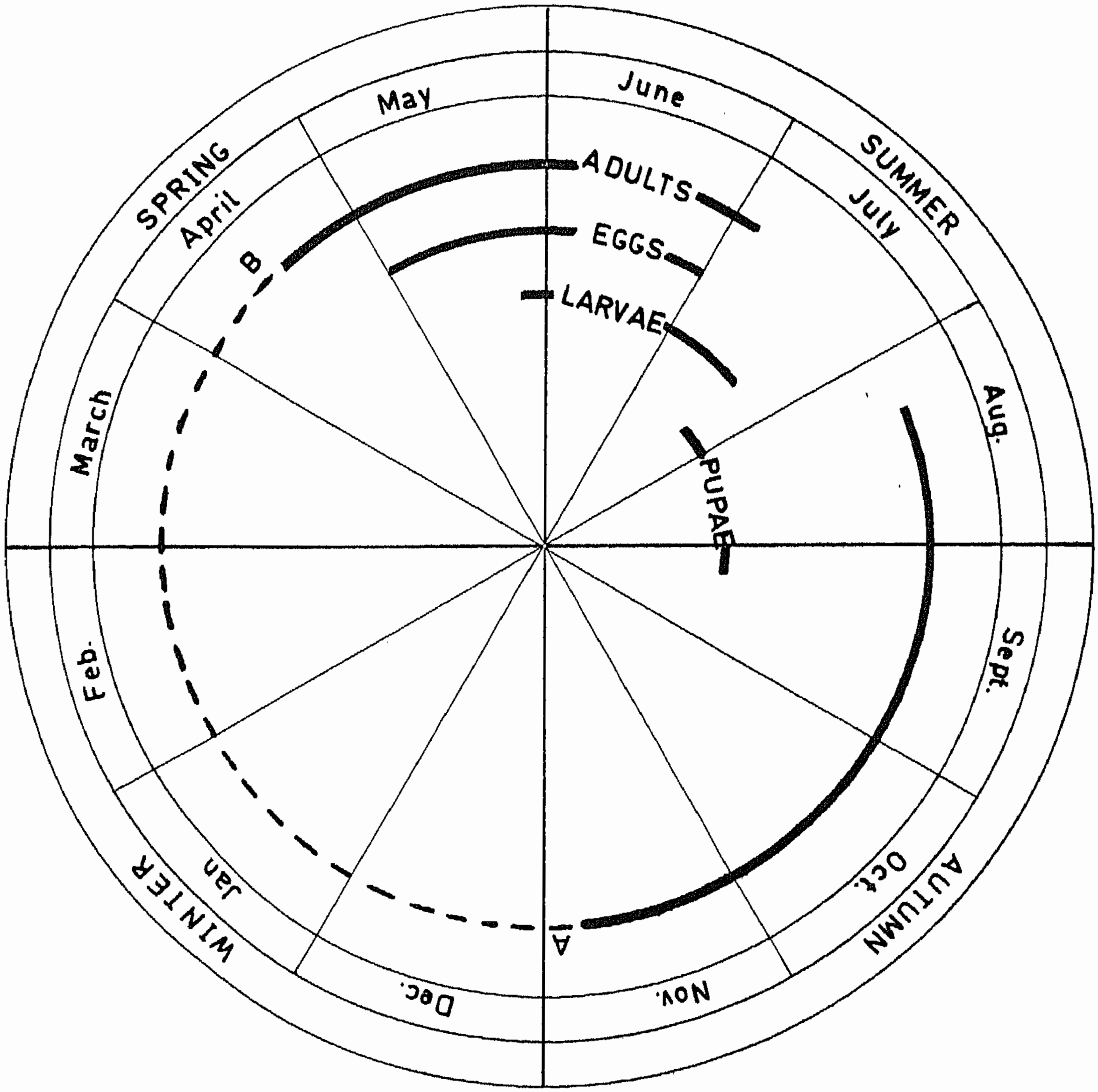
C······D: Adults in very low frequencies

APPENDIX 2B - Seasonal life history of *S. lineata* in Israel.



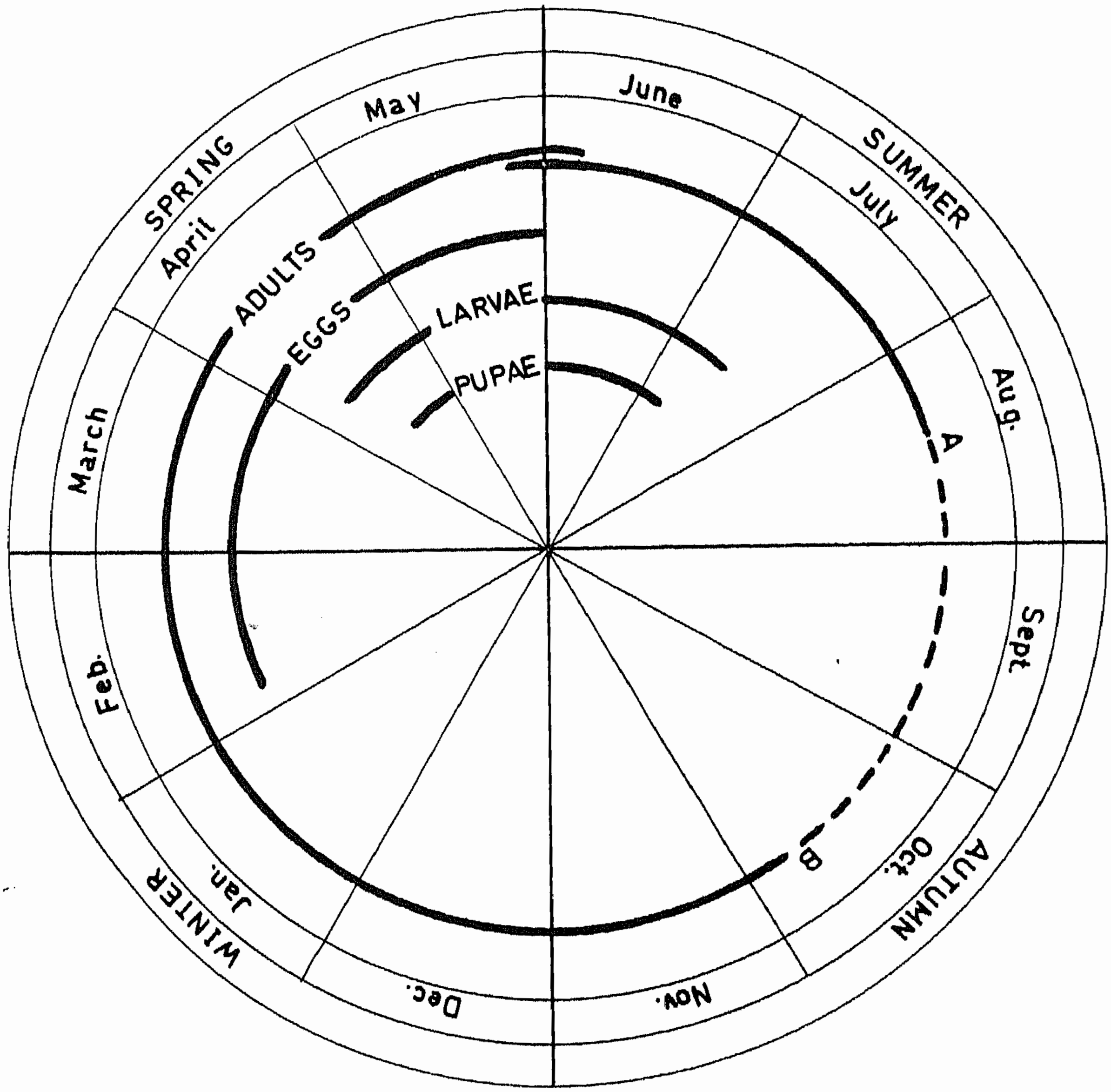
A---B: Adults in diapause

APPENDIX 2C - Seasonal life history of <u>S. lineata</u> in England.



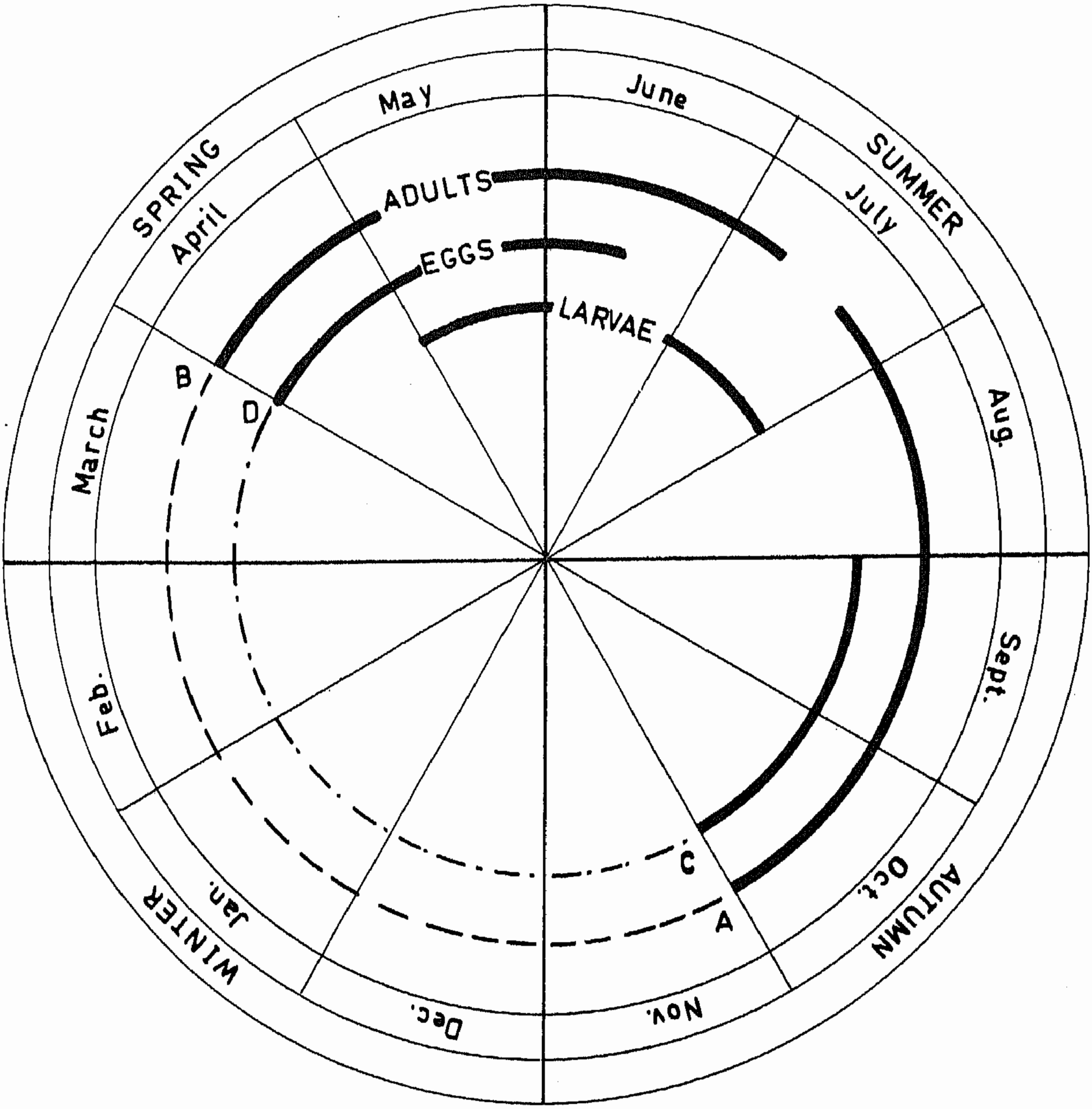
A – – – B = Adults in diapause over winter

APPENDIX 2D - Seasonal life history of *S. lineata* in the Pacific North West of North America.



A— — —B = Adults aestivating

APPENDIX 2E - Seasonal life history of <u>S.hispidula</u> in Britain.

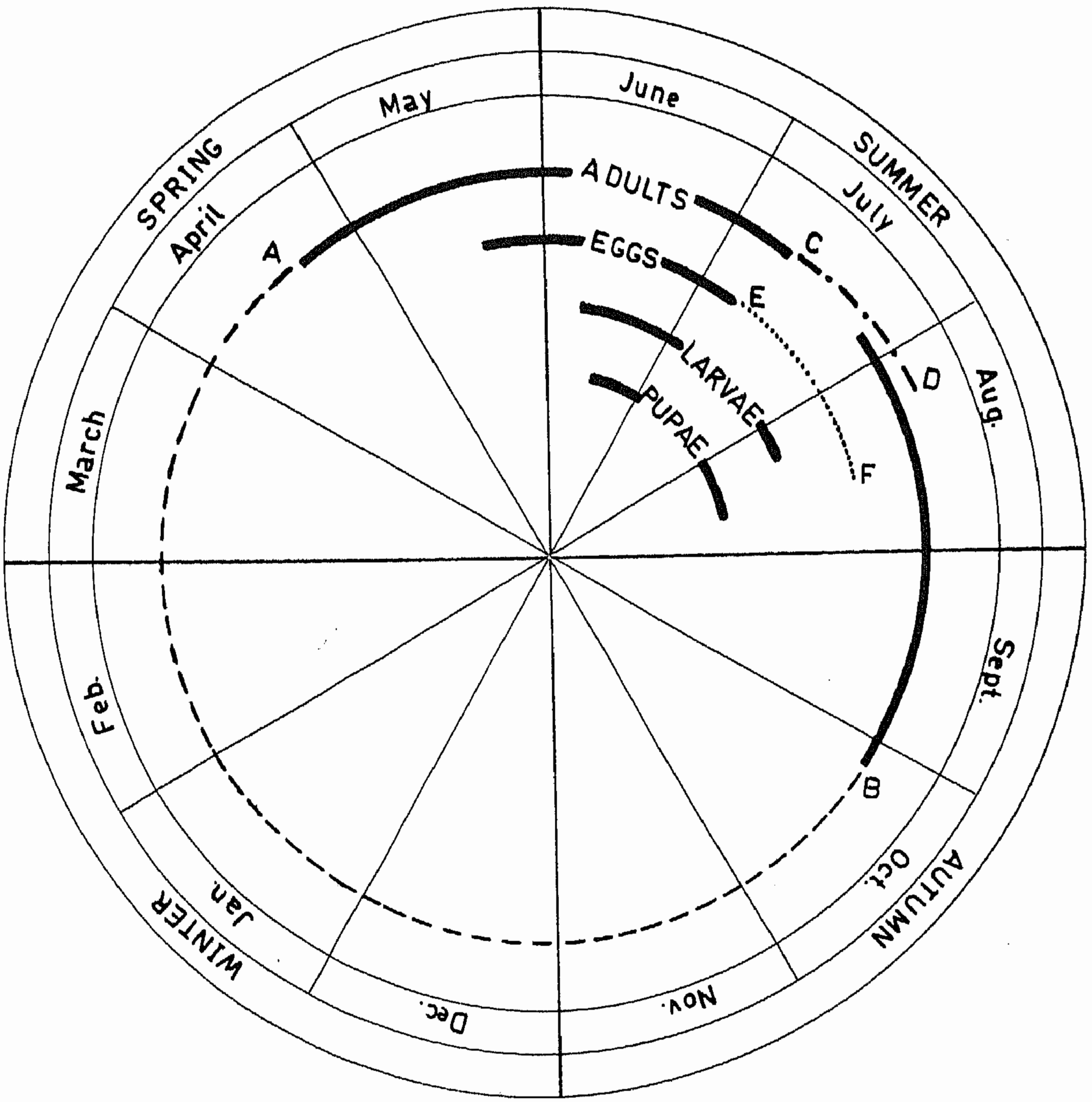


PUPAE NOT KNOWN

A — —B = Adults over winter

C —·—·D = Autumn laid eggs over winter

APPENDIX 2F - Seasonal life history of <u>S. cylindricollis</u> in Canada.

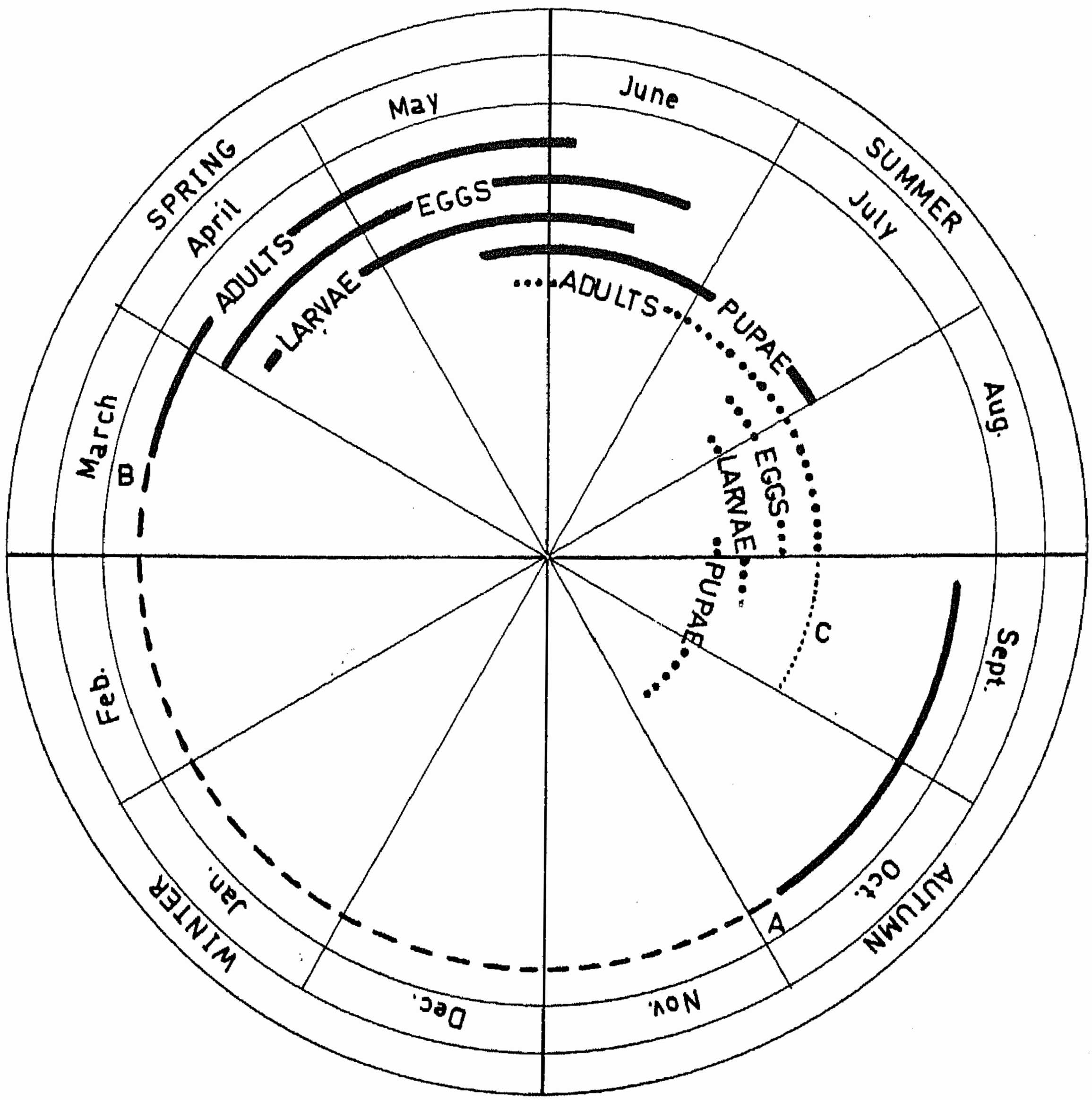


A — — — B = Adults in hibernation

C — · — · — D = Adults dying of old age

E · · · · · · · F = Eggs dessicated and do not form larvae which mature.

APPENDIX 2G - Seasonal life history of *S. cylindricollis* in Uzbekistan U.S.S.R.



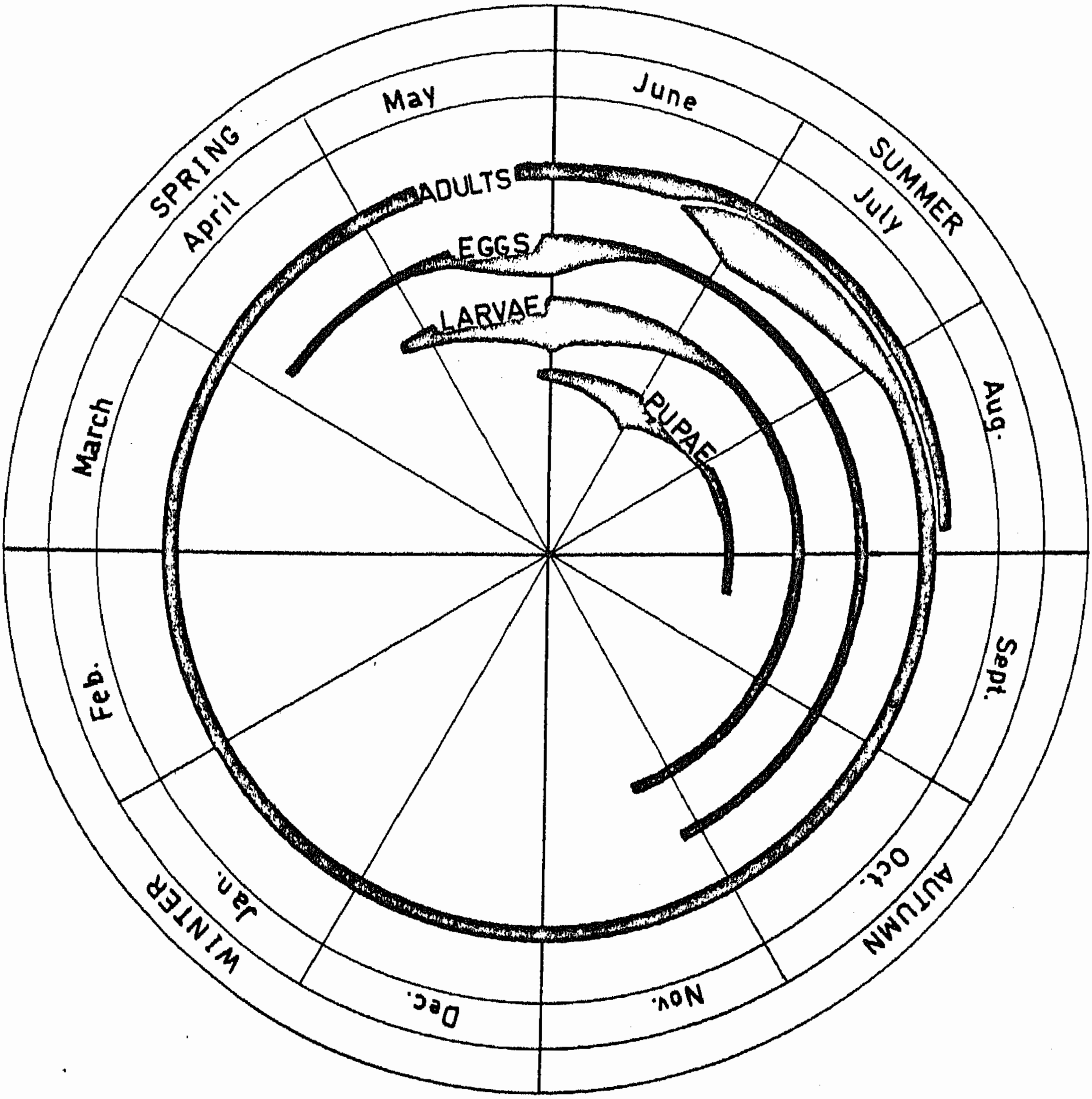
A– – –B= Adults in hibernation

C·······= Not known when adults die

▬▬▬ First generation

•••••• Second generation

APPENDIX 2H - Seasonal life history of *Hypera postica* in Colorado *



* From Metcalf and Flint (1962)