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Age, sexual development, and seasonal occurrence of the pine weevil *Hylobius abietis* (L.)

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Abstract

Age composition, seasonal occurrence, sexual development and flight muscle condition were investigated in populations of *Hylobius abiets* collected on a clear-cut area during three consecutive years after cutting. Weevils that had been reproductive during any previous season were classified as old and distinguished from young weevils based on the degree of elytral scale wear. Collections were made from late April until early October. Weevils developed their flight muscles before reaching sexual maturity. The proportion of young and old weevils with well-developed flight muscles was already high by the beginning of May. None of the examined young weevils emerging during autumn had well-developed flight muscles or mature reproductive organs. A large proportion of the weevils arriving at the fresh clear-cutting overwintered and remained there throughout the following season. It is concluded that they also oviposited again in the stumps, giving rise to a new generation emerging during autumn of the third season and spring of the fourth season after cutting.

1 Introduction

The pine weevil *Hylobius abietis* (L.) is attracted to fresh conifer clear-cuttings by odours emanating from cut timber, stumps and slash. Fresh stumps and their roots constitute the most important source of breeding material. The predominant features of the life cycle in southern and central Sweden have been described by EIDMANN (1974): "The flight period occurs during a several week period around late May-early June. Oviposition begins after flight period, around mid-June, and continues until early August."

The larvae overwinter in stumps and pupate between mid-June and late July of the following year. Some of the newly emerged weevils creep up to the soil surface between the end of July and late September the same year. After feeding, these weevils then overwinter in the ground. The other new-generation adults remain in their pupal chamber and do not emerge to the ground surface until spring of the third year, when the other weevils that had overwintered in the litter also appear on the surface again. The new generation then leaves the clear-cutting during the flight period. Parent weevils hibernate in the ground and may oviposit again the following year. It is uncertain whether the parent weevils after hibernation stay on the breeding area or leave it.

Pine weevils can live for several years; experiments in outdoor cages have shown that they can survive up to three winters (CANCOV 1970). MUNROE (1914), BUTOVITSCH (1928), SCHWECHTEN (1933), CHRISTIANSEN (1971) and LÅNGSTRÖM (1982) all used the presence of the *corpus luteum* to document that old females can be present early in the season on breeding areas of different ages. They also noted that the scales on old weevils were highly worn.

LÅNGSTRÖM (1982) used the condition of the elytral scales to estimate age. He recognized three weevil age classes: young weevils, having intact scales; intermediate weevils, having slightly worn scales; and old weevils, having very worn scales.

Several studies have been made on sexual development in pine weevils (e.g. MUNROE 1914); however, none has distinguished the phases of sexual development between the

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different generations that occur simultaneously in the field. SOLBRECK (1980) studied the flight capacity of the weevils in the laboratory during the flight period, but no investigations of the flight muscle development have been reported earlier.

The main goals of the present study were to investigate age composition, sexual development, seasonal occurrence and flight muscle development in populations of pine weevils on clear-cut areas during several years after cutting.

2 Material and methods

2.1 Collection of weevils

The investigation was made on two mixed-conifer clear-cuttings about 20 km east of Uppsala, Sweden. One was a freshly cut area (1983), while the other was studied during three successive growing seasons (1983 to 1985); one (A + 1), two (A + 2) and three (A + 3) years after cutting. The age of the clear-cutting areas is given according to the definitions used earlier by BEJER-PETERSEN et al. (1962). The growing season immediately following cutting, when fresh breeding substrate is available, is called year A.

Freshly cut and split billets of Scots pine, *Pinus sylvestris* (L.), (40 cm long, 20 cm diam) were used to attract weevils. The method has previously been used in attempts to estimate pine weevil populations (BUTOVITSCH 1931; SWAINE 1951; EIDMANN 1968; SZMIDT 1981; LÅNGSTRÖM 1982). Six rows of five billets each were laid out with 3 m between billets in a row. Weevils were collected at least once a week from late April until early October. Freshly cut billets were added to already existing piles of billets once every 14 days. The length of the main flight period was estimated by periodic inspection of an attractive pile of sawdust at a nearby sawmill.

To determine how late weevils continue to emerge from their subterranean overwintering sites during spring, the number of weevils caught weekly in tents placed over stumps of Norway spruce, *Picea abies* (Karst.), was estimated on the A + 2 site. The tents, described by LINDELÖW and WESLIEN (1986), were in place from late May until the end of June.

2.2 Oviposition in old roots

In a small laboratory experiment, the ability of weevils to breed in old roots was investigated. Roots were collected on 1 June and frozen (−20 °C) for one week prior to the test in order to kill any eggs or larvae already present in the roots. Ten weevils of each sex were then introduced into each of two sawdust-filled boxes, one containing a section of A + 2 root and the other containing a section of A + 3 root (roots were 50 cm long, and 5 cm in diam). After a week these parent weevils were removed. The experiment at constant temperature 20 °C was begun during the second week of June and was terminated after the new generation started emerging, about 7 months later.

2.3 Age determination by scale condition

In a pilot study prior to this investigation, in which collections of weevils on an A + 2 year old clear-cutting were made, the methods described below were developed and tested (NORDENHEM, unpubl.). The results showed that young weevils emerging in spring and in autumn could easily be recognized by their small and undeveloped reproductive organs and the excellent condition of their scales. An important character proved to be the colour of the scales (see below). There was a high degree of correspondence between age determinations using scale characters and those based on reproductive organ features. However, there were some cases of uncertainty during season A after oviposition had started. These cases were determined based on scale condition alone.

In the present study a weevil is classified as old if it had reached reproductive maturity during any previous season. Using a modification of the age determination method described by LÅNGSTRÖM (1982), weevils were divided into two age groups before dissection: old weevils with whitish scales, more or less worn, and young weevils with yellow-brownish scales, with little or no wear.

2.4 Dissection

Each time weevils were collected on the billets, random samples of 60 males and 60 females of each age class were dissected. When fewer weevils were caught, all were dissected. During dissections, the phase of sexual development and the condition of the flight muscles were determined. A stereomicroscope (16× magnification) was used to make these observations.

2.5 Sexual development in females

The phase of sexual development of each female (according to CHRISTIANSEN 1971 and LÅNGSTRÖM 1982), i.e. prereproductive, reproductive or postreproductive, was determined by examining the sexual organs at dissection (fig. 1).

1. Prereproductive phase: In young females, ovaries vary from small and undeveloped to larger with more or less developed eggs. Old females have relatively large ovaries without eggs or with more or less developed eggs. Young and old females have no eggs in the common oviduct. The *corpus luteum (cl)* is absent in young females, whereas old females have a dark *cl.*
2. Reproductive phase: In young and old females, the ovaries are large, and eggs are present in the common oviduct. In young females, the *cl* gradually darkens after oviposition has begun. Old females have a dark *cl.*
3. Postreproductive phase: Both young and old weevils have large ovaries. A few eggs can be present, although not in the common oviduct. The *cl* is dark in both young and old females.

2.6 Sexual development in males

Prereproductive young males have small, whitish testes (fig. 1). In the reproductive phase the testes are large, and the center gradually darkens as the season progresses. Postreproductive young males have large testes with a brownish center. The testes of old males, initially are large and have a brownish center; they do not change noticeably during the season. In this study males were classified as having either: 1. small undeveloped testes or 2. large well-developed testes.

2.7 Flight muscle condition

The flight muscles were also examined at dissection and broadly classified as follows:

1. Undeveloped: white muscle cell mass of variable size, no fibers visible.
2. Well developed: fibers large and rose-coloured with no space between them, firmly attached to skeleton.
3. Reduced: small, thin, whitish fibers, clearly separated from each other and weakly attached to skeleton.

3 Results

3.1 Seasonal occurrence of weevils

Weevils were found on billets from late April to early October (fig. 2). In spring, young and old weevils appeared at about the same time, but after mid-September only young, recently emerged adults were found (fig. 2). During spring A+2, weevil emergence occurred throughout May and June, as observed using tents placed over stumps.

The fresh clear-cutting (A) was invaded by both young and old weevils. In contrast, during the earlier part of year A+1 all weevils found at the billets were old. During autumn A+1 newly emerged young weevils were found at the billets (table).

The numbers of young weevils found during years A+2 and A+3 were dramatically reduced after the main flight period, before the new emergence in autumn (table). No such reduction after the main flight period was found for old weevils during year A+1.

Young newly emerged weevils were found during autumn of years A+1, A+2 and A+3, with the largest numbers occurring during A+1 and A+2 (fig. 2, table).

3.2 Oviposition in old roots

Breeding studies on old roots revealed that weevils can even develop in material from seasons A+2 and A+3. Two individuals emerged from A+2 root, and one emerged from A+3 root, 7 months after removing the parent animals. The numerous old, empty larval galleries present showed that the roots had been heavily occupied during previous seasons.

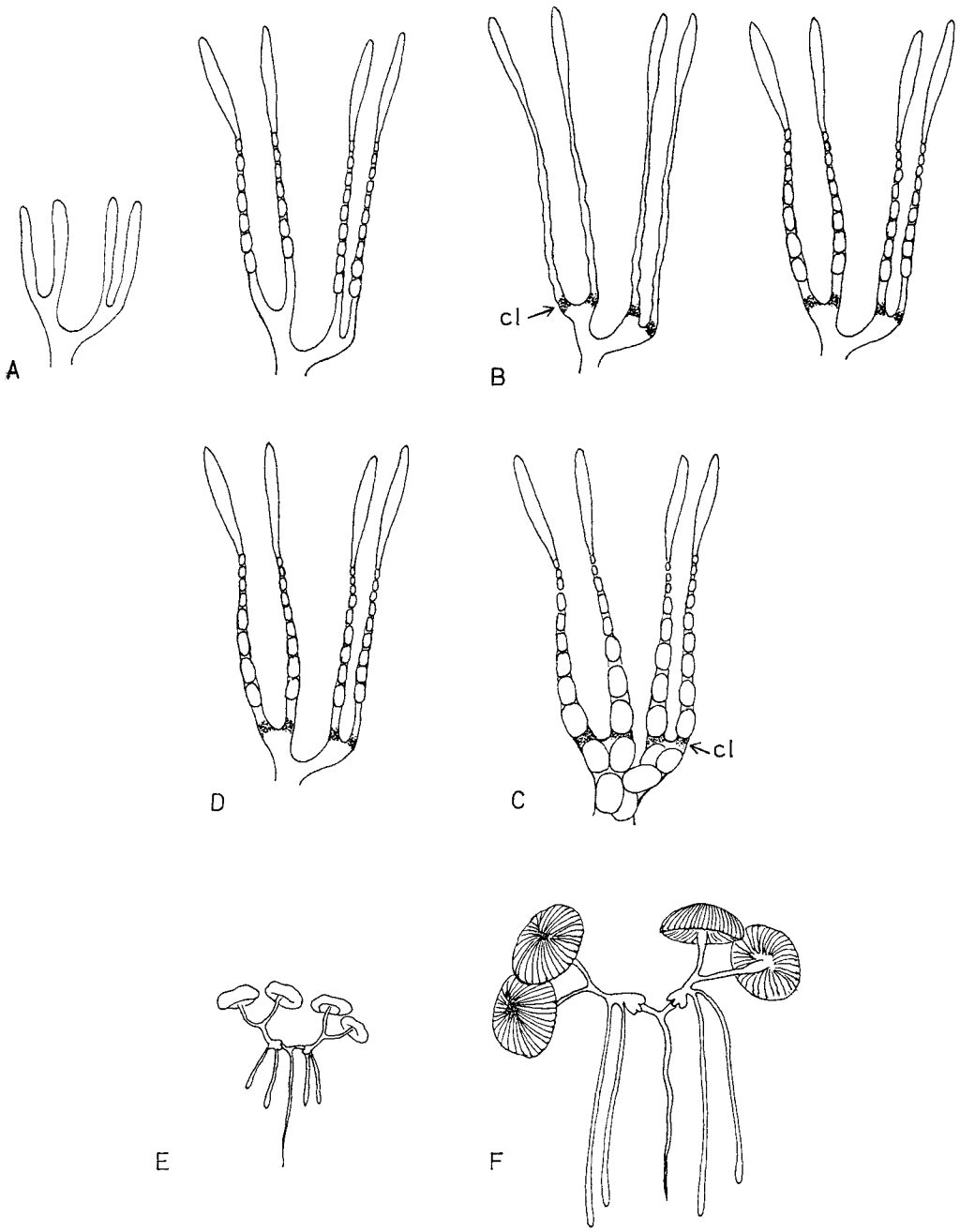

Fig. 1. Developmental phases in *H. abietis*. A–D: ovaries; E–F: testes; A: Prereproductive, young females; B: Prereproductive, old females; C: Reproductive, young and old females; D: Postreproductive, young and old females; E: Prereproductive (undeveloped) males; F: Reproductive (well-developed) males. *cl* = *corpus luteum*

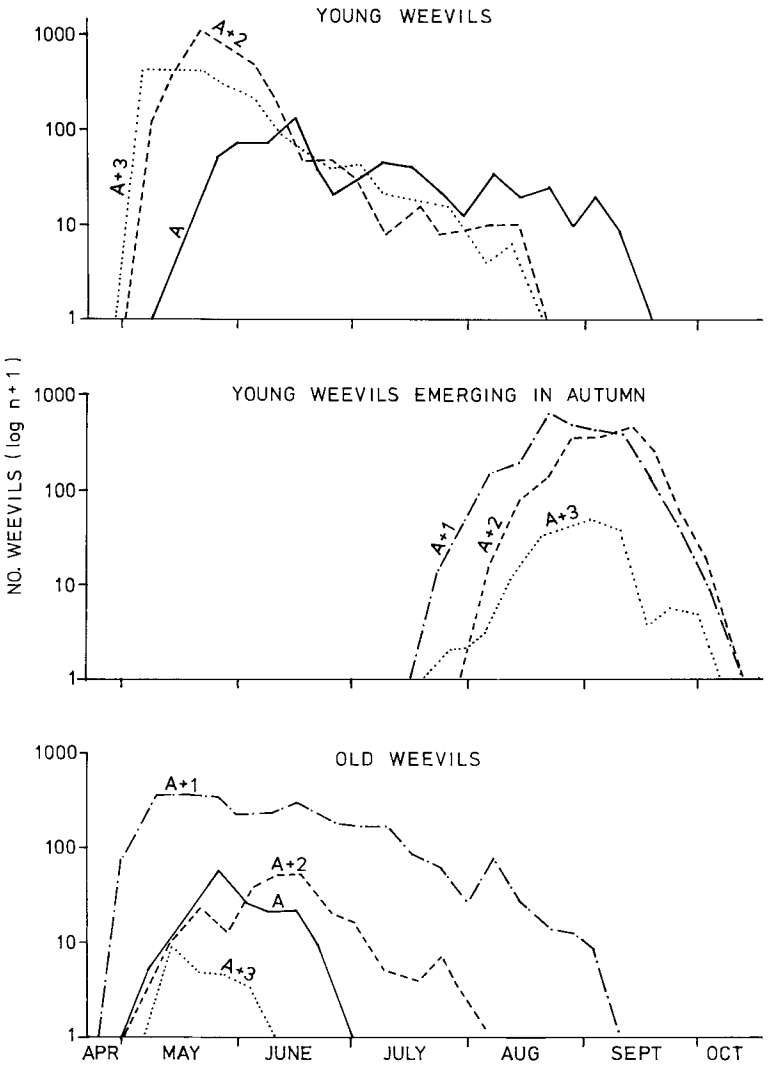

Fig. 2. Seasonal variation in numbers of *H. abietis* caught on pine billets

3.3 Reproductive development

Nearly all of the young females captured during seasons A + 2 and A + 3 from late April until the end of June were prereproductive (fig. 3). Most of these individuals were in an early prereproductive stage, i.e. egg differentiation had barely begun. Old females collected during the same period of year A + 1 were almost all reproductive.

The reproductive phase in old as well as young females generally lasted until early or mid-August (fig. 3). Young males appeared to reach reproductive maturity sooner than females. Young males already had well-developed testes by early May. The testes of males, that had been reproductively active the previous year were classified as well-developed throughout the season.

Numbers of weevils caught at billets before and after the main flight period during the first season after cutting and each of the three years thereafter, for old and young weevils of each sex

Year	Sex	Old weevils			Young weevils			Young weevils emerging during autumn
		Before	After	Total	Before	After	Total	
A	males	41	36	77	54	302	356	0
	females	60	43	103	27	281	308	0
	total	101	79	180	81	583	664	0
A+1	males	666	825	1491	0	4	4	1476
	females	498	815	1313	0	6	6	1117
	total	1164	1640	2804	0	10	10	2593
A+2	males	47	48	95	1746	135	1881	892
	females	56	38	94	1443	66	1509	757
	total	103	86	189	3189	201	3390	1649
A+3	males	11	1	12	1105	85	1190	105
	females	14	3	17	875	67	942	93
	total	25	4	29	1980	152	2132	198

None of the examined young weevils emerging from the soil during autumn had mature sexual organs.

3.4 Flight muscle condition

The proportion of male and female weevils with well-developed flight muscles was already high by the beginning of May (fig. 3). Among the young weevils collected years A + 2 and A + 3, the proportion with well-developed flight muscles increased steadily until the end of June, whereas this proportion steadily decreased in old weevils (A + 1) during the same period. After the flight period the proportion of weevils with well-developed flight muscles decreased rapidly.

Muscle degeneration appeared to proceed more rapidly in females than in males. Many of the older weevils seemed to lack flight muscles, i.e. no fibers or undifferentiated muscle cell mass was visible.

Flight muscle development was completed before reaching sexual maturity. Prior to the beginning of July, all young weevils collected during years A + 2 and A + 3 that were found to be reproductive also had well developed flight muscles (fig. 3). Flight muscle development in young weevils emerging from the ground during autumn was still incomplete at the onset of winter.

4 Discussion

GUSLITZ (1969) estimated the time for newly emerged females to reach reproductive maturity during spring, to two weeks. He also mentioned that females that had oviposited during the previous season began oviposition earlier than newly emerged females. Results of the present study suggest that the period for reaching reproductive maturity is around 2–3 weeks in populations of young weevils and slightly shorter in populations of older weevils.

Based on the proportion of sexually mature and immature weevils collected during A + 1 and A + 2, one gains the impression that old females reach sexual maturity sooner than young ones (fig. 3). This may, however, be largely due to the fact that the old weevils emerge from the ground during a short period probably owing to their tendency to hibernate in the uppermost layer of the mineral soil (v. OPPEN 1885; SCHWECHTEN 1933). Young weevils have a more extended period of appearance, from late April until the end of June, because a large proportion may overwinter as adults in their pupal chambers. Most

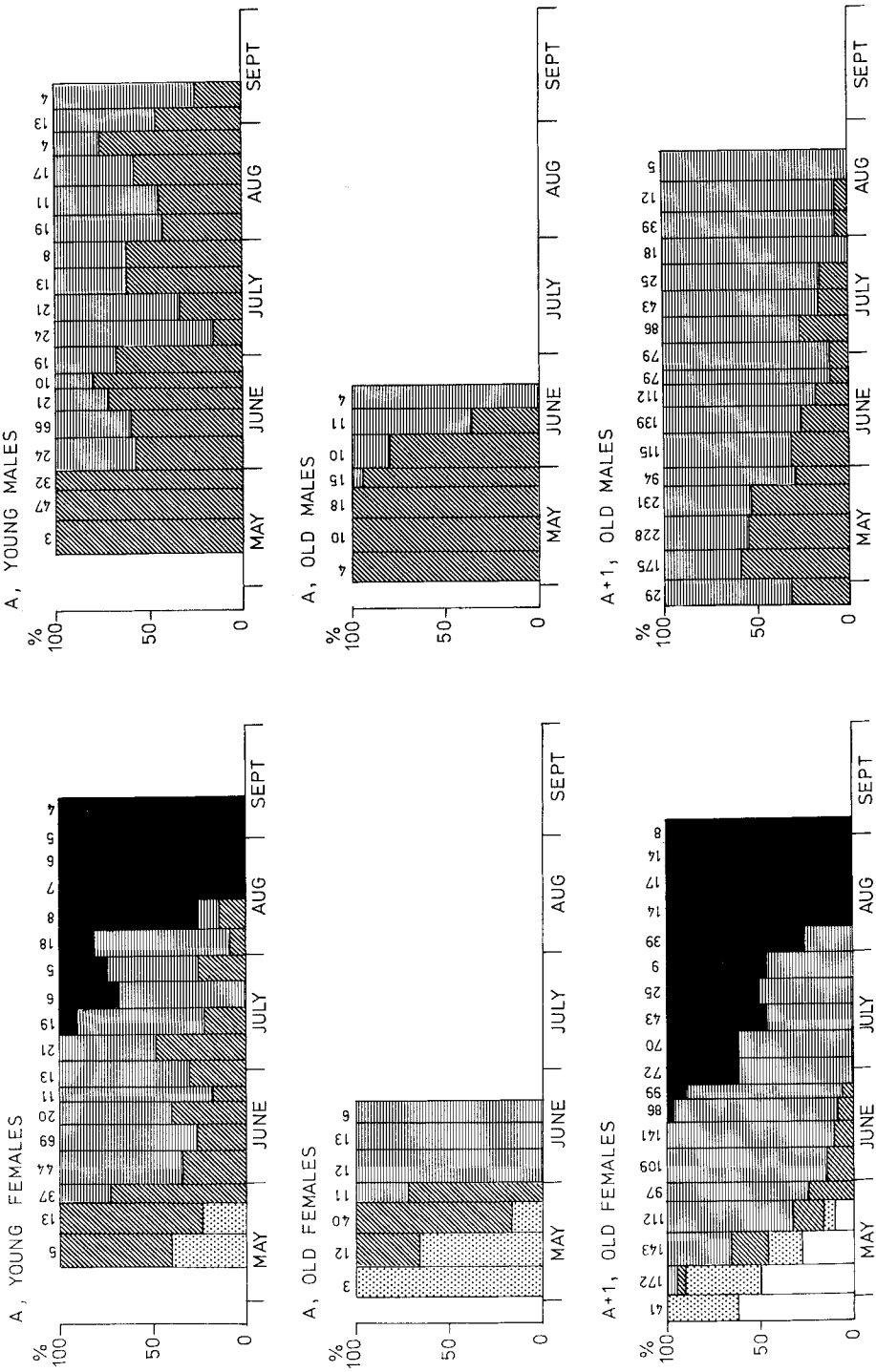

Fig. 3. Sexual maturity and flight muscle development in pine weevils during 3 consecutive years after cutting (years A to A + 3). Numbers above columns indicate catches. Catch periods yielding 4 weevils or less are excluded. For legend see opposite page

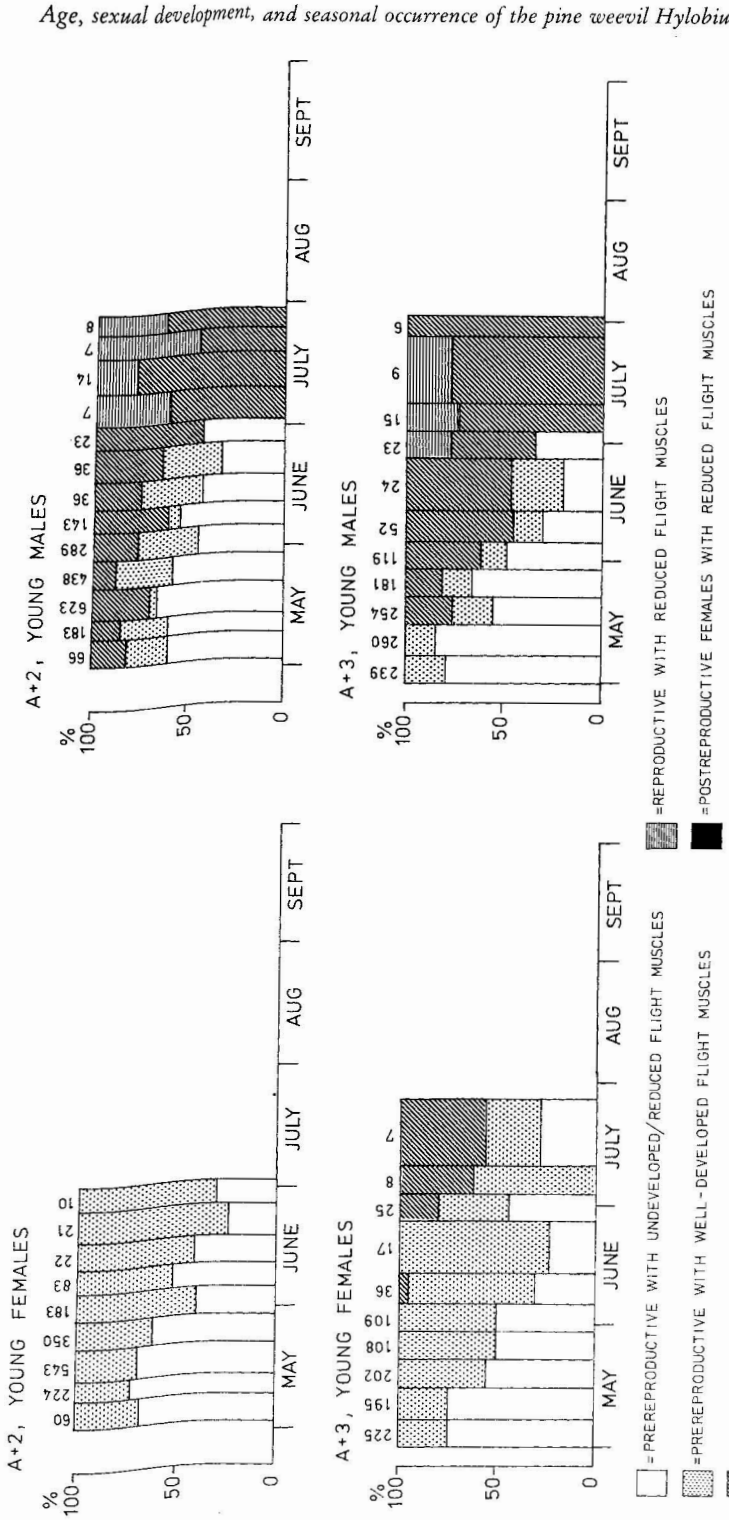

Fig. 3. (continued)

young females left the clear-cutting before having reached reproductive maturity. Many of the old weevils do not seem to develop flight muscles; thus they remain on the clear-cutting. Consequently, weevils with immature reproductive organs can be found throughout the spring.

The number of weevils captured after the flight period on clear-cuttings during seasons A + 2 and A + 3 was very low compared with the numbers captured during the corresponding period in seasons A and A + 1. These results suggest that 1. most young weevils left the area, 2. only a few old weevils survived until A + 2 and A + 3.

Nearly all young females collected during years A + 2 and A + 3 were in their prereproductive phase, whereas almost all of the females collected from the fresh clear-cutting and from sawdust piles during the flight period were reproductively mature. Thus egg development appeared to proceed very rapidly, during or just after the individual weevil's flight period.

Males dominated the catch on the fresh clear-cutting early in the flight period (fig. 3). EIDMANN (1974), GYLDBERG and THORELL (1978), and SOLBRECK and GYLDBERG (1979) reported similar observations on fresh sawdust piles. Except for the young weevils emerging during autumn, only 10 out of 2814 weevils captured during season A + 1 were young. This confirms the general opinion (e.g. EIDMANN 1974) that clear-cuttings more than one year old usually are not particularly attractive to migrating weevils. It can thus be assumed that the large number of old weevils found on the clear-cutting during A + 1 had arrived the previous year and overwintered. Old animals were also found on the same clear-cutting during years A + 2 and A + 3, however, in much smaller numbers (table, and fig. 4). GUSLITZ (1969) reported 80–90 % survival of weevils overwintering in cages in the field. The present study shows that a large proportion of the weevils arriving at the fresh clear-cutting overwintered and remained there throughout the following season (A + 1).

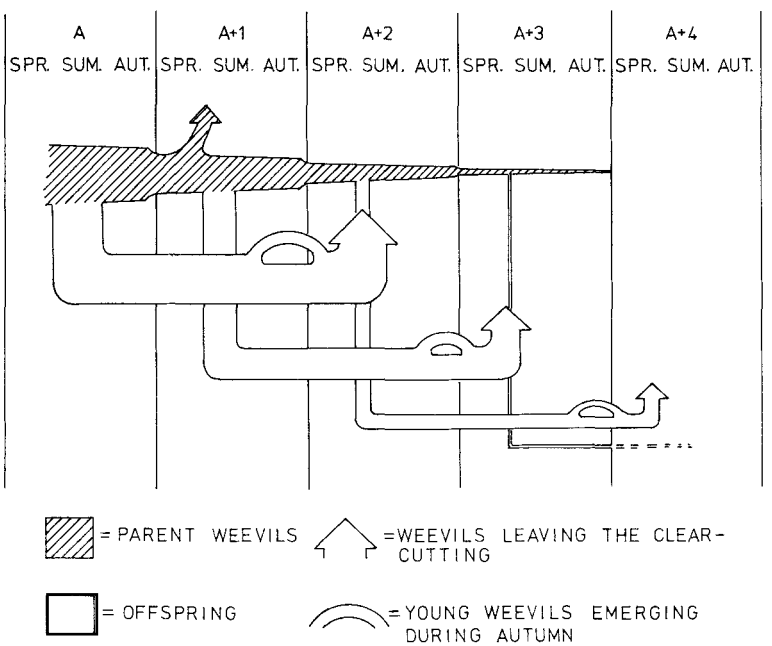

Fig. 4. Schematic representation of the pine weevil population on a clear-cutting during successive years after cutting. The figure is based on the assumption that all weevils have a two-years generation period

The breeding experiment showed that a new generation of weevils can even emerge from 4-year-old roots. Thus the large numbers of young pine weevils trapped during autumn A + 2 and spring A + 3 probably developed from eggs laid by overwintered weevils in A + 1. Similar conclusions were made by NORDLANDER (1987).

This investigation confirms earlier results and assumptions (e.g. SKOGSSTYRELSEN 1978 and NORDLANDER 1987) that the pine weevil population on a clear-cutting can still be high during spring A + 3, but then decreases markedly by autumn A + 3. Under such circumstances, it should be possible to reduce the risk for weevil damage to seedlings by delaying planting until autumn A + 3.

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Zusammenfassung

Alter, Geschlechtsreife und jahreszeitliches Auftreten des Großen Braunen Rüsselkäfers Hylobius abietis (L.)

Auf Kahlschlägen in Mittelschweden wurden während der ersten drei Jahre nach dem Abtrieb das jahreszeitliche Auftreten von *Hylobius abietis* untersucht sowie Altersstruktur, Geschlechtsreife und Zustand der Flugmuskulatur in den Populationen. Käfer, die sich schon in früheren Jahren vermehrt hatten, wurden als alt klassifiziert und von jungen Käfern auf Grund des Zustandes der Deckflügelbeschuppung unterschieden. Die Käfer wurden von Ende April bis Anfang Oktober an Fangknüppeln eingesammelt.

Keiner der im Herbst gefangenen und untersuchten Jungkäfer hatte eine gut entwickelte Flugmuskulatur oder ausgereifte Geschlechtsorgane. Die Käfer entwickelten ihre Flugmuskulatur bevor sie die Geschlechtsreife erreichten. Schon Anfang Mai hatte ein hoher Anteil der Käfer eine gut entwickelte Flugmuskulatur. Ein großer Anteil der Käfer, die in den frischen Kahlschlag eingewandert waren, überwinterten und blieben während der ganzen folgenden Vegetationsperiode auf der Fläche. Es wird angenommen, daß sie auch wieder Eier in die Stubben und Wurzeln legten und damit eine neue (Schwester-)Generation anlegten, die im Herbst des dritten und im Frühjahr des vierten Jahres nach dem Kahlschlag ausschlüpfte.

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