

Flight ability and reproductive development in newly-emerged pine weevil *Hylobius abietis* and the potential effects of climate change

Janine Y. Tan, David Wainhouse, Keith R. Day* and Geoffrey Morgant†

Forest Research, Centre for Forestry and Climate Change, Alice Holt Lodge, Wrecclesham, Farnham, Surrey GU10 4LH, U.K., *School of Environmental Sciences, University of Ulster, Cromore Rd., Coleraine, County Derry BT52 1SA, Northern Ireland and †Centre for Human and Ecological Sciences, Alice Holt Lodge, Wrecclesham, Farnham, Surrey GU10 4LH, U.K.

- Abstract**
- 1 Adult pine weevils *Hylobius abietis* emerge from conifer root-stumps, on which larvae develop, over an extended period during summer and autumn. Newly-emerged weevils were tested for their ability to fly and assessed for wing muscle and reproductive development. In addition, the effect of summer–autumn maturation feeding on reproductive development was assessed in field bioassays.
 - 2 There was considerable variation in development between newly-emerged weevils that was related to the timing of emergence. The first weevils, emerging in early July, weighed less than later-emerging ones, had undeveloped flight muscles and did not fly. Over the emergence period, wing muscle size and flight ability increased markedly, with 50–60% flying by mid-September. Differences between emerging adults are likely to have been affected by temporal changes in the quality of the bark on which the larvae feed.
 - 3 Reproductive development lagged behind that of wing muscles but, in early August, there was a rapid increase in the proportion of weevils with immature eggs and a corresponding increase in oocyte size. However, although wing muscles were fully formed in later-emerging weevils, immature eggs were only approximately 10% of the volume of mature eggs.
 - 4 In field bioassays of summer–autumn maturation feeding, eggs continued to develop and some weevils laid mature eggs. Feeding and development during the pre-overwinter period is likely to influence winter survival and also dispersal and reproduction in the following spring.
 - 5 The potential effects of climate change on the weevil life cycle are briefly discussed. Weevils are likely to benefit from the higher temperatures and later autumns predicted under climate change, resulting in an increase in damage to transplants.

Keywords Climate change, dispersal, maturation feeding, oogenesis, *Pinus nigra*, *Pinus sylvestris*.

Introduction

The pine weevil *Hylobius abietis* (L.) (Coleoptera: Curculionidae) is a ‘silvicultural’ pest because local population size and the amount of feeding damage to young transplants is determined largely by the influence of silviculture on the availability of the roots and associated stumps (root-stumps) of the conifers in which they breed (Eidmann, 1985; Långström & Day, 2004). In unmanaged forests, the availability of root-stumps

is often limited but, in extensive plantation forests managed by clearfelling and replanting, a large potential breeding resource is available in most years.

Temperature is the main determinant of the length of the life cycle and weevils may be uni- or semivoltine (Leather *et al.*, 1999). In southern England, weevils typically emerge during July to October and overwinter in the soil close to the emergence site. Weevils subsequently re-emerge and disperse to oviposition sites in late spring. In univoltine development, which can occur in some years (D. Wainhouse, personal observation), the progeny of these weevils emerge in the autumn. In

Correspondence: David Wainhouse. Tel.: +44 (0) 1420 526233; fax: +44 (0) 1420 23653; e-mail: david.wainhouse@forestry.gsi.gov.uk

semivoltine development, larvae overwinter and adults emerge in the following spring or autumn. Newly-emerged weevils are reproductively immature and a period of 'maturation' feeding is necessary before dispersal to recent clearfells for oviposition (Nordenhem, 1989). Although maturation feeding is known to be an essential prerequisite for reproductive development in *H. abietis* (Örlander *et al.*, 2000; Wainhouse *et al.*, 2001, 2004), its significance for development of flight capacity is not known. In Sweden, emerging *H. abietis* appear to lack well developed flight muscles, although dissection of weevils after overwintering suggests that they develop before sexual maturity is reached (Nordenhem, 1989). A clear understanding of wing muscle and reproductive development in *H. abietis* during the emergence period and before and after overwintering is of both ecological and applied importance. The timing of wing muscle development influences the occurrence of local flights, and therefore the food resources that weevils are able to exploit, as well as dispersal to spatially separated breeding resources and this could have a significant effect on breeding success (Eidmann, 1977; Solbreck & Gyldeberg, 1979; Solbreck, 1980).

The present study aimed to determine the degree of wing muscle and reproductive development in weevils that emerge during the summer and autumn in southern England as well as the influence on development of feeding on Scots pine *Pinus sylvestris* L. and Corsican pine *Pinus nigra* ssp. *laricio* Maire prior to overwintering. These interactions are of particular interest in the context of climate change-induced temperature increases, which have the potential to extend the time available for summer–autumn maturation feeding, shorten the overwintering period and advance the stage of reproductive development of re-emerging weevils in the spring. Such influences on the life cycle should increase the frequency of univoltine development in this important pest and extend the period during which feeding on transplants can occur.

Materials and methods

All sampling and field experiments were conducted at Thetford Forest, Norfolk, U.K. (52°25'26"N, 0°39'38"E) between 2004 and 2005.

Emerging weevils

Weevils were caught in emergence traps placed over root-stumps of Scots pine that had been felled in March of the year prior to weevil collection. The traps were a simple arrangement of a freshly cut pine log (approximately 10 × 20 cm), placed next to a root-stump and the whole covered by a 1-m² piece of horticultural shade netting, the edges of which were buried in the soil. The pine log was changed at 3-week intervals. Newly-emerging weevils accumulated under the pine log and, for the main experiments, were collected weekly, between July and September 2004, from 64 traps and stored on moist tissue paper in plastic boxes at 2–5 °C for up to 2 weeks to arrest development before assay. In the subsequent year, weevils were collected during July on a Scots pine clearfell for use in feeding bioassays. Only female weevils were used in experiments.

Flight, wing muscle development and development of eggs

Prior to assay, up to 20 females selected at random from each emergence trap collection were weighed and kept at 20–25 °C under bright artificial light [approximately 1 m below ten Sylvania F58W Gro-lux T8 fluorescent tubes (Sylvania, Germany)] for a minimum of 1 h. Flight tests were conducted, under the same temperature and light conditions, in a U-shaped 'wind tunnel' (length 60 cm, width 31 cm, height 28 cm), open at the top, with an approximately laminar airflow of 1–2 m/s maintained by a 15-cm diameter 12 V DC fan blowing through a honeycomb 'aeroweb' baffle. Individual weevils were suspended by a fine wire glued to the pronotum and moved rhythmically backwards and forwards in the airflow for up to 3 min. Individual weevils were classified as 'flying' only when wing unfolding was followed by rapid wing beats maintained for more than 10 s during the assessment period.

After flight testing, female weevils were stored at –18 °C prior to assessment of reproductive and wing muscle development. Dorsal dissection of the metathorax under 50% alcohol exposed the wing muscles, which, as in other Coleoptera, were composed of fibres attached at both ends directly to the cuticle (Pringle, 1957). Wing muscle development was determined by measuring the width of four randomly chosen fibres from the dorsal longitudinal muscle, which runs from the prephragma to the postphragma (Jackson, 1933; Reid, 1958).

Ovaries were dissected from the abdomen under Ringer's solution and the presence or absence of developing eggs and the width and length of the largest in each ovariole was determined. Egg/oocyte volume was calculated as $0.1667 \pi lw^2$, where l was the longest, and w the widest point (Wainhouse *et al.*, 2001).

Reproductive development during post-emergence maturation feeding

Reproductive development was bioassayed in the field on the 2-year-old internodes of 8–12-year-old pines during the summer–autumn period. Newly-emerged weevils were transferred from storage at 2–5 °C to ambient laboratory conditions for 24 h, after which moribund or inactive weevils were removed. Experimental weevils were subsequently held at 5–10 °C before transport to the field site the next day. On randomly selected trees, needles were removed from experimental internodes on the third whorl of branches above ground level. The internodes varied in diameter in the range 7–11.5 mm and were free from natural weevil feeding scars. Weevils were enclosed individually in plastic mesh tubes (6 × 10 cm) encircling the internode, with the ends sealed by a plug of high-density foam rubber. A tube of polystyrene foam containing moistened cotton wool inside each cage provided protection from direct sun when weevils were not feeding.

Corsican and Scots pine in 2004 and Scots pine in 2005. In 2004, the experimental trees were growing in a Corsican pine stand planted in 1992 with naturally-regenerated Scots pine of a similar size growing among the planted trees. On 24 August, one weevil was caged on each of 30 Corsican and 29 Scots

pine trees and cotton wool remoistened weekly. To maintain the supply of bark on which weevils fed, cages were moved to an equivalent internode on a new tree after 15, 29 and 43 days and, after 59 days, weevils were transferred to the laboratory and stored at -18°C prior to dissection. Weevils were dissected to measure the width of wing muscle fibres and the mean volume of the four largest eggs or oocytes. In addition, the presence of eggs in the common oviduct or of a corpus luteum was noted. Weevils were classified as reproductively mature if eggs were present in the common oviduct and with eggs/oocytes in the ovarioles.

In 2005, the experimental trees were located in a stand of Scots pine planted in 1995. Single weevils were caged on each of 40 trees on 29 July 2005. Cages were moved to new trees after 14, 28 and 42 days and removed after 56 days. Weevils were stored at -18°C before assessment of wing muscle width and reproductive development, as in 2004.

Nitrogen content of bark and temperature records. One internode similar to that used for bioassay, from a different branch of the same experimental whorl, was taken from each experimental tree at the start of the experiment and at each subsequent transfer to new trees in 2004 and 2005. Samples were stored at -70°C prior to analysis. Bark was removed from each internode and dried for 1 h at 100°C then at 70°C for a further 48 h to constant mass. For the first two sample dates in each year, bark from groups of five to seven trees selected at random was amalgamated to give three (2004) or five (2005) replicate samples for nitrogen analysis. The process was repeated for the second two sample dates in each year.

Maximum and minimum temperatures during the assay periods were obtained from the nearest Meteorological Office station, (Santon Downham, $52^{\circ}27'32''\text{N}$, $0^{\circ}40'26''\text{E}$), which was 7 km from the 2004 site and 0.75 km from the experimental site in 2005. Mean daily temperatures were determined for each year.

Statistical analysis

Two basic types of model (as subsequently described where appropriate) were used in analysis of the main results. For binary data (ability to fly or the presence of eggs), a binomial generalized linear model (GLM) with logit link was applied to the grouped data for each sampling day. The logit link function related the probability of success, P , to the linear model, L , by $\log [P/(1 - P)] = L$. For the continuous variables wing muscle width and egg volume, linear and nonlinear regression models were fitted to the mean data for each sample date, with the number of weevils in a sample used as a weight. The regression models considered included linear, quadratic, exponential ($Y = a + be^{-cX}$) and logistic ($Y = a/(1 + be^{-cX})$). The models used were chosen to give the most appropriate fit in terms of shape and goodness of fit. All data were analyzed using GENSTAT statistical software (Payne, 2007).

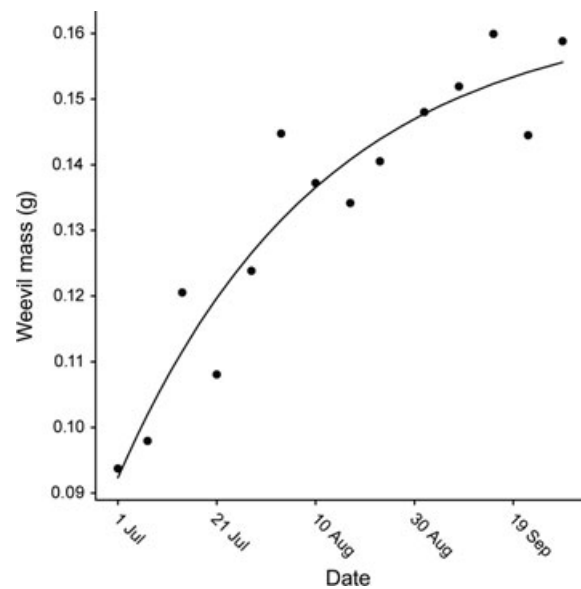


Figure 1 The relationship between emergence date and mean female weevil mass (WM). The relationship was described by the exponential model $WM = 0.164 - 0.071e^{-0.024D}$ ($R^2 = 84.1$, $P < 0.001$), where D = sampling day (day 1 = 1 July).

Results

Emerging weevils

The mean mass of newly-emerged weevils increased over the summer–autumn emergence period (Fig. 1), so that, by the end of September, weevils were approximately 50% heavier than those that had emerged at the beginning of July.

Flight, wing muscle development and development of eggs

The mean proportion of weevils flying changed over the emergence period and the data were fitted to a quadratic model on the logit scale (Fig. 2a). The first weevils to emerge did not fly but, from mid-July onwards, the proportion that flew increased up to a maximum of 50–60%. The data on wing muscle width, which was fitted to a logistic model (Fig. 2b), showed that there was a similar trend in increasing muscle width over the sample period, with the first-emerging weevils having relatively undeveloped wing muscles, whereas those of later-emerging weevils appeared fully formed (Fig. 3).

The data on the proportion of weevils with visible oocytes were fitted to a quadratic model on the logit scale (Fig. 2c) and that on the size of the developing eggs to a logistic model (Fig. 2d). No oocytes were visible in the first weevils to emerge but, towards the end of July, there was a rapid increase in the number of weevils with oocytes so that, by mid-September, they were present in 60–70% of weevils, with the percentage declining thereafter. There was a similar trend in the size of oocytes in emerging weevils, with oocytes increasing in size during August.

The relationship between wing muscle and egg development over the emergence period is shown in Fig. 4, with the data fitted to an exponential model. In the first weevils to emerge,

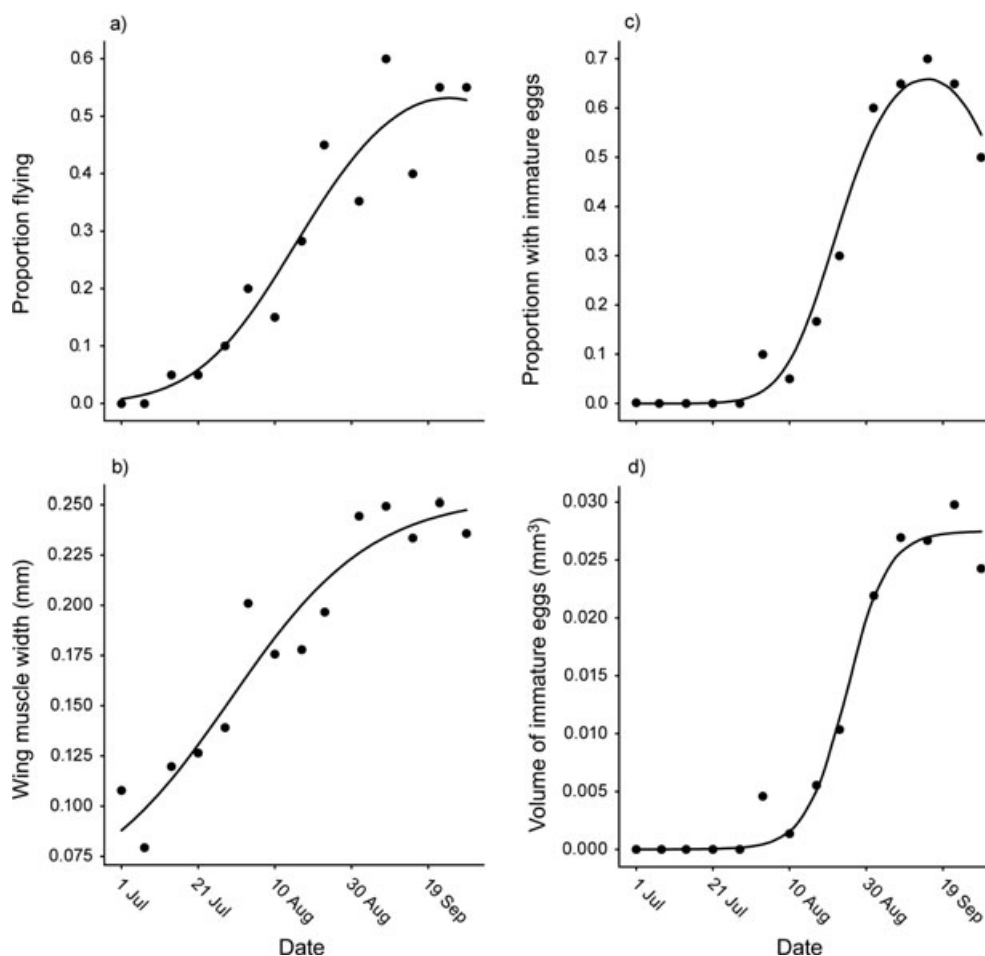


Figure 2 The relationship between weevil emergence date and flight ability, and wing muscle and reproductive development. (a) The mean proportion (P) of weevils flying. The data were fitted to the quadratic model, $\text{logit } P = -4.82 + 0.1159 D - 0.0007 D^2$ ($P < 0.001$). (b) Mean dorsal longitudinal muscle width (DL). The data were fitted to the logistic model, $DL = 0.052 + 0.202/(1 + e^{-0.54(D-28.5)})$ ($R^2 = 88.5$, $P < 0.001$). (c) The proportion (P) of weevils with immature eggs. The data were fitted to the quadratic model, $\text{logit } P = -12.85 + 0.3565 D - 0.0024 D^2$ ($P < 0.001$). (d) The mean volume of immature eggs (EV). The data were fitted to the logistic model, $EV = 0.027/(1 + e^{-0.188(D-54.9)})$ ($R^2 = 97.6$, $P < 0.001$). D = sample day (day 1 = 1 July).

eggs were either absent, or present in only a few weevils (Fig. 2c). In this analysis, therefore, egg volume was considered to comprise a composite index of reproductive development that represented the proportion of weevils with eggs and any differences in egg size. The temporal relationship between wing muscle and egg development was indicated by the line connecting the mean values in numbered sampling sequence in Fig. 4. This shows that wing muscle development was much more advanced than egg development and, although wing muscles appeared to be fully formed in later-emerging weevils, the immature eggs were only approximately 10% of the volume of mature eggs.

Reproductive development during post-emergence maturation feeding

Corsican and Scots pine in 2004 and Scots pine in 2005. In 2004, all weevils were still reproductively immature after

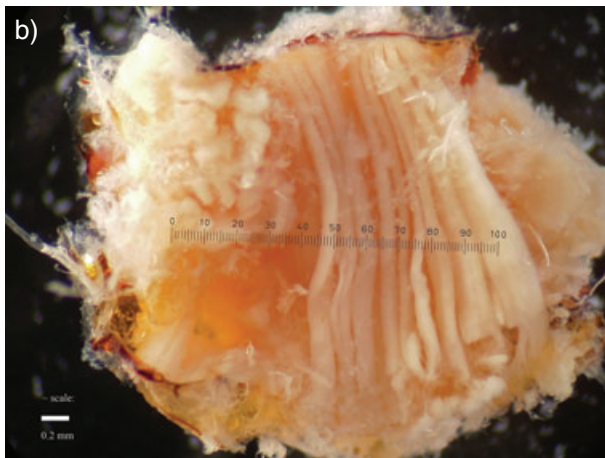
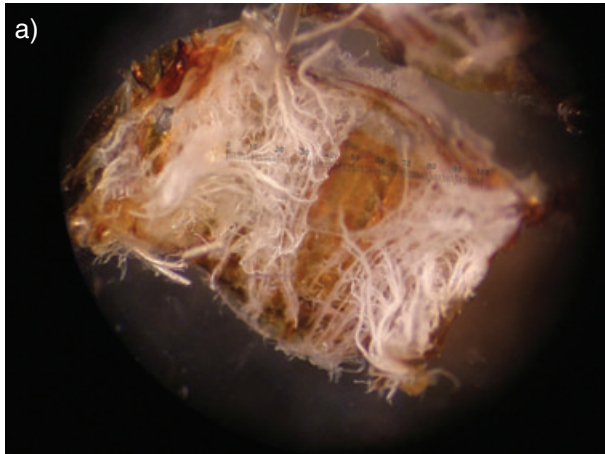
feeding for 59 days (Table 1) but eggs were larger in weevils feeding on Scots than Corsican pine ($t = 3.35$, d.f. = 50, $P < 0.01$). In the subsequent year, over 50% were reproductively mature after 57 days and most weevils had already laid eggs. The size of eggs in the females that were still reproductively immature in 2005 is shown in Table 1.

Nitrogen content of bark and temperature records. Over the 2-month assay period, there was a small increase in the nitrogen concentration of Scots pine bark in both 2004 and 2005 ($F_{2,12} = 18.1$, $P < 0.001$) but no change in Corsican pine (Table 2). In 2004, the nitrogen concentration in Scots pine was significantly higher than that in Corsican pine ($F_{1,13} = 136.7$, $P < 0.001$).

Air temperature during the assay period in 2004 and 2005 (Fig. 5) showed that temperatures were generally higher in 2005, reflecting the fact that assays were started 1 month earlier than in 2004.

Table 1 Reproductive development of newly-emerged weevils caged onto Scots (SP) or Corsican pine (CP) during autumn 2004 and 2005

Year	Species	Date	Mean air temperature (°C)	Number of weevils	Days	Weevils		
						% Immature	% Mature	Immature egg volume (mm ³)
2004	SP	24 August to 21 October	12.9	27	59	100	0	0.059 ± 0.003
	CP	24 August to 21 October	12.9	25	59	100	0	0.044 ± 0.003
2005	SP	29 July to 23 September	15.7	40	57	42.5	57.5	0.079 ± 0.004

**Figure 3** Dorsal-longitudinal wing muscles in *Hylobius abietis*. (a) Immature muscle in which fibres were thin and white. (b) Mature muscle with large fibres that were pink in colour.

Discussion

Over the autumn emergence period, there were marked increases in the size of female *H. abietis*, and in the degree of wing muscle and reproductive development. As a result, a high proportion of the newly-emerged weevils were flight capable by early September, although none were reproductively mature. The observed trends in weevil size and development are likely to have been influenced by several factors. The time of oviposition by the parent generation would have an important influence on the timing of emergence, as would the temperature at the different depths below the soil surface

Table 2 The nitrogen concentration in bark of trees used in feeding bioassays in 2004 and 2005

Year	Species	Sample	Nitrogen % dry mass	<i>n</i>
2004	SP	1	0.64 ± 0.020	3
		2	0.77 ± 0.033	3
	CP	1	0.45 ± 0.006	3
		2	0.47 ± 0.006	3
2005	SP	1	0.57 ± 0.006	5
		2	0.65 ± 0.011	5

SP, Scots pine; CP, Corsican pine.

where larvae and pupae develop (Hanson, 1943; Bakke & Lekander, 1965; Christiansen & Bakke, 1968; Pye & Claesson, 1981). The size of adults would be most affected by the nutritional quality of the larval food resource (Thorpe, 1999; Strohm, 2000; Thorpe & Day, 2002; Nijhout, 2003; Karino *et al.*, 2004). Preformed defences present in the living bark may be active for a period after felling, and this 'residual' resistance (Wainhouse, 2004) could have affected development of the offspring of the first females to oviposit after felling in March. These larvae are likely to have been among the first to emerge as adults and to be smaller than those emerging later. The availability as well as the quality of the bark on which larvae feed would also be influenced by competitors. Larvae developing in remnants of crowded roots with little food tend to have shorter developmental times and produce smaller adults than unaffected larvae (Rothe, 1910). Similarly, decay fungi, which are usually most abundant in roots close to the cut surface (von Sydow, 1993), can affect larvae feeding in this zone and those unable to locate unaffected bark may pupate earlier, and at lower mass, than those feeding at a greater depth on unaffected bark. In bark beetles, larval competition for food often results in the emergence of smaller adults (Anderbrant & Schlyter, 1989; Amezaga & Garbisu, 2000), an effect that can be more pronounced in late than early-emerging adults (Anderbrant *et al.*, 1985). The fact that later-emerging pine weevils were larger than those emerging earlier suggests that a reduction in the amount or quality of food over the development period was not an important factor. Indeed, larvae feeding later in the season may have benefited from increases in the nitrogen content of pine root-stumps that are reported to occur in the months after felling (Albrektson *et al.*, 2000).

Weevil size is likely to have had some influence on weevil development. Preliminary analysis of the data on individual weevils (unpublished) indicated that there was a significant positive relationship between weevil mass and wing muscle development in the early sampling period. This was

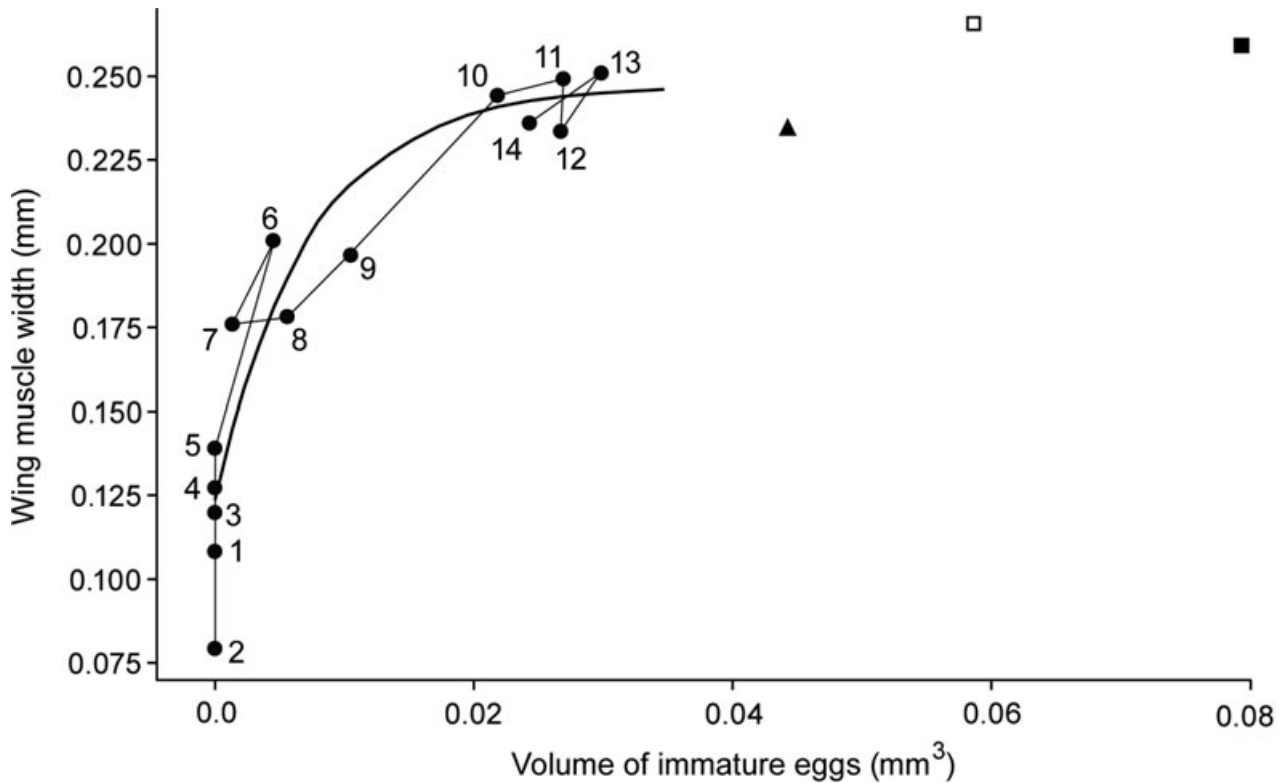


Figure 4 The relationship between mean width of the dorsal longitudinal muscles (DL) and the mean volume of immature eggs (EV) in newly-emerged females. The data were fitted to the exponential model, $DL = 0.243 - 0.120e^{-153.68EV}$ ($R^2 = 87.8$, $P < 0.001$). The mean values for each emergence date are connected in sequence to indicate changes over time – numbers represent the sampling sequence from the start of trapping (=1). Data on mean wing muscle and reproductive development for weevils in maturation feeding assays (see text) are shown for comparison. ▲, Corsican pine 2004; □, Scots pine 2004; ■, Scots pine 2005. Data are for immature eggs, which were present in 100% of females in 2004 and 42.5% in 2005.

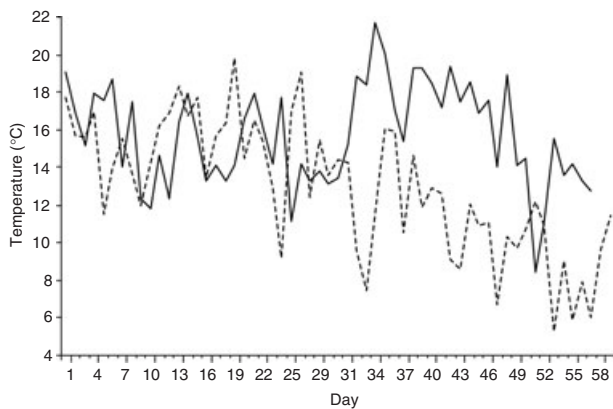


Figure 5 Mean daily air temperature from the start of the autumn bioassays in 2004 (broken line) and 2005.

not, however, evident in the later samples and there was no significant relationship between weevil mass and oocyte volume. One possible cause of variation in development could be post-eclosion feeding before weevils emerge above ground. Such pre-emergence feeding has been observed in newly-eclosed bark beetles, including *Hylastes* spp., *Ips paraconfusus*, *Dendroctonus jeffreyi*, *Tomicus piniperda*, *Scolytus multistriatus*

and *Phloeosinus sequoiae* (Hanson, 1943; McNee *et al.*, 2000). Feeding on fine roots by *H. abietis* has been observed in the field (Örlander *et al.*, 2001; Nordlander *et al.*, 2003; Wallertz *et al.*, 2006) and the nitrogen content of the inner bark of root-stumps and the lower stem is usually above the threshold for wing muscle and reproductive development (Wainhouse *et al.*, 2004; Tan, 2006). Pre-emergence feeding, however, is unlikely to have produced the observed trends in weevil development over the emergence period.

Wing muscle development occurred in advance of that of reproductive development, as indicated by the temporal sequence shown in Fig. 4. By the end of the emergence period, wing muscles were similar in size to those of flight-competent weevils in spring (Tan, 2006) and these weevils clearly have the potential for flight. This contrasts with findings reported from Scandinavia, which indicate that autumn-emerging weevils lack developed flight muscles (Nordenhem, 1989). Although oocytes increased in size over the emergence period, they only reached a maximum of approximately 10% of the size of mature eggs (Wainhouse *et al.*, 2001). However, further reproductive maturation can occur in weevils that feed during the autumn, the potential for which is shown in the feeding bioassays. Of particular interest is the finding that, in 2005, some weevils that began feeding in July had laid eggs by September. In 2004, the

later start of the feeding trial and the resulting lower temperatures during the assay period were probably the main reasons why weevils failed to mature eggs in that year. Autumn maturation feeding may allow early-emerging weevils to 'catch-up' developmentally with later-emerging ones, although the smaller weevils would be less fecund. Most weevils are therefore likely to have well developed wing muscles and partially developed eggs when they enter the overwintering period.

Egg maturation during the autumn has not previously been reported under field conditions where, among other factors, the location of food resources by walking weevils is likely to be limiting, especially in a large clearfell. The results of the feeding assays, however, suggest that under climate change, higher temperatures together with earlier springs and later autumns could have a significant influence on weevil seasonal development. With modest climate warming, earlier emergence and an extended autumn feeding period is likely to result in increased overwintering survival of weevils that are also reproductively more advanced. Earlier re-emergence in the following spring, together with a shorter period required for reproductive maturation prior to dispersal, would further extend the time available for larval development during the summer period. As a result of these additive effects, univoltine development, with spring oviposition by the parent generation, and the emergence of the new generation adults in the autumn followed by overwintering and oviposition in spring would be likely in most years. With more extensive warming, weevils have the potential for egg maturation, dispersal and oviposition during the autumn of the year of emergence. The shortened generation time is likely to result in higher weevil populations and the potential for increased damage to transplants during the spring and autumn maturation feeding periods.

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