

# Interaction between flight, reproductive development and oviposition in the pine weevil *Hylobius abietis*

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- Abstract**
- 1 The development of reproductive and flight capacity of pine weevils *Hylobius abietis* during the spring and their dispersal to, and subsequent development at, new clearfell oviposition sites comprise key phases in their life cycle in managed forests. At an old clearfell site where autumn-emerging weevils had overwintered, weevils were trapped as they re-emerged in the spring and tested for their ability to fly and then dissected to determine the degree of wing muscle and egg development.
  - 2 Re-emerging weevils were most abundant in pine growing at the edge of the clearfell and, over most of the trapping period (April to June), their capacity for flight (proportion flying and wing muscle width) was more advanced than in weevils from the clearfell itself, with a similar trend in the degree of reproductive development (proportion with mature eggs and egg volume).
  - 3 In weevils from the clearfell, flight capacity and reproductive development increased concurrently to a peak around mid-May. In weevils from pine, wing muscles were already well developed at the start of trapping, although few of them flew. Their more advanced development was attributed to the increased opportunities for maturation feeding after emergence in the previous autumn.
  - 4 In the spring, weevils reached the canopy of trees for maturation feeding by walking and, to a lesser extent, by flight. Weevils dispersed by flight to oviposition sites in mid-May when most of them were reproductively mature. After arrival, flight ability and wing muscle size declined rapidly but egg production was maintained until most weevils had stopped flying. When wing muscles reached their minimum size, there was a marked decline in egg size, suggesting that wing muscle breakdown is important in maintaining egg production at oviposition sites. Prospects for further wing muscle and reproductive development are discussed.

**Keywords** Maturation feeding, oogenesis, *Pinus sylvestris*, wing muscle development.

## Introduction

In northern European forests managed on a cycle of clearfelling and replanting, the juvenile stages of the pine weevil *Hylobius abietis* develop predominantly within the bark of the stumps and associated roots (root-stumps) on recent pine and spruce clearfells. The newly-emerging adults, which can be reproductively active over 2 years (Christiansen, 1971; Nordenhem, 1989), subsequently disperse to new clearfells where they

oviposit during the early summer. This simple sequence of events in managed forests reflects ecological and physiological adaptations to their natural environment of unmanaged conifer forests, where weevils breed in moribund or windblown trees whose availability would normally be unpredictable in space and time. Weevils locate these resources by responding to monoterpenes and ethanol released from the moribund bark (Tilles *et al.*, 1986). The bark available on a single root-stump is limited, usually only supports one generation (Eidmann, 1977) and is likely to be utilized by insect and fungal competitors (Hanson, 1943; Croke & Kirkland, 1956). After oviposition,

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exploitation of the bark resource is influenced by maternal effects on egg size (Wainhouse *et al.*, 2001), affecting both larval survival and rate of development, and by intra- and inter-specific competition.

In managed, even-aged plantations, suitable root-stumps for breeding are abundant, although usually spatially separated from sites of weevil emergence. Pine is the natural host and, when developing on this species in southern England, emergence usually occurs in the autumn (D. Wainhouse, personal observations). Newly-emerged adults are synovigenic and, in suitable weather, they can feed on the bark of young conifers or on twigs of mature trees before they overwinter. The main period of this 'maturation' feeding is, however, considered to occur in the spring after they re-emerge, or after a main spring emergence. Although newly-emerged weevils are generally flightless, those emerging in late autumn have much more well-developed flight muscles than those that are among the first to emerge, and so have at least the potential for flight (Tan *et al.*, 2010). Maturation feeding is necessary for egg development (Munro, 1928; Leather *et al.*, 1999) and, for some weevils, is probably also important for the development of flight muscles (Nordenhem, 1989; Örländer *et al.*, 2000). The relationship between flight ability, reproductive development and duration of the oviposition period is not well understood and yet is a key determinant of the timing of dispersal and oviposition on new clearfells and thus is important in the context of pest management. In addition, this phase of the life cycle is also most likely to be affected by seasonal changes in temperature and the length of the growing season, which are predicted consequences of climate change.

The present study had two principal aims: (i) to determine the relationship between maturation feeding, wing muscle development and flight capacity, and reproductive development in weevils that are re-emerging during the spring at an overwintering site and (ii) to determine how the relationship between flight capacity, wing muscle development and oviposition changes once weevils have arrived at a clearfell oviposition site in eastern England.

## Materials and methods

Overwintering and oviposition sites were located at Thetford Forest, Norfolk, U.K. (52°25'N, 0°39'E), and were sampled during 2004. The overwintering site had been felled between April and August 2002 and the oviposition sites between November 2003 and February 2004.

### *Overwintering site: spring re-emergence, maturation feeding and dispersal*

Experiments were performed on an 8.5-ha Scots pine (*Pinus sylvestris* L.) clearfell where weevils had emerged during autumn 2003 and subsequently overwintered. The sample site had been replanted with 2-year-old cell grown Corsican pine (*Pinus nigra* ssp. *laricio* (Poiret) Maire) (height 8–20 cm, root collar diameter 3–5 mm) during the winter early in 2004. It was bordered by young (approximately 10 years) or mature (approximately 70 years) plantations of Corsican or Scots pine, which

included some areas of intermixed naturally regenerated Scots pine. Weevils were sampled on the site both to monitor their development and population trends before and after dispersal to oviposition sites.

*Re-emerging weevils.* The spatial distribution of weevil overwintering sites was unknown, so those re-emerging in the spring were sampled on two representative parts of the experimental site: within the replanted clearfell area (clearfell transects) and along the edge of an adjacent stand of mainly young Corsican pine (pine transects). Weevils were trapped from April to June using sections of pine stem (= log traps, approximately 10 × 25 cm) placed in a shallow depression on the soil surface (Långström, 1982; Nordenhem, 1989; Wilson and Day, 1995). In the clearfell, there were four transects (approximately 50 m long and 3–4 m apart) at right angles to, and starting approximately 10 m from, the adjacent pine stand. There were ten log traps in each transect and, in alternate transects, traps were placed next to or between root-stumps. Along the edge and within the adjacent pine, there were two parallel transects (approximately 200 m long, 3 m apart) each with 20 log traps. Weevils were collected weekly and stored at 2–5 °C for up to 2 weeks to prevent further development before assay. Log traps were replaced with newly felled ones at approximately 3-week intervals.

*Maturation feeding and dispersal.* Within the experimental site, maturation feeding could occur on pines of different age and size including the transplants on the clearfell area. Sampling was confined to the young trees (approximately 10 years old, height 2–3 m, lower stem diameter 10–15 cm) adjacent to the clearfell. Three plots (10 × 5 m), two of Corsican and one of Scots pine, were established and some trees in each plot removed to leave 12–15 trees, which were lightly pruned to prevent contact between branches of neighbouring trees. On approximately half the trees in each plot (six to seven trees), which were selected at random, barriers were fitted to the main trunk so that weevils were prevented from walking up to the crown and could only reach it by flight. Barriers comprised lengths of polythene (10 × 40 cm) wrapped around the stem 30 cm from the ground, above which strips of polyvinyl chloride (20 × 50 cm) were formed into a cone around the stem and secured to give an insect-proof seal. The barrier was covered with sticky Hyvis® (Aquaspersions Ltd, U.K.), which was re-applied weekly. The remaining trees had no barriers, allowing access to the canopy by both walking and flying weevils. The three plots contained a total of 20 trees with barriers and 22 without. Branches of all trees within plots were beaten to remove weevils from the canopy and subsequently resampled during April to June by beating branches over collecting sheets once or twice per week. On each sampling occasion, catches from all three plots were pooled.

### *Oviposition sites: arrival and oviposition*

Three oviposition sites were sampled. They were compartments of Corsican pine, 6–12 ha in size, which had been clearfelled

2–5 months previously. Compartments of mature pine bordered at least two sides of each site and they were located 0.75–7 km from the nearest older clearfell from which weevils could be dispersing. At each site, 30–60 log traps were deployed over an area of up to 50 × 100 m, and weevils were collected weekly from April to September 2004. Log traps were renewed every 2–3 weeks. Weevils were stored at 2–5 °C from the day of collection for up to 2 weeks before assay.

#### Flight ability and wing muscle development

Assessments of the potential for flight and the degree of wing muscle development were made for weevils from the overwintering site and oviposition sites. Before assay, up to 40 females each from the pine (range 6–40) and clearfell (range 1–33) transects at the overwintering site and up to 60 (range 7–60) at the oviposition sites were selected at random from each log trap collection date. Weevils were weighed and kept at 20–25 °C under bright artificial light (approximately 1 m below ten Sylvania F58W Gro-lux T8 fluorescent tubes; Havells Sylvania Europe Ltd, Germany) for a minimum of 1 h. The method of flight testing was as described by Tan *et al.* (2010). Briefly, individual weevils were suspended by a fine wire attached to the pronotum in a U-shaped wind tunnel, open at the top and with an approximately laminar airflow of 1–2 m/s. Weevils were moved rhythmically backwards and forwards in the airflow for up to 3 min, after which 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.

Weevils were stored at –20 °C after flight testing, before assessment of reproductive and wing muscle development. The metathorax was dissected from the dorsal side under 50% alcohol to expose 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).

#### Reproductive maturation and oviposition

Ovaries were dissected under Ringer’s solution from the abdomen of flight-tested weevils and from up to 20 weevils from canopy beating samples that had been stored at –20 °C. The width and length of the four largest mature eggs or oocytes were measured, and 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. Egg/oocyte volume was calculated as  $0.1667\pi lw^2$ , where  $l$  is the longest, and  $w$  is the widest point of the egg (Wainhouse *et al.*, 2001) and the mean volume of four eggs (immature or mature) was used in analysis of reproductive development. Three immature weevils trapped at oviposition sites in September were assumed to be the offspring of the first adults on the site and were excluded from the analysis.

#### Statistical analysis

All data were analyzed using the GenStat statistical package (Payne, 2007). Details of the models fitted are given as appropriate. For proportional data (i.e. flight ability and the presence of mature eggs), a binomial generalized linear model was used with a logit link function ( $\text{logit}(p) = \log(p/(1-p))$ ), where  $p$  is the proportion). Where appropriate, overdispersion was taken into account when testing the significance of effects. For wing muscle width and egg volume, general linear regression models were used after confirming that transformations were not required. This was determined by scatter plots of the variables against explanatory variables and normal probability plots for either the variables or their residuals from fitted models. Further, quadratic models were fitted to check for deviation from linearity. Where necessary, these quadratic models were adopted.

## Results

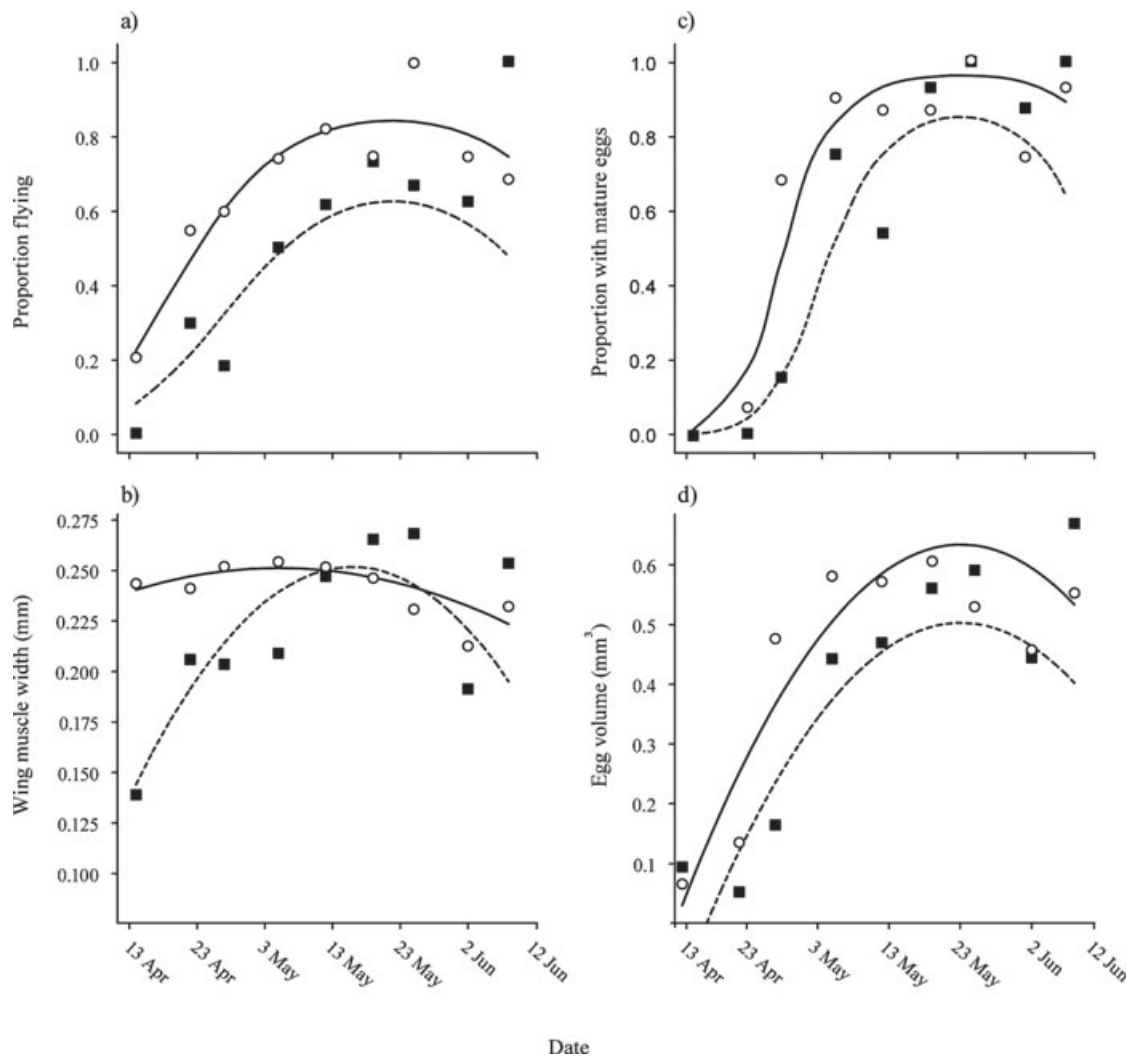
#### Overwintering site: spring re-emergence, maturation feeding and dispersal

*Re-emerging weevils.* The total catches of weevils in the pine and clearfell transects are shown in Table 1. A log-linear model with overdispersion was fitted to the data and showed that catches in pine were significantly greater than those from the clearfell (deviance ratio (DR)<sub>1,8</sub> 25.2,  $P < 0.001$ ). There was also a significant effect of trapping date on the numbers caught (DR<sub>8,8</sub> 4.7,  $P < 0.05$ ), with catches at both sites peaking during late April and early May.

The data on mean proportion of weevils flying on each sample date were best fitted by the quadratic model shown in Fig. 1(a). The proportion of weevils flying increased over the sampling period, with a higher proportion of weevils flying in samples from the pine transects than from the clearfell (DR<sub>1,12</sub> 23.5,  $P < 0.001$ ). A quadratic model was fitted to the data on variation in wing muscle width using the number of weevils dissected as a weighting factor. A model with separate terms was required to describe changes in wing muscle size over the sampling period in the pine and clearfell transects (variance ratio (VR)<sub>2,18</sub> 10.9,  $P < 0.005$ ) (Fig. 1b). In pine, wing muscles were well developed at the start of trapping and

**Table 1** Total number of re-emerging male plus female weevils caught at log traps ( $n = 40$  per location) from the four transects within the clearfell and the two transects along the edge of an adjoining pine stand

Date	Transect	
	Clearfell	Pine
14 April	17	42
22 April	41	126
27 April	73	98
5 May	11	85
12 May	34	129
19 May	34	59
25 May	12	22
2 June	16	30
8 June	2	39



**Figure 1** Variation in flight and reproductive development of weevils at an overwintering site during the spring re-emergence and dispersal period. Data are for the pine (○) and clearfell transects (■). (a) The mean proportion of weevils flying. The fitted model was  $\text{logit } P = S_i + 0.16D - 0.002D^2$ . (b) Mean dorsal longitudinal muscle width. The fitted model for pine was  $DL = 0.24 + 0.001D - 0.00002D^2$  and for the clearfell  $DL = 0.14 + 0.007D - 0.0001D^2$  (overall  $R^2 = 77.9$ ). (c) The mean proportion of weevils with mature eggs. The fitted model was  $\text{logit } P = S_i + 0.40D - 0.005D^2$ . (d) Mean egg volume. The fitted model was  $EV = S_i + 0.03D - 0.0004D^2$  ( $R^2 = 81.8$ ). Egg volumes over  $\sim 0.4 \text{ mm}^3$  indicate mature eggs.  $P$ , mean proportion;  $S_i$ , Site (pine or clearfell);  $D$ , sample day (day 1 = 14 April);  $DL$ , dorso-longitudinal wing muscle width;  $EV$ , egg volume.

changed little over the sampling period, whereas those from the clearfell were initially less well developed but their width increased to a peak by mid-May. The proportion of weevils with mature eggs followed a similar trend to that of flight (Fig. 1c), with a significantly higher proportion of weevils with mature eggs in samples from pine ( $DR_{1,12} 9.2$ ,  $P < 0.01$ ). A quadratic model was fitted to the data on egg volume using the number of weevils dissected as a weighting factor (Fig. 1d). Eggs increased rapidly in size, with weevils from pine having significantly larger eggs than those from the clearfell over the sampling period ( $VR_{1,12} 7.6$ ,  $P < 0.02$ ).

**Maturation feeding and dispersal.** Weevils were collected from trees without barriers from the first sampling date on 14 April, although few were caught on trees with barriers until the 14

May and none were found on them after this date (Table 2). The number of weevils on trees without barriers and the number at log traps also declined after this time, suggesting significant dispersal by flight in mid-May. At this time, over 80% of weevils were estimated to be reproductively mature (Fig. 1c).

#### *Oviposition sites: arrival and oviposition*

The overall mean number of weevils trapped at the three oviposition sites (Fig. 2) showed that few weevils were caught in early April but that they were abundant on the site from mid-May to the end of July before declining to low levels by the end of August.

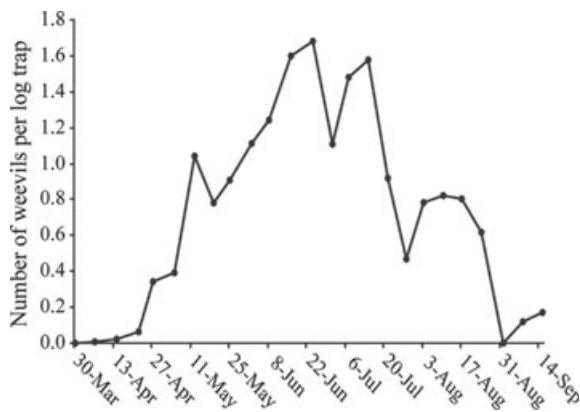
Variation in the mean proportion of weevils that flew or had mature eggs over the trapping period was analyzed by



**Table 2** The number of female weevils and the percentage that were reproductively mature in beating samples from trees with ( $n = 20$ ) and without ( $n = 22$ ) barriers (see text). For trees without barriers, numbers were adjusted to weevils per 20 trees. The number of female weevils caught at log traps in pine is also shown

Sample date	Canopy beating				Pine transects Log trap ( $n = 40$ )
	Number in Canopy		Percent reproductively mature		
	No barrier	Barrier	No barrier	Barrier	
14 April 2004	21	2	0	0	16 <sup>a</sup>
22 April 2004	13	3	7	33	61
27 April 2004	14	4	33	0	23
5 May 2004	—	—	—	—	32
12 May 2004	5	4	40	25	53
14 May 2004	15	14	47	50	—
19 May 2004	3	0	33	—	24
25 May 2004	5	0	60	—	6
2 June 2004	3	0	67	—	8

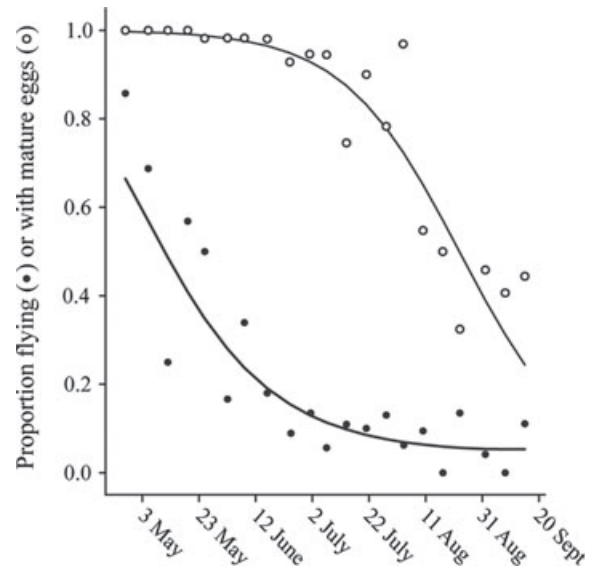
<sup>a</sup>Estimated number of females in a total catch of 42 males + females. Estimate based on the mean proportion of females at log traps over all sample dates.



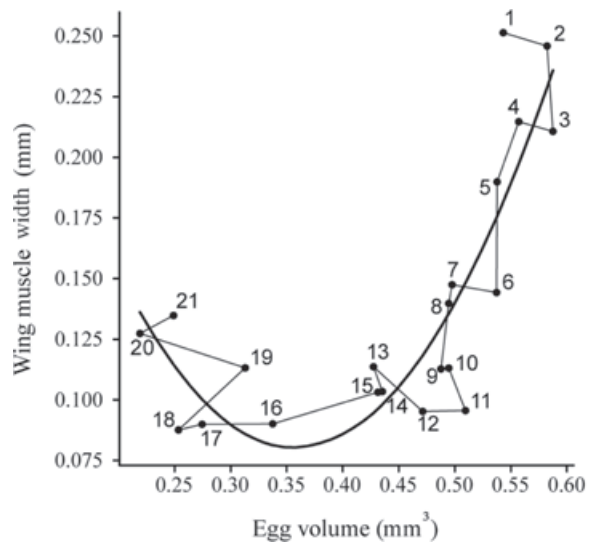
**Figure 2** Mean number of weevils (male + female) per log trap at oviposition sites during 2004 ( $n = 30$ –60 log traps at each of three sites).

logistic regression. The proportion of weevils flying over the sampling period, which was described by a quadratic model ( $DR_{2,18} 19.7, P < 0.001$ ) (Fig. 3), showed a marked decline over the first 10 weeks of trapping. Variation in the proportion of reproductively mature females was described by a linear model ( $DR_{1,19} 120.1, P < 0.001$ ) (Fig. 3) showing that the proportion of weevils with mature eggs remained relatively high during the first 11 weeks of sampling, declining to low numbers over the next 10 weeks, during which time the majority of weevils had stopped flying.

The relationship between muscle width and egg volume was best described by a quadratic model ( $VR_{2,20} 26.2, P < 0.001$ ) (Fig. 4). Mean values of muscle width for each sampling date were connected in sequence, revealing a marked decline in



**Figure 3** The mean proportion of weevils at oviposition sites that flew (closed circles) or had mature eggs (open circles). Data were analyzed by logistic regression using a quadratic model for the proportion of weevils flying ( $\text{logit } P = 1.45 - 0.06D + 0.0002D^2$ ) and a linear model for the proportion with mature eggs ( $\text{logit } P = 6.43 - 0.049D$ ) (data on females with mature eggs were backtransformed).  $P$ , mean proportion;  $D$ , sample day (day 1 = 27 April).



**Figure 4** The relationship between width of the dorsal longitudinal muscles and egg volume for weevils at oviposition sites. The relationship was described by the quadratic model  $DL = 0.455 - 2.096EV + 2.934EV^2$  ( $R^2 = 71.6\%$ ). The mean values for each sample date are connected in sequence to illustrate changes over time; numbers represent the sampling sequence from the start of trapping (= 1).  $DL$ , dorso-longitudinal wing muscle width;  $EV$ , egg volume.

muscle width relative to egg volume after arrival at oviposition sites. Towards the end of the trapping period, there was evidence of an increase in wing muscle development while egg volume continued to decline.

## Discussion

At the overwintering site, the higher catches of weevils in pine transects at the edge of the clearfell were probably a result of movement of the weevils to the edge of the clearfell after emergence from root-stumps during the previous autumn. These weevils scored higher than those from the clearfell transects on both measures of flight capacity (proportion flying and wing muscle width) and of reproductive development (proportion with mature eggs and egg volume) over most of the trapping period. This was probably a consequence of the wider availability of maturation feeding sites in the pine. Weevils that remained on the clearfell would have had little opportunity to feed during the autumn before the site had been replanted over winter and, in addition, the population feeding on transplants during the spring may have included a few weevils that were newly emerged.

One notable difference between weevils from the pine and clearfell transects was that those from pine had well developed flight muscles from the beginning of the trapping period (mid-April). Because many of these were likely to have entered the overwintering period with relatively well developed flight muscles after a period of autumn feeding (Tan *et al.*, 2010), this suggests that weevils utilize reserves from stored fat rather than from the breakdown of wing muscles to survive over winter. It is possible, however, that some weevils feed on fine roots below ground during the winter (Örlander *et al.*, 2001; Nordlander *et al.*, 2003; Wallertz *et al.*, 2006) or on twig material above ground on suitably warm days. Despite having well-developed wing muscles, the probability of flight for weevils trapped in the pine transects was initially low. This contrasts with observations on autumn-emerging weevils, where wing muscle development and the probability of flight are highly correlated (Tan *et al.*, 2010), and may indicate that overwintering weevils need to restore depleted fat reserves before dispersal by flight can occur. For weevils in the clearfell, where young transplants would be the main food source, wing muscles and eggs increased in size together so, although wing muscles usually develop before eggs mature (Nordenhem, 1989; Tan *et al.*, 2010), they can develop in parallel.

For weevils feeding in the canopy of trees at the margins of the clearfell during the spring, the larger number of weevils beaten from trees without trunk barriers indicates that most had walked up to the canopy to feed, although a few weevils were evidently flying from mid-April onwards. The sudden increase in the number of weevils on trees with barriers in mid-May and a subsequent decrease in the number caught at the log traps indicates that there had been a significant dispersal from the re-emergence site. This timing suggests that the majority of dispersing weevils were reproductively mature (Fig. 1c, d and Table 2), although further maturation feeding would be necessary for some individuals. At the time of dispersal, air temperature was above the threshold for weevil flight of approximately 18–19 °C (Solbreck & Gyldberg, 1979). Temperatures above this threshold were, however, reached on several days during late April (J. Tan, unpublished data) when flight-mature weevils were present in the population, suggesting that the reproductive state of the weevils may influence the timing of dispersal in the U.K. In Scandinavia, spring dispersal may occur before (Nordenhem, 1989; Örlander *et al.*, 2000)

or after most weevils are reproductively mature (Christiansen, 1971), with the timing of dispersal being determined by suitable temperature and wind conditions (Solbreck & Gyldberg, 1979).

The relative abundance of reproductively mature weevils at the oviposition sites from mid-May is consistent with a significant dispersal of weevils from re-emergence sites at this time. At the oviposition sites most weevils lost the ability to fly, as reported in previous studies (Långström, 1982; Nordenhem, 1989). Although weevils stopped flying soon after arrival at oviposition sites, egg production was maintained over a much longer period, with the proportion of reproductively mature weevils decreasing markedly only after most weevils had stopped flying (Fig. 3). The relative timing of these events suggests the possibility that a loss of flight ability linked to wing muscle breakdown plays a role in maintaining egg production over the summer. This is supported by the relationship between the size of wing muscles and egg volume during the oviposition period (Fig. 4). There was an initial rapid decline in muscle width with relatively little change in egg volume and, until early July, eggs remained within the size range (0.45–0.67 mm<sup>3</sup>) expected for mature eggs (Wainhouse *et al.*, 2001). When muscle width approached a minimum, however, mean egg volume fell below that of mature eggs, providing strong circumstantial evidence that the breakdown of wing muscles allows resources to be re-allocated to egg production (Marden, 2000).

Some bark and ambrosia beetles also resorb wing muscles after arrival at a suitable breeding site (Chapman, 1956; Reid, 1958; Atkins & Farris, 1962; Borden & Slater, 1969; Forsse & Solbreck, 1985; Slansky & Haack, 1986; Robertson, 1998) and this is usually assumed to contribute to oogenesis (Wheeler, 1996; Marden, 2000). Under suitable conditions, bark beetles can redevelop wing muscles relatively quickly, allowing redispersal and formation of 'sister' broods (Bakke, 1983). There was some evidence that wing muscles were beginning to redevelop in *H. abietis* once egg laying had ceased (Fig. 4). Although sister broods do not occur in *H. abietis*, a further cycle of oogenesis is possible in the subsequent year (Guslits, 1969; Christiansen, 1971) in this relatively long-lived weevil (Eidmann, 1979; Leather *et al.*, 1999). Dispersal and reproduction in these older weevils will depend, among other things, on their ability to exploit available food sources. Post-reproductive weevils are initially flightless so that, in large clearfells that have not been replanted and lack significant natural regeneration, weevils must locate surrounding conifer stands by walking. Proposed alternative food sources (Munro, 1928; Leather *et al.*, 1994; Manlove *et al.*, 1997; Toivonen & Viiri, 2006) are of unknown nutritional quality and at least some appear to be toxic; their importance in enabling the regeneration of wing muscle and reproductive capacity is therefore unknown.

In the experiments reported in the present study, oviposition behaviour in the field was uncontrolled and we cannot exclude the possibility that weevils fed over this period, helping to maintain egg production. Under experimental conditions, weevils feed throughout the oviposition period (Wainhouse *et al.*, 2001; Bylund *et al.*, 2004). The inner bark of root-stumps in which weevils oviposit as well as the bark of fine roots were the only potential food sources at the site before replanting. Albrektsen *et al.* (2000) reported that the nitrogen content of the fine

roots of *P. sylvestris* increased for a period after felling so that, by locating recent clearfells, weevils may be able to exploit a 'flush' of nitrogen in fine roots. We found no evidence of an increase in nitrogen concentration in the inner bark of a small sample of root-stumps during the oviposition period (J. Tan, unpublished data), although the overall concentration of nitrogen, which varied in the range 0.6–1.1% nitrogen dry weight, would be sufficient to maintain reproductive and wing muscle development (Wainhouse *et al.*, 2004; Tan, 2006). Given that starved weevils re-absorb their eggs (Tan, 2006), it is likely that at least some feeding occurs. The small increase in wing muscle width at the end of the reproductive period, which may indicate the start of redevelopment of wing muscles, also suggests that some feeding was occurring.

In a changing climate, warmer spring and summer weather could lead to earlier re-emergence and dispersal to oviposition sites, extending the period for larval development so that univoltine development would become more widespread. An extended period of maturation feeding in mild autumn weather is likely to result in overwintering of reproductively more advanced weevils (Tan *et al.*, 2010), reducing the time required for maturation feeding in the subsequent spring. Climate change is therefore likely to have a significant impact on voltinism and possibly the abundance of pine weevil, requiring changes to the silvicultural management of this important pest.

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