

Food-plant effects on larval performance do not translate into differences in fitness between populations of *Panolis flammea* (Lepidoptera: Noctuidae)

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Abstract

In the UK, *Panolis flammea* (Denis & Schiffermüller) is a pest of monocultures of non-native lodgepole pine *Pinus contorta* Douglas, but not of the indigenous host Scots pine *P. sylvestris* L. This difference in population dynamics may be due to the adaptation of *P. flammea* populations to the phenology, chemical composition and natural enemy complement of lodgepole pine. To ascertain if there was local adaptation of *P. flammea* populations to lodgepole pine, this study tested for improved performance of both larvae and adults on the host plant species from which they were sourced, compared with their performance on the alternative host plant species. No difference was found in the relative mean performance of populations sourced from Scots pine or lodgepole pine plantations, when fed on Scots or lodgepole pine foliage. Larvae grew faster on Scots pine but this difference did not translate into differences in pupal weight, female body weight or fecundity. Indeed, those insects that had fed on lodgepole pine had a longer lifespan than those that had fed on Scots pine, which, if translated into greater probability of mating or higher fecundity, could contribute to the observed outbreak dynamics in the field. The prediction that the observed outbreak dynamics of *P. flammea* can be explained by the existence of populations locally adapted to lodgepole pine was not supported. These results cast doubt on the use of larval growth parameters as surrogates of fitness in Lepidoptera.

Introduction

Panolis flammea (Denis & Schiffermüller) (Lepidoptera: Noctuidae) has a long history as a pest of Scots pine *Pinus*

syvestris L. (Pinaceae) in continental Europe (Klimetzek, 1972). This contrasts with the situation in the UK, where it has never caused economic damage on Scots pine, but since the 1970s has become a serious pest of plantations of the introduced lodgepole pine *Pinus contorta* Douglas (Pinaceae) in northern Scotland (Stoakley, 1977; Watt & Leather, 1988; Hicks, 2001).

Contrary to what might be expected from the different population dynamics of this insect on its two main hosts, previous research has shown that Scots pine is the superior host for larval performance (Watt, 1989a; Watt *et al.*, 1991b). This suggests that plant quality *per se* cannot adequately explain the outbreak behaviour seen in the UK. What is

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likely is that several factors contribute to the contrasting dynamics of populations associated with Scots and lodgepole pine. For example, research has shown that the Scots and lodgepole pine-dominated forests differ in their natural enemy assemblages and in the impact of these natural enemies on host populations (Watt, 1989a; Watt *et al.*, 1991b; Walsh *et al.*, 1993; Aegerter, 1997; Docherty & Leather, 1997).

This disparity in the performance of *P. flammée* on its two main hosts in the UK suggests that, despite being congeneric, the host plants are, from the insects perspective, distinct both in quality (chemical composition and phenology) (Watt, 1989b) and natural enemy assemblage. Wainhouse & Jukes (1997) reported variation at a geographical scale in the genetic population structure of *P. flammée* and provided evidence of the relatively low dispersal power of this insect. They suggested that the considerable variation in genetic structure between populations could be important in determining the response of this insect to the establishment of exotic plantations. This, together with the distinct nature of the two plant communities and the outbreak dynamics of *P. flammée* on lodgepole pine for over 20 years, leads to the hypothesis that this insect has become locally adapted to this novel host (see Leather *et al.*, 1998). Local adaptation (and population differentiation) are here defined as the evolutionary increase in insect performance on one host plant (lodgepole pine) with a concomitant decline in adaptation to the other host plant (Scots pine). This trade-off in performance on the different hosts would be revealed by a population \times host plant interaction in an ANOVA (Via, 1990).

There is evidence from other systems that differentiation among conspecific populations of polyphagous insect herbivores does occur, leading to the formation of sympatric races associated with a host plant (Rausher, 1982; Feder *et al.*, 1990; Mopper *et al.*, 1995; Traxler & Joern, 1999). The bulk of studies examining the question of population differentiation and formation of insect demes have tended to concentrate on sedentary taxa, e.g. thrips (Karban, 1989) and scale insects (Hanks & Denno, 1994) under the assumption that low vagility was a pre-requisite for genetic isolation. Some evidence suggests that dispersal ability is a poor indicator of the potential for differentiation of insect populations with studies reporting local adaptation at fine spatial scales (Mopper *et al.*, 1995; Mopper, 1996; Van Zandt & Mopper, 1998).

Nevertheless, gene flow, with its potential to homogenize the genetic structure of populations means that a strong counterbalancing selection pressure, possibly plant mediated, is required before differentiation according to host plant could be observed (Ehrlich & Raven, 1969; Mopper, 1996; Mopper *et al.*, 2000). Such selective pressure has been demonstrated in other systems due to differences in phenology, (Mitter *et al.*, 1979; Dumerle, 1983; Feder *et al.*, 1990) host plant chemical composition (Feeny, 1970), or in the natural enemy assemblage (Mopper *et al.*, 1995).

Experimental evidence for population differentiation would be supplied by consistent differences in genetically-controlled life history parameters among conspecific populations (Futuyma & Peterson, 1985; Mopper *et al.*, 1995; Mackenzie, 1996; Traxler & Joern, 1999). Any local adaptation to a host plant would manifest itself as a population-level increase in fitness on that host, relative to ancestral or alternative host species. For example, although

P. flammée is historically adapted to Scots pine, local adaptation by insects sourced from lodgepole pine plantations would reveal itself as higher relative fitness, compared to insects sourced from Scots pine, when reared on lodgepole pine (Rausher, 1982; Via, 1984, 1990; Futuyma & Phillipi, 1987; Traxler & Joern, 1999). Commonly surrogate estimates of fitness (e.g. larval growth rates) are used to test for differences in relative performance on different host plants and hence evidence of local adaptation. These surrogate measures need to be accurate predictors of fitness for the insect species being examined if they are to provide evidence for local adaptation. The estimates usually used in such studies are those such as larval growth rate (Rausher, 1982) and survivorship (Mopper, 1995; Traxler & Joern, 1999) being relatively easy to measure, rather than those that perhaps show a closer relationship to fitness (e.g. lifetime fecundity). Furthermore, most studies do not then go on to test the relationship between such larval surrogates and fitness.

This paper describes a series of experiments aiming to describe the extent of differentiation among populations of *P. flammée* according to host plant species. The experiments using both larval and adult stages of *P. flammée* were designed to test two hypotheses:

1. Scottish populations of *P. flammée* show local adaptation to the host plant species from which they originated, shown by better performance on the natal host plant compared to the novel host plant species.
2. Differences in quality between the host plant species, demonstrated by differential larval growth rates, have consequences for adult reproduction and therefore fitness.

Materials and methods

Insect sampling and culture lines

In June and July 1998, cultures of *P. flammée* were established by collections of eggs and larvae from two Scots pine and two lodgepole pine forests (table 1). These sites were spatially separated from forests of the alternative type by a minimum of 10 km, sufficiently isolated given the dispersal power of this insect (Watt *et al.*, 1989; Wainhouse & Jukes, 1997). Subsequently, insects were collected from a further eight forests that summer. However, significant mortality was recorded from the cultures gathered from the field in 1998, with eight populations lost as viable breeding stock due to entomopathogenic fungi (Hicks & Watt, 2000). The larvae obtained were placed into culture chambers at ambient temperature in an insectary at the Centre for

Table 1. The original source host plant species and geographical location of the *Panolis flammée* populations used in this study.

Population	Source host	Source location	Latitude and longitude
Teindland	Scots pine	Moray	57°13.6'N 03°10.8'W
Glen Affric	Scots pine	Highland	57°35.6'N 05°07.4'W
Dalchork	Lodgepole pine	Highland	58°04.2'N 04°24.0'W
Dallas	Lodgepole pine	Moray	57°33.2'N 03°27.8'W

Ecology and Hydrology, Banchory (57°3.0'N 2°30.2'W), and reared through to pupation on the appropriate host plant. Adults emerging in April 1999 and 2000 were placed in breeding cages and provided with 10% honey solution to promote longevity and fecundity (Leather, 1984). The moths were provided with their source host plant for oviposition.

Larval performance: survival, growth and pupal weights

The populations used in these experiments, together with their geographic locations and host plants are listed in table 1. Two experiments were conducted: in 1999, the first experiment examined larval performance (survival, growth rate and pupal weight) only, whilst in 2000 a second assessment of larval performance was carried out, with a subsequent experiment in 2001 (see below) which continued performance measurements from these larvae into the adult stage.

The design of both the 1999 and 2000 experiments was the same, namely a full reciprocal transfer of larvae with cultured eggs from each population (table 1), placed on 12 replicate three-year old saplings of the natal host and 12 saplings of the novel host plant (giving 48 replicates per host plant species). The replicate trees were all planted in a standard compost substrate. Fifteen eggs were placed on each replicate tree and enclosed in polyester Organza™ cages. The number and pooled fresh weights of surviving larvae were recorded on 10, 17, 28 June and 6 July in 1999 and on 15, 22, 29 June and 6 July in 2000. Pupal weights were recorded on 13 October 1999 and 28 September 2000. The mean relative growth rates (MRGR) of the larvae were calculated from the following formula (Fisher, 1920; Radford, 1967):

$$MRGR = \frac{\ln W_f \pm \ln W_i}{t_2 \pm t_1}$$

where W_f = weight on final weighing occasion, W_i = weight at hatch, and $t_2 - t_1$ = the time between the two weighing occasions.

Adult performance: body weight, longevity and fecundity

After the second larval trial in 2000, an experiment was carried out to find out if adult performance was significantly affected by host plant species. Beginning on 4 April 2001, moths were sexed, females weighed and paired with a male from the same source population in individual breeding chambers (polypropylene pot 8 cm diameter, 10.5 cm depth). An excised shoot from three-year old pine saplings was provided for oviposition, with the cut end placed in a covered container of water. Moths were provided with 10% sugar solution as a food source. Within a given population females were weighed then placed in randomized blocks into an outdoor insectary at the Centre for Ecology and Hydrology Banchory. The experiment was monitored daily until the 19 May, with the numbers of eggs laid (removed daily) and time to death of a given female being recorded, with the end of the experiment determined by the death of the last female. This experiment looked for differences between populations in female weight, total egg production and adult survival, measured as longevity of females.

Hypothesis 1: population-level adaptation to host plant species

The first hypothesis, that *P. flammaea* populations show local adaptation to the host plant from which they are sourced, was tested using insect populations as the independent sampling units. One-way ANOVA was performed on the difference between the average performance measure (larval growth rate, pupal weight and adult female weight, longevity and fecundity) for each population reared on Scots versus lodgepole pine. The hypothesis of local adaptation predicts that the difference in population performance on Scots or lodgepole pine will favour the host plant species from which the populations originated. Statistical power was low at the level of source population (two populations per host species), but estimates of mean larval growth rates were more precise due to replication within populations. Data from both larval trials were analysed together with year as a blocking factor.

Hypothesis 2: differences between populations and effect of host plant species

The second hypothesis that population-level differences in larval performance translated to differences in adult performance parameters was tested, using the number of replicate plants in the experiments, in ANCOVA to compare performance measures between populations. Tests of larval performance (growth rate and pupal weight) included the year of experiment as a blocking factor, and the main effects and interaction of population and host plant species used to feed the larvae. The average number of larvae surviving on each tree over the course of the experiment was tested as a covariate. Analyses of adult female parameters tested the main effects and interaction of population and larval host plant species. Analyses of female longevity and fecundity also tested female weight as a covariate.

Data analysis

Data were analysed as general linear models using GLIM 3.77 (Royal Statistical Society) and were transformed where required to fulfil model assumptions of normality. Standard model checking procedures were applied. Model simplification was not required in tests of adaptation to host plant species. ANCOVA models were simplified by removing, if not significant, the contribution of the covariate and the interaction between population and host plant species. These contributions are only reported if significant. The main effects of population and food plant species are reported whether significant or not.

Results

Hypothesis 1: population-level adaptation to host plant species

Population-level adaptation of *P. flammaea* to natal host plant species was not apparent from our results. No difference was found in the relative mean performance of populations originating from Scots or lodgepole pine plantations, fed on Scots or lodgepole pine foliage in any of the parameters measured (table 2). Female body weight approached significance, however the tendency was towards greater body weight when they had fed as larvae on the

alternative host plant rather than on their natal host plant, a pattern not consistent with the hypothesis of local adaptation (fig. 1, table 2).

Hypothesis 2: differences between populations and effect of host plant species

Variability in larval growth rate between populations was found, independent of any effect of host plant species ($F_{3,167} = 3.804$, $P = 0.01$; fig. 2a). The population sourced from Glen Affric grew at the slowest rate while those insects originally sourced from Dalchork developed the fastest. An effect of host plant was found at the level of larval food-plant: larvae feeding on Scots pine grew significantly faster than those feeding on lodgepole pine ($F_{1,167} = 15.92$, $P < 0.001$; fig. 2a). There was no evidence of density-dependence in larval growth rate ($F_{1,163} = 0.972$, $P = 0.326$). There was no effect on pupal weight of the source of the larval population ($F_{3,167} = 0.690$, $P = 0.559$; fig. 2b) or food-plant ($F_{1,167} = 0.726$, $P = 0.396$; fig. 2b) or larval density ($F_{3,163} = 3.392$, $P = 0.067$).

No significant difference in adult female body weight of *P. flammæ* existed between populations ($F_{3,164} = 1.813$, $P = 0.147$; fig. 2c) nor was an effect of larval food-plant on female weight found ($F_{1,164} = 0.024$, $P = 0.878$; fig. 2c). Adult female longevity was significantly affected by larval food-plant: longevity of females that as larvae had fed on Scots pine, was lower than for those fed on lodgepole pine ($F_{1,153} = 5.478$, $P = 0.021$; fig. 2d). There was no overall effect of population origin on female longevity ($F_{3,153} = 0.255$, $P = 0.895$). A significant interaction between population and larval-food plant in female fecundity was found ($F_{3,161} = 3.161$, $P = 0.016$; fig. 2e). Those populations sourced from lodgepole pine did not differ in fecundity according to which larval food had been eaten. In contrast, the fecundity of Scots pine-sourced populations differed according to larval food-plant.

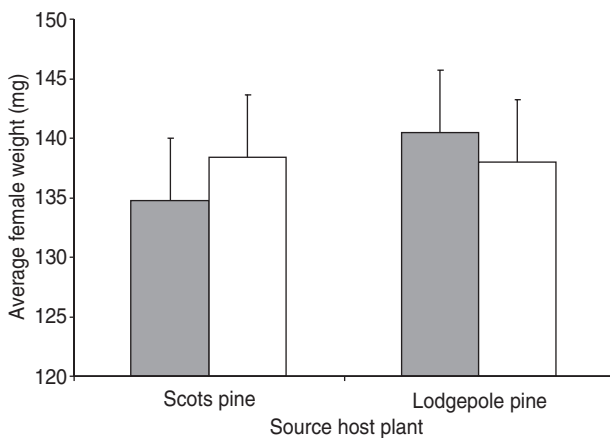


Fig. 1. The population level response of *Panolis flammæ* for each source host plant species (Scots or lodgepole pine) and larval food-plant combination (Scots (■) or lodgepole pine (□)). Evidence for locally adapted populations would be provided by improved performance on the source host species relative to the alternative host plant species. As an example, the lack of this interaction with respect to weight is shown ($F_{1,2} = 13.69$, $P = 0.066$). Full details of tests of local adaptation for all life history parameters are shown in table 2. Data are estimates of means and standard errors from a one-way ANOVA that used the difference in performance between trial hosts as the response variable.

Table 2. The difference in performance between populations of *Panolis flammæ* on their source host, compared to their performance on their non-source host in the experiments (see text for details).

Life history parameter	df	F	P
Larval growth rate	1,5	0.592	0.476
Pupal weight	1,5	0.001	0.972
Adult female weight	1,2	13.69	0.066
Adult female longevity	1,2	2.923	0.229
Adult female fecundity	1,2	0.232	0.678

Tests were one-way ANOVAs on life history parameters using population as the independent unit. Year was included as a blocking factor in the tests of larval parameters but not adult parameters. Data presented are estimates of mean and standard errors from the ANOVA model.

However, the two Scots pine populations showed contradictory patterns, with those insects from Glen Affric attaining greater fecundity when reared on Scots pine while the reverse was true for insects from Teindland (fig. 2e).

Discussion

Contrary to what may be expected from the outbreak dynamics of *P. flammæ*, these data demonstrate that Scots pine is the superior host plant for larval development. The larval growth rate of *P. flammæ* was greater on Scots pine regardless of whether the larvae had originally been sourced from Scots or lodgepole pine (fig. 2a) confirming earlier work (Watt, 1989a; Watt *et al.*, 1991b; Leather *et al.*, 1998). This refutes the idea that host plant quality can be the direct cause for the outbreak dynamics of *P. flammæ*. However, variance in quality between provenances of lodgepole pine does seem to be a factor in explaining the susceptibility of different areas to outbreaks of this insect (Leather, 1985; Leather *et al.*, 1985). The populations examined in this study also showed significant variability in larval growth rate (fig. 2a). This was, however, independent of any effect of host plant and consequently does not imply any life history adaptation.

These data do not support the first hypothesis, namely that populations of *P. flammæ* have become adapted to their locally abundant host plants. This study looked for a population-level interaction between source host plant species and host plant species fed on during the experiments, in their effect on surrogate measures of *P. flammæ* fitness. A significant and consistent interaction would provide strong evidence of local adaptation to the host plant (Rausher, 1982; Via, 1984, 1990; Mackenzie, 1996; Traxler & Joern, 1999). No such interaction between insect population and host plant species in any of the larval or adult parameters measured was found (fig. 1, table 2). Consequently there is no evidence to suggest that locally adapted populations of *P. flammæ* exist in Scotland. However, this may be because of low replication of populations in this study.

Replication must be at the level of the population to allow meaningful conclusions to be drawn about adaptation to population-level effects, such as host plant species. Statistical power in the tests of adaptation to host plant species presented here are low, although replication within populations allowed better estimates of fitness parameters to be analysed. If subsequent genotypic analysis provides

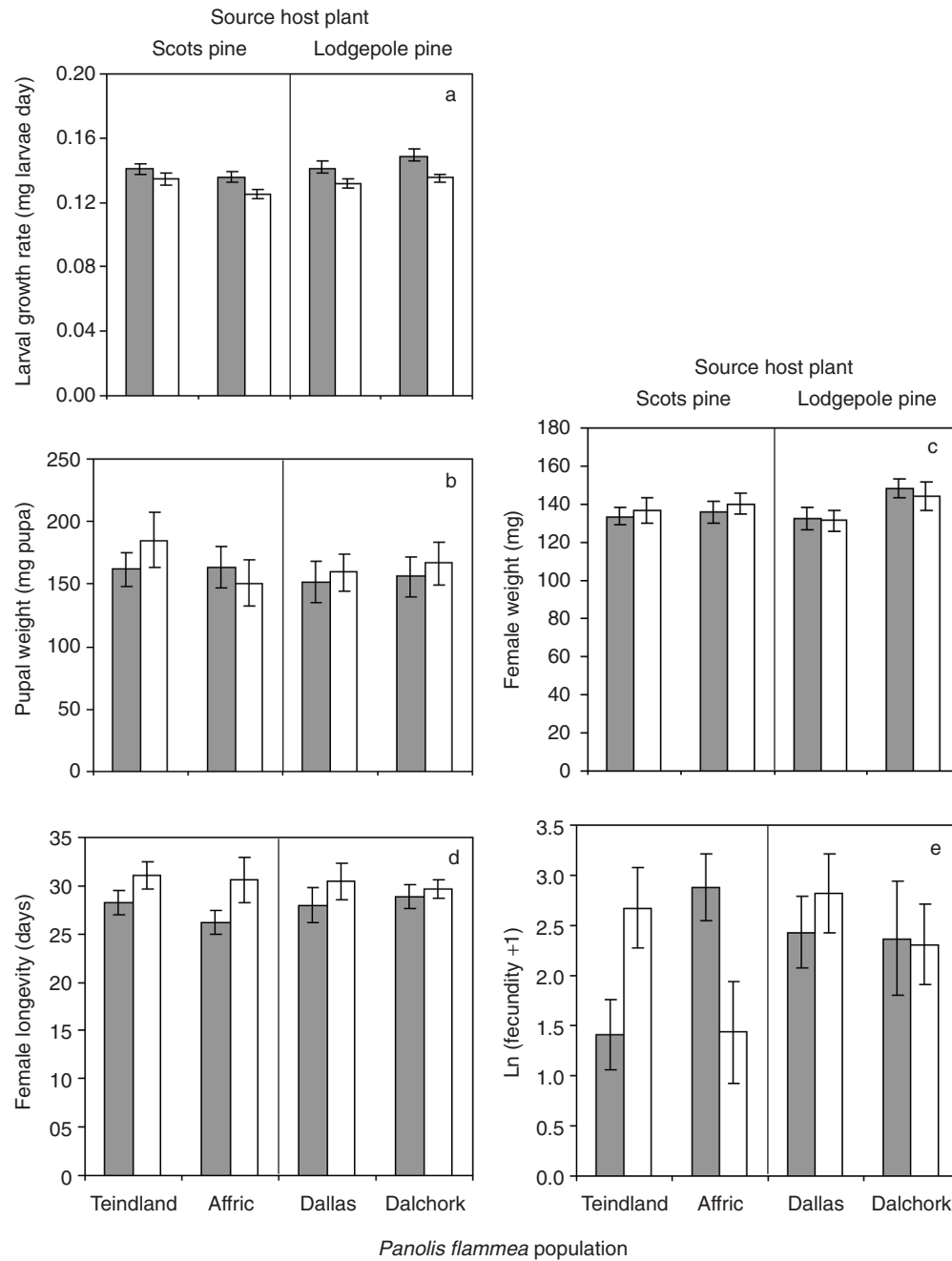


Fig. 2. The effect of *Panolis flammea* population and larval food-plant (Scots (■) or lodgepole pine (□) on (a) larval growth rate (b) pupal weight (c) female weight (d) female longevity (e) fecundity). Data are means with standard errors.

further evidence of geographic variation in *P. flammea* population structure (Wainhouse & Jukes, 1997; B.J. Hicks *et al.*, unpublished data), this investigation may bear repeating with increased replication at the level of source population (Van Zandt & Mopper, 1998).

Problems of replication aside, the lack of evidence suggesting that host-associated populations may have arisen is, perhaps, surprising. This system appears a good candidate to study local adaptation of insect populations; the host plant species significantly differ in phenology and

chemical composition (Watt, 1989b; Watt *et al.*, 1991a), which translates into differential larval mortality (Watt, 1992) and these plant species tend to be planted as monocultures. Such differences between these host plants in combination with locally abundant host patches may be expected to select for a loss of generalism and concomitant evolution of local adaptation (Via, 1990).

Apart from differential larval performance, preference for the natal host by the adult would maintain and drive the host-associated differentiation of a given population (Via,

1990). In this system the host plant is important for female selection of oviposition site, with a greater number of eggs laid on the more suitable host for larval development (Leather & Burnand, 1987). Female *P. flammaea* select hosts using chemical cues, discriminating between provenances of lodgepole pine and this discrimination may relate to differences in host quality for larval growth and development (Leather, 1985; Leather *et al.*, 1985). This study found evidence of host plant effects on fecundity, but the pattern was not consistent: populations ultimately sourced from Scots pine showed contradictory variation in fecundity according to larval food-plant (fig. 2e). An effect of larval food-plant on adult life-span was found with greater longevity in females that had as larvae consumed exclusively lodgepole pine foliage. Clearly this is an important result, if greater longevity translates into increased fecundity or increased probability of mating then the act of feeding on lodgepole may contribute to the observed outbreak dynamics in the field. This contrasts with a previous finding that insects that had fed on Scots pine compared to lodgepole pine achieved higher fecundity (Leather *et al.*, 1998). However, this study shows there is great variability between populations of this insect in the response to various life history parameters, including adult longevity. The discrepancy between this study and Leather *et al.* (1998) may be partly explained by the earlier study using a single population ultimately sourced from lodgepole pine. In effect, Leather *et al.* (1998) were only sampling at one point in the spectrum of population responses of this insect.

The second hypothesis, that larval performance parameters were a good indicator of overall fitness, was not supported. For example, our data show that differential larval growth does not translate into pupal weight or in any clear and consistent way to adult fecundity. More specifically, this lack of an effect of larval performance on subsequent adult reproduction implies that earlier studies in this system (Watt 1987, 1989a; Watt *et al.*, 1991a,b) that relied on larval performance measures to make inferences regarding the population dynamics of *P. flammaea* may be inaccurate because of the lack of consideration of the adult stage. This paper suggests caution should be exercised in the extrapolation of data from one stage in the life cycle of holometabolous insects to general conclusions on ecological and evolutionary dynamics. Consideration should be given to every stage in the life cycle if accurate conclusions are to be drawn. The need for whole life cycle studies is highlighted by the commonly contradictory findings of studies investigating the *P. flammaea*–*Pinus* system, which also serves to demonstrate the complexity of this system and probable lack of a single explanation of the ecological and evolutionary dynamics of this important pest.

Acknowledgements

The authors would like to thank David Elston (BioSS), Laurent Crespin and Rosie Hails for advice and comments on statistical analysis. Thanks also to Penny Luntz, Rachel King and Carolyn Dawson for assistance with the performance trials. Thanks to two anonymous referees whose comments improved this manuscript. This work was funded via the NERC EDGE thematic programme (grant number: GST/02/1838).

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(Accepted 4 August 2003)
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