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The pollen beetle, *Meligethes aeneus*, changes egg production rate to match host quality

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Abstract Motivation-based models dominate current theory concerning host plant selection for oviposition by herbivorous insects. A female searching for a host plant will be more likely to accept a host which is of inferior quality for her offspring if motivation is high, e.g. a large eggload or long time since last oviposition. This implies that insects will accumulate eggs if exposed to hosts of low acceptability and after a time lay eggs on such hosts. An alternative strategy for insects when exposed to less acceptable hosts is to stop producing, instead of accumulating, eggs. Thus, resources would be saved until a more acceptable host is found. If this hypothesis is true, a herbivorous insect would cease egg production when exposed to hosts of low acceptability and resume egg production when exposed to hosts of high acceptability. Previous exposure should not affect oviposition rate when an insect encounters a new host of a different quality. In an earlier study pollen beetles, *Meligethes aeneus* (F.) (Coleoptera: Nitidulidae), did not accumulate eggs in the absence of high quality hosts. In this study we monitored the daily oviposition rate of female pollen beetles on hosts plants of low (*Sinapis alba* L.), intermediate (*Brassica nigra* Koch) or high (*B. napus* L.) acceptability over a 5-day period. Individuals were then switched to an oviposition resource of a different acceptability. Beetles moved from high- to low-acceptability plants reduced their oviposition rate considerably. In the opposite case, low to high acceptability, the rate of oviposition increased markedly after the switch. When *M. aeneus* were moved from the high-acceptability host to that of intermediate acceptability oviposition rate was modified accordingly. However, when moved to the intermediate host from a host of low acceptability oviposition on *B. nigra* was much less than would normally be expected. A possible mechanism for this finding is discussed. *M. aeneus*, by adjusting oviposition rate to host acceptability, maximizes the average host quality for offspring, even at the cost of a lower egg-laying rate.

Key words Host-switching · Oogenesis · Oviposition · Egg load · *Meligethes aeneus*

Introduction

Having encountered a potential host plant, the response of an individual gravid insect is most broadly characterized as acceptance or rejection of the oviposition resource (Miller and Strickler 1984; Singer 1986). An insect making a decision concerning oviposition on a potential host effectively faces a trade-off between an immediate increment in fitness (from oviposition) and a possible loss of fitness determined by the probability of subsequently encountering and utilizing a better host (Mangel 1987). As the period of time without oviposition increases, the motivation (Singer et al. 1992) of the insect may change, with a subsequent modification of the probability of host acceptance. A number of accepted theoretical frameworks for individual host plant selection, such as the rolling fulcrum (Miller and Strickler 1984) and the hierarchy-threshold model (Courtney et al. 1989), represent this relationship. These motivation-based models explore an oviposition strategy where increasing motivation (Singer et al. 1992) or modified physiological condition (Miller and Strickler 1984) over time results in a broadening range of acceptable host plants. Motivation-based models of host plant selection currently remain the only theoretical framework for considering the effect of prolonged exposure to host plants of low acceptability.

Egg load is accepted as one important physiological factor which influences host selection by insects (Minkenberg et al. 1992; Jaenike and Papaj 1992) and positive correlations between high egg loads and acceptance of lower-ranking hosts have been found when egg loads

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increase with host deprivation (e.g. Fitt 1986). However, it has been shown that host deprivation can curb egg maturation in some insect species, thereby reducing or halting the accumulation of eggs (Fitt 1986; Weston and Miller 1987; Weston et al. 1992; Koštál 1993; Hopkins and Ekbom 1996; Alonso-Pimentel et al. 1998) and overriding one factor linked to changes in motivation.

The suppression of egg production in the absence of host stimuli may be a strategy to divert energy from egg production into host finding when suitable hosts are rare. For this to be a viable strategy the process must be quickly reversible, that is, after a period of low egg production the insect should be able to restart egg production when acceptable host plants are once again available. A Japanese species of thistle-feeding herbivorous lady beetle, *Henosepilachna niponica*, varies egg production as a mechanism for keeping the population in equilibrium with the available food resources (Ohgushi 1991). The resource availability of the thistle varied considerably over a 5-year period, yet the monophagous *H. niponica* maintained a constant density relative to the availability of this resource, mostly by changes in oviposition rate (Ohgushi 1991, 1995). When beetles, which had stopped laying eggs because of resource depletion, were moved to undamaged plants the beetles resumed egg production (Ohgushi 1995).

The oligophagous pollen beetle, *Meligethes aeneus* (F.) (Coleoptera: Nitidulidae), responds to host deprivation by reducing egg production (Hopkins and Ekbom 1996). *M. aeneus* is a small beetle, 1.5–2.5 mm long and univoltine, overwintering in forest debris as an adult. When spring temperatures reach 14°C *M. aeneus* migrates and feeds on the pollen of early-flowering plants before moving to *Brassica* crops at the onset of bud formation. *M. aeneus* then both feeds and oviposits on crucifer flower buds, and is reproductively active for up to 2 months. The gravid females lay clutches of up to six or more eggs, preferentially on buds 2–3 mm in length (Ekbom and Borg 1996). Larger and smaller buds are mostly used for adult feeding, together with open flowers. Estimates of lifetime egg production vary, but a total in excess of 200 eggs is possible.

Individual *M. aeneus* exposed to *Sinapis alba*, a poor host plant, lay eggs at a rate less than a third of that on more acceptable host plants (Ekbom and Borg 1996). *M. aeneus* reduces egg production in line with the rate of oviposition when deprived of oviposition sites or offered less acceptable host plant species (Hopkins and Ekbom 1996). Motivational change, in terms of egg load is consequently not a factor that affects *M. aeneus* host acceptance, contrary to the motivation-based models. Thus, we hypothesize that host plant acceptance by *M. aeneus* is not governed by changes in motivation due to increasing egg load. Instead, egg production is suppressed until a suitable oviposition resource is encountered. If this is the case then a further question arises: does the sequence in which *M. aeneus* encounters host plants of differing acceptability influence the oviposition rate on the current host plant? This paper addresses that question.

Materials and methods

Biological materials

Insects

M. aeneus were collected from trap plants of *Brassica juncea*, a plant species not otherwise used in the study, during early June in 1996 and 1997 (peak pollen beetle oviposition). Gravid females were identified by placing insects individually in a 40-ml plastic vial with buds of *B. juncea*. After 24–36 h buds were dissected and those individuals which had laid eggs were introduced to the experiment as reproductively active females. The pollen beetles were then arbitrarily assigned to one of six plant exposure schemes after a 24-h period without exposure to an oviposition resource.

Plants

Three cruciferous oilseed species, which have been shown to have a range of acceptability for oviposition by *M. aeneus* (Ekbom and Borg 1996), were used in this experiment. The three oilseed species used, in order of receiving least to most eggs (i.e. increasing acceptability), were *Sinapis alba* L. (white mustard, cv Mustang), *Brassica nigra* Koch (black mustard, breeding line 91–40112) and *B. napus* L. (oilseed rape, cv. Paroll). All the seed for these experiments were supplied by Svalöf-Weibull AB.

Experiments

Individual females were assigned to one of six oviposition site exposure regimens at the beginning of the experiment:

1. Continuous exposure to *B. napus* for 5 days, then switched to *B. nigra* for 5 more days ($n = 7$)
2. *B. nigra* followed by *B. napus* ($n = 13$)
3. *B. napus* followed by *S. alba* ($n = 12$)
4. *S. alba* followed by *B. napus* ($n = 5$)
5. *B. nigra* followed by *S. alba* ($n = 8$)
6. *S. alba* followed by *B. nigra* ($n = 9$)

Between 22 and 29 individuals were originally assigned to each regimen; however, some females died or went missing before the full cycle was completed. The numbers shown in brackets are the number that completed a full 10 days, and only those were used in the analyses of oviposition rates.

Females were exposed singly to oviposition sites, which consisted of one cut raceme with no flowers present and approximately 10–15 buds covering a range of sizes. The oviposition cage (cylindrical frames covered with netting, diameter 13 cm; height 30 cm) contained a cut raceme of the test plant species, placed in a 40-ml plastic vial filled with water, with cotton wool to prevent beetles from falling in. Females were constantly exposed to an oviposition site, except for a short period each day (<15 min) whilst the raceme was being changed. All flowers and buds that had been exposed to the females were carefully inspected and the number of eggs that had been laid was recorded.

Statistical analyses

Not all females introduced into the experiment completed a 10-day cycle. We wished to know whether the plant species influenced the outcome. The fate of females on the first plant to which they were exposed, of any of the three species, can be summarized as one of the following: (1) female alive and had laid eggs, (2) female alive but had laid no eggs, (3) female dead. A χ^2 analysis was applied to the resulting contingency table.

Data from individuals that survived 10 days (i.e. were alive at the end of their second 5-day period) were analysed in the following manner. Mean number of eggs laid on a plant species over the 5 days of exposure when the plant species was first were compared to means for when the plant species was second in the exposure regime (Fig. 1). Groups for each plant species were tested for significant differences using a χ^2 approximation of a median scores one-way analysis (SAS, release 6.10, procedure NPAR1WAY).

For each individual female the cumulative number of eggs laid over 5 days on the preferred host in an exposure pair was divided by the total number of eggs laid, thereby creating a response variable. This variable indicates the proportion of all the eggs laid by a female on the preferred host. In order to ascertain whether this percentage was influenced by the order in which the plants were offered, the response variable for individuals on one exposure pair was tested against the response variables for the opposite pair (for example individuals exposed to *B. napus* first and *S. alba* second were compared to individuals exposed to *S. alba* first and B. *napus* second, Fig. 2). The proportions from all individuals were transformed using an arcsine-square root transformation and subjected to a *t*-test (SAS, release 6.10).

Results

Fate of individuals after 5 days on different host plants

Mortality of adult *M. aeneus* on *S. alba* and *B. nigra* over the first 5 days was greater than on *B. napus*. There was also a higher probability of oviposition on *B. napus* over the first 5 days than on the other two species (Table 1). The distribution of responses on the three species was significantly different (χ^2 = 26.57, *df* = 4; *P* = 0.001).

Oviposition rate on different host plants

Whether *B. napus* was presented to pollen beetles directly or after 5 days on another plant, the mean number of eggs laid was not significantly different (χ^2 = 2.5, *df* = 2; *P* = 0.29, Fig. 1). The same was true for *S. alba* (χ^2 = 0.04, *df* = 2; *P* = 0.98). For *B. nigra*, however, fewer eggs were laid when a female had previously been exposed to *S. alba* (χ^2 = 6.05, *df* = 2; *P* = 0.049).

Pollen beetles consistently laid most of their eggs on *B. napus* when compared to *S. alba* irrespective of the order in which the plants were offered (*t* = 0.45, *df* = 15, *P* = 0.66) (Fig. 2a). The pattern was somewhat different when comparing *B. napus* and *B. nigra*. While the highest percentage of eggs was laid on *B. napus* this was only slightly higher than the percentage laid on *B. nigra* (Fig. 2b). The difference between the

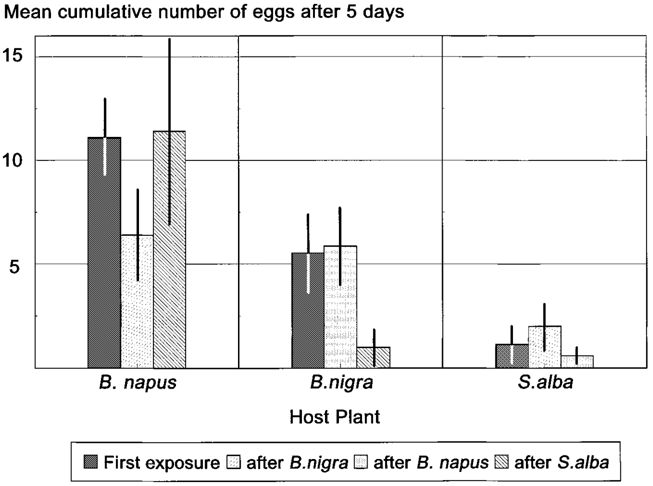

Fig. 1 The mean number of eggs laid by *Meligethes aeneus* on host plants during 5 days of exposure. The *first bar* in each group is the mean number of eggs when first exposure was to the host plant named under the group. The *following two bars* in each group are mean number of eggs laid on the host plant named under the groups during 5 days after previous exposure on another plant. *Lines* indicate SEs

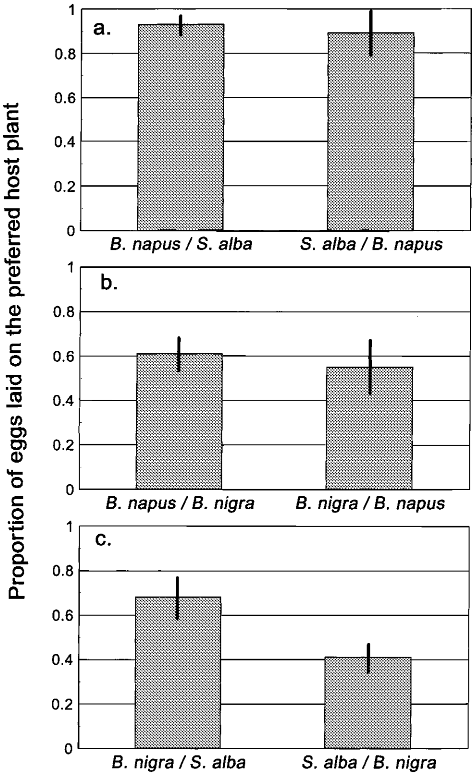

Fig. 2a–c Comparison of the proportion of eggs laid by *M. aeneus* individuals on the preferred plant in a pair. *Lines* indicate SEs. **a** The most preferred host, *Brassica napus*, compared to the least preferred host, *Sinapis alba*. **b** The most preferred host, *B. napus*, compared to the intermediately preferred host, *B. nigra*. **c** The intermediately preferred host, *B. nigra*, compared with the least preferred host, *S. alba*

Table 1 The fate of individual *Meligethes aeneus* females during the first 5-day period on one of three species of crucifers during the course of this study. Numbers of females in each category is shown (χ^2 = 26.57, *df* = 4; *P* = 0.001) as well as percentage in category for each plant species

Plant species	Alive and laid egg(s)	Alive but no eggs	Dead
Brassica napus	30	4	8
	71.4%	9.5%	19.1%
B. nigra	17	12	13
	40.5%	28.6%	30.9%
Sinapis alba	10	20	22
	19.2%	38.5%	42.3%

two exposure regimens was not statistically different ($t = 0.21$, $df = 18$, $P = 0.84$). Females laid more eggs on *B. nigra* than on *S. alba*, when *B. nigra* was presented first, but not when *S. alba* was presented first (Fig. 2c). This difference was statistically significant ($t = 2.57$, $df = 15$, $P = 0.02$).

Discussion

During the course of this study, the oviposition rate of *M. aeneus* generally changed in line with the acceptability of the host plant offered. In two of the three test sequences this occurred irrespective of the order in which hosts of differing acceptability were offered. When the switch included a host of high acceptability, offer sequence had no significant effect on the proportion of eggs laid on the preferred host compared with the alternate. There was, however, a clear exception to this when individuals were placed on *B. nigra* (intermediate acceptability) following a period on *S. alba* (low acceptability). If *B. nigra* was offered to an individual after a period on *S. alba* fewer eggs were laid over 5 days than when *B. nigra* was the first plant offered or followed 5 days on *B. napus* (Fig. 1). In addition the proportion of eggs laid on *B. nigra* compared to *S. alba* was significantly lower if the host of intermediate acceptability followed the host of lowest acceptability (Fig. 2).

The continued suppression of oviposition on the host of intermediate acceptability after a period on the low-acceptability host is the opposite of what would be predicted by motivation-based models. Motivation-based models would predict higher oviposition on *B. nigra* when it followed *S. alba*, because motivation would have changed over the course of the previous 5 days. Singer et al. (1992) define motivation as ''a non-specific readiness to oviposit'' and concluded that for the checkerspot butterfly, *Euphydryas editha*, motivation was higher in the absence of a preferred host plant. This evidence is frequently extrapolated as a general rule for phytophagous insects. Application of either the rolling fulcrum model (Miller and Strickler 1984) or hierarchy-threshold model (Courtney et al. 1989) to a pattern of increasing motivation should lead to an increasing probability of low-quality hosts being accepted over time and to immediately increased oviposition when a higher-quality host is presented after a period of host deprivation.

Several distinct explanations are possible for the results found in the *B. nigra*/*S. alba* switches of this study, operating singly or in combination. Firstly, following decreased oviposition on *S. alba*, the period tested may simply be too short to increase oviposition after moving to the intermediate host plant. However, if this were the case we would expect lower oviposition when beetles switched to *B. napus* after *S. alba*, and this was not the case. Secondly, it has never been conclusively shown that *S. alba* does not have a direct antibiotic (Painter 1941) effect on *M. aeneus*. From the results of this study, it is apparent that adult mortality is higher on *S. alba* than on other plant species confirming a strong, but not significant, trend towards shorter lifespan on *S. alba* in a previous study (Ekbom and Borg 1996). In addition, the larvae of *M. aeneus* grow more slowly and have higher mortality on *S. alba* than on other crucifers (Ekbom 1998). The extreme polyphagy of adult *M. aeneus* for food plants has generally resulted in adult antibiosis being disregarded as the mechanism behind low oviposition. Although there is only weak evidence to support an antibiotic effect, it should not be dismissed. However, if low oviposition on *S. alba* is because of antibiotic compounds or poor nutrition, any carryover should also be apparent when individuals are moved to *B. napus*, and we did not find this to be the case. Finally, on a host plant of intermediate acceptability the individual females may receive less clear cues than are found at the extremes. In consequence they may not clearly perceive the improvement in host quality.

We previously suggested that cessation of egg production in *M. aeneus* is an adaptation to short periods of poor resource quality, such as might occur if a specific developmental stage of the plant was required (Hopkins and Ekbom 1996). Although insects with short reproductive periods can gain an advantage from laying large numbers of eggs quickly, even on hosts of poor quality, this advantage may be reduced for insects with longer reproductive periods (Larsson and Ekbom 1995). There may be advantages to storing the compounds associated with egg production, rather than simply producing eggs that only generate a small increment in fitness. The sweet potato whitefly, *Bemisia tabaci*, builds up reserves of vitellogenin, vitellin and lipids in the absence of acceptable oviposition sites (Veenstra and Byrne 1998).

Several species of Coleoptera, in addition to *M. aeneus*, exhibit resource-modified oviposition strategies. The larvae of the beetle *Stator limbatus* are polyphagous seed feeders and the adults produce fewer, but larger, eggs to overcome the high mortality which normal larvae suffer when penetrating the seed coat of some species (Fox et al. 1997). Alternatively, varying egg production can stabilize populations of insects which are generally long-lived in the adult stage, but utilise unpredictable oviposition resources (Ohgushi 1991). No clear mechanism behind this type of flexibility has been shown in phytophagous insects. However, burying beetles rapidly complete ovarian maturation upon encountering a suitable oviposition resource (Scott and Traniello 1987; Trumbo et al. 1995). In one such species of burying beetle, *Nicrophorus orbicollis*, behavioural assessment of an oviposition resource was linked to a rapid increase in the haemolymph titres of juvenile hormone (JH) (Trumbo et al. 1995). They concluded that this rise in JH was suggestive of a role for JH in coordinating reproduction on an unpredictable resource. The white pine weevil, *Pissodes strobi*, has been found to have reduced ovarian development on a poor oviposition resource, a reduction that could be corrected by the topical application of JH (Sahota et al. 1998). Sahota et al. (1998) concluded that feeding on the resistant oviposition resource disrupts the normal function of the JH system by way of an antibiotic mechanism of resistance. However, if *P. strobi* requires host encounter to stimulate the function of the JH system in the same way that burying beetles do, then it is possible that they are also a species where simple host quality and availability is driving the reproductive system.

In this study we have shown that individual *M. aeneus* match oviposition rate to the changes in available oviposition resource. Motivation-based models (e.g. Miller and Strickler 1984; Courtney et al. 1989) essentially allow for the maximization of oviposition rate at the price of utilizing inferior oviposition resources. Alternatively, insects may optimize fitness by maximizing the quality of the larval host, even if it is at the expense of a lowered oviposition frequency. Preference, the relative likelihood of accepting a particular host that has been encountered, has been defined as the combination of the intrinsic acceptability of a plant, modified by the motivational state of the insect (Singer et al. 1992). *M. aeneus* displays different oviposition rates on host plants of differing acceptability, yet does not develop greater egg loads in the absence of a highly acceptable oviposition site, nor does the probability of *M. aeneus* accepting a low-ranked host increase over time (Hopkins and Ekbom 1996). The motivation of *M. aeneus* is not modified by egg accumulation, nor does it vary with time, so acceptance and preference are effectively reduced to the same value. If no host plant of high acceptability is found, current eggs are retained and production of eggs is reduced or ceases. The resources an insect thus spares may be stored (Veenstra and Byrne 1998) or diverted to somatic repair and maintenance (Carey et al. 1998).

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References

Alonso-Pimentel H, Korer JB, Nufio C, Papaj DR (1998) Role of colour and shape in host-enhanced oogenesis in the walnut fly, *Rhagoletis juglandis*. Physiol Entomol 23:97–104

Carey JR, Liedo P, Müller H-G, Wang J-L, Vaupel JW (1998) Dual models of aging in Mediterranean fruit fly females. Science 281:996–998

Courtney SP, Chen GK, Gardner A (1989) A general model for individual host selection. Oikos 55:55–65

Ekbom B (1998) Clutch size and larval performance of pollen beetles on different host plants. Oikos 83:56–64

Ekbom B, Borg A (1996) Pollen beetle (*Meligethes aeneus* Fab.) oviposition and feeding preference on different host species. Entomol Exp Appl 78:291–299

Fitt GP (1986) The influence of a shortage of hosts on the specificity of ovipositional behaviour in species of *Dacus* (Diptera, Tephritidae). Phys Entomol 11:133–143

Fox CW, Thakar MS, Mousseau, TA (1997) Egg size plasticity in a seed beetle: an adaptive maternal effect. Am Nat 149:149–163

Hopkins RJ, Ekbom B (1996) Low oviposition stimuli reduce egg production in the pollen beetle *Meligethes aeneus*. Phys Entomol 21:118–122

Jaenike J, Papaj DR (1992) Behavioural plasticity and patterns of host use by insects. In: Roitberg BD, Isman MB (eds) Insect chemical ecology, an evolutionary approach. Chapman and Hall, New York, pp 245–264

Koštál V (1993) Oogenesis and oviposition in the cabbage root fly, *Delia radicum* (Diptera: Anthomyiidae), influenced by food quality, mating and host plant availability. Eur J Entomol 90:137–147

Larsson S, Ekbom B (1995) Oviposition mistakes in herbivorous insects: confusion or a step towards a new host plant? Oikos 72:155–160

Mangel M (1987) Oviposition site selection and clutch size in insects. J Math Biol 25:1–22

Miller JR, Strickler KL (1984) Finding and accepting host plants. In: Bell WJ, Cardé RT (eds) Chemical ecology of insects. Chapman and Hall, New York, pp 127–157

Minkenberg OPJM, Tatar M, Rosenheim JA (1992) Egg load as a major source of variability in insect foraging and oviposition behavior. Oikos 65:134–142

Ohgushi T (1991) Lifetime fitness and evolution of reproductive pattern in the herbivorous lady beetle. Ecology 72:2110–2122

Ohgushi T (1995) Adaptive behavior produces stability in herbivorous lady beetle populations. In: Cappuccino N, Price PW (eds) Population dynamics, new approaches and synthesis. Academic Press, New York, pp 303–319

Painter RH (1941) The economic value and biological significance of insect resistance in plants. J Econ Entomol 34:358–367

Sahota TS, Manville JF, Peet FG, White EE, Ibaraki AI, Nault JR (1998) Resistance against white pine weevil: effects on weevil reproduction and host finding. Can Entomol 130:337–347

Scott MP, Traniello JFA (1987) Behavioural cues trigger ovarian development in the burying beetle, *Nicrophorus tomentosus*. J Insect Physiol 33:693–696

Singer MC (1986) The definition and measurement of oviposition preference in plant feeding insects. In: Miller J, Miller TA (eds) Insect-plant interactions. Springer, Berlin Heidelberg New York, pp 65–94

Singer MC, Vasco D, Parmesan C, Thomas CD, Ng D (1992) Distinguishing between "preference" and "motivation" in food choice: an example from insect oviposition. Anim Behav 44:463–471

Trumbo ST, Borst DW, Robinson GE (1995) Rapid elevation of juvenile hormone titer during behavioral assessment of the breeding resource by the burying beetle, *Nicrophorus orbicollis*. J Insect Physiol 41:535–543

Veenstra KH, Byrne DN (1998) Effects of starvation and oviposition activity on the reproductive physiology of the sweet potato whitefly. Phys Entomol 23:62–68

Weston PA, Miller JR (1987) Influence of ovipositional resource quality on fecundity of the seedcorn fly. Environ Entomol 16:400–404

Weston PA, Keller JE, Miller JR (1992) Oviposition stimulus deprivation and its effect on lifetime fecundity of *Delia antiqua* (Meigen) (Diptera: Anthomyiidae). Environ Entomol 21:560–565