Life history correlates and reproductive biology of *Laelius pedatus* (Hymenoptera: Bethylidae) in The Netherlands

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Abstract. Bethylid wasps are a medium sized family of parasitic Hymenoptera, with biological control potential, which have recently proved excellent model systems for testing evolutionary and life history theory. We report observations on a species of *Laelius* from The Netherlands. The species is morphologically indistinguishable from *Laelius pedatus*, previously reported only from the New World. Reciprocal crosses between the Dutch wasps and *L. pedatus* from Madison, Wisconsin, USA confirmed that the Dutch population belongs to *L. pedatus*. We compared the life history of the Dutch wasps with those from Madison by rearing them on *Trogoderma glabrum*, but found no significant differences. The Dutch wasps successfully parasitize *Trogoderma angustum*, an invasive museum and domestic pest found in situ, but suffer high developmental mortality on *T. glabrum*. Wasp egg size was positively correlated with the size of ovipositing female, which was also negatively correlated with the developmental mortality of offspring. Larger wasps also carried more mature eggs. Time taken to lay the clutch increased with the size of the eventual clutch laid and was longer in unmated than mated females. When some wasps died before completing development, surviving members of the brood grew to a larger size and took longer to complete development. The number of males per brood increased with previous oviposition experience, an indication of sperm depletion through life. We discuss the implications of these trends for parasitoid life history theory.

INTRODUCTION

Bethylid wasps (Hymenoptera: Bethylidae) are a globally distributed family of aculeate ectoparasitoids with about 2,000 known species (Evans, 1978; Gauld & Bolton, 1988; Gordh & Móczár, 1990). Bethylid species have attracted the attention of applied entomologists because their hosts (the larvae, and more rarely pupae, of Lepidoptera and Coleoptera) include many important pests of crops and stored products (e.g. Murphy & Moore, 1990; Pérez-Lachaud & Hardy, 1999). In addition, bethylid wasps display behaviours and life histories which have attracted the attention of evolutionary biologists (e.g. Hardy & Mayhew, 1998; Mayhew & Hardy, 1998).

A major barrier to both the effective use of Bethylidae in biological control and to using them to develop evolutionary theory is that biological details are available only for only a small proportion of species, and even then our knowledge is usually very superficial (such as location of collection, host species, and host habitat). Here we report observations on a species of *Laelius* collected in The Netherlands. We perform experiments to determine the identity of the wasp. We observe the life history of the wasp, investigate correlations between life history traits, and observe how they are affected by wasp size, host size and host species. We then discuss the relevance of our findings to the biological control of host species and to developing life history theory.

Biology of *Laelius*

Laelius Ashmead (Hymenoptera: Bethylidae: Epyrinae) is a genus of small black wasps containing 15 described extant species and another two fossil species known from Baltic amber (Gordh & Móczár, 1990). Some taxonomists regard the genus *Allepyris* Kieffer, containing 5 species, as synonymous with *Laelius* (e.g. Perkins, 1976; Fitton et al., 1978). *Laelius* have been collected throughout the New World, Europe, North Africa and India, and *Allepyris* in Europe, North Africa, Japan and the Canary Islands. Species in both genera are idiobiont ectoparasites on the larvae of dermestid beetles (Coleoptera: Dermestidae) and a few other coleopteran species, associated with dead wood or other stored products (Gordh & Móczár, 1990). Their association with destructive pests makes them potential biological control agents. With the exception of *L. utilis* Cockerell, an American species which has been found in Sweden amongst imported American timber, no species has previously been found in both the New and Old Worlds (Gordh & Móczár, 1990). Further biological details are known for only a few species. Females typically lay small numbers (1–6) of eggs per host, paralyzing the host sometimes several hours before ovipositing (Mayhew & Hardy, 1998). During the intervening time the host may be transported to a concealed location (Mertins, 1980). Sex ratios are typically female

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biased, with males emerging prior to females and mating with them upon emergence (Hardy & Mayhew, 1998).

Laelius pedatus (Say) is the best known species in the genus. *L. pedatus* was previously recorded widely in North America and also Brazil (Evans, 1978; Gordh & Móczár, 1990), where it is the only species in its genus known from the southern hemisphere. Body length varies from 1.8–3.3 mm (Evans, 1978), and males are on average smaller than females (Mertins, 1980; Hardy & Mayhew, 1998). Adult females are known to attack the larvae of at least 7 species of dermestid beetles with varying degrees of developmental mortality (d.m.): *Anthrenus verbasci* L. (d.m. = 0.068, Morgan & Cook, 1994), *A. flavipes* (Leconte) (d.m. = 0.134, Morgan & Cook, 1994; d.m. = 0.132, Mayhew & Godfray, 1997), *A. sarnicus* (Mroczk) (d.m. = 0.068, Morgan & Cook, 1994), *Trogoderma variabile* Ballion (d.m. = 0.276, Klein et al., 1991) and *T. glabrum* Herbst (d.m. = 0.631, Klein et al., 1991). Al-Kirshi et al. (1997) reared the wasp successfully on *Trogoderma angustum* (Solier) and *T. granarium* Everts. Mertins (1982) also reports that four *Trogoderma* species are attacked with rare partial success and that little or no interest is shown in *Attagenus megatona* F. or *Thylodrias contractus* Motschulsky (he also reports that the species is unable to attack *A. flavipes*, c.f. Morgan & Cook, 1994; Mayhew & Godfray, 1997). Mortality on the three *Anthrenus* spp. is significantly overdispersed, meaning that it tends to be aggregated on individual hosts, although is not clutch size or host weight dependent (Hardy et al., 1998; c.f. Morgan & Cook, 1994). Hosts are located at least partially by kairomones (Qi Yuntai & Burkholder, 1990; Qi Yuntai et al., 1990).

The oviposition behaviour of *L. pedatus* has been the focus of several evolutionary studies. Clutch size ranges from 1–6 depending critically on the size of the host, and even when developmental mortality is very low, larger offspring result from larger hosts suggesting that clutch size does not completely compensate for the larger resources provided by larger hosts given that the entire host is usually consumed (Mayhew, 1998). The variability in mean offspring size on each clutch decreases with increasing clutch size as predicted by resource allocation models for small broods (Mayhew, 1998). In gregarious clutches, offspring sex ratio almost exactly equals the reciprocal of clutch size and is extremely precise with nearly every clutch receiving a single male and one or more females (Morgan & Cook, 1994; Mayhew & Godfray, 1997; Hardy et al., 1998). The latter conforms to the expectations of single foundress local mate competition. The male is usually the last egg to be oviposited (Mertins, 1980; Mayhew, 1996). In solitary clutches, males are laid on very small hosts and females on larger hosts, a strategy known as conditional sex expression, which suggests that females benefit more from large size than males (Mayhew & Godfray, 1997). Female wasps encountering a clutch of eggs laid by a conspecific female will invariably remove them prior to laying her own clutch, a tactic known as ovicide, considered adaptive because egg removal takes little time but reduces competition for resources among

her offspring (Mayhew, 1997). This means that only a single female will successfully produce offspring on each host. The inbreeding and ovicidal behaviour displayed by *L. pedatus* and many other bethylids implies that relatedness between brood mates is high, which may provide a reason for the stability of small gregarious broods in the face of other pressures for siblicidal behaviour between broodmates (see Mayhew et al., 1998).

MATERIAL AND METHODS

In situ cultures

Cultures of *Laelius* wasps were initiated at one site of capture in The Netherlands (a house in Amsterdam). Three independent lines of wasps were kept, each derived from a single Dutch female: two caught in the same house in Amsterdam and one in a house in Zoetermeer (Heitmans & Mayhew, unpubl.). All three wasps produced female offspring, hence had been inseminated prior to capture. Two lines were maintained for a full year (the Zoetermeer line went extinct within 2 generations due to lack of males) using three species of hosts: many *T. angustum* were captured from an infested dried insect collection at the same site, and these were supplemented with some *T. glabrum* cultured in the laboratory (see below) and some *A. verbasci* captured elsewhere. Female wasps were kept in 80 × 25 mm glass tubes with foam stoppers, supplied with a slip of tissue paper and a drop of honey. The foam stoppers prevented entry or exit of conspecific wasps, but allowed movement of certain parasites, predators and pathogens (see below). Wasps were presented serially with individual hosts as availability allowed. Hosts were inspected daily and, if they carried a clutch of wasp eggs, were removed to another tube to be reared through. Temperature in the house ranged from 19–28°C, lighting was incidental (the wasps were kept out of direct sun), and varied from 11–16 h during the year. Humidity was not controlled or measured.

The following data were collected: female size (mesosoma length), wasp line identity, the number of broods the female had previously laid, brood size and date laid, number of adult wasps emerging, their size (mesosoma length) and sex, host length and host width.

A total of 61 female wasps laid a total of 405 broods, of which we had full data (on all the above variables) for 333 broods laid by 44 females. Twenty-nine female wasps, of variable age and size, were also dissected under a binocular microscope and the number of ovarioles and mature eggs in the abdomen counted. We also had data on time (in days) from presenting a wasp with a host until oviposition, for 58 broods (all on *T. angustum*) from one of the Amsterdam lines.

Laboratory cultures

A laboratory culture of *L. pedatus* was set up from a single female collected in a house in Amsterdam. Five generations of the wasp were reared on *T. angustum* collected from the same location. After the fifth generation we maintained wasps *on T. glabrum* for 3 generations (maintained under the same conditions) due to a shortage of *T. angustum*. All hosts were maintained on a mixture of herring meal and powdered milk at 30°C without incidental light or humidity control. Mated female wasps were placed with single hosts on the first day after wasp emergence in a 5 cm Petri dish lined with tissue paper. The dishes were maintained at 25°C, 70% rh and 16L : 8D photoperiod. Voucher specimens of the culture were deposited at The Natural History Museum, London, UK, at the Nationaal Natuurhistorisch Museum, Naturalis, Leiden, The Netherlands, and at

the Zoological Museum (University of Amsterdam), Amsterdam, The Netherlands.

Laboratory experiments

Mating experiments

We performed mating experiments to test the identity of the Dutch wasps. A culture of *L. pedatus* from Madison, Wisconsin, USA was used as test material for crosses with the laboratory culture from Amsterdam. The Madison stock has been used for several previous biological studies of *L. pedatus* (e.g. Mertins, 1980, 1982; Klein & Beckage, 1990; Qi Yuntai & Burkholder, 1990; Qi Yuntai et al., 1990; Klein et al., 1991; Al-Kirshi et al., 1997). An unmated female wasp was placed at the bottom of a 80 × 25 mm glass tube, and then an unmated male wasp introduced into the top of the tube. Time from introduction of the wasp until mating was recorded, as well as time spent during mating. After mating, the male was removed and the female was then placed in a 50 mm Petri dish lined with tissue paper with a single host and left until oviposition occurred, after which the female was removed. Some females were presented with up to 6 hosts in series as host availability allowed. Four crosses were performed: the two reciprocal crosses between cultures and the two within cultures to serve as controls. Seven to nine replicates were performed of each cross. Wasps surviving to pupation were placed in separate rearing tubes. To observe the fertility of F1 females (male F1 offspring are not hybrids in haplodiploid species because they are produced parthenogenetically), these were mated with their brothers and then presented with hosts in the same way. We then compared the time to mating, time spent mating, developmental mortality, and sex ratio across treatments.

Comparisons on *T. glabrum*

To observe if the biology of the Dutch wasp differed from that of *L. pedatus* from Madison, we reared both on *T. glabrum* (of which we had many individuals) under identical conditions as above, and recorded the following variables which were then compared across cultures: size (mesosoma length) of ovipositing female, clutch size, egg length, egg width, host weight (as a covariate), age at death of each developing offspring (recorded daily) number, sex and size of emerging offspring, time from presentation of host to oviposition, time from oviposition to adult emergence. Thirty-eight clutches of the Dutch strain were reared, and 23 of the Madison strain.

Biology on *T. angustum*

We reared five generations of the Dutch laboratory culture on *T. angustum*, the host found at the site of collection in Amsterdam. The first generation of clutches ($n = 10$) were the progeny of a single female and were not included in our experimental data. The remaining clutches ($n = 44$) were all the first brood laid by different females and were analyzed statistically. These 44 wasps were all descendents of the first female: they comprised 9 daughters, 14 grand-daughters, 11 great-grand-daughters and 10 great-great-grand-daughters. We measured the size (mesosoma length) of each ovipositing female, clutch size, host weight, host length, host width, number, sex and size of emerging adults, and days from oviposition to emergence. Longevity of adult wasps reared on this host was measured by placing females in 2 cm diameter glass tubes after they had laid a single clutch of eggs, and males after they had mated once. They were supplied with honey at 25°C as above.

Analysis

Analysis was performed using general linear modelling in the GLIM statistical package (see Crawley, 1993). We initially assumed Poisson error variance for count data and binomial error variance for proportion data. Statistical models were built by stepwise subtraction from a full model including all potential explanatory variables for which we had data, starting with the least significant terms. Significance was assessed by the change in deviance when a variable was removed from the model, under normal errors by an *F* test, and under Poisson and binomial errors by a χ^2 test. Only significant terms were allowed to remain in the model, which is then termed minimally adequate. The appropriateness of Poisson or binomial errors was assessed by a heterogeneity factor, equal to the residual deviance divided by the residual degrees of freedom. If the heterogeneity factor was > 1.3, the model was rescaled using the value of Pearson's χ^2/df (see Crawley, 1993). The percentage of the total deviance explained by a factor (% dev) is used as an informal measure of explanatory power for Poisson and binomial errors, equivalent to *r*-squared in normal errors. Longevity was analyzed by fitting a Weibull distribution to the wasp age at death. The shape parameter of the Weibull distribution is 1 when the risk of death is constant over time, > 1 when it increases with time and < 1 when it decreases with time. Factors which led to a significant decrease in deviance when fitted to the model were again assessed with a χ^2 test.

When comparing life history differences in the Dutch and Madison wasps, we accepted a significant difference between strains if removal of the binary factor "strain" from the model led to a significant reduction in deviance. Egg volume, *V*, was estimated from the formula $V = 4/3\pi ab^2$ where a = half the maximum egg length and b = half the maximum egg width, which assumes an ovoid egg shape.

The analysis of in situ cultures is complicated by the fact that females laid several broods each, making it possible that broods are not statistically independent. To avoid this, any analysis was carried out using female wasps rather then the broods they laid as replicates, averaging variables over all the broods each laid.

To test whether brood sex ratio and mortality variances were significantly different from binomial, we used the Meelis test (see Nagelkerke & Sabelis, 1991). In the Meelis test, *R* is the variance ratio, calculated as the observed variance over that expected under a binomial distribution. Therefore $R = 1$ when variance is binomial, $R < 1$ when underdispersed (similar distribution across broods) and $R > 1$ when overdispersed (dissimilar distribution across broods). The test statistic *U* allows us to judge the significance of any deviation from binomial variance. We used the Meelis test on the raw brood data for the in situ cultures regardless of the non-independence of broods laid by different females because there is currently no way to perform a nested analysis of brood sex ratio variance. We define sex ratio as the proportion males [m/(m + f)].

RESULTS

In situ cultures

Clutch size typically ranged from 1 to 6 eggs, although one clutch each of 7 and 8 eggs were found (the latter might represent cases of self-superparasitism). Mean host size was the only factor which significantly explained mean brood size per female, and host length explained more variance than host width (length: $r^2 = 0.380$, $F_{1,43} = 16.33$, $P < 0.01$. Width: $r^2 = 0.322$, $F_{1,43} = 13.85$, $P < 0.01$).

Out of 1,162 offspring laid, 536 died before adult emergence. We observed how death occurred in 451 cases: predatory mites killed 50 eggs or larvae, and hyperparasitoids *Melittobia acasta* (Walker) (Hymenoptera: Eulophidae) killed 41 larvae or pupae. In one brood all 3 eggs

turned an unusual red colour and did not hatch, perhaps due to a bacterial infection. The host sometimes became unsuitable either through desiccation or microbe infection, resulting in the death of 37 offspring. Female wasps killed 12 of their own eggs. Twenty-six offspring died because the positioning of the eggs precluded feeding upon hatching. The majority of offspring died during the egg and larval stages through unknown causes, which probably included damage caused by host movements (particularly severe in *T. glabrum* and probably one cause of high mortality on this host), inability to pierce the host integument, starvation through competition, desiccation and microbe infection. Eighty-one eggs and 188 larvae died in this way. Thirteen pupae also died in their cocoons from unknown causes.

The only variable which significantly affected mean offspring mortality per female was the proportion of eggs which were laid on *T. glabrum* as opposed to *T. angustum* hosts (the relationship was positive: % dev = 27.6, χ^2_1 = 20.1, $P < 0.001$). Mean ($\pm$ SE) brood developmental mortality was 0.7514 $\pm$ 0.039 on *T. glabrum* (n = 92 broods) and 0.395 $\pm$ 0.027 on *T. angustum* (n = 240 broods).

Females laid up to 24 clutches and 58 eggs in their lifetime. Lifetime number of adult offspring produced per female in culture depended significantly on the number of broods laid (i.e. the number of hosts presented) (b = 0.110, % dev = 42.77, χ^2_1 = 46.74, $P < 0.001$), the proportion of eggs which were laid on *T. glabrum* (b = -1.415, % dev = 14.89, χ^2_1 = 16.27, $P < 0.001$), host length (b = -0.718, % dev = 7.28, χ^2_1 = 7.96, $P < 0.005$), mean clutch size per host (b = 0.272, % dev = 4.80, χ^2_1 = 5.25, $P < 0.025$), and host width (b = 1.550, % dev = 4.36, χ^2_1 = 4.76, $P < 0.05$), but female wasp size was (marginally) not significant (b = 1.323, % dev = 2.56, χ^2_1 = 2.79, 0.1 > $P > 0.05$).

When analyzing the data on sex ratio at emergence, we excluded 5 females which produced only male offspring and which were therefore probably not inseminated. We initially included all gregarious broods from females which produced at least one surviving female offspring, regardless of the degree of mortality. Sex ratio (per female) was negatively correlated with clutch size (b = -0.362, χ^2_1 = 6.18, $P < 0.025$), positively correlated with offspring survival (b = 1.00, χ^2_1 = 4.14, $P < 0.05$), and negatively correlated with female body size (b = -2.12, χ^2_1 = 4.12, $P < 0.05$). The number of males per brood was normally 0 (n = 174) or 1 (n = 91), although a number of broods had more, with 2 males (n = 26), 3 males (n = 6), 4 males (n = 2) and even 5 males (n = 1) sometimes emerging from clutches produced by females which did produce at least one female offspring. Mean number of males per brood was positively correlated with the number of broods a female laid during her life ($F_{1,33}$ = 17.68, $P < 0.01$), and positively correlated with the survival of offspring ($F_{1,33}$ = 15.31, $P < 0.01$).

Amongst gregarious broods in which no mortality occurred (n = 80 broods, 29 females) and at least one female offspring was produced by the ovipositing female, mean sex ratio did not significantly depend on mean
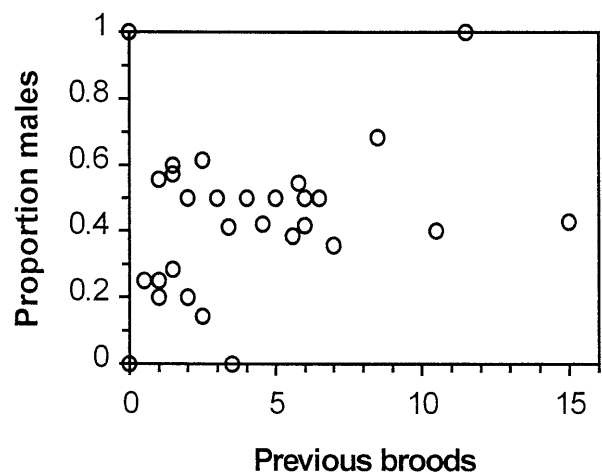

Fig. 1. Offspring sex ratios at adult emergence (proportion males) per ovipositing female in gregarious broods without developmental mortality against the number of broods previously laid by the female. There is a significant rise in proportion males with previous oviposition experience, suggestive of sperm depletion.

clutch size (χ^2_1 = 1.741, $P > 0.1$). However, it was positively related to the mean number of clutches previously laid by a female (χ^2_1 = 6.840, $P < 0.01$) (Fig. 1), was different in the wasp lines (χ^2_1 = 4.774, $P < 0.05$) and decreased as the proportion of *T. glabrum* hosts increased (χ^2_1 = 4.146, $P < 0.05$). The former trend, also found in the complete data set, is suggestive of sperm depletion over time, because unfertilized eggs are male. Examination of the raw brood size data suggested that sperm depletion was indeed occurring: one female laid 14 clutches, but only males were produced from the seventh brood on, or 20th egg laid, 17 days after the first brood. Another female laid 12 broods but produced only males in the last three broods (after having laid 29 eggs, the tenth clutch laid 44 days after the first). Other less clear-cut examples occurred in which the number of males per brood seemed to increase over time although females were sometimes also laid. The number of males per brood was most commonly 1 in every brood size, although varied between 0 and 2 in clutches of 2 eggs, 0 and 3 in clutches of 3 eggs, 1 and 4 in clutches of 4 eggs, and 1 and 2 in clutches of 5 eggs. Only 1 clutch of 6 eggs suffered no mortality, and that produced 3 males. The number of males per clutch was not affected by any variable investigated. There was evidence for sex ratio precision (R = 0.770), and this was significant using a one-tailed test (U = -1.808, $P < 0.05$), but not using a two-tailed test.

A total of 39 single egg broods were laid, of which 17 (laid by 12 females) survived to adulthood. Four males and 13 females emerged, but the proportion males (per ovipositing female) did not signficantly depend on any variable investigated.

When analyzing number of mature eggs in the wasp abdomen, or number of ovarioles, we found large underdispersion under Poisson errors, suggesting that such an error structure was inappropriate. Therefore the

5
4   2 4   3 3 3
3 1 2 2 3 3   1
2 1   1
1
0

Mature eggs

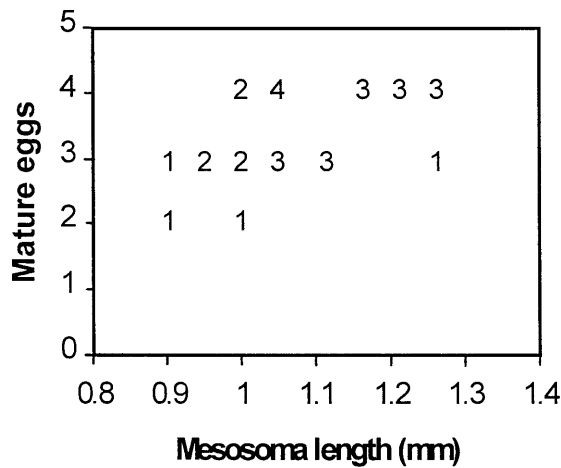0.8 0.9 1 1.1 1.2 1.3 1.4

Mesosoma length (mm)

Fig. 2. The number of mature eggs in the abdomen of female wasps against wasp size. Numbers are superimposed data points.

data were analyzed under normal errors using a square root transformation. Number of mature eggs varied from 2 to 4, and increased significantly with wasp size ($F_{1,27}$ = 11.55, $P < 0.01$) (Fig. 2). The number of visible ovarioles also increased with wasp size ($F_{1,27}$ = 14.29, $P < 0.01$), varying from 4 to 6, although ovarioles without mature eggs were sometimes difficult to distinguish after dissection. We therefore view this as a minimum estimate of ovariole number. It is notable that the maximum number of ovarioles coincides with the typical maximum clutch size. The (square root) number of mature eggs was also positively correlated with the (square root) number of visible ovarioles ($F_{1,27}$ = 31.98, $P < 0.01$). Time to lay a clutch took up to 4 days, and was positively correlated with the clutch size laid (% dev = 27.55, χ^2_1 = 5.697, $P < 0.025$).

Mating experiments

All time measurements were right skewed and so were ln-transformed prior to analysis. Mating occurred in all crosses between strains as within strains. Time to mating (ln-transformed) did not significantly differ between treatments ($F_{3,28}$ = 2.46, $P > 0.05$), and neither did time spent during mating (ln-transformed) ($F_{3,28}$ = 1.46, $P > 0.05$) (Table 1). Survival of offspring to adult emergence did vary significantly between treatments (χ^2_3 = 15.12, $P < 0.01$), with survival being lowest in the two inter-culture crosses (Table 1). The sex ratio of emerging offspring did not differ between treatments (χ^2_3 = 5.19, $P > 0.1$).

F1 females from between-strain crosses were only obtained from those with males from Madison and females from Amsterdam (very few offspring at all survived to adulthood on *T. glabrum* hosts). Four of these F1 females were allowed to mate with their brothers and then provided with hosts. All 4 laid eggs and 3 produced 1 surviving offspring each, all of which were female. Thus, the F1 females were both viable and fertile.

Comparison of strains on *T. glabrum* in the laboratory

There was never a significant difference between wasp strains in any of the life history variables we investigated. However, some other findings are noteworthy:

Proportion developmental mortality (0.743 ± 0.037) was explained by three factors: the generation in which a clutch was laid, being highest in the first generation (χ^2_2 = 9.377, $P < 0.01$); female size, being lower in clutches laid by larger females (χ^2_1 = 7.703, $P < 0.01$); and egg length, being lower with increasing egg length (χ^2_1 = 6.282, $P < 0.025$). Wasp strain was marginally non-significant (χ^2_1 = 3.112, $P < 0.1$).

Estimated egg volume was significantly higher in clutches laid by larger females ($F_{1,60}$ = 4.67, $P < 0.05$) (Fig. 3), but was not affected by the clutch size laid ($F_{1,54}$ = 0.164, $P > 0.05$), whether the wasp was mated ($F_{1,55}$ = 0.210, $P > 0.05$), the generation in which a clutch was laid ($F_{2,58}$ = 2.267, $P > 0.05$), or wasp strain ($F_{1,59}$ = 0.272, $P > 0.05$). Egg length was also significantly correlated with female size ($F_{1,60}$ = 8.00, $P < 0.01$), but egg width was not ($F_{1,60}$ = 1.05, $P > 0.05$).

Time taken to lay a clutch increased significantly with the clutch size ($F_{1,59}$ = 9.10, $P < 0.01$) (Fig. 4), and was longer in unmated females than in mated females ($F_{1,59}$ = 14.94, $P < 0.01$). A non-linear clutch size term (clutch size squared) did not improve the fit of the model ($F_{1,57}$ = 0.724, $P > 0.05$).

Biology of Dutch wasp on *T. angustum* in the laboratory

The single female from which our laboratory culture originated was 2.36 mm in length and had a mesosoma length of 0.9 mm. She lived a subsequent 74 days after capture and laid 24 eggs in 10 clutches ranging from 1–5 eggs per host, giving rise to 17 adult offspring of which six were male and eleven female. In subsequent generations, female wasps were only given a single host so that clutches could be treated as statistically independent.

Clutch size in generations 2–5 ranged from 2–6 eggs and significantly increased with both host weight (% dev = 0.846, χ^2_1 = 21.89, $P < 0.001$), host width (% dev =

TABLE 1. Comparison of mating and resulting offspring produced within and between *L. pedatus* strains (means ± SE).

| Treatment	n	Ln (time to mate, s)	Ln (time mating, s)	Eggs laid	F1 offspring emerging	F1 females emerging
Amsterdam ♂ Amsterdam ♀	7	3.753 ± 0.970	4.964 ± 0.096	4.429 ± 1.131	1.429 ± 0.571	1.286 ± 0.474
Madison ♂ Madison ♀	8	5.072 ± 0.317	5.275 ± 0.108	6.125 ± 1.481	2.000 ± 0.567	1.250 ± 0.412
Amsterdam ♂ Madison ♀	9	3.820 ± 0.322	5.114 ± 0.123	7.444 ± 0.959	0.111 ± 0.111	0.000 ± 0.000
Madison ♂ Amsterdam ♀	8	2.799 ± 0.691	5.161 ± 0.066	5.625 ± 1.945	1.125 ± 0.666	0.750 ± 0.412
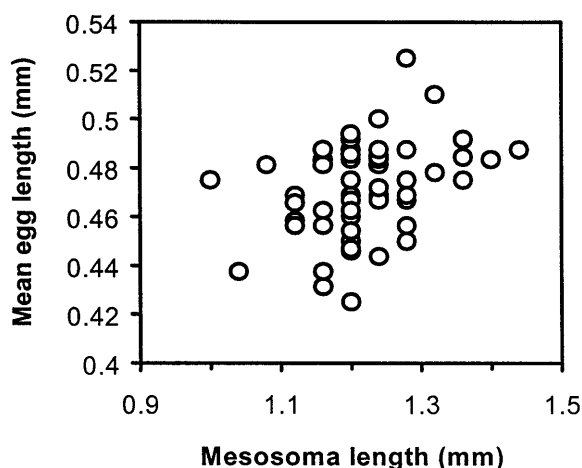
Fig. 3. Egg length against the size of the mother in *Laelius pedatus*. Data are from both Dutch and Madison strains of the wasp from clutches laid on *Trogoderma glabrum*.

0.847, χ^2_1 = 21.93, P < 0.001), and host length (% dev = 0.739, χ^2_1 = 19.12, P < 0.001), of which host width was marginally the better predictor, and host length the worst. Mean offspring size per brood did not significantly depend on clutch size ($F_{1,42}$ = 0.510, P > 0.1), but increased significantly with host weight (r^2 = 0.116, $F_{1,42}$ = 5.530, P < 0.05) when fitted on its own. However, this relationship was not significant when developmental mortality was controlled for, which was positively related to offspring size (r^2 = 0.290, $F_{1,43}$ = 12.49, P < 0.01) (Fig. 5). The variance in the mean offspring size for each brood did not significantly depend on clutch size (Levene's statistic = 0.9874, P (2-tailed) = 0.426). Mean (± SE) developmental mortality was 0.0534 ± 0.0192, did not vary with clutch size (χ^2_1 = 0.165, P > 0.1) or host weight (χ^2_1 = 0.883, P > 0.1)) and the mortality distribution across broods was not significantly different from binomial (R = 0.913, U = –0.642, P > 0.05). Mean (± SE) development time was 46.86 ± 0.22d and was positively correlated with both the mean size (thorax length) of offspring in a brood (r^2 = 0.230, $F_{1,42}$ = 12.57, P < 0.01) and the proportion of developmental mortality (r^2 = 0.115, $F_{1,42}$ = 5.47, P < 0.05). Mean (± SE) secondary brood sex ratio was 0.4240 ± 0.0324, decreased significantly with clutch size (χ^2_1 = 7.554, P < 0.01), and the secondary brood sex ratio variance was significantly underdispersed (R = 0.594, U = –2.59, P < 0.01). The mean (± SE) number of males per clutch was 1.205 ± 0.101 and did not significantly depend on clutch size (χ^2_1 = 0.593, P > 0.1).

Mean (± SE) wasp longevity was 63.3 ± 2.12 d, ranging up to 101 d, and followed a Weibull distribution with shape parameter 3.69 indicating that the risk of death increased with age (χ^2_1 = 132.86, P < 0.001). Adding either sex (χ^2_1 = 9.75, P < 0.01), or wasp thorax length (χ^2_1 = 6.70, P < 0.01) to the model led to a weak but significant reduction in deviance (size: % dev = 0.87, sex: % dev = 1.26, with females living longer than males).

CONCLUSIONS AND DISCUSSION

Species identity

We have described aspects of the biology of a species of *Laelius* from the Netherlands. The species morphology is identical with *L. pedatus*, and no differences in life history were detected when the wasps were reared on *T. glabrum*. In addition, mating occurs readily and gene flow is possible between the Dutch wasps and *L. pedatus* from the USA. These similarities suggest that the Dutch wasp is *L. pedatus*. The cross between Amsterdam males and Madison females produced no female offspring. Incomplete post-zygotic isolation is commonly observed amongst sister-species crosses in other taxa (see Coyne, 1994). However such sister species often possess a mating barrier which is clearly not the case here. In addition, it is not clear that the low survival of offspring observed is due to hybrid inviability: the wasps were reared on *T. glabrum* where survival of offspring is very low, so the absence of surviving female offspring in one cross may not signify the absence of female offspring. The absence of a barrier to mating, morphological similarity, and the absence of a complete post-zygotic barrier probably justifies the use of the same species name, which makes this the first record of *L. pedatus* from the Old World.

Geographic range and host range

L. pedatus is the most studied wasp in its genus and one of the best known in the family. It was previously reported only from the New World, and our records make it the first species in its genus to be established in both the New and Old Worlds. Very few other bethylids are so widespread – they include several species of *Cephalonomia* Westwood, *Holepyris* Kieffer and *Plastanoxus* Kieffer (worldwide), and *Prorops nasuta* Waterston (New World and Africa). All are associated with stored products or crops. *L. pedatus* parasitizes pests of stored products, and it seems likely that its presence in Europe is due to human influence, as is the record of its close relative, *L. utilis* in Sweden amongst imported timber (Gordh & Móczár, 1990). Of interest is the fact that the associated host of *L. pedatus* in The Netherlands is *T. angustum*, itself a pest introduced from the New World. Given the worldwide distribution of many dermestid beetles, further records of range expansion of *Laelius* spp. are to be expected.

The fact that *L. pedatus* parasitizes *T. angustum* very successfully makes it a potential biological control agent for this pest, as has been suggested for its other dermestid hosts (e.g. Al-Kirshi et al., 1997). The fact that the species is already established in Europe means that concerns over its possible introduction to the Old World are now irrelevant. In The Netherlands, *T. angustum* is the most important pest in many museum and private collections of pinned insects and stuffed vertebrates (Weidner, 1993), where it has become much more numerous than the museum beetle *Anthrenus museorum* L. *L. pedatus* shows the following characteristics which make it a good candidate to suppress *T. angustum* populations: offspring sur-
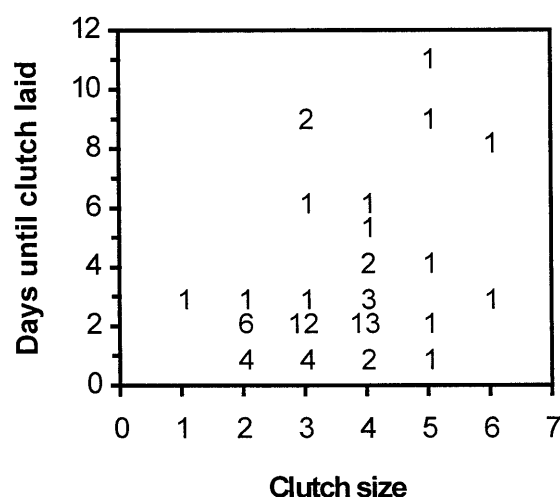
Fig. 4. Time taken to lay a clutch of eggs against the number of eggs eventually laid in the clutch in *Laelius pedatus*. Numbers indicate the total superimposed data points. Data are from both Dutch and Madison strains of the wasp from clutches laid on *Trogoderma glabrum*.

vival is high; large (hence destructive) hosts can be successfully attacked, and result in larger wasp broods. Hosts do not recover fully once stung; the parasitoid development time is sufficient to realize several generations per year in heated buildings. The wasp can also reproduce without alternative food or water by feeding on host haemolymph.

Fecundity, survival and development

Our data have shown a positive correlation between the body size of female wasps and the size of eggs they lay. A few other intraspecific studies of parasitoids show a positive correlation between body size and egg size (e.g. O'Neil & Skinner, 1990; Visser, 1994; Otto & Mackauer, 1998). Like many other idiobiont ectoparasitoids (Flanders, 1942; Mayhew & Blackburn, 1999), *L. pedatus* lays anhydropic eggs (see Jervis & Kidd, 1986), which are large, and yolky with a thick chorion. The functional significance of large egg size in ectoparasitoids is intuitively connected with the ecological constraints of desiccation tendency and nutrient availability (e.g. Grbic & Strand, 1998). Endoparasitoid eggs are surrounded by a nutrient rich aqueous environment which can be exploited with a reduction in egg size. In ectoparasitoids all the nutrients for early development must be supplied by the egg yolk, and the egg must be protected from desiccation.

The reasons for the observed allometric egg size variation are unclear. Such variation occurs both across as well as within species (Blackburn, 1991). Developmental or other constraints may certainly be involved. For example, small wasps may have physical difficulty laying very large eggs. However, an alternative is that egg size influences fitness, and larger wasps allocate more resources to each egg as part of an adaptive strategy (e.g. Charnov, 1991; Kozlowski & Weiner, 1997). On *T. glabrum*, mortality of the young wasps is high because hosts sometimes recover from paralysis prior to the completion of wasp

development (see also Klein & Beckage, 1990), suggesting that mortality is linked to reduced envenomization. It might be that larger females are better able to paralyze hosts. When female size is controlled for, egg size is positively correlated with survival probability, which is correlational but nonetheless suggestive evidence. To be confident about the effect of egg size, a manipulation experiment would have to be performed in which the individual wasp which paralyzes the host is different from the individual which layed the eggs, so the effects of envenomization and egg size can be properly separated (see Mayhew, 1997). In parasitoids, models of lifetime reproductive success suggest that incorporating egg size can be important in the way life history strategies are interpreted (Sevenster et al., 1998). We suggest that the search for fitness consequences of egg size and the reasons for intraspecific egg size allometry should be a priority in parasitoid life history studies.

Our data have shown that the size of female wasps is positively correlated with the survival of their offspring after controlling for egg size. Much research has been invested in describing the relationship between adult size and fitness in parasitoid wasps. The vast majority of studies have been laboratory based (reviewed in Godfray, 1994; Visser, 1994), and comprise studies on separate fitness related variables under standard conditions, such as longevity or maximum lifetime fecundity. More recent studies have incorporated field information including dispersal ability into estimates (e.g. Visser, 1994; Kazmer & Luck, 1995; West et al., 1996; Bennett & Hoffman, 1998; Ellers et al., 1998), or measured further variables in the laboratory (Petersen & Hardy, 1996). Our study suggests that female size can affect the survival of offspring that are laid. We suggest that body size may be correlated with the ability of wasps to paralyze hosts successfully. This hypothesis has yet to be tested directly.

Our data also show that when some offspring die before completing development on a host, the remaining offspring take longer to complete development. Our data additionally suggest that this is due to the larger size which survivors attain when they do not have to compete with siblings for food. The contrasting developmental strategies of parasitoids with different life histories have been the subject of a vigorous research programme (see Salt, 1941; Vinson & Iwantsch, 1980a, b; Thompson, 1990; Mackauer et al., 1997). Depending on their ecology and that of the host, some parasitoids may be selected for rapid development, which may bring advantages of reduced mortality or higher rates of population increase (see Harvey et al., 2000). Idiobionts attack hosts which do not increase in size after parasitism. They are regarded as developing at the maximum physiological rate, resulting in a trade-off between adult size and development time, with adult size being determined by available resources or some physiological upper limit (Mackauer et al., 1997). Our results are consistent with this model, as are other studies on idiobiont ectoparasitoids (e.g. Harvey et al., 1998; Otto & Mackauer, 1998). Koinobionts attack hosts which continue to develop, and a range of developmental
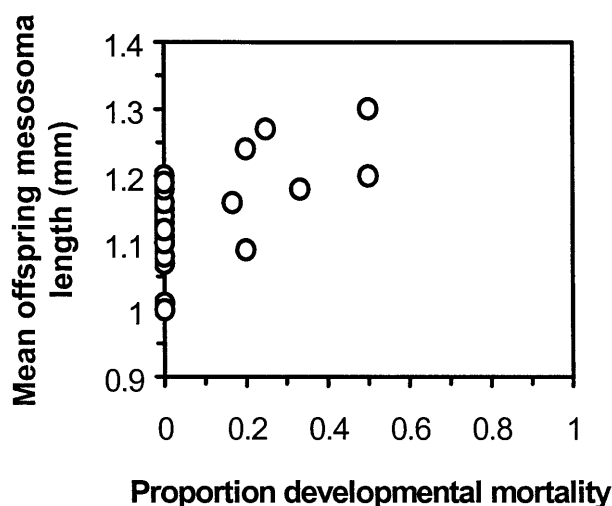
Fig. 5. The size of offspring emerging per clutch against the proportion of individuals in the clutch which died before completing development in *Laelius pedatus*. Data are from Dutch wasps reared on *Trogoderma angustum*.

strategies may occur, so that similar trends to idiobionts may be observed, or development rate may increase in larger hosts so that development time is constant (see Sequeira & Mackauer, 1992; Harvey et al., 1994; Mayhew & van Alphen, 1999). A third koinobiont model has been proposed by Harvey et al. (2000), who suggested that some koinobionts develop very rapidly once the host has grown to sufficient size, often failing to consume the whole host and pupating outside it. Together, these studies suggest that a cost to larger body size in terms of longer development may sometimes occur, and may be important if rapid development is a target for selection. This possibility is not usually considered in optimal life history models for parasitoids (see Godfray, 1994).

Our data additionally show that females take longer to lay a clutch of eggs after encountering a host if they lay larger clutches and longer if they are unmated. The first trend has been found in another bethylid wasp, *Goniozus nigrifemur* Ashmead (Luft, 1993), where the time taken to mature the large eggs is a likely explanation for the extended handling time. It has been suggested that extended handling time in larger clutches might provide an explanation for the fact that *L. pedatus* allocate more per capita resources to offspring developing in larger clutches or on larger hosts (Mayhew, 1998). The mechanism for the latter requires that handling time, or the fitness costs of handling time, should be proportionally greater for each extra egg added in a clutch. Our data do not provide evidence for a non-linear relationship between handling time and clutch size, though they do not exclude that either (Fig. 4).

The fact that unmatedness increases the time females take to lay a clutch is also of interest. Since unmated female *L. pedatus* do not lay different numbers of eggs or differently sized eggs than mated wasps, it seems likely that this reflects a greater reluctance to lay unmated broods. Unmated broods in haplodiploid species result in

all male offspring. In outbreeding species with a panmictic mating structure, single sex broods suffer no fitness costs, but in locally mating species such as bethylids, single sex broods may have reduced fitness because offspring can only find mates away from the emergence site. In consequence, unmated female wasps should allocate greater time to searching for mates than searching for hosts. Guertin et al. (1996) found that even in an outbreeding wasp, unmated females may be reluctant to search for hosts rather than mates. Our data suggest some support for this prediction in a wasp with at least partial local mating.

Sex ratio

In common with previous sex ratio studies on *L. pedatus*, we found that one male per clutch was common in gregarious broods, and there was evidence of sex ratio precision, suggestive of local mate competition. However, all male broods, all female broods, and single egg broods were also produced, suggestive of non-local mating. To resolve this paradox, information on mating stucture is required (Mayhew & Godfray, 1997). We have shown here that females sometimes become sperm depleted late in life, laying all-male broods. This may partly account for the fact that sex ratio precision in this study was much less than reported in previous studies of *L. pedatus*, which only considered the first brood laid by each female (see Hardy et al., 1998). Females which are only capable of laying male broods take longer to lay clutches, suggesting a lower motivation to oviposit. In our cultures and mating experiments we readily observed multiple mating by females. Thus, mating opportunities are likely to exist away from the natal patch, giving single sex broods non-zero fitness. The high frequency of single males in gregarious broods and low sex ratio variance however suggest that local mating opportunities are more common than non-local mating opportunities.

Our studies failed to find a relationship between host size and offspring sex in single-egg clutches, a trend found previously in *L. pedatus* (Mayhew & Godfray, 1997) and in many other parasitoid spp. (see King, 1987). In addition to the possibility that this trend is genuinely absent, there are three possible methodological reasons: the lower number of replicates in this study leading to low power, different measures of host size, and the fact that females in our study laid several broods each. At present we are unable to narrow the list of possible causes.

Conclusion

Finally, we address some wider issues raised by this study. Through the simultaneous measurement of many life history variables, we have shown novel phenotypic relationships between life history variables which may reflect trade-offs, other constraints or variable adaptive strategies. We believe that these relationships have potentially important consequences for the way parasitoid life history theory should develop. The incorporation of such intercorrelations between traits, and their fitness effects, should lead to two satisfying developments: first, models incorporating more biological detail, leading to greater

predictive power; and second, models considering the evolution of suites of traits simultaneously. We consider both to be desirable trends in life history study.

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