Larval Competition, Adult Fitness, and Reproductive Strategies in the Acoustically Orienting Ormiine *Homotrixa alleni* (Diptera: Tachinidae)

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Homotrixa alleni *is a gregarious endoparasitoid fly that attacks adult male* Sciarasaga quadrata *(Orthoptera: Tettigoniidae) in southwestern Western Australia. Gravid female flies acoustically orient to their host's call and deposit live first-instar larvae upon or near their calling host. Up to 16 larvae may be found developing in the one host, and since only calling adult male* S. quadrata *are parasitized, host size and hence larval resources are essentially fixed at parasitism. This study examines parasitism by* H. alleni *in relation to intraspecific larval competition and adult fitness. The mean number of larvae emerging per host failed to increase significantly beyond a clutch size of four. Mean pupal weight and survival to the adult stage decreased linearly with increasing clutch size across the entire range of clutch sizes examined. Within a clutch, heavier pupae successfully completed pupal development significantly more often than lighter pupae. Pupal weight was directly related to adult size, with adult males being significantly larger than adult females at any given pupal weight. Female body size was positively correlated with fecundity. The size distribution of emerging females was normally distributed, while the distribution of searching gravid females collected at acoustic traps in the field was significantly skewed toward larger flies, suggesting yet another fitness benefit associated with large size. Using fecundity and survival to adulthood as our measure of fitness we calculated the optimal clutch size maximizing fitness per*

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host to be seven, which exceeds the majority of observed clutch sizes in the field. Uncertainties associated with larvae successfully entering the host following larviposition are likely to reduce clutch sizes of H. alleni *below this optimum in the field.*

KEY WORDS: intraspecific larval competition; adult fitness; optimal clutch size; reproductive strategy; Tachinidae.

INTRODUCTION

Intraspecific larval competition can have a profound effect on the individual and hence the dynamics and stability of insect populations (Hassell, 1975; Smith and Lessels, 1985). When resources are limited, an individual's contribution to the next generation may suffer via density-dependent effects on survivorship and fecundity. Consequently, larval competition in insects is a major functional determinant of life-history strategies and behavior [see Prout and McChesney (1985) for a review in *Drosophila*; see also Smith and Lessels (1985)].

Intraspecific competition may take on a variety of forms characterized at their extremes as either scramble or contest competition, depending on the utilization of resources by competing larvae (Nicholson, 1954). Scramble competition arises when resources are equally partitioned among competing larvae, with all competitors suffering the consequences of limitation equally. Contest competition is characterized by the disparate allocation of resources among competing larvae, with some individuals obtaining more resources at the expense of others. Scramble competition is characterized by an abrupt change from complete survival to no survival when there are no longer sufficient resources for survival, whereas under contest competition the number of surviving larvae remains constant with increasing larval density (Hassell, 1975).

Intraspecific larval competition in insects influences many aspects of adult fitness (examples in Diptera include Sigurjóndsóttir, 1984; Prinkkilä and Hanski, 1995; Nilssen, 1997), especially for gregarious parasitoids when host size is fixed and larvae must compete for resources during development. Increases in the intensity of intraspecific competition have frequently been shown to reduce the adult body size of parasitoids (Waage and Ng, 1984; Bai and Mackauer, 1992; Adamo *et al.*, 1995; Nakamura, 1995, Iwao and Ohsaki, 1996). Moreover, female body size is positively correlated with fecundity and longevity (see Visser, 1994). Given these potentially deleterious effects on fitness, it is understandable that intraspecific competition may alter the reproductive strategy adopted by a female parasitoid (Godfray, 1994). Optimality models (Parker and Courtney, 1984; Charnov and Skinner, 1985; Waage

and Godfray, 1985), taken in conjunction with empirical results (Waage and Godfray, 1985; le Masurier, 1987), suggest that larger clutch sizes evolve when the deleterious effects of intraspecific competition decrease.

Homotrixa alleni Barraclough is a gregarious parasitoid fly that attacks adult male *Sciarasaga quadrata* Rentz in southwestern Western Australia (Allen, 1995a, 1995b). Gravid female flies acoustically orient to the call of male *S. quadrata*, and when a calling male is located, females larviposit on and around the host by forcibly expelling live first-instar larvae from their abdomens (Allen *et al.*, 1999). Once in the host, fly larvae take 2 weeks to complete their development, with the host dying soon after they exit to pupate. *H. alleni* is unlike other idiobiont parasitoids, that is, parasitoids where host size is fixed at the time of oviposition, in that it does not often physically encounter the host during the process of oviposition (Allen *et al.*, 1999). Consequently, clutch size decisions must be made without an accurate assessment of host size, without information on whether the calling male is already parasitised, and with a level of uncertainty as to how many of the deposited larvae will successfully enter and develop within the host. Furthermore, the dynamics of the host–parasitoid system shifts over the course of the 3- to 4-month calling season as parasitism levels increase and the number of available hosts left in the field decreases. As a consequence, the average number of fly larvae developing within a host increases over the calling season from about 2 to 4 or 5 per host and ranges between 1 and 16 (Allen, 1995a).

The main aim of this study was to quantify the effects of larval competition on adult fitness in *H. alleni*. To achieve this aim we measured three potential components of adult fitness: adult size, fecundity, and the host-searching activity of gravid females in the field. Measuring the searching activity of gravid females in the field has only recently been used to estimate the fitness of parasitoids (see Visser, 1994; Kazmer and Luck, 1995; West *et al.*, 1996) and overcomes some of the inherent limitations that arise from extrapolating fitness consequences entirely from laboratory experiments (Visser, 1994; Godfray, 1994). Finally, we relate our predictions concerning optimal clutch size to the reproductive strategy of larviposition and to observed clutch sizes found in the field.

MATERIALS AND METHODS

Larval Competition

Collections of calling male *S. quadrata* were undertaken within a 2-km area of coastal heath at Cape Naturaliste (33°33′S, 115°01′E) in the southwest of Western Australia. Parasitism of *S. quadrata* was determined by

examining collected males each day, for up to 7 days, for the presence of abdominal holes or respiratory spiracles produced by the action of fly larvae by the fourth of the 14 days of larval development within a host (Allen, 1995a). The final number of supernumerary spiracles present on the host after collection provided an accurate measure of the number of larvae developing within a given host and was used as our estimate of clutch size (Allen, 1995a). Clutch size, as used in this paper, therefore does not necessarily reflect the actual number of larvae deposited by a fly. Furthermore, it is possible that some clutches may have resulted from superparasitism. In the field, the number of larvae within a host increases toward the end of the calling season (Allen 1995a). Therefore, to minimize the potential for superparasitism among our samples, we collected the majority of hosts (82%) prior to the end of the calling season. In addition, all fly larvae emerged from hosts within 24 h, thereby narrowing the temporal opportunity for superparasitism within our clutches to a similar period of time. Parasitized male *S. quadrata* were maintained in the laboratory at 20°C following the methods of Allen (1995a). Upon completion of fly larval development in the host, we recorded the number of fly larvae that emerged from the host and the number of fly larvae to pupate successfully and measured the weight of each pupa within 48 h. of emergence. Upon emergence, each fly was sexed and then frozen prior to size measurement.

Size Measurements

For each fly we measured head capsule width and the length of its left and right fore-, mid-, and hind tibiae. Legs were mounted on slides in Hoyer's solution prior to measurement. Tibiae were measured with an eyepiece graticule at 30× magnification under a binocular microscope with a 0.007-mm accuracy, and head width was measured at 20× magnification with a 0.01-mm accuracy.

Host-Searching Activity of Gravid Female Flies in the Field

To determine the impact of adult female fly size on host-searching activity in the field, the size distribution of gravid female flies arriving at sound-traps was compared to the size distribution of female flies emerging from hosts. Searching gravid female flies were collected in mid-February 1995 using artificial chirper units broadcasting the synthesized call of *S. quadrata* (see Allen, 1998). The sample of emerging female flies in the field was attained from field parasitized *S. quadrata* that had fly larvae emerge during the months of November and December.

Female Fecundity

Virgin female *H. alleni* do not mate readily in the laboratory (G.R.A., personal observation) so all fecundity measures were made on gravid female flies collected at acoustic traps in the field during the 1994–1995 *S. quadrata* calling season. Flies were placed in the freezer within 24 h of collection. Upon their return to the laboratory, flies were dissected in a small watchglass containing distilled water so as to expose the highly coiled uterus containing the developing first-instar larvae or planidia (see Ferrar, 1987). Once the uterus was fully exposed, it was ruptured, the planidia within it dispersed, and the number of full-size dark (mature) and white (immature) planidia counted as an overall index of fecundity (see Allen *et al.*, 1999).

RESULTS

Larval Competition

The mean number of larvae that successfully pupated per host increased with clutch size up to a clutch size of four per host (Fig. 1a). Above a clutch size of four the average number of pupae emerging per host remained similar, though variability around the mean dramatically increased. If both sexes emerged from within a given host, their pupal weight did not differ significantly [nonspecific ranking test for unequal cell frequencies: $n = 28$ hosts, $H = 0.013$, df $= 1$, $P > 0.90$ (Meddis, 1984)], and as a result the mean pupal weight was pooled at each clutch size. The mean weight of emerging pupae rapidly decreased with increasing clutch size (Fig. 1b). Solitary larvae developed, on average, to over twice the pupal weight of those developing within clutch sizes of 10 or more (Fig. 1b). An increase in clutch size resulted in a decline in the proportion of larvae that developed into an adult fly (Fig. 1c). However, this relationship is characterized by a step function where there is no change in survivorship up to a clutch size of five, but above this clutch size survivorship declines rapidly, with over a twofold difference in survival rate between minimum and maximum clutch sizes (Fig. 1c). Within any one host, the heavier pupae to emerge were significantly more likely to develop successfully into an adult fly (nonspecific ranking test for unequal cell frequencies: $n = 25$ hosts, $H = 7.87$, df $= 1$, $P < 0.005$). Chi-square goodness-of-fit tests within each clutch size showed no difference from an expected 0.5 sex ratio and were not significantly heterogeneous ($\chi^2 = 11.68$, df $= 8$, $P > 0.10$), therefore justifying pooling (Zar, 1984). The overall sex ratio ($n = 212$, males $= 106$, females $= 106$) did not differ significantly from a sex ratio of 0.5 ($\chi^2 = 0.0$, df $= 1$, $P > 0.90$).
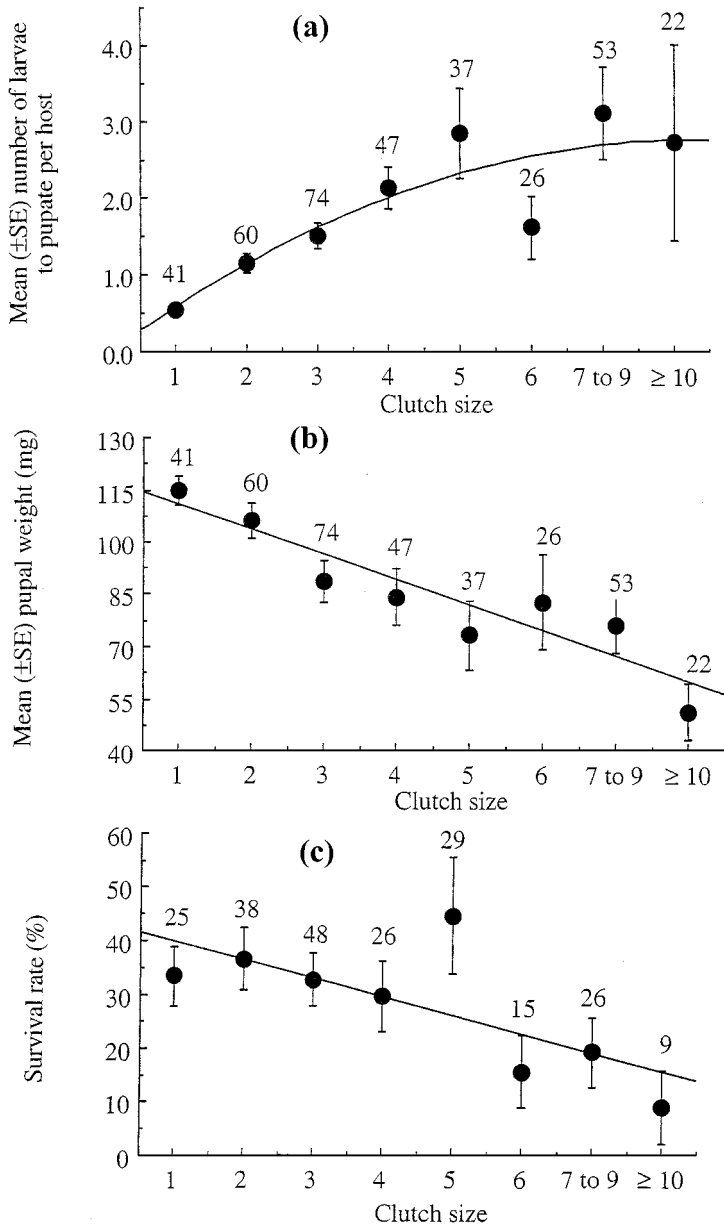
Fig. 1. The relationship between clutch size and (a) the Mean (±SE) number of pupae emerging per host (regression: $y = -0.029x^2 + 0.581x + 0.082$; adjusted $r^2 = 0.69$, $P = 0.02$), (b) the mean (±SE) weight of pupae emerging from hosts (regression: $y = -5.113x + 110.733$; adjusted $r^2 = 0.83$, $P < 0.0001$), and (c) the mean (±SE) survival rate to the adult stage (regression: $y = -0.026x + 0.408$; adjusted $r^2 = 0.53$, $P = 0.02$). The number of individuals measured per clutch size is given above each clutch size.

Adult Fitness

The head width of adult flies successfully emerging from pupae increased significantly with the cube root of pupal weight (Fig. 2a). There was a significant effect of sex on head width ($F = 9.265$, df $= 1,57$, $P < 0.004$), with males being significantly larger than females for any given pupal weight (see Fig. 2a). There was a significant, though weak, positive correlation between female body size and fecundity, with the number of larvae within the uterus of gravid females varying from 94 to 600 (Fig. 2b).

Tibia length in *H. alleni* was sexually dimorphic, with females having relatively longer tibiae than males (unpaired t test: foretibiae, $t = -3.79$, $P < 0.0003$; midtibiae, $t = -8.65$, $P < 0.0001$; hind tibiae, $t = -8.55$, $P < 0.0001$; dfs $= 94$) (Table I). Within each sex the fore-, mid-, and hind tibia differed significantly in length (repeated-measures ANOVA: female, $F = 310.82$, df $= 2,126$, $P < 0.0001$; male, $F = 6.85$, df $= 2,62$, $P < 0.0021$). The foretibia was significantly shorter than the mid- and hind tibiae in both sexes, while the hind tibia was significantly shorter than the midtibia in females only (Table I). The size variation present in the tibiae of females was lower than the variation in head width (female CVs: foretibia $= 5.5\%$, midtibia $= 5.2\%$, hind tibia $= 4.6\%$, head $= 8.7\%$) and the variation present in the equivalent traits in males (male CVs: foretibia $= 11.3\%$, midtibia $= 9.4\%$, hind tibia $= 6.6\%$, head $= 9.7\%$).

The host-searching activity of gravid females in the field was also influenced by body size. The size distribution of female flies emerging from field-collected hosts was normally distributed ($g_1 = -0.415$, $t = 0.943$, $n = 28$, $P > 0.20$), whereas that of gravid females arriving at acoustic traps had a significant negative skew ($g_1 = -1.22$, $t = 3.19$, $n = 38$, $P < 0.005$). Therefore, large females were overrepresented among the gravid female searching population in the field.

Optimal Clutch Size

To estimate the optimal clutch size in *H. alleni* [defined as the clutch size that maximizes the gain in fitness from each host (Godfray *et al.*, 1991)], the fitness–fecundity gains from female offspring emerging from hosts at different clutch sizes were calculated. It was assumed that the fitness of daughters provided a direct measure of maternal fitness since maternal fitness should increase with the fecundity of her daughters (Vet *et al.*, 1994). Knowing that *H. alleni* has a sex ratio of 0.5 and up to 16 larvae have been found developing per host in the field (Allen, 1995a), the number of female pupae produced per host, over this range, was calculated by halving the estimation from the
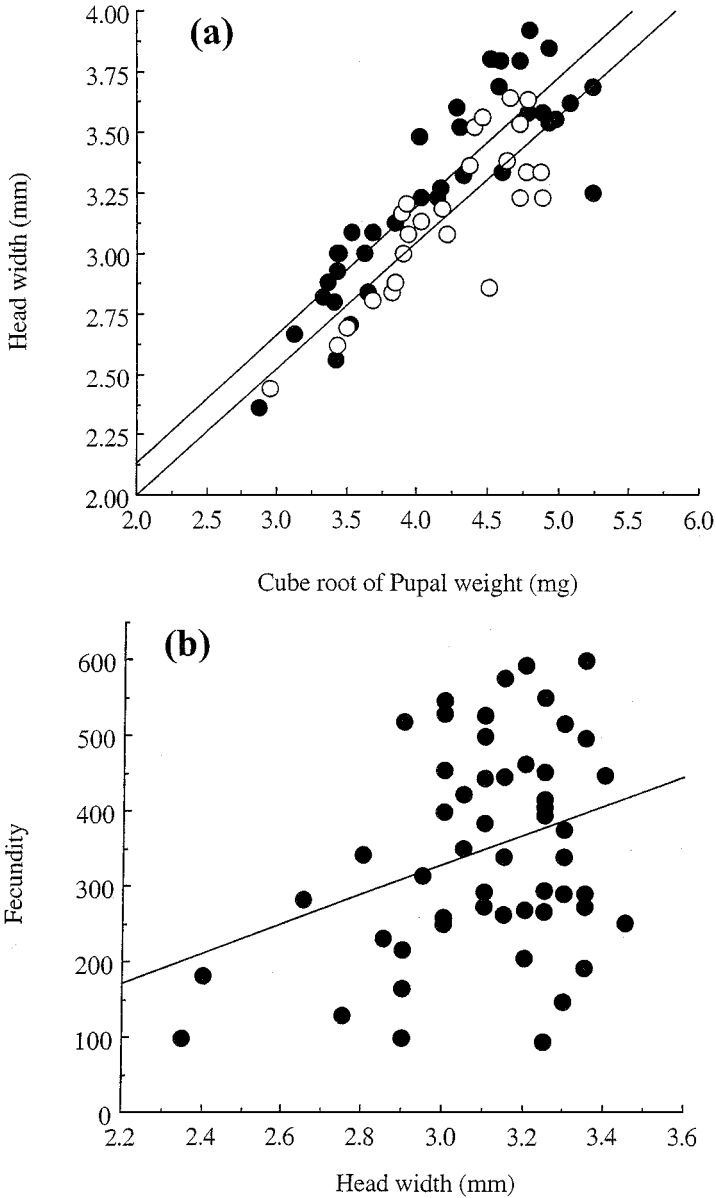
Fig. 2. The relationship between the head width of adult flies and (a) the cube root of pupal weight (regression: (●) male—$y = 0.531x + 1.066$; adjusted $r^2 = 0.76$, $n = 36$, $P = 0.001$; (○) female—$y = 0.525x + 0.942$; adjusted $r^2 = 0.68$, $n = 25$, $P = 0.001$) and (b) female fecundity (regression: $y = 196.426x - 262.264$; adjusted $r^2 = 0.09$, $n = 53$, $P = 0.02$).

Table I. The Mean (±SE) Relative Size of Tibiae in Male and Female *H. alleni*[a]

|	Foretibia	Midtibia	Hindtibia
Male			
Size	0.780 ± 0.016^a	0.845 ± 0.014^b	0.818 ± 0.01^b
(*n*)	(32)	(32)	(32)
Female			
Size	0.832 ± 0.006^a	0.960 ± 0.006^b	0.904 ± 0.005^c
(*n*)	(64)	(64)	(64)

[a] Relative trait size is calculated by dividing mean tibia length by head width. Different-letter superscripts indicate significant differences within a sex between the morphological traits at $P < 0.05$. Sample sizes are given in parentheses.

equation for Fig. 1a. The pupal weight, body size, and fecundity of daughters emerging from these pupae were estimated from the equations for Figs. 1b, 2a, and 2b, respectively. However, this assumes that all pupae successfully develop into adult flies, whereas we found that the proportion of flies that successfully emerges from pupae decreases with clutch size according to the equation, $y = -0.021x + 0.667$ ($F = 33.56$, df $= 2{,}6$, $P = 0.002$). By adjusting the number of female pupae produced per host by this mortality factor and multiplying the result by the estimated fecundity of the daughters, we calculated the maternal fitness gains per host and per egg over the known range of clutch sizes (Fig. 3). The standard errors for maternal fitness gains per host at each clutch size were calculated using the standard errors in each of the four independent regression equations in Figs. 1a, 1b, 2a, and 2b. The maternal fitness gains per egg were calculated by dividing the fitness gains per host by the clutch size. The curve for fitness per host generates an optimal clutch size of seven, while the optimal clutch size for fitness per egg is one.

DISCUSSION

Larval Competition and Adult Fitness

The outcome of larval competition has been examined in at least three other tachinid species, *Archytas marmoratus, Epicampocera succinata*, and *Compisulura concinnata*, and has yielded mixed results. Hughes (1975) suggested that scramble competition predominated in *A. marmoratus*, with all larvae dying prior to emergence, once a critical clutch size was reached. Reitz (1995), however, concluded that scramble competition was unlikely in this species because pupal weights and adult eclosion rates did not differ significantly between singly parasitized and superparasitized hosts. Iwao and
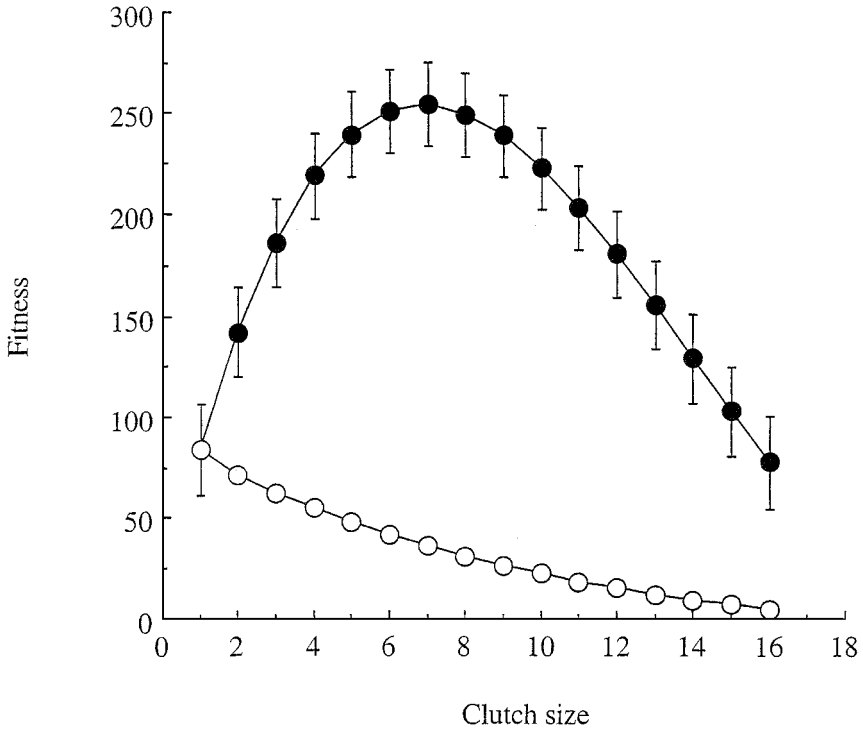
Fig. 3. The relationship between clutch size and the total number (±SE) of progeny produced by daughters per host (●) and daughters per egg (○). Regression for the fitness per host: $y = -2.91x^2 + 45.688x + 66.736$; adjusted $r^2 = 0.94$, $n = 16$, $P = 0.0001$. Regression for the fitness per egg: $y = -4.964x + 76.132$; adjusted $r^2 = 0.96$, $n = 16$, $P = 0.0001$.

Ohsaki (1996) concluded that the solitary specialist *E. succinata* exhibited contest competition, whereas the gregarious generalist *C. concinnata* exhibited scramble competition. This study, however, suggests that larval competition in tachinids may not be characterized easily by just one type of competition. In *H. alleni*, survivorship remained constant up to a clutch size of five and then declined rapidly, suggesting that scramble competition may in fact give rise to contest competition at larger clutch sizes. Furthermore, variability in the number of larvae to pupate within a clutch was particularly evident as the clutch size exceeded four, suggestive of contest competition.

   Adult size in *H. alleni* is determined largely by success in larval competition. However, for any given pupal weight, males emerge to be significantly larger adults than females. Furthermore, where both sexes emerged from the one host their pupal weights were not significantly different. *Homotrixa alleni* therefore differs from other tachinids, where females either are larger in

body size (McLain *et al.*, 1990; Gross *et al.*, 1996; but see Nakamura, 1995) or develop from heavier pupae (Pintureau and Grenier, 1992; Nakamura, 1995), but agrees with Adamo *et al.* (1995) for the ormiine fly *Ormia ochracea*. One size-related sexual dimorphism in ormiines is their ear, which is situated on the ventral prosternum and is significantly larger in females (Robert *et al.*, 1994). Our leg measurements of *H. alleni* revealed yet another size-related sexual dimorphism, with females having relatively longer tibiae than males. Thus, for *H. alleni* the smaller size of females eclosing from equivalent pupal weights may represent a cost associated with the development of larger ears and longer tibiae. Evolutionary theory predicts that structures contributing most to fitness should fluctuate less than structures of less importance (Soulé, 1982; Soulé and Cuzin-Roudy, 1982). Although we did not measure ear size, the CVs for female tibia lengths were about half that for head width and, similarly, about half that of the equivalent traits in males, suggesting a stronger regime of natural selection acting on tibia length in females to canalize their development. For female flies the advantage of long legs may lie in a better ability to larviposit, which is achieved by expelling larvae forward of themselves from underneath their abdomen (Allen *et al.*, 1999) and/or to localize sound during the rocking behavior they undertake when approaching a calling host (G.R.A., personal observation). Conversely, the advantage of large body size in males may lie in their ability to control better-quality territories since known ormiine mating systems appear to be based around males defending "hilltop" resources (Lederhouse *et al.*, 1976; Wood, 1987).

　　Adult body size is shown to correlate with the two field-measured fitness components in *H. alleni*. First, as has been demonstrated in the laboratory in a number of tachinid (King *et al.*, 1976; Mani and Nagarkatti, 1983; Reitz and Adler, 1995; Nakamura, 1995) and hymenopteran parasitoids (Godfray, 1994), larger females are more fecund. Second, the trapping of host-searching, gravid female flies in the field indicated a second advantage associated with large body size. The size distribution of emerging females was normally distributed, whereas it had a significant negative skew among the host-searching population attributable to the over representation of large females. While this pattern could be generated by various factors, such as smaller females being selected out of the adult population prior to host-searching or larger females actually searching for a disproportionately longer period of time, it does suggest that larger females are more likely to locate and parasitize a greater number of hosts in the field. Indeed this has been demonstrated in the field in at least two hymenopteran parasitoids, *Aphaereta minuta* (Visser, 1994) and *Achrysocharoides zwoelferi* (West *et al.*, 1996). However, Kazmer and Luck (1995) found that body size in the wasp *Trichogramma pretiosum* was not a reliable indicator of individual or cohort fitness in the field.

Larval Competition and Reproductive Strategies

Where adverse effects on adult fitness are associated with larval competition, a reproductive trade-off is expected that will maximize the number of offspring produced and minimize the negative effects of intraspecific competition (Takagi, 1985). The optimal clutch size resulting from this reproductive trade-off will maximize parental fitness by producing offspring of higher fitness (Godfray, 1994). In our study the strategy maximizing fitness in *H. alleni* would be to get seven larvae to enter each host successfully. In reality, however, the average clutch size found in hosts in the field is considerably lower than the optimal, averaging between 1.7 ± 0.2 and 5.6 ± 1.3 per host over the calling season of *S. quadrata* (Allen, 1995a). However, not all non-clutch maximization solutions are necessarily nonoptimal. A match between observed and theoretical clutch sizes is expected only when animals lay a single clutch in their lifetime or when the opportunity to lay an additional clutch is rare (Vet *et al.*, 1994; Godfray, 1994). However, lower-than-optimal observed clutch sizes have been documented in the majority of studies where clutch size and fitness have been examined (e.g., Waage and Ng, 1984; Dijkstra, 1986; Taylor, 1988; Hardy *et al.*, 1992).

One reason for the lower observed clutch sizes may be that female egg supply is limiting (Iwasa *et al.*, 1984; Waage and Godfray, 1985) but this is unlikely in *H. alleni* since the number of full-size larvae in the uterus ranges between 90 and 600, with 60% of these being dark and capable of survival after larviposition (Allen *et al.*, 1999). Nonoptimal clutch sizes may also arise in response to costs associated with host-searching. Models incorporating the temporal costs associated with locating a suitable host predict that parasitoids should alter clutch size to maximize fitness gains per unit time (Charnov and Skinner, 1984, 1985; Iwasa *et al.*, 1984; Parker and Courtney, 1984). For *H. alleni* the host density declines as the calling season progresses and the average clutch size correspondingly increases, suggesting that searching costs shift during the calling season (Allen, 1995a,b). However, the observed shift in average clutch size may also be associated with the incidence of multi-parasitism because nightly acoustic trapping of flies in the field (see Allen, 1998) shows an increase in the incidence of multiple fly arrivals at sound traps toward the end of the *S. quadrata* calling season (G.R.A., personal observation). A third consideration is that our measure of offspring fitness is driven by the fecundity of daughters and does not include sons. Thus, our assumption that the relationship between size and reproductive success is similar between males and females may not be valid. If this relationship is not identical, then one would expect a somewhat different figure for optimal clutch size.

The final and most important consideration regarding nonoptimal clutch sizes in *H. alleni* is that, to behave optimally, females must be able to assess accurately (i) the host quality and (ii) the number of larvae successfully entering the host (Lack, 1947). Host quality assessment in ormiines is unlikely, especially since females have little or no contact with their host during larviposition (Adamo *et al.*, 1995; Allen *et al.*, 1999). Even more important, though, is that accurate adjustment of the number of larvae in the host (the measure of clutch size used in our study) by females would be hindered by not knowing how many of the deposited larvae will gain entry into the host (Adamo *et al.*, 1995). Godfray and Ives (1988) modeled the effects of uncertainty during oviposition on clutch size and demonstrated that, where fitness costs of overshooting the optimum are not the same as the costs of undershooting it, then uncertainty can influence the optimal clutch size. For *H. alleni* our results suggest that the fitness costs of under- or overshooting the optimal number of larvae in the host are similar. Hence, suboptimal clutch sizes may reflect the difficulty that larvae have of gaining entry into the host, with the magnitude of the larval loss, between deposition and entry into the host, governing whether the number of larvae within the host is above or below optimal.

ACKNOWLEDGMENTS

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