Chapter 5

HOW DIFFERENT HOST SPECIES INFLUENCE PARASITISM PATTERNS AND LARVAL COMPETITION OF ACOUSTICALLY-ORIENTING PARASITOID FLIES (TACHINIDAE: ORMIINI)

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ABSTRACT

Sexual signals are often critical for mate attraction and reproduction but their conspicuousness can expose the signallers to parasites and predators. In orthopteran insects males typically produce acoustic signals to attract females for mating. Tachinid flies of the family Ormiini act as illicit receivers by detecting the mating songs of their bushcricket and gryllid hosts. Ormiini flies can be characterised as opportunistic hunters; the taxonomic specificity of these flies is moderately low and they can have a range of alternative hosts.

This chapter is in two parts. In the first I quantify the influence host species has on body size and life history traits of different populations of *Therobia leonidei*, the only European Ormiini fly species. For parasitoids host size can constrain offspring growth, subsequently influencing the evolution of body size and life history traits. I compared fly populations developing in two hosts: *Poecilimon mariannae* and in the lighter *P. thessalicus*. The fly populations investigated had no substantial morphological or molecular-genetic differences. The general pattern of larval competition was similar in both hosts; increasing parasitoid brood size reduced pupal weight and survival to adulthood. Consistent with a local adaptation hypothesis, pupal weight in the heavier host was about 30% heavier than are those parasitizing the lighter host. Similarly, the critical weight necessary for successful hatching of fly maggots was significantly lower in the lighter host. In contrast, brood size was similar between host species.

In the second part I review studies of gryllid and tettigoniid parasitizing Ormiini flies. The general pattern of host usage for temperate species is quite similar, with pupae from single infected hosts weighing around 10 percent of host weight. One remarkable

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exception is the Australian *Homotrixa alleni*, a very large fly that parasitizes extremely heavy bushcricket species. In this fly species single pupa weigh less than four percent of host weight, leading to higher mean parasitoid clutch sizes. Coupled to this reduced parasitoid-to-host weight ratio is prolonged host survival and an increase in the probability of superparasitism.

INTRODUCTION

Insect parasitoids are an active field of ecological and evolutionary research due to the recognition that host-parasitoid systems offer unparalleled opportunities to examine fundamental questions in animal behaviour and evolutionary ecology (Eggleton & Belshaw 1992). However, most research has focused on Hymenoptera parasitoids (Godfray 1994, Hassell 2000, Hochberg & Ives 2000). These parasitoids have a relatively limited range of hosts and the parasitoid habit appears to have evolved only once in the Hymenoptera (Eggleton & Belshaw 1993). In contrast Dipteran parasitoids are exceedingly diverse in both their hosts and their evolutionary origins (Feener & Brown 1997). Tachinidae is one of the most diverse and ecologically important parasitoid families in the order Diptera. As parasitoids they are important natural enemies in most terrestrial ecological communities. One of the few traits that unites this diverse assemblage of flies is that all tachinids are parasitoids of arthropods, especially insects. Because of their predominance as parasitoids of the larval stage of Lepidoptera and other major groups of insect herbivores, tachinids often play significant roles in regulating herbivore populations, with over 100 species employed in biological control programs of crop and forest pests (Stireman et al. 2006). Despite their diversity and ecological impact relatively little is known about the basic ecology of tachinids.

Variation among hosts is an important determinant of phenotypic variation in insects that use discrete resources, such as parasitoids (Godfray 1994). Host size is a major source of phenotypic variation as it may constrain the evolution of body size and life history traits (Hardy et al. 1992, Allen and Hunt 2001, Mackauer and Chau 2001, Häckermann et al. 2007). One of the major decisions gregarious parasitoids have to make is how many eggs or larvae to lay on or in a host (Godfray et al. 1991). Host size is often considered to be a key factor influencing parasitoid fitness (Godfray 1994), so female parasitoids are expected to lay the number of eggs that maximizes their gain in fitness. The resulting intraspecific larval competition from gregarious oviposition influences many aspects of adult fitness, especially when host size is fixed. Intraspecific competition occurs when two or more individuals of the same species strive for the same resource. Intraspecific competition can be in the form of a scramble (resources divided equally) or a contest (resources divided unequally). Under contest competition there are winners and losers. Scramble competition arises when a resource is equally partitioned among competing larvae, with all competitors suffering the consequences of limitation equally. In species with scramble competition, individuals in populations adapted to large hosts are generally larger than those adapted to small hosts.

Several theoretical and empirical studies have focussed on clutch-size patterns in hymenoptera parasitoids (summarized in Godfray 1994). In contrast, dipteran parasitoids have

received less attention (Feener & Brown 1997). Tachinids differ from Hymenoptera in lacking the rigid ovipositor that provides information about host parasite status and quality, and in often depositing mobile planidia larvae rather than eggs (Stireman et al. 2006). These differences may lead to female Tachinids not being able to reliably assess the number of larvae entering a given host (Adamo et al. 1995b).

Research on the small tribe Ormiini within the Tachinidae was undertaken by evolutionary biologists (Cade 1975, Zuk & Kolluru 1998) who realized that their unique exploitation of acoustic mating songs for finding hosts may impose strong natural selection on signalling (Zuk et al. 1993, 1995), signal structures (Rotenberry et al. 1996; Zuk et al. 1998, 2001; Lehmann & Heller 1998) and even the evolution of alternative mating strategies (Cade 1975, 1981; Zuk et al. 2006). Tachinid flies of this tribe rely on acoustic cues to locate hosts (Cade 1975, Walker 1986, Gray et al. 2007) and their ear is tuned towards the frequency of host's song (Lakes-Harlan and Heller 1992, Robert et al. 1992, Stumpner et al. 2007). Deposition of live planidia (larviposition) is elicited by host calling (Allen et al. 1999). After landing, female Ormiini flies deposit planidia either directly on the host or spread a number of larvae in their vicinity (Adamo et al. 1995b; Cade 1975), where they are able to survive for up to two hours (Allen et al. 1999). In one study more than fifty percent of flies had no direct contact with the host, but laid a number of planidia nearby (Allen et al. 1999). Planidia penetrate the host's interscleral membranes and a few days later produce a connection with the air outside through a funnel in the host's abdomen (Leonide 1969). Infected hosts inevitably die following parasitoid emergence.

The objective of the first part of this review is to quantify the relative contribution of environmental (host species) effects to differences in body size and life history traits between populations of the Ormiini *Therobia leonidei* MESNIL, 1964 developing on lighter and heavier host species. This European fly species has been found to attack the singing sex of three different families of bushcrickets (Leonide 1969, review in Lehmann 2003). Infection by planaria is indicated by their breathing funnel which can be seen as a brown dot on the ventral side of the male's abdomen, normally four days after infection (Lehmann and Heller 1998, Lehmann 2006). The average survival time following the appearance of the breathing funnel is seven days. The longest time that parasitized males have survived is 14 days after fly attack (Lehmann and Lehmann 2006). Developing fly larvae reduce male bushcricket survival and reproductive effort. Parasitism reduces a male host's investment capability into spermatophore production (Lehmann and Lehmann 2000a) which results in a shorter female mating refractory period and fewer eggs being laid (Lehmann and Lehmann 2000b). Infected males call less and are discriminated against by females (Lehmann and Lehmann 2006). Although *T. leonidei* is considered a generalist because of the number of known hosts, host use varies substantially between localities, and most populations attack single or a few hosts and are thus selective relative to the diversity of bushcricket species available to them (Lehmann 2003). This may lead to adaptation to local hosts (Fox & Czesak 2000).

In populations of the Greek phaneropterine bushcricket *Poecilimon mariannae* WILLEMSE AND HELLER, 1992 males were found to be parasitized in large proportions, up to 65% at the end of their breeding season (Lehmann & Heller 1998). Mute females were never found to be infected (Lakes-Harlan and Heller 1992, Lehmann and Heller 1998). I was able to study the parasitism behaviour in a further, closely related host species *P. thessalicus* BRUNNER VON WATTENWYL, 1891 (Lehmann et al. 2001). Although this species showed a remarkable variation in body size between populations (Lehmann and Lehmann in press.), all

body sizes are smaller than in *P. mariannae*. Larger hosts are expected to be more advantageous in terms of offspring fitness than smaller hosts because they contain a greater quantity of resources. In gregarious species, fitness is affected not only by host size but also by the number of parasitoids developing in a single host for hymenoptera (Zaviezo & Mills 2000, Bell et al. 2005, Häckermann et al. 2007) and tachinid parasitoids (Nakamura 1995, Reitz & Adler 1995, Allen & Hunt 2001, Kolluru & Zuk 2001). Therefore, I assessed the influence of host species differing in body size on the success of the parasitoid female in terms of brood size and number of surviving offspring.

Part II

What is known about Ormiini tends to be widely dispersed in specialized articles and even unpublished reports. In the second part of this chapter I review Ormiini ecology, focusing on parasitism patterns and host usage. What we know comes largely from four Ormiini-host systems: my own studies on *Therobia leonidei,* which attacks several bushcricket hosts in Europe, the Australian *Homotrixa alleni* which is a parasitoid of the large weight bushcricket *Sciarasaga quadrata* (work of Geoff Allen and collaborators), and two species of the genus *Ormia* which infects crickets or mole crickets (see especially the work of Adamo, Cade, Fowler, Frank, Kolluru, Walker and Zuk).

I review four main areas: (*a*) life history data, (*b*) parasitism rates and seasonality of occurrence, (*c*) evolution of reproductive strategies including brood sizes and superparasitism. Superparasitism is defined as the deposition of a clutch of eggs by a female parasitoid in or on a host already parasitized by itself or a conspecific female (van Alphen & Visser 1990, Godfray 1994), and (*d*) oviposition strategies.

The evolution of acoustic hunting, biogeography and host ranges in Ormiini have been reviewed previously (Lehmann 2003).

MATERIALS AND METHODS

Part I

Parasitoid Flies
Therobia leonidei is a parasitoid fly (Diptera: Tachinidae: Ormiini) distributed in Southern Europe in the Mediterranean Countries. The northernmost record is from the Tessin (Switzerland), in the East it is recorded from Turkey, the Ukraine and Azerbaidzhan (Lehmann 1998 and references therein).

After locating a male bushcricket, the female fly deposits planidia larvae on the abdomen of the male, which burrow inside the host. A few days later, the larvae produce a connection with the air outside the host through a 'breathing funnel' in the host abdomen (Leonide 1969). Subsequently, the infection by the fly is indicated by a brown dot on the ventral side of the male's abdomen (Lehmann 2006), in *Poecilimon mariannae* after four days (Lehmann & Heller 1998).

The Bushcricket Host Species

Therobia leonidei was found to parasitize 13 host species from three different bushcricket subfamilies (Lehmann 2003). After screening a large number of populations for parasitoid occurrence in Greece (see Lehmann 1998, Lehmann & Heller 1998), we analyzed parasitism patterns and host usage in two species of the phaneropterine genus *Poecilimon*. The bushcrickets *Poecilimon mariannae* WILLEMSE ET HELLER, 1992 and *P. thessalicus* BRUNNER VON WATTENWYL, 1891 are medium-sized species (mean body length around 2 cm), morphologically and ecologically quite similar and are members of the *Poecilimon propinquus*-group, which contains eight species (Lehmann AW 1998, Lehmann AW et al. 2006). I compared fly parasitism adapted to either the heavier bushcricket host *P. mariannae* (average weight of 560 mg) with a population adapted to the much lighter host *P. thessalicus* (average weight of 500 mg). The first host species *P. mariannae* is confined to areas of central Greece and inhabits roadside verges and grassy patches (Willemse & Heller 1992). The population studied was on a grassy ridge near Vrissiá (22°19' E, 39°15° N, Nomos Lárissa; see Lehmann and Heller 1998). The second and lighter host species was examined in Elatohori (Central Greece, Pieria-Mountains, 22°16 E, 40°19 N), where it is found on shrubs and bushes (Lehmann et al. 2001). There is considerable variation in body size between *P. thessalicus* populations (Lehmann & Lehmann in press). However the Elatohori population was one of the few parasitized populations of this species (Lehmann unpubl. data).

Parasitism Patterns

Field samples of adult male bushcrickets were screened for the presence of breathing funnels as an indicator of parasitoid infection. The breathing funnel appears four days after infection (Lehmann & Heller 1998). To measure levels of parasitism the populations of *P. mariannae* at Vrissia and *P. thessalicus* at Elatohori were investigated over three consecutive years 1994-1996. The rate of parasitism was observed over the whole season, from the beginning of male calling until the fading of male populations (see Lehmann and Lehmann 2006 for a life table analysis of the larger host species *P. mariannae*).

In 1995 all individuals were not only checked for presence or absence of parasitoid breathing funnels, but additionally the number of maggots in a male was counted via the number of breathing funnels. To verify that the number of fly larvae corresponded to the number of observed breathing funnels I dissected twenty males from each species. The number of visible funnels was always identical with the number of maggots found inside the males.

As it was not possible to determine whether all of the larvae inside a host were the progeny of a single parasitism event I refer to brood size and avoid the term clutch size. Furthermore, clutch size, defined as the number of planidia placed in a single event, might be larger than brood size because not all planidia might be successful in entering a host. After emergence and pupating, all pupae were weighed (wet weight) and hatched flies were sexed. For comparison host males were weighed on a Kern EG 300-3M scale (± 1 mg).

RESULTS

Parasitism in two closely related bushcrickets infected by *Therobia leonidei* in Greece.

Parasitism Patterns

Male parasitism in *P. mariannae* reached 57, 50 and 54 percent in three consecutive years (Figure 1a). Rates of parasitism increased nearly linear as the calling season progressed. While there is variation in parasitism rate in the middle of the calling season the general pattern is similar between years.

In the second host species, *P. thessalicus,* substantial variation was observed in the parasitism pattern between three consecutive summers (Figure 1b). In 1994 the level of parasitism was low and did not exceed more than 10 percent during the whole season. In 1996 parasitism was slightly higher than the previous two years but showed a similar pattern to 1994 with a peak parasitism rate in the middle of the calling season. In contrast, parasitism in 1995 showed a linear increase reaching a plateau of 40 percent infection by the end of the season.
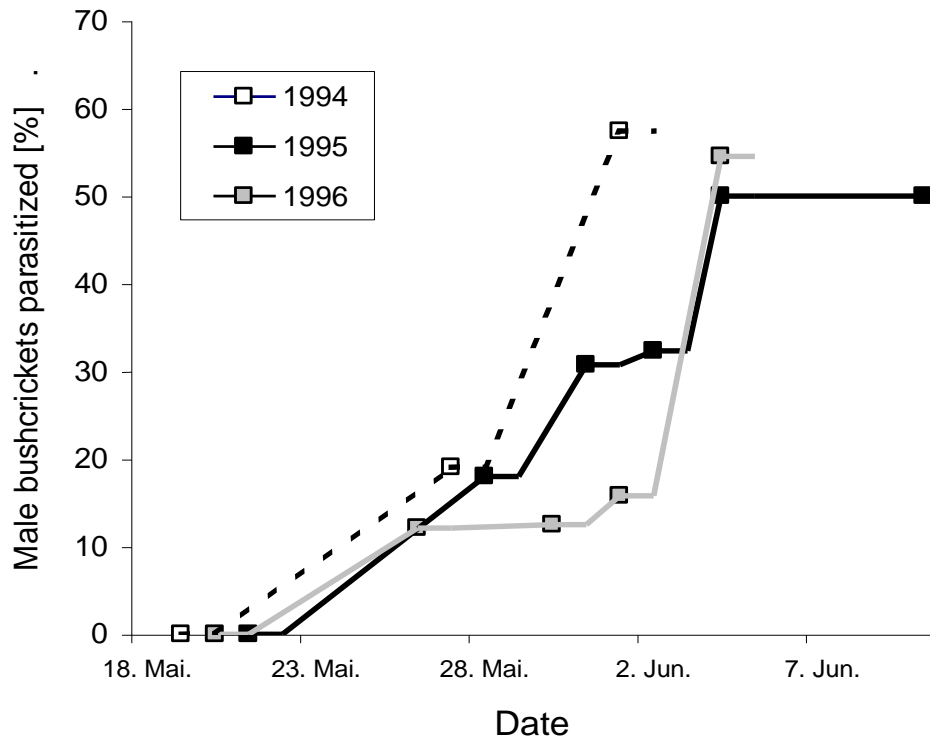

Figure 1a. Percent parasitism of male *Poecilimon mariannae* by *Therobia leonidei* in the years 1994-1996. The beginning of the time - axis corresponds with the moulting of the first males to adulthood. The very last data represent the last sight of adult males. Sample sizes were *1994:* n = 50, 21, 54 - *1995:* 50, 50, 13, 34, 36, 12 - *1996*: 50, 33, 8, 57, 33.
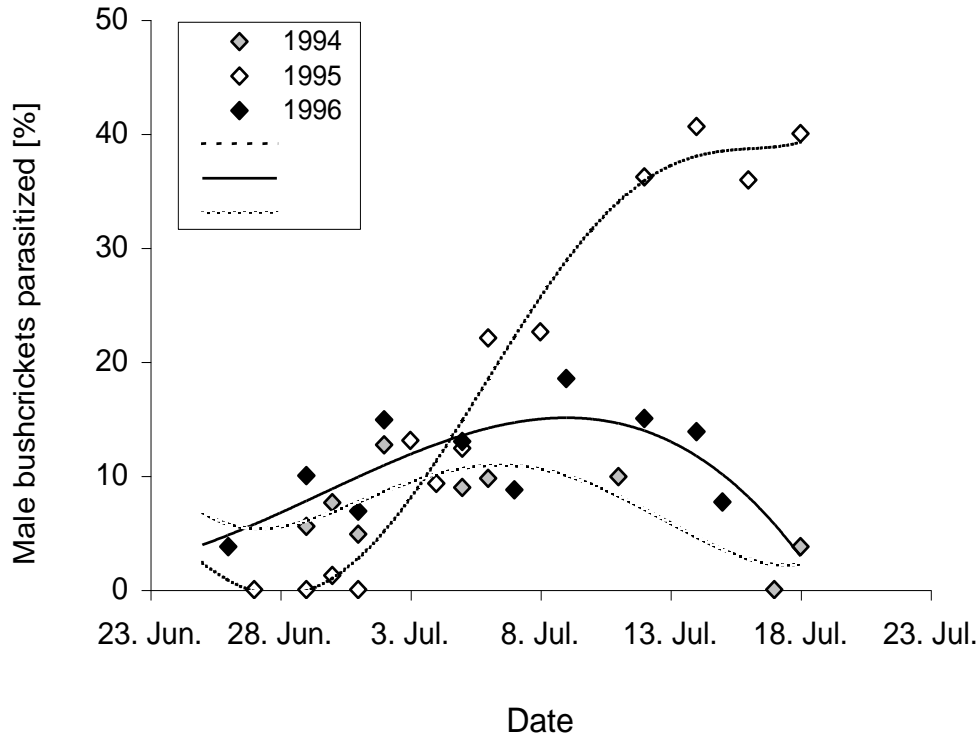
Figure 1b. Percent parasitism of male *Poecilimon thessalicus* by *Therobia leonidei* in the years 1994-1996. The beginning of the time - axis corresponds with the moulting of the first males to adulthood. The very last data represents the last sight of adult males. Sample sizes were *1994*: n = 54, 118, 41, 78, 82, 111, 58, 53 - *1995*: 65, 17, 80, 64, 130, 161, 113, 77, 84, 105, 32, 64, 25 - *1996*: 53, 100, 58, 94, 100, 80, 81, 60, 65, 39.

Over the whole calling season of 1995, more than 50 percent of *P. mariannae* males had only one fly maggot (you need to be consistent and use only "larva" or "maggot"), a further 22 percent harboured two fly larvae, while hosts with three or more maggots were rarely found (Figure 2). As a maximum, seven breathing funnels were observed in individuals in 1995, although I have found a male *P. mariannae* in another population with twelve breathing funnels (unpubl. obs.). In the smaller host *P. thessalicus* fewer males had solitary fly larvae (38 percent) but the incidence of three or more parasitoids was nearly identical between host species.

While the proportion of parasitized males increased over the host's calling season, the mean brood size showed no trend over the season (Figure 3). Mean clutch size was statistically independent of time for both males of *P. mariannae* (Kruskal-Wallis-Test: H = 15.5, df = 13, p = 0.28) and *P. thessalicus* (Kruskal-Wallis-Test: H = 9.96, df = 8, p = 0.27). Over the whole season, parasitoid brood size (mean ± SE) in the heavier host species *P. mariannae* (2.13 ± 0.18) was marginally higher than in the lighter host *P. thessalicus* (1.92 ± 0.09), but this difference was not significant (Mann Whitney-U-test: Z = -0.15, p = 0.88).
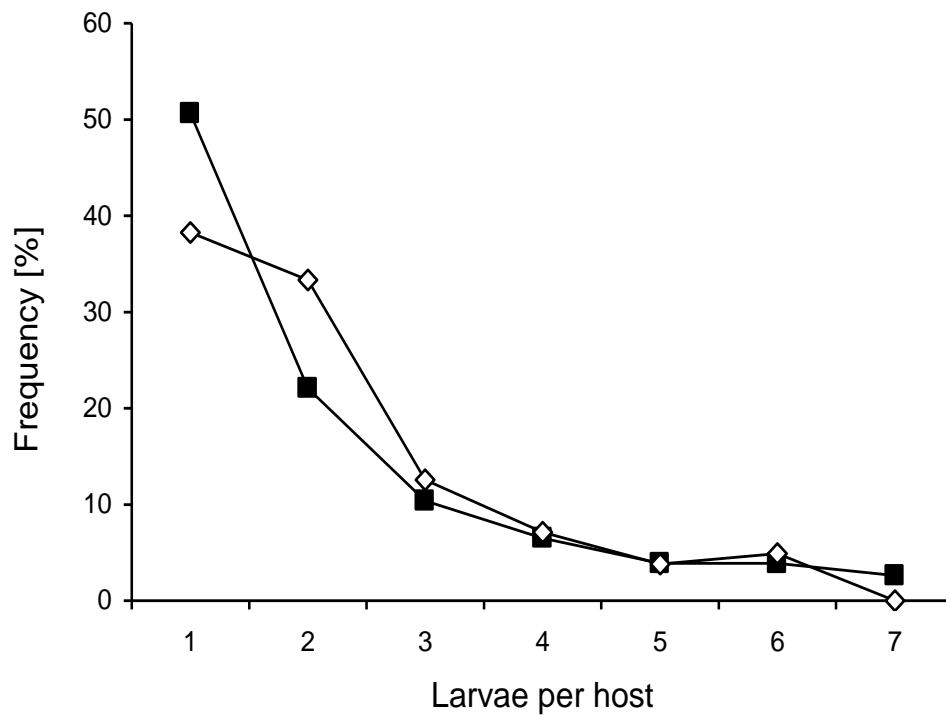
Figure 2. Frequency distribution of brood sizes of the dipteran's parasitoid *Therobia leonidei* in male bushcrickets of *Poecilimon mariannae* (■, n = 77) and *P. thessalicus* (◇, n = 183).

Brood size in *P. thessalicus* was to some extent variable over the season (Figure 4) and brood sizes larger than three may represent superparasitism (Figure 4 hatched bars). For the whole sampling season its amount was 8.6 percent, with a maximum of 17.6 percent. However, proposed superparasitism occurred in the middle and at the end of hosts calling season, when daily attack rates were highest (indicated by the strongest daily increase in absolute parasitism rates, see Figure 1b).

Nonetheless, superparasitism was obviously disadvantageous, as never more than one maggot hatched from *P. thessalicus*, regardless of brood size. In the larger host *P. mariannae*, two or even three maggots occasionally emerged from parasitized hosts. In no case involving brood sizes greater than one did I find all larvae surviving to pupation. For *P. mariannae* hosts where the brood size was equal or larger than four (proposed to be superparasitism) never more than a single parasitoid hatched.
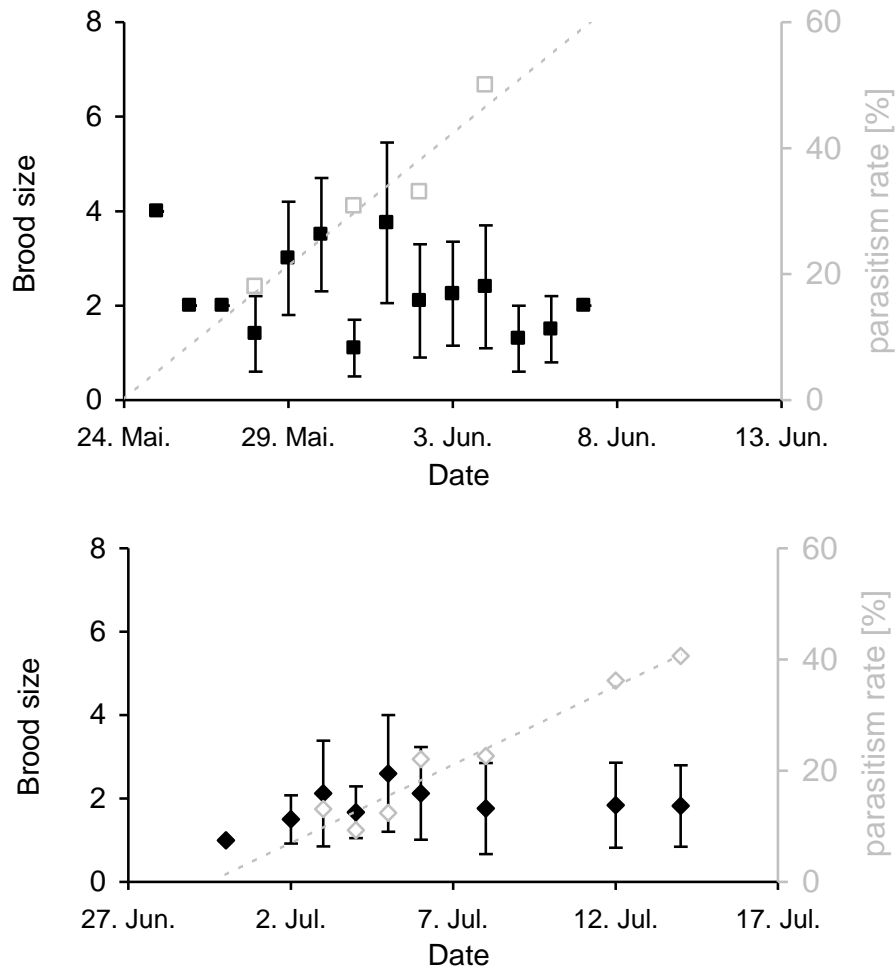
Figure 3. Brood size (mean ± SD) of *Therobia leonidei* over a period of two weeks in males of *Poecilimon mariannae* (top) and *P. thessalicus* (bottom). The parasitism rate of the whole populations in 1995 and the regressions line were plotted for comparison (see Figure 1). Sample sizes *P. mariannae*: n = 1, 1, 1, 10, 3, 2, 9, 3, 16, 3, 22, 3, 2, 1- *P. thessalicus*: 1, 4, 17, 15, 15, 17, 37, 45, 11.

Larval Competition

There is no correlational evidence that higher host weight resulted in higher parasitoid weight within a species. Parasitoid pupae hatched from single infected hosts showed no increase in weight with increasing host weight (Figure 5). A linear regression accounted for two ($y_{mariannae} = 47.88 + 0.01$ x, $R^2 = 0.02$, n = 33) or seven percent of the total variation ($y_{thessalicus} = 26.51 + 0.03$ x, $R^2 = 0.07$, n = 27). Bushcricket males of *P. mariannae* were significantly heavier (563.91 ± 69.33 mg; mean ± SD) than *P. thessalicus* males (502.78 ± 78.84 mg) (t-test: T = 3.19, df = 58, p = 0.0023) at infection. The pupae from the relatively heavier host *P. mariannae* were even relatively heavier in relation to host body weight (9.59 vs. 8.33 %).
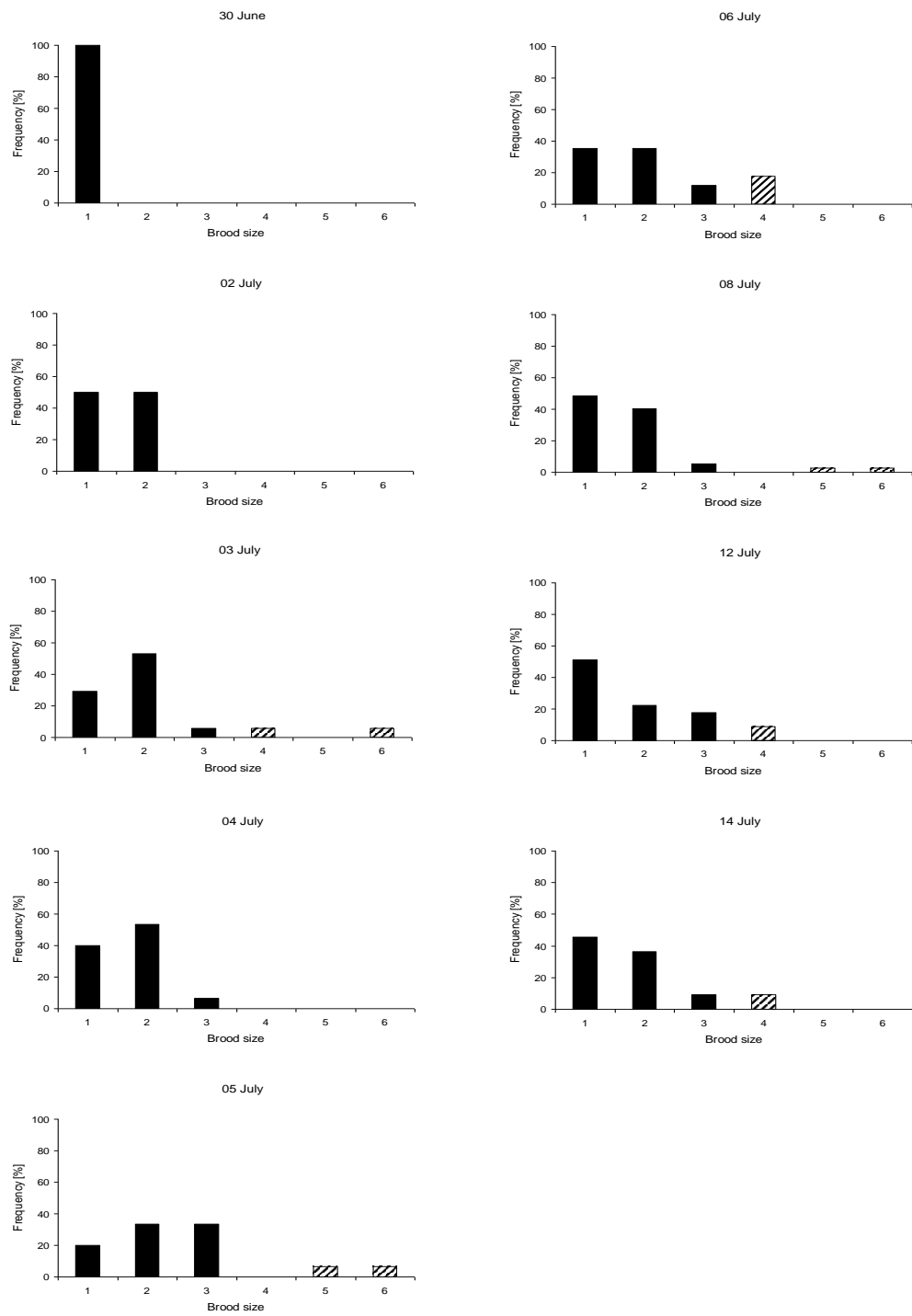
Figure 4. Seasonal progress of parasitoid brood size in *P. thessalicus* and the probable amount of superparasitism (hatched bars).

Parasitoid size was influenced by host size, resulting in substantially heavier pupae from *P. mariannae* compared to pupae from the smaller host species *P. thessalicus* (pupal weight: 53.39 ± 5.36 versus 41.30 ± 8.95 mg mean +- SD, two-way ANOVA $_{\text{host species}}$: $F_{1,47} = 32.73$, p = 0.000). The sex of the resulting fly had no significant influence on pupal weight (ANOVA $_{\text{fly sex}}$: $F_{1,47} = 1.21$, P = 0.28).

Bushcricket body weight did not predict the number of parasitoid larvae for either host (*P. mariannae* linear regression: $R^2 = 0.000$, n = 44, Figure 6top; *P. thessalicus* (regression: $R^2 = 0.003$, n = 104, Figure 6bottom).

Pupal weight declined significantly with increasing brood size in both host species (Figure 7) (two-way ANOVA$_{\text{clutch size}}$: $F_{4,175} = 17.15$, p = 0.000) with solitary pupae around 20 percent heavier than pupae from multiple-infected hosts. In all brood sizes pupae developing in *P. mariannae* were on average 32 to 44 percent heavier than those developing in *P. thessalicus* (two-way ANOVA$_{\text{host species}}$: $F_{1,175} = 86.44$, p = 0.000).

Pupal weight was a predictor for emergence success of adult flies (Figure 8). In pupae heavier than 35 mg hatching success was high in *P. mariannae* (≥ 80 %), whereas hatching success in *P. thessalicus* was much lower for any given weight. The minimum pupal weight result in a live fly was 27 mg in *P. mariannae* and less than half of that (11 mg) in *P. thessalicus*. No obvious differences between the sexes in both species could be found.

Pupal weight declined with brood size, and pupal weight was crucial for hatching success of adult flies. Therefore an increase in brood size resulted in a decline in the proportion of larvae that developed into adult flies in both host species (Figure 9). Fly larvae emerged from hosts more often if they had developed alone. Most parasitoids developed successfully from solitary infected male hosts into adult flies (73 % and 60 %), whereas in fivefold or more parasitized males only 13 and 10 percent successfully emerged as adults.
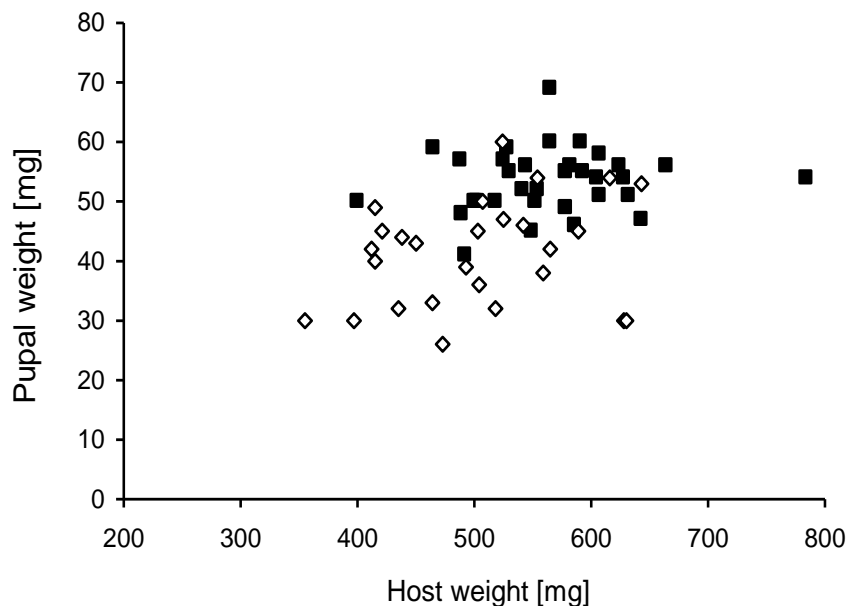

Figure 5. Pupal weight [mg] in relation to host weight [mg] from single infected host males of *Poecilimon mariannae* (■, n = 33) and *P. thessalicus* (◇, n = 27).
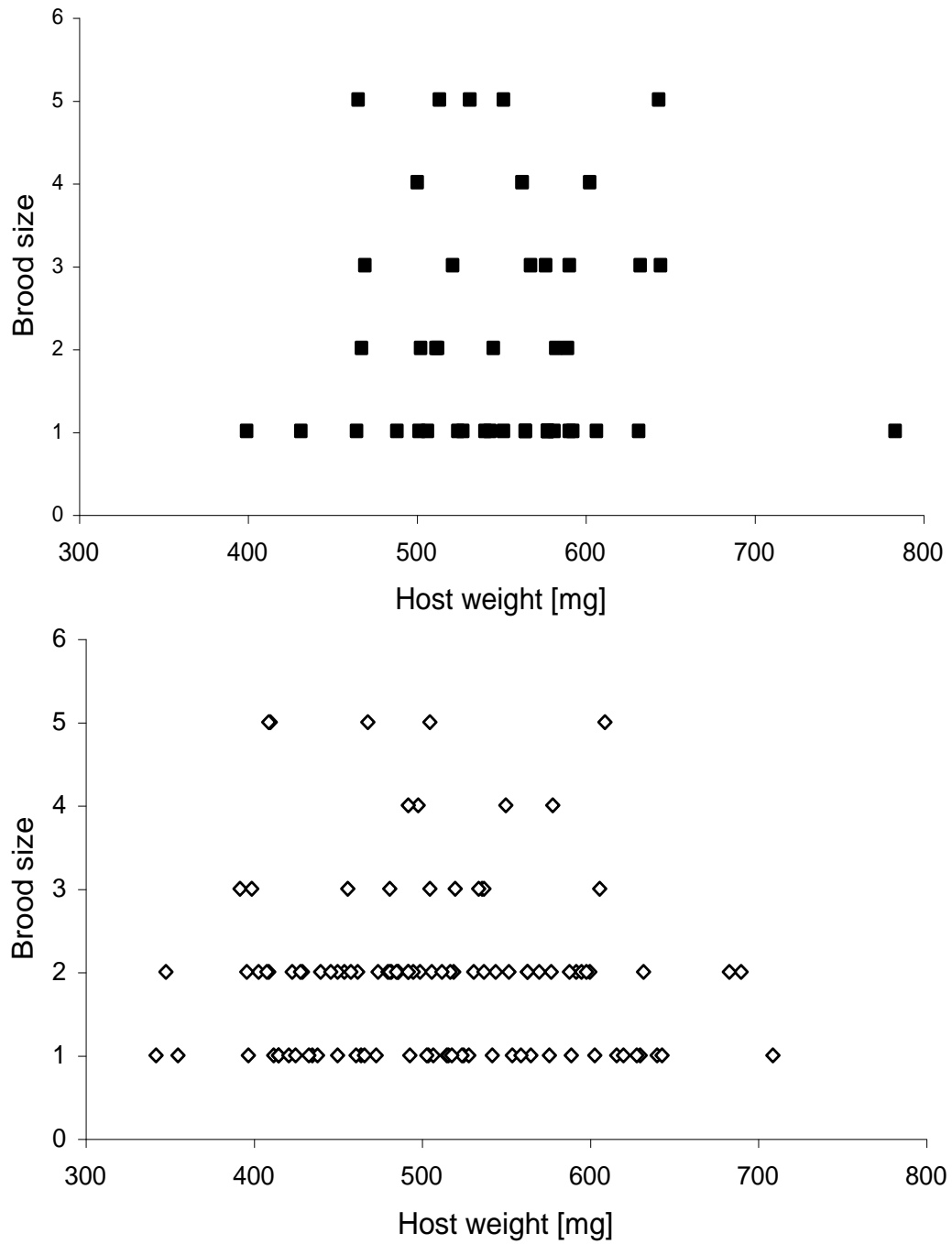
Figure 6. Brood size of *Therobia leonidei* in relation to host weight in *Poecilimon mariannae* (■, n = 44) and *P. thessalicus* (◇, n = 104).

Figure 7. Mean (± SD) weight of pupae emerging from *Poecilimon mariannae* (■) or *P. thessalicus* (◇) males in relation to brood size. Sample sizes *P. mariannae*: n= 34, 23, 11, 9, 7 - *P. thessalicus*: 99, 91, 21, 13, 4.
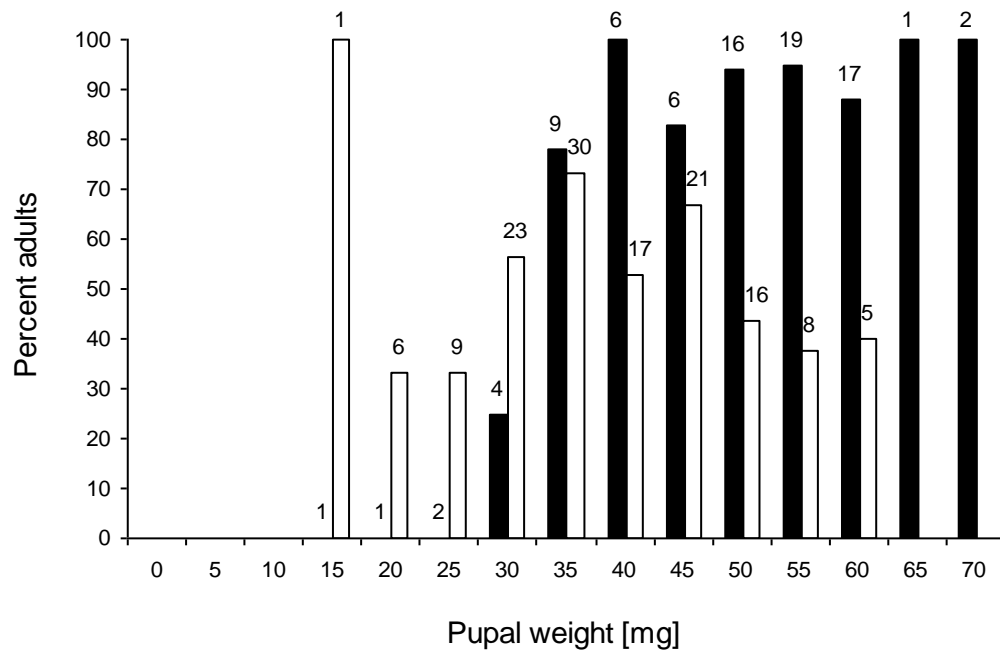
Figure 8. Hatching success of adult flies depending on pupal weight in *Poecilimon mariannae* (black bars, n = 84) and *P. thessalicus* (white bars, n = 136). Sample sizes presented above each bar.
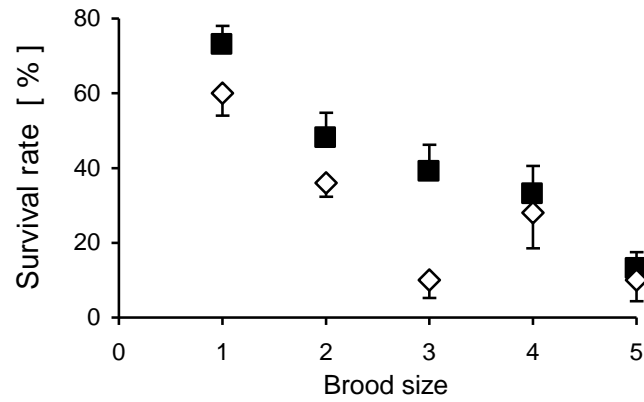
Figure 9. Mean (± SD) survival rate to adult flies from *Poecilimon mariannae* (■) or *P. thessalicus* (◇) males in relation to brood size. Sample sizes *P. mariannae*: n = 69, 26, 13, 10, 11 - *P. thessalicus*: 177, 93, 26, 9, 6.

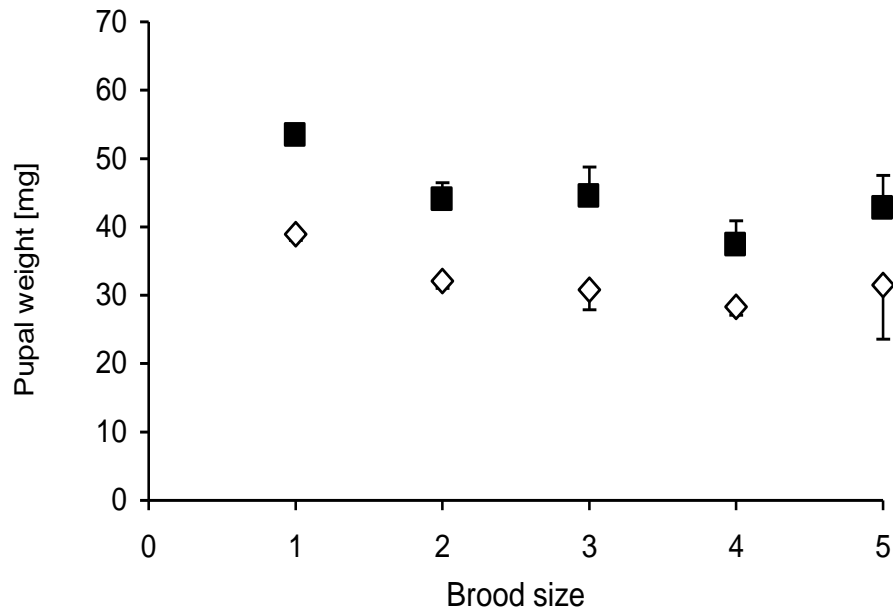Figure 10. Mean (± SD) number of (top) pupae and (bottom) adult flies emerging from *Poecilimon mariannae* (■) or *P. thessalicus* (◇) males in relation to brood size. Sample sizes *P. mariannae*: n = 69, 26, 12, 10, 11 - *P. thessalicus*: 112, 62, 18, 8, 6.
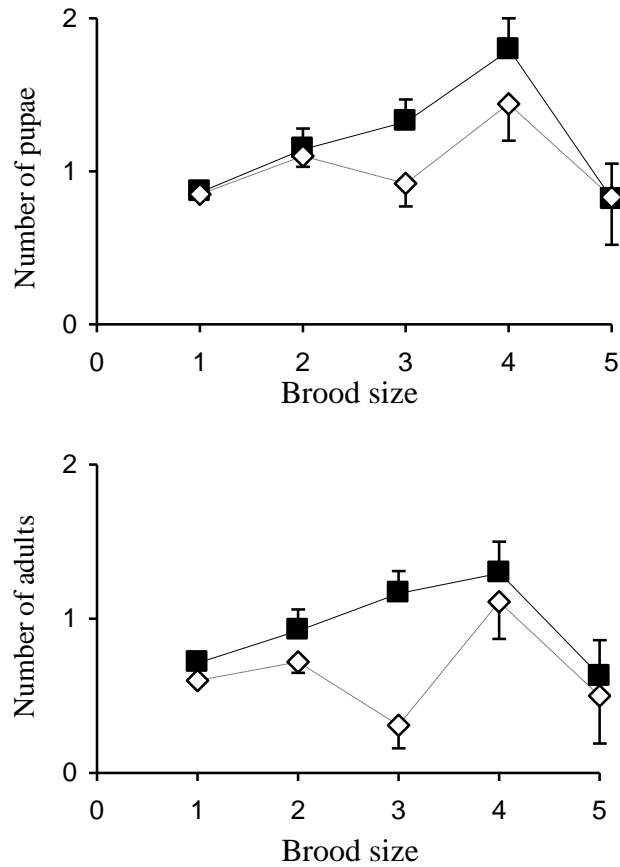
The total number of hatched maggots (Figure 10top) increased up to a brood size of four maggots (two-way ANOVA$_{\text{clutch size}}$: $F_{4,266} = 8.56$, $p < 0.001$) independent of host species (ANOVA$_{\text{host species}}$: $F_{1,266} = 1.59$, $p = 0.21$). In accordance with the number of pupae, the number of adult flies (Figure 10bottom) nearly doubled in fourfold parasitized males compared to solitary infected ones for both host species (two-way ANOVA$_{\text{clutch size}}$: $F_{4,279} = 3.41$, $p = 0.0096$). A brood size larger than four reduced the number of adult flies to a value lower than for single infections. However, the number of adult flies was significantly influenced by host species (ANOVA$_{\text{host species}}$: $F_{1,279} = 7.44$, $p = 0.0068$), because a very reduced number of flies hatched from *P. thessalicus* males infected with three larvae.

For parasitoids from single infected hosts, the sex ratio of hatching flies was nearly equal, with 46.7 and 47 percent females for the two host species. A greater number of female flies emerged when brood size was larger than three in the heavier host *P. mariannae* or larger than two for the lighter host *P. thessalicus* (Figure 11). However, the increase in female parasitoid flies was not statistically significant for either species (*P. mariannae* $\chi^2 = 6.94$, df = 4, $p = 0.14$, n = 60; *P. thessalicus* $\chi^2 = 8.56$, df = 4, $p = 0.07$, n = 124), probably due to low sample sizes for higher brood sizes.
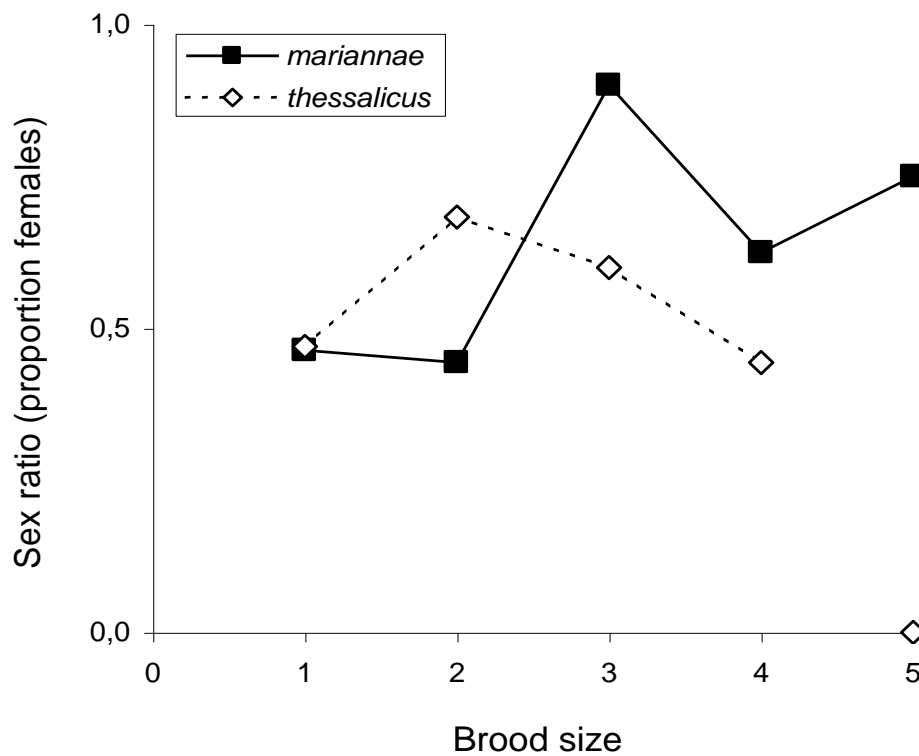

Figure 11. Sex ratio as an amount of females emerging from the heavier host *Poecilimon mariannae* (■) or the lighter host *P. thessalicus* (◇) in relation to brood size. Sample sizes *P. mariannae*: n = 28, 9, 10, 8, 4 - *P. thessalicus*: 66, 41, 5, 9, 3.

Host-parasitoid Aspects of Ormiini Flies - A Review

Life History

Even after three decades of active research starting with Cade (1975), we still have only limited knowledge on Ormiini life histories. The host ranges of over 80 percent of Ormiini species are not known, and the host range can only be approximated in four to five species. The majority parasitize singing bushcrickets, with the derived pattern of cricket parasitism occurring only in a subgroup of the genus *Ormia* (Lehmann 2003). Targeted hosts are likely to be singing males, which are active at night. Summaries of life history data for five Ormiini-Orthoptera systems are in Table 1.

Despite the different hosts used by *Therobia leonidei* and *Ormia ochracea* they have much in common: host weight, parasitoid pupal mass, relative pupal weight, and mean brood sizes are nearly equal. In contrast, the Australian *Homotrixa alleni* has a slower life-cycle, with a much longer developmental time inside the host and a prolonged pupal duration even if corrected for rearing temperatures. This might be directly related to the very large host species that they exploit, leading to a low relative pupal weight. The longer developmental time of the maggots might also give rise to the two-fold larger brood size, even if the number of maggots placed by a single fly female is similar to *Ormia ochracea.* This large brood size in *Homotrixa alleni* is best interpreted as resulting from superparasitism.

The direct pupal development found in all studies of Ormiini (Wineriter & Walker 1990, Allen 1995, Lehmann unpubl. data) is puzzling. Direct developing flies might eclose and be searching for hosts beyond the time singing males are present in the field, so we would expect an off-season pupal stage. We do not know whether this direct development is an artificial response to our rearing conditions or flies are using alternative hosts over the season. Experiments manipulating pupal duration in the field have been unsuccessful (Allen 1995, Lehmann unpubl. data).

Parasitism Rates and Seasonality

Ormiini flies are strictly nocturnal, most active shortly after sunset (Fowler 1987a; Cade et al. 1996; Allen 1998; Kolluru 1999). Due to the phonotactic host locating tactics of the flies, mostly singing males suffer from parasitism (Cade 1975, Lakes-Harlan & Heller 1992, Robert et al. 1992, review in Lehmann 2003). Parasitism patterns differ between the studied host-parasitoid systems according to seasonality and life-history of host populations. The greatest differences exist between crickets (including mole crickets) (Figure 12) and bushcrickets (Figure 13). Both groups differ fundamentally in their habitat use. Bushcrickets climb up and inside vegetation with males singing from relatively exposed positions. This might be an advantage for song propagation but in turn exposes singing males well to the sound locating parasitoid flies. In contrast crickets and mole crickets shelter inside self-constructed burrows. This habit might protect crickets to some extent from the parasitoids.

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Table 1. Life history data of four Ormiini species

	Therobia leonidei	Ref.	Therobia leonidei	Ref.	Ormia ochracea	Ref.	Ormia depleta	Ref.	Homotrixa alleni	Ref.
Fly species	*Therobia leonidei*		*Therobia leonidei*		*Ormia ochracea*		*Ormia depleta*		*Homotrixa alleni*	
Host species	*Poecilimon mariannae*		*Poecilimon thessalicus*		*Teleogryllus oceanicus*		*Scapteriscus spp.*		*Sciarasaga quadrata*	
Host Family	Tettigoniidae Bushcricket		Tettigoniidae Bushcricket		Gryllidae Cricket		Gryllotalpidae Molecricket		Tettigoniidae Bushcricket	
Host weight [mg] (mean ± SD)	563.91 ± 69.33 (n=33)	(1)	502.78 ± 78.84 (n=77)	(1)	544.17 ± 133.51 (n=6)	(4)	range 540 - 1590	(8)	3540 ± 50 (n=35)	(12)
Pupal weight [mg] (mean ± SD)	53.39 ± 5.36 (n=33)	(1)	41.30 ± 8.95 (n=77)	(1)	47.86 ± 11.43 (n=14)	(4)	means around 52 mg	(8)	116 ± 5 (n=19)	(12)
Relative pupal weight (%)	9.47	(1)	8.21	(1)	8.80	(4)	(nearly 5 %)	(8)	3.28	(12)
Pupal to host weight	independent	(1)	independent	(1)			linear increase	(8)		
Brood size (mean ± SD)	2.13 ± 1.58 (n=77)	(1)	2.20 ± 1.38 (n=183)	(1)	1.77 ± 1.2 (n = 214)	(5)			3.48 ± 2.67 (n=114)	(12)
					1.73 ± 1.0 (n = 22)	(6)				
	range 1-7	(1)	range 1-6	(1)	ranges 1-5, 1-8	(5,6)	range 0-2	(9)	range 1-12	(12)
Brood size and season	independent	(1)	independent	(1)					increases	(12)
Brood size to host weight	independent	(1)	independent	(1)	independent	(5,6)			independent	(12)
Fecundity of parasitoid (mean ± SD) (=number of planidia)					165 ± 192 (n=248)	(5)	175.5 ± 90.96 (n=111)	(10)	range 94-600 (n=53)	(13)
					range 0-430		range 28-488			
					219 ± 38 SE (n=11)	(7)	148.2 ± 90.2 (n=30)	(10)		
					range 65-517		range 32-400			
							range 36-486	(11)		

				187 ± 45 SE (7) (n=6, lab) range 70-310	
Parasitoid fecundity to body size			increases (5)		increases (13)
Planidia laid / field			5.2 ± 2.8 (n=8) (6) range 3-8		
Planidia laid / laboratory			6.1 ± 5.2 (n=8) (6) range 2-18		4.3 ± 0.7 (n=90) (14) range 0-10
Parasitoid inside host [d]	11 (3)		7-9 at 25°C (7)	8-9 at 23-25°C (7)	up to 17 days (12)
Time until breathing funnel [d]	4 (2)				
Breathing funnel until death [d]	7 (3)				up to 13 days (12)
Pupal developing at 25°C [d]	13 {at 17°/28° C}		12-15 (7)	11-13 (7)	21 ± 0.7 (12) 22 ± 0.2

Data are compiled from following references: (1) this book chapter part I, (2) Lehmann & Heller 1998, (3) Lehmann & Lehmann 2006, (4) Kolluru pers. comm., (5) Kolluru & Zuk 2001, (6) Adamo et al. 1995b, (7) Wineriter & Walker 1990, (8) Welch 2006, (9) Frank pers. comm., (10) Fowler 1987, (11) Fowler & Garcia 1987, (12) Allen 1995, (13) Allen & Hunt 2001, (14) Allen et al. 1999.
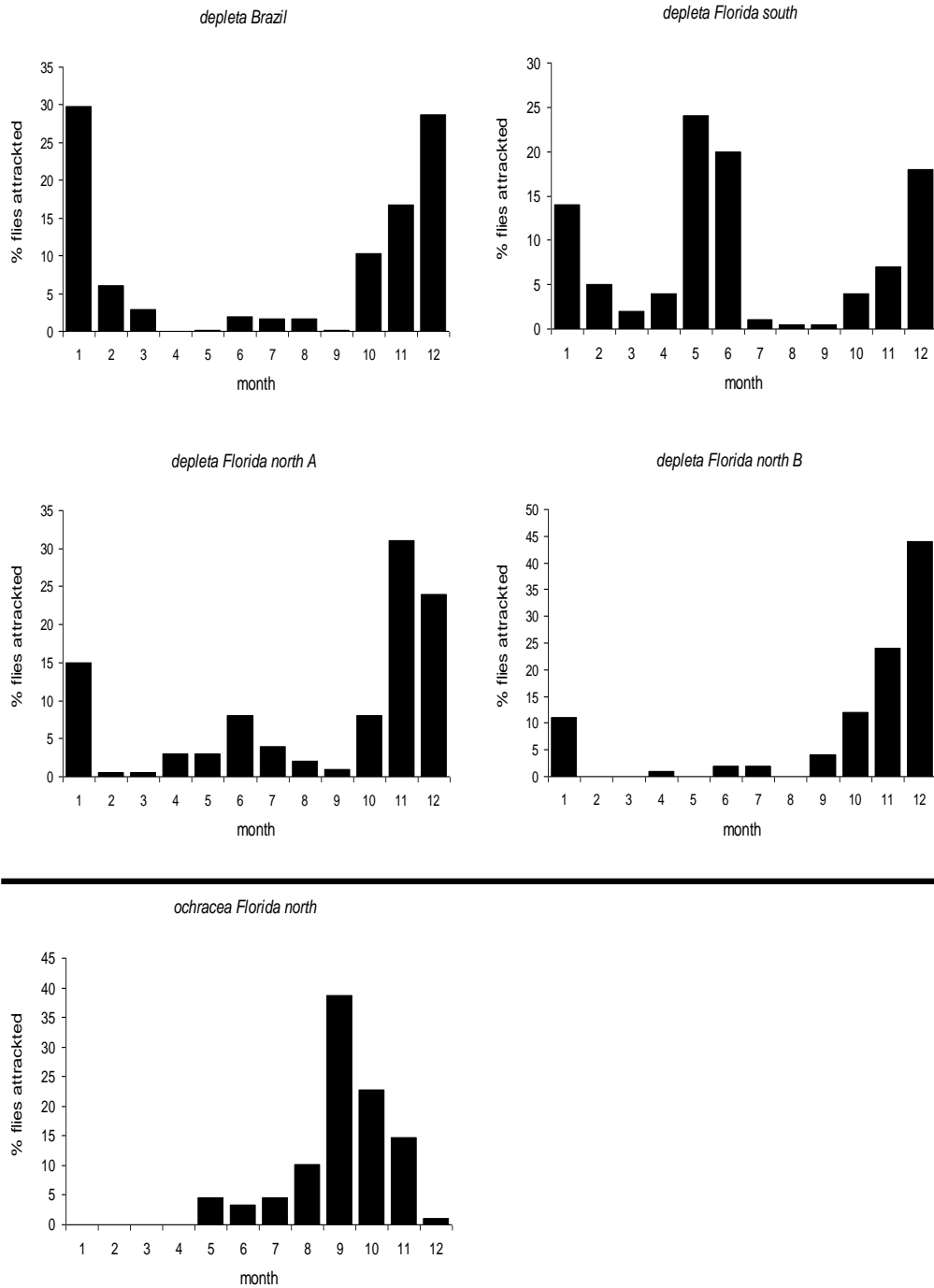
Figure 12. Seasonal captures of female parasitoid flies on sound traps using synthesized songs. Mole cricket songs were tested in Brazil (Fowler 1987b) and extensively in different localities in Florida (Walker et al. 1996), attracting females of *Ormia depleta*. Songs of the cricket *Gryllus rubens* (below the bold line) were also tested in Florida (Mangold 1978, see Walker 1986 for similar data) attracting *Ormia ochracea*. Fly numbers attracted and courted were normalized to percentage values over the whole season for comparison.
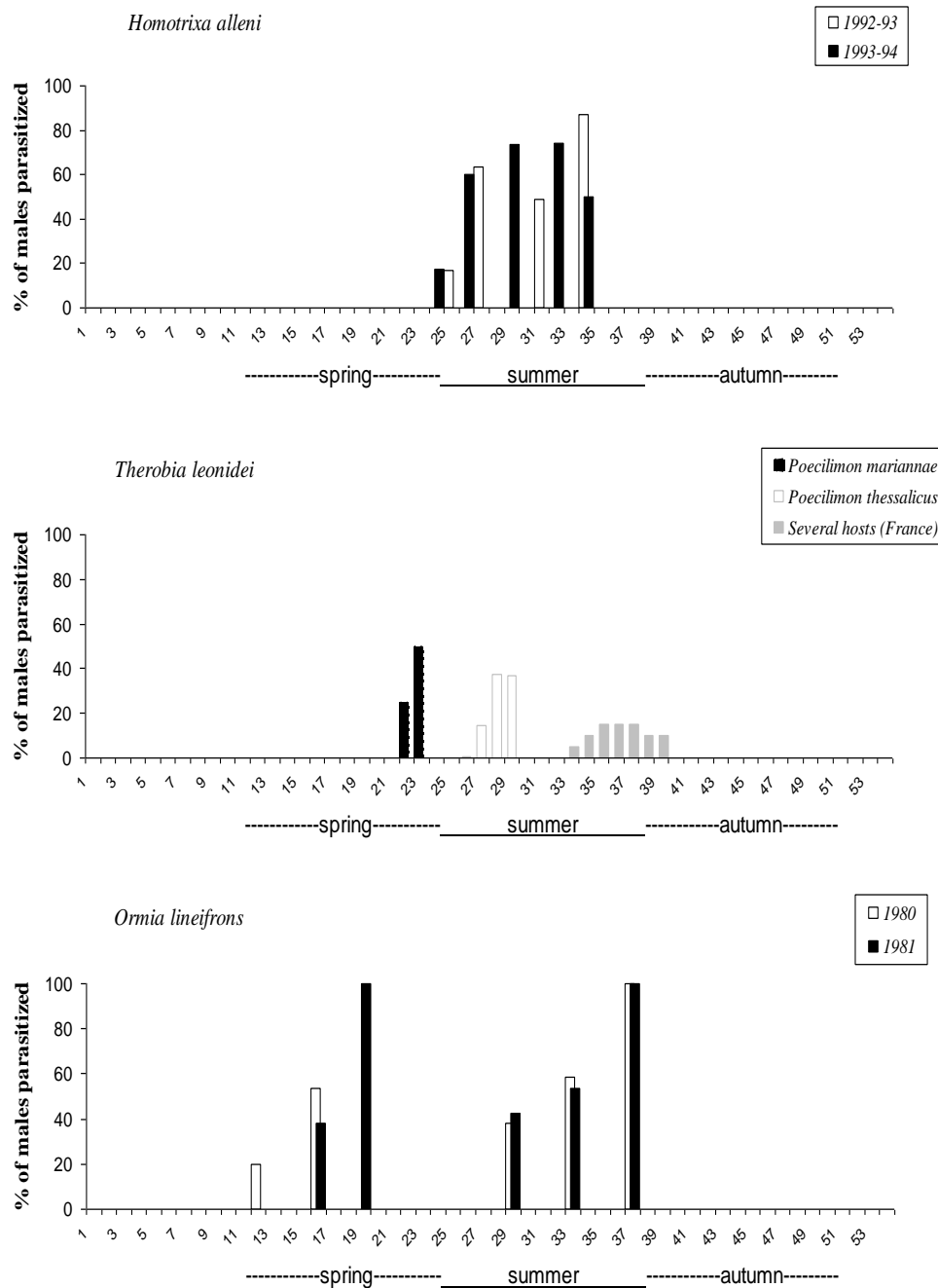
Figure 13. Percent parasitism in three different bushcricket parasitoids. On top the parasitism rates of the Australian Fly *Homotrixa alleni* in its main host *Sciarasaga quadrata* in two consecutive seasons (reanalyzed data from Allen 1995). In the middle the parasitism patterns of the European *Therobia leonidei* in different hosts (original data, Leonide 1969 for France). In northern Florida *Ormia lineifrons* is bivoltine utilizing the same host *Neoconocephalus triops* (reanalyzed data from Burk 1982).

It is not surprising, therefore, that bushcrickets are the hosts for the majority of Ormiini flies (Lehmann 2003) and that parasitism rates are quite high in all studied species,

particularly at the end of the season (Figure 12). In Australia the bushcricket *Sciarasaga quadrata* is the main host of *Homotrixa alleni*, with parasitism occurring over the whole southern summer from November to February.

The European fly species *Therobia leonidei* has been observed parasitizing several bushcricket species. The main hosts in Greece are members of the phaneropterine genus *Poecilimon,* who have a calling season of up to four weeks (Lehmann & Lehmann 2006). *P. mariannae* is a lowland species whose breeding season commences earlier than the higher altitude *P. thessalicus*. However, in France the fly has been observed in late summer and autumn in other bushcricket species as well (Figure 12 middle). In North America the bushcricket *Neoconocephalus triops* is parasitized by *Ormia lineifrons*. Fly parasitism is bivoltine in northern Florida (Figure 12 bottom), but extends at least over four summer months in southern Florida (Burk 1982). No data currently exist for tropical bushcricket species.

In bushcrickets singing males are generally the sole host. There are a few exceptions such as where low numbers of acoustically responding females or even nymphs are found parasitized (reviewed in Lehmann 2003).

Reported parasitism rates are generally much lower in crickets than in bushcrickets. Parasitism rates in the North American fly species *Ormia ochracea*, which attacks several crickets of the genus *Gryllus* in the United States and a novel host on Hawaii, are low, generally not exceeding 16 percent (Adamo et al. 1995b, Cade 1975, Hedrick & Kortet 2006, Walker & Wineriter 1991, Zuk 1994). Female crickets are significantly less often parasitized than males, but they may still show infection levels of three to ten percent (Adamo et al. 1995b, Walker & Wineriter 1991, Zuk 1994). However, in Brazil 0.3 to 0.6 percent of female mole crickets (*Scapteriscus* 3 spp.) were found to be parasitized while no parasitized males were found (Fowler & Garcia 1987). There is an interesting difference between the cricket and the bushcricket systems. Female crickets may become parasitized if they walk through an area where a fly has recently deposited maggots (Adamo et al. 1995b), as can silent satellite males also (Cade 1975, Zuk 1994).

In the previous paragraph, I reviewed how seasonal occurrence differs between parasitoid-host systems. Even so large differences are observed in regard to parasitism rates between species in the field. What then are the reproductive patterns of Ormiini flies?

Brood sizes in field samples of five host-parasitoid systems are similar (Figure 14). Most hosts bear a single parasitoid larva and the distribution function is a negative exponential curve. This pattern is especially similar for the European *Therobia leonidei* attacking two bushcricket species and the American *Ormia ochracea* that parasitizes two cricket species. However, the brood size curve in the Australian *Homotrixa alleni* is rather flat and large brood sizes of seven and more parasitoids per host male are regularly found. This pattern is obviously the result of extended superparasitism by *Homotrixa alleni* (see discussion).

Therobia leonidei in *Poecilimon mariannae*

Therobia leonidei in *Poecilimon thessalicus*

Ormia ochracea in *Teleogryllus oceanicus*

Ormia ochracea in *Gryllus integer*

Homotrixa alleni in *Sciarasaga quadrata*
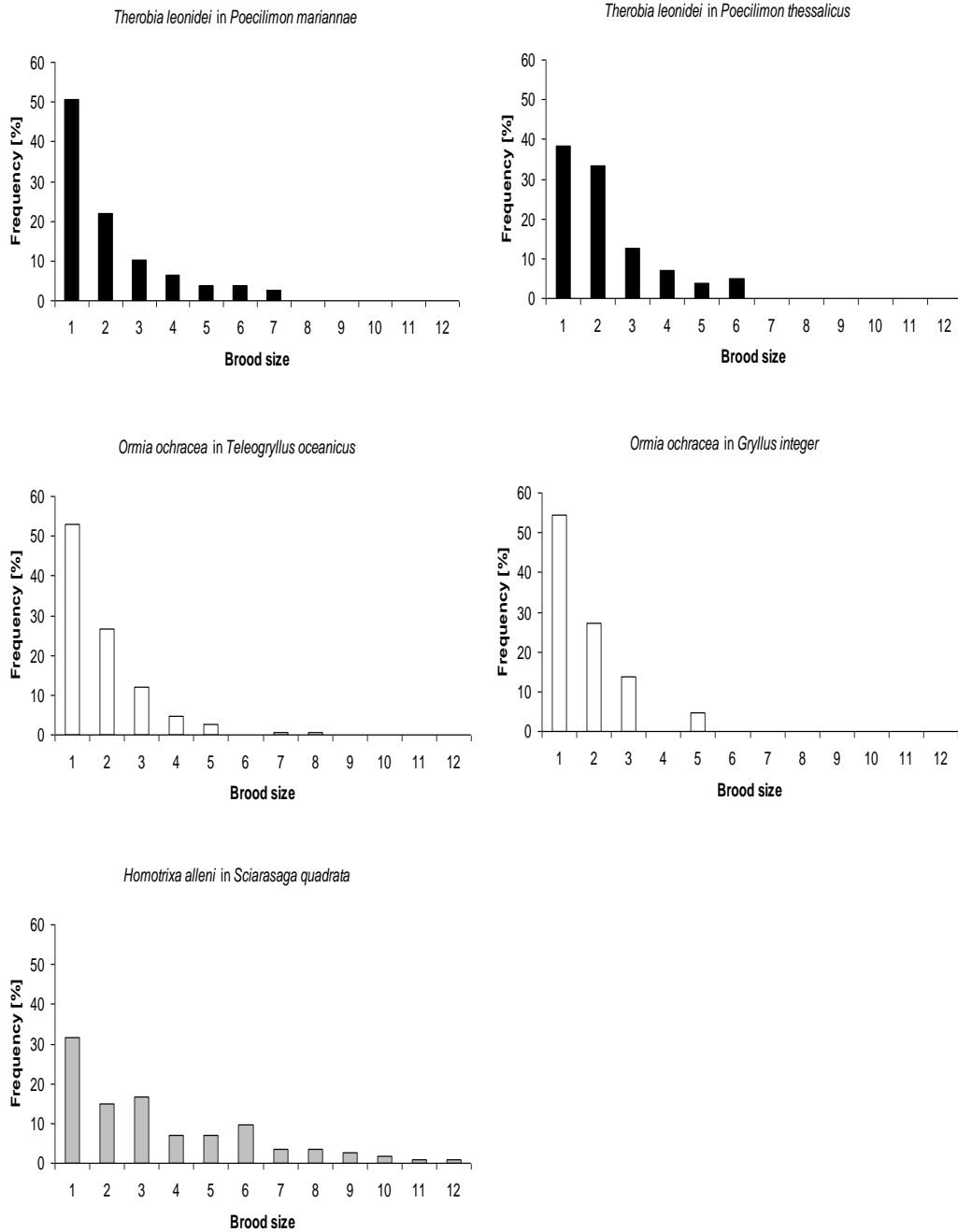
Figure 14. Frequency distribution of brood sizes of three different Ormiini parasitoids (*Therobia leonidei, Ormia ochracea* and *Homotrixa alleni)* in male bushcrickets in Europe (black, original data), Australia (grey, reanalyzed after Allen (1995a)) and in male crickets from North America (white, reanalyzed from Adamo et al. (1995b)) and from Hawaii, where the fly is introduced from North America and the non-original host introduced from Australia (white, reanalyzed from Kolluru & Zuk (2001)).

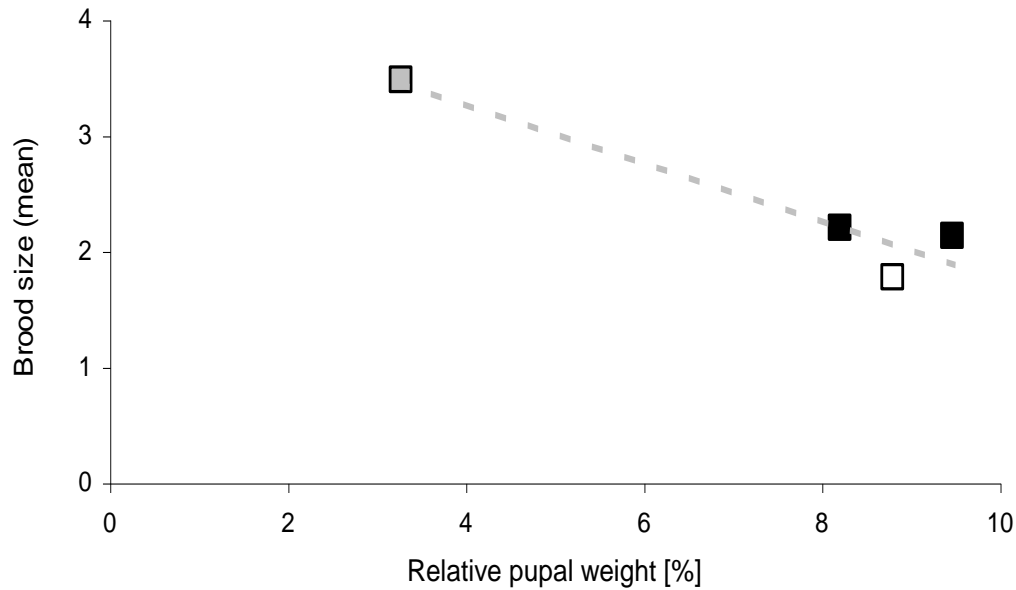Figure 15. Correlation between the parasitoid mass (divided by host mass) and brood sizes in field samples. There is a strong negative correlation ($y = -0.23x + 4.21$, $R^2 = 0.98$), with relatively lighter parasitoids having more parasitoid maggots per host. Data of parasitoid flies of male bushcrickets in Europe (black, original data) and Australia (grey, reanalyzed after Allen (1995a)) and in male crickets from Hawaii (white, original data from Kolluru, pers. comm.).

Pupae of the European fly *Therobia leonidei* weigh on average 8.2 or 9.5 percent of their host males, depending on host species. This is similar to the relative mass of *Ormia ochracea* pupae, which weigh 8.8 percent of their host *Teleogryllus oceanicus* from Hawaii (Kolluru pers. comm.). *Ormia depleta* pupae obtained from artificially infected *Scapteriscus abbreviatus* weighed roughly five percent of host weight (Welch 2006). The Australian *Homotrixa* is once again an exception. Its pupae are twice as heavy as those from other Ormiini species. Nonetheless, *Homotrixa* hosts are so large that the relative parasitoid pupae mass 3.2 percent of host weight (Figure 15).

Classical clutch size theory (Lack 1947) predicts that a female should lay the number of eggs that maximizes her gain in fitness from the whole clutch. From field studies we can not be sure how many parasitoid females have contributed to the observed number of fly larvae within a host. However, the same fitness curve should apply regardless of whether a single or multiple females parasitize a host. Fitness curves for Ormiini flies are only available for *H. alleni* (Allen & Hunt 2001) but we can use the number of larvae to pupate per host as an approximation for other species (Figure 16). In all five systems the mean brood size in the field is much lower than the number of parasitoids that yields the maximum offspring number. This lower-than-optimal clutch size is a unifying pattern, independent of the response curves which are quite steep for *O. depleta*, *O. ochracea* and *H. alleni* or rather flat for *Therobia*.
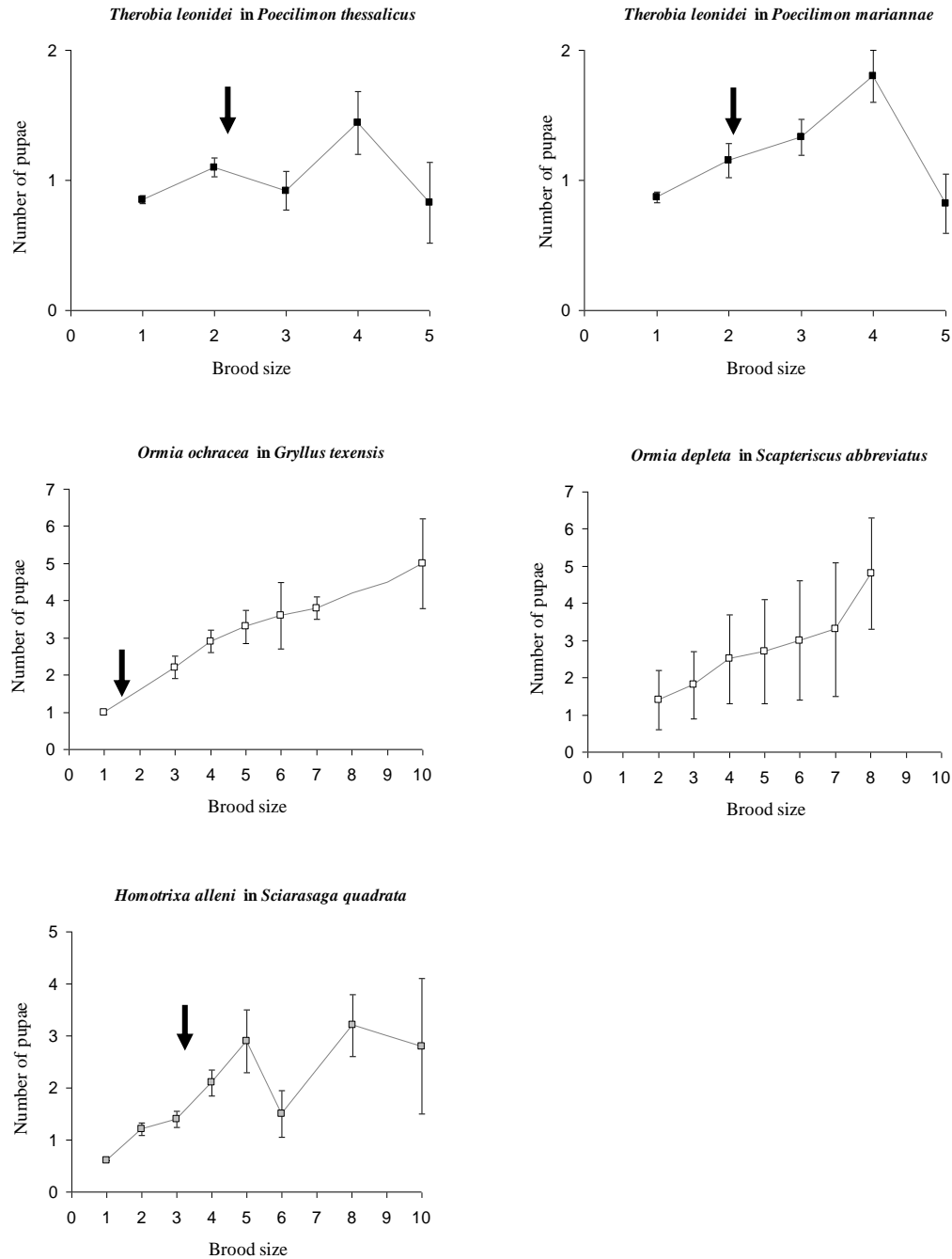
Figure 16. Mean (± SD) number of parasitoid pupae emerging from males of five different host species in relation to brood size. The arrow marks the mean brood size found in the field. The brood size data from the mole cricket *Scapteriscus abbreviatus* are from flying and not from grubbed individuals. This gave the possibility, that the real mean brood size is higher. Data of parasitoid flies in two bushcricket species in Europe (black, original data from chapter I) and one Australian bushcricket (grey, reanalyzed after Allen & Hunt (2001)). The data from *Ormia* fly species attacking crickets (white) and mole crickets were analyzed from Adamo et al. (1995b) and Welch (2006).

Oviposition Strategies

Tachinid flies show a diversity of oviposition strategies, even if they lack any specialized ovipositor. We can distinguish between species that lay eggs on the host (direct oviposition) versus those that lay eggs away from the host (indirect oviposition). The Ormiini show an advanced developing mode in that they exhibit ovovivipary, placing active first-instar planidia on or near to their hosts (Cade 1975, Adamo et al. 1995b, Allen et al. 1999). The indirect mode of oviposition is linked to a larger clutch size in *Ormia ochracea* (Adamo et al. 1995b), but the presence or absence of a host does not change the number of indirectly positioned planidia in *Homotrixa alleni* (Allen et al. 1999). We have no clear picture of how often or when female Ormiini use the direct or the indirect oviposition mode. However, fecundity seems to be quite similar between Ormiini flies (Allen & Hunt 2001, Fowler 1987b, Fowler & Garcia 1987, Kolluru & Zuk 2001, Wineriter & Walker 1990), with means of 148 to 219, ranging up to 600 planidia (see table 1). This number corresponds well with the summary given for tachinid flies having a direct-external oviposition mode using incubated eggs (Stireman et al. 2006).

Parasitoid fecundity also increases with body size - measured either as female head width (Allen & Hunt 2001) or female thorax length (Kolluru & Zuk 2001). The number of placed planidia may be three to four times higher than the brood size observed in cricket hosts (Adamo et al. 1995b, Kolluru & Zuk 2001). This does not necessarily mean there can be 75% larval mortality since some may infect by-passing females or satellite non-singing males (Adamo et al. 1995b, Zuk 1994).

DISCUSSION

Given the relatively small size of parasitoids, finding a suitable host might be a heavy task for most species. Hymenoptera are famous for their ability to use chemical cues either emitted directly from the host or from the host's microhabitat. Host plant odours are important as such chemicals (Godfray 1994). Ormiini flies in contrast rely on acoustic signals of their hosts for localization (Cade 1975) and act as illicit exploiters of the host communication system (Haynes & Yeargan 1999). Ormiini flies can very accurately hear (Mason et al. 2001) and attack hosts by homing in on their calling song (Müller & Robert 2001). Even while walking (Mason et al. 2005), *Ormia* flies are capable of distinguishing sound sources (Arthur & Hoy 2006). Signals derived directly from hosts are considered reliable indicators of their location and identity (Feener & Brown 1997). It is therefore not astonishing, that high levels of parasitism are found in most Ormiini-host systems studied (Allen 1995, Adamo et al. 1995b, Burk 1982, Kolluru & Zuk 2001), including my results on Greek bushcrickets presented here. Male parasitism in *P. mariannae* increased linear over the season and levelled between 50 and 57 percent in three consecutive years. This host species produces more complex and longer lasting (= poly-syllabic) songs compared to the monosyllabic *P. thessalicus*. This might explain largely the differences in the total amount of parasitized males (Lehmann & Heller 1998). However, substantial fluctuation exist in the parasitism rate between years in the monosyllabic *P. thessalicus*, similar to fluctuations between years found for another monosyllabic host *P. veluchianus* (Lehmann & Heller 1998). Because flies rely so strongly on sound as a host clue, a fluctuation might be related to differences in the amount

the bushcricket males spend calling. Such variation in the time spend calling might be induced by environmental variables like weather conditions. Alternatively this levels are intrinsically linked to between years fluctuations in population densities of flies.

Once an adult fly has detected and localized a host, we expect a dynamic interaction between the host as the variable environment for the developing larvae and the decisions to be made by the mother. In general, oviposition behaviour in parasitoids is dynamic, responding to variation in host quality and availability (Papaj 2000). Parasitoids display remarkable inter- and intraspecific variation in their reproductive and associated traits. Adaptive explanations have been proposed for many of parasitism patterns and linked to key aspects of host ecology (Jervis et al. 2008). However, there are fundamental differences between the large body of results in Hymenoptera (e.g. Godfray 1994), and those in Diptera (Feener & Brown 1997), especially Tachinidae (Stireman et al. 2006).

Oviposition Strategies

Unlike parasitic Hymenoptera, tachinids lack a primitive piercing ovipositor. This missing prevents the injection of paralytic poisons, mutualistic polyDNA viruses, and other accessory substances. Instead of immobilizing their hosts and/or its immune system, tachinids allow them to continue to feed and grow while they develop inside (Stireman et al. 2006). Host performance decreases over time (Cade 1984, Adamo et al. 1995a, Allen 1995, Kolluru et al. 2002, Orozco & Bertram 2004, Lehmann & Lehmann 2006), probably in a response to the rapid growth of the maggots inside and the degrading effect on host physiology. Tachinidae flies can be distinguish according to their reproductive mode, especially whether they deposit eggs, larvae or even pupae (Meier et al. 1999). They can also be divided into species that oviposit directly on the host versus those that deposit in the surrounding of the host. These diverse oviposition strategies have evolved in concert with host-searching and attack strategies, changes in fecundity, and the types of hosts attacked (Stireman et al. 2006). Ormiini deposit active first-instar planidia (ovovivipary), flexible either direct on (Cade 1975) or in the surrounding of a host (Adamo et al. 1995b, Allen et al. 1999) and the planidia must gain entry into the host. The indirect mode of oviposition is connected to a larger clutch size in *Ormia ochracea* (Adamo et al. 1995b), but the presence or absence of a host does not change the number of indirectly positioned planidia in *Homotrixa alleni* (Allen et al. 1999). Field collected Ormiini females had up to 600 planidia, with means of 148 to 219 (Allen & Hunt 2001, Fowler 1987b, Fowler & Garcia 1987, Kolluru & Zuk 2001, Wineriter & Walker 1990) and larger wild-caught flies had higher fecundity (Allen & Hunt 2001, Kolluru & Zuk 2001).

Regarding the number of offspring deposited, Ormiini are gregarious parasitoids with mixed sex broods (Godfray 1994). Brood sizes are low compared to other tachinids, with a maximum of 12 breathing funnels observed in a single host (Allen 1995, Lehmann unpubl. data, Figure 14). The majority of hosts bear only a single parasitoid larvae. The brood size distribution is especially similar for the European *Therobia leonidei* attacking two bushcricket species and the American *Ormia ochracea* in two cricket species. Maggots in both Ormiini species reach similar maggots weights, with pupae from single infected hosts weighing in mean between 8.2 and 9.5 percent of host mass (Table 1). The large and heavy Australian bushcricket *Sciarasaga quadrata* however is parasitized by a larger number of maggots, but

the relative parasitoid pupae mass is only 3.2 percent. This leads to the assumption of a correlation between relative parasitoid-to-host mass and the mean brood size (see Figure 15).

Ormiini may be unable to accurately access host size or quality, especially when females indirectly oviposit. The indirect infection mode further add to the infection uncertainty as some planidia might not reach the targeted singing male (Adamo et al. 1995b). The number of planidia placed around a targeted host is three to four times higher, than the brood size in field sampled cricket hosts (Adamo et al. 1995b, Allen et al. 1999). This means an approximated 75 percent of planidia mortality and therefore it is not astonishing, that no evidence of clutch sizes adjustment could be found, different to hymenopterans (Godfray 1994). Parasitized male crickets were slightly larger than unparasitized males (Kolluru & Zuk 2001), a result not found in a field experiment with bushcrickets (Lehmann et al. 2001). There was no correlation between host size and the number of larvae in all species tested (Table 1).

Larval Competition/Clutch Size Theory

One of the major decisions a gregarious parasitoid have to make is how many offspring to oviposit on an encountered host (Godfray 1994). Classical clutch size theory predicts, that a mother should lay the number of eggs, that maximizes her gain in fitness not from the single offspring, but from the whole clutch (Lack 1947). For insects that use discrete resources, such as parasitoids and seed feeders (see Amarillo-Suarez & Fox 2006), host size and host quality are major sources of phenotypic variation and constrain offspring growth (Hardy et al. 1992, Tsai et al. 2001). The fundamental assumption of parasitoid clutch size theory is that offspring fitness is a function of clutch size. There is a large body of evidence, that hymenopteran parasitoids adjust their clutch size to host size and host quality (Hardy et al. 1992, Godfray 1994, Mesterton-Gibbons et al. 2004, Traynor & Mayhew 2005, Häckermann et al. 2007).

Ormiini show a negative relationship between clutch size and progeny fitness, consistent with hymenopterans, but no adjustment of clutch size to host size (different from hymenopterans). The number of maggots placed on or around a singing host was similar between Ormiini species attacking larger (Allen et al. 1999) or smaller host species (Adamo et al. 1995b). Within species the number of maggots a host harboured was independent of host weight (Table 1), whereas between species the relatively heavier host species -the bushcricket *S. quadrata*- contained more parasitoids (Figure 15). However, this host survives longer after parasitoid attack (Allen 1995) than other Ormiini hosts (Lehmann & Lehmann 2006, Wineriter & Walker 1990), with an increased possibility, that the larger parasitoid number is the result of superparasitism (see discussion below) and not the outcome of clutch size adjustment by the parasitoid fly. Mixed results are obtained for pupal weight in regard to host weight. In my field studies, there was no relationship between parasitoid pupal weight and host weight (Figure 5), whereas in artificial infected mole crickets heavier hosts produced heavier fly maggots (Welch 2006). In phorid flies laboratory reared offspring were also positively related to the size of the host worker ant (Morrison & Gilbert 1998).

Larval competition in all studied Ormiini increased with brood size and led to reduced survival (Figure 9, Allen 1995b, Welch 2006) and pupal weight (Figure 7, Hunt & Allen 2000, Allen & Hunt 2001, Welch 2006) or pupal size (Adamo et al. 1995b, Kolluru & Zuk 2001). Hatching success of adult flies decreased with pupal weight in three Ormiini species

(Figure 8, Adamo et al. 1995b, Allen & Hunt 2001) and larger flies had higher fecundity (Allen & Hunt 2001, Kolluru & Zuk 2001). In conclusion, adult size and probably fitness is determined largely by the success in larval competition. The only available estimate of fitness in an Ormiini species was undertaken by Allen & Hunt (2001). To compare datasets, I used the number of larvae to pupate per host, instead of fitness curves. As in the hymenopterans (Godfray 1994), the observed brood size in the field was smaller than hosts can support to pupation in five Ormiini species (Figure 16). More precisely, between a third and half of all hosts contained only one parasitoid fly (Figure 14). There are many speculations why parasitoids may be selected to produce smaller clutches than the modelled optimum. One reason in Ormiini might be the fact that larger females survive better or are able to locate hosts better (Allen & Hunt 2001). A minimum size might be critical for hearing, given the fact, that the Ormiini ear is one of the smallest in the world (Lakes-Harlan & Heller 1992, Robert et al. 1992, 1998, Mason et al. 2001). A second explanation might be, that clutch size is hard to adjust to hosts, because the fly not always made contact with the targeted host. To have more planidia than optimum reaching and entering the host, will penalize all offspring with the risk of no survivors at all. This uncertainty over the number of planidia reaching a host undoubtly select for lower clutch sizes. It should also taken into account, that all measurements of offspring number and size are done using well-fed hosts in the laboratory. Environmental conditions might limit host performance and would influence the optimal parasitoid number. Given the broad host range, a moderate clutch size might also contribute to host flexibility and gave the flies the opportunity to invade new areas with alternative hosts of reduced size and weight. At least the cricket parasitoid *Ormia ochracea* shows a remarkable number of regional hosts over North America (Gray et al. 2007) and has even been able to adapt to a novel host after being introduced to Hawaii (Zuk 1994).

Sex Ratios

Males and females are produced in approximately equal numbers in most species with separate sex and any deviation from this equal sex ratio deserves explanation (Hardy 2002, Sheldon & West 2002). The better-studied hymenopteran parasitoids show sex-ratios varying with host size, host quality and local mate competition (Ode & Hunter 2002, Shuker et al. 2006). Most parasitic wasps are haplo-diploid, and ovipositing mothers can selectively fertilize eggs (Ode & Hunter 2002), whereas diplo-diploid species are constraint in there mechanisms of sex determination (Cook 2002, Cockburn et al. 2002, West & Sheldon 2002). In tachinids, the limited amount of studies did found equal sex ratios (Nakamura 1995), also in Ormiini (Adamo et al. 1995b, Allen & Hunt 2001). In phorid flies, females emerge from larger hosts (Morrison & Gilbert 1998) and laboratory studies revealed a pattern of sex ratio variation as a function of host size (Morrison et al. 1999). Sex ratios for single infected hosts were nearly equal for *Therobia leonidei* in my studies regardless of host species. Even if not statistically significant, I found a higher amount of female flies in larger brood sizes. This variation might not be the result of a deviated primary sex ratio controlled by the mothers, but due to differential mortality of the sexes in response to larval competition (e.g. Miura 2003). Larger brood sizes led to smaller offspring, so males in *Therobia leonidei* might be under a stronger selection for larger size than females. One possible explanation comes from the fact, that Ormiini form mating swarms (Lederhouse et al. 1976), like in a number of flies (Downes

1969). Therefore only large males are likely to gain access to females as in two Australian tachinids (Alcock & Smith 1995), leading to strong selection on male body size, levelling the ability to survive by small male maggots.

Superparasitism

Superparasitism is defined as the deposition of a clutch of eggs by a female parasitoid in or on a host, already parasitized by itself or a conspecific female (van Alphen & Visser 1990, Godfray 1994). Because the progeny of a superparasitizing female are normally at a competitive disadvantage relative to the progeny of the previous parasitoid, natural selection should favour females with the ability to discriminate against parasitized hosts. Such host discrimination have been widely documented for parasitic Hymenoptera, where parasitoids use a variety of cues to distinguish between parasitized and unparasitized hosts (Godfray 1994). Superparasitism in gregarious hymenopteran parasitoids can be an advantage adaptation, until the host carrying capacity is reached (Speirs et al. 1991, Dorn & Beckage 2007). In contrast to Hymenoptera, superparasitism appears to be a more regular phenomenon in parasitic Diptera (Feener & Brown 1997). This widespread occurrence of superparasitism in flies supports the impression, that most flies lack the ability to discriminate against parasitized hosts. Because female fitness is not only correlated to offspring quality but also to the total produced number of offspring, this lack of discrimination must not be a disadvantage. Parasitoid flies may optimizing their fitness by producing a lot of less fecund offspring (Nufio & Papaj 2004), most likely when host availability is low. Even so, the ability to discriminate between parasitized and unparasitized hosts may be less advantageous in species that attack agile or actively defended host, which is the case in carnivorous bushcrickets.

In the Ormiini, ovipositing females make not always direct contact with the host, and therefore they have little opportunity to recognize prior parasitization. Female Ormiini might discriminate against less favoured hosts by exploiting the information contained in hosts song. Indeed, Ormiini flies preferred the same song patterns as cricket host females, having higher chirp rates, longer chirp duration, and higher chirp amplitudes (Wagner 1996, Wagner & Basolo 2007). Host males more attractive for conspecific females also suffer from higher parasitism rates (Lehmann et al. 2001). Song production and structure (Cade 1984, Kolluru et al. 2002, Orozco & Bertram 2004, Lehmann & Lehmann 2006) and attractiveness of song (Lehmann & Lehmann 2006) decreases with the time since parasitism, so at least older parasitized hosts may be not superparasitized. The opportunity to use song for detecting superparasitism however, may be limited in the first days and Adamo et al. (1995b) found no evidence, that females of *O. ochracea* discriminate between unparasitized and parasitized cricket males. We have no data on direct observations of superparasitism in Ormiini, and it is ambiguous to determine, whether a field-collected host is superparasitized. However, several approaches are used to estimate superparasitism in gregarious species (Dorn & Beckage 2007). By classifying parasitoid maggots using their developmental stage inside the host, superparasitism was estimated to be between 4.7 (Kolluru & Zuk 2001) and 25 percent in north American field crickets (Adamo et al. 1995b). Using an threshold approach, I estimated an amount of 8.6 percent superparasitized males over the whole season, with a maximum of 17.6 percent in the bushcricket *P. thessalicus*. Superparasitism was obviously disadvantage,

as never more than just one maggot hatched from this species. In conclusion, superparasitism might best be seen as nonadaptive in Ormiini, related to the non-contact oviposition and the lack of clear clues in the song to identify freshly parasitized hosts.

Multiparasitism

An other case of larval competition is found in cases where parasitized hosts are infected by a second species. Such multiparasitism was also reported between different species of Tachinidae (Iwao & Ohsaki 1996, Reitz 1996, Kan et al. 2003). Adult bushcrickets are found to be multiparasitized by tachinids and strepsipterans (Solulu et al. 1998), but both without the ability to hear their hosts. Even if Ormiini show broad host ranges, in no case were two Ormiini species found within one host. The only case of multiparasitism was observed between the Ormiini *H. alleni* and a sarcophagid fly species in the Australian bushcricket *S. quadrata* (Allen & Pape 1996). I also found Sarcophagidae as parasitoids of bushcrickets in Greece and Slovenia (Lehmann unpubl. data), but in those examples the sarcophagids must have entered the immature stages, as they hatched from nymphal field samples. In several hundred *Poecilimon* bushcrickets parasitized by the Ormiini *T. leonidei*, I never observed an other parasitoid species hatching. It is questionable why Sarcophagidae, in which at least one species have independently evolved a hearing organ (Lakes-Harlan et al. 1999, Robert et al. 1999) and parasitizes singing cicada in North America (Soper et al. 1976, Lakes-Harlan et al. 2000, Köhler & Lakes-Harlan 2001, 2003, Schniederkötter & Lakes-Harlan 2004, de Vries & Lakes-Harlan 2005) has not evolved the ability to exploit singing orthopterans as well. However, adult bushcrickets and crickets live quite hidden in their habitats, preventing probably most parasitoids to get access. The exploitation of acoustic signalling is therefore a private channel for Ormiini, which limits interspecific competition.

Host Ranges

Dipteran parasitoids generally attack a wider range of hosts compared to the more diverse parasitic wasps (Eggleton & Belshaw 1993). Many tachinid species are polyphagous, and a number of them show a striking variation in host ranges (Stireman et al. 2006). Host ranges in Ormiini are still poorly known (Lehmann 2003), so I must concentrate on the four systems studied in more detail. The comparative approach showed, that parasitism of bushcrickets is the ancestral stage and the switch to the ground living crickets and mole crickets is a derived pattern (Lehmann 2003), even if we lack a robust phylogeny for the flies. There is a strong difference between Ormiini parasitizing bushcrickets and those parasitizing crickets or mole crickets. The two bushcricket parasitoids *T. leonidei* and *H. alleni* have both broad host ranges (review in Lehmann 2003). Their hosts vary in regard to host feeding type (carnivore-herbivore), body size, and thus are from distantly related bushcricket subfamilies. The only limitation for parasitism seems to be the song pattern produced, but host species have either the male-only-calling or the female-responding communication system. It is therefore very likely, that much more host species will be found in the future, even in this well explored systems. This flexibility will also allow the flies to explore new or alternative host species easily, if only the song type fit into the physiological and anatomical properties of hearing.

However, little data exist for tropical areas, which would be a perfect test of our predictions. In general, males are the effected sex, with few exceptions, where acoustically responding females (Léonide 1969), non-singing females (Lehmann 2003) or even nymphae (Shapiro 1995), found as being parasitized.

    Parasitism patterns differ in the two cricket-flies (including mole crickets). Their habit to shelter inside self-constructed burrows might protect crickets to some extend from the parasitoids. Therefore reported parasitism rates are lower than in bushcrickets (Adamo et al. 1995b, Cade 1975, Hedrick & Kortet 2006, Walker & Wineriter 1991, Zuk et al. 1993, Zuk 1994). Females are less often parasitized than males, but suffer to a much larger degree than bushcricket females (Adamo et al. 1995b, Walker & Wineriter 1991, Zuk 1994). Females and silent satellite male crickets may become parasitized, if they walk through an area, where a fly has recently deposited maggots (Adamo et al. 1995b, Cade 1975, Zuk 1994). The host ranges are more constrained, limited to closely related host species mostly from one genus. However, the fly *O. ochracea* uses crickets with locally differing song pattern (Gray et al. 2007) and has been adapted to a novel host after introduction into Hawaii (Zuk et al. 1993, Zuk 1994). In the cricket flies the hearing threshold is focussed on the song frequencies of crickets (Robert et al. 1992), restricting the parasitism to this group. Ormiini are obviously able to avoid an immune response during the first days, during which they remain in the thorax muscles (Léonide 1969, Adamo et al. 1995a). After the fly maggot have migrated into the abdomen, they turn the immune response of their host, to build the respiratory funnel from products of the host's immune response (Feener & Brown 1997). Hymenopteran parasitoids use a huge variety of mechanisms to escape the encapsulation process (Schmidt et al. 2001, Dubuffet et al. 2008), which obviously holds for Ormiini (Bailey & Zuk 2008) and allows them to infect a brood range of host species.

Phenotypic Plasticity

    For insects that use discrete resources, such as parasitoids, host size is a major source of phenotypic variation and constrain offspring growth, influencing the evolution of body size and life history traits (Hardy et al. 1992, Tsai et al. 2001). Similar problems apply to seed feeders (Amarillo-Suarez & Fox 2006). Individuals in populations adapted to large hosts are generally larger than those adapted to small hosts, especially in species with scramble competition (Godfray 1994, Häckermann et al. 2007). In my study system, hatching maggots of the Ormiini *T. leonidei* in a population adapted to the larger host *P. mariannae* were much heavier than in a population adapted to the smaller host *P. thessalicus*. This difference in offspring weight is likely the response to large versus small hosts, in agreement with the usual expectations for scramble-competing species (Hardy et al. 1992, Tsai et al. 2001). Notably, maggots from the lighter host *P. thessalicus* were able to hatch at a much reduced minimal weight, in a range where no hatching was observed for maggots from the heavier host species. This plasticity likely buffers these flies from high mortality or low fitness, that they would otherwise experience, when encountering alternative host populations. Thus it provides the opportunity to infect a broad range of local host species, relatively independent of host body weight. Those adaptive plasticity should promote establishment and persistence in new environments (Ghalambor et al. 2007). The role of phenotypic plasticity is broadly covered by life history theory (Roff 2002), and such change in ecologically significant parameters can

occur over tens of generations or fewer and is now widely documented in nature (Carroll et al. 2007). We need further experiments to disentangle the basis of such response, because much plasticity perceived as adaptation could be environmentally induced (nongenetic) plastic responses rather than (genetic) evolutionary adaptations (Gienapp et al. 2008). However, this is the first example I know of, that a fly parasitoid is found to respond in life history traits to its local host species.

Research Opportunities

The limitations for research within the Ormiini-host systems differ. Bushcrickets are easier to detect, at least in open habitats where the hosts can be sampled in reasonable numbers (Allen 1995, Burk 1982, Lakes-Harlan & Heller 1992, Lehmann & Heller 1998). The light colour of most bushcricket undersides is ideal for counting the melanized breathing funnels of the parasitoids (see Lehmann 2006). In contrast, crickets and mole cricket calls from inside of burrows are harder to find or capture (Walker & Wineriter 1991), and non-calling individuals might be underrepresented. Sound traps as time-effective alternatives for sampling face two serious problems. Firstly, parasitoid flies are also attracted along with their hosts, leading to parasitism inside traps (Walker & Wineriter 1991). Secondly, parasitism strongly affects host performance (Adamo et al. 1995a; Kolluru et al. 2002, 2004; Lehmann & Lehmann 2000a, 2000b, 2006), reducing calling duration and quality (Cade 1984, Kolluru et al. 2002, Lehmann & Lehmann 2006, Orozco & Bertram 2004). Even if it is not measured yet, host flight is an energy-demanding behaviour (Reinhold 1999) and so fewer parasitized hosts may be sampled. Therefore, parasitism rates and brood sizes might be underestimated in samples from sound traps. In the bushcricket systems, operating sound traps is technically more demanding, as the ultrasound song needs more sophisticated equipment for broadcasting. In my study species, *Therobia leonidei* no flies could be caught with different traps (similar to those described by Fowler 1988; Walker 1988, 1989) and flies could not be reared under semi-field conditions (Lehmann unpubl. data). Therefore any research on this fly must be field-based and limits the experimental possibilities.

To date, Ormiini research has yielded interesting results, regarding host selection, host switching from bushcrickets to crickets and the observation, that the uncertainty of host parasitism limits the potential for clutch size adaptation in this group. Still far more results are available for hymenopteran parasitoids, but flies and especially tachinids might be a good addition to understand general trends in parasitoid-host relationships. Ormiini form only a small group, but due to their influential position in evolutionary biology (Zuk & Kolluru 1998) and biological control (Parkman et al. 1996, Walker et al. 1996), we know more about this small group than about most other parasitoid flies (Feener & Brown 1997, Stireman et al. 2006). The potential for further research is therefore manifold and I encourage future researchers to study this group, especially results from tropical areas have the potential to contribute substantially to the understanding of host-parasitoid relationships and that of illicit receivers of acoustic communication in particular.

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