

Evol Ecol (2008) 22:153–166
DOI 10.1007/s10682-007-9164-x

ORIGINAL PAPER

Comparing and contrasting development and reproductive strategies in the pupal hyperparasitoids *Lysibia nana* and *Gelis agilis* (Hymenoptera: Ichneumonidae)

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Received: 12 May 2006 / Accepted: 12 February 2007 / Published online: 11 April 2007
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Abstract In most animals, the optimal phenotype is determined by trade-offs in life-history traits. Here, I compare development and reproductive strategies in two species of solitary secondary hyperparasitoids, *Lysibia nana* and *Gelis agilis*, attacking pre-pupae of their primary parasitoid host, *Cotesia glomerata*. Parasitoid larvae of both species exploit a given amount of host resources with similar efficiency. However, adults exhibit quite different reproductive strategies. Both species are synovigenic, and female wasps emerge with no mature eggs. However, *G. agilis* must first host-feed to produce eggs, while *L. nana* does not host-feed but mobilizes internal resources carried over from larval feeding to initiate oogenesis. Further, *G. agilis* is wingless, produces large eggs, has a long life-span, and generates only small numbers of progeny per day, whereas these traits are reversed in *L. nana*. Given unlimited hosts, the fecundity curve in *L. nana* was “front-loaded,” whereas in *G. agilis* it was depressed and extended over much of adult life. In *L. nana* (but not *G. agilis*), wasps provided with honey but no hosts lived significantly longer than wasps provided with both honey and hosts. Differences in the fecundity curves of the two hyperparasitoids are probably based on differing costs of reproduction between them, with the wingless *G. agilis* much more constrained in finding hosts than the winged *L. nana*. Importantly, *L. nana* is known to be a specialist hyperparasitoid of gregarious *Cotesia* species that pupate in exposed locations on the food plant, whereas *Gelis* sp. attack and develop in divergent hosts such as parasitoid cocoons, moth pupae and spider egg sacs. Consequently, there is a strong match between brood size in *C. glomerata* and egg production in *L. nana*, but a mismatch between these parameters in *G. agilis*.

Keywords Development · *Cotesia glomerata* · Hyperparasitoid · Lifetime reproductive success · Synovigenic · Trade-off

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Introduction

Understanding how limited metabolic resources are allocated for vital functions remains one of the foundations of both empirical and theoretical aspects of evolutionary ecology (Roff 1992; Stearns 1992). In most organisms, the optimal phenotype is determined by a trade-off in life-history traits, such as between early and late reproduction and between reproduction and survival (van Noordwijk and de Jong 1986; Lessells 1991; Rivero and West 2005). Consequently, an organism may invest more internal resources towards egg production early during adult life at the cost of a reduced life-span (Lessells 1991). A trade-off occurs when two traits are limited by the same resource, such as time or energy, because these can only be utilized once (Levins 1966; Lessells 1991). The relative importance of trade-offs in life-history traits critically depends on the quality of the habitat in which the organism lives, feeds and reproduces, in terms of resource availability (Pexton and Mayhew 2002; Holomuzki and Biggs 2006). Further, the risk of mortality experienced by the organism early during development may also influence metabolic investment towards maintenance or reproduction (Black and Dodson 1990; Riessen 1992; Vollrath and Parker 1992). Ultimately, life-history trade-offs may play an important role in shaping the structure of ecological communities (Bonsall et al. 2004).

Some of the best studies on life-history trade-offs and the importance of larval and adult feeding on reproduction have been conducted with parasitic wasps or “parasitoids” (Jervis and Kidd 1986; Chan and Godfray 1993; Collier 1995; Ellers et al. 1998; Rivero and West 2005). Parasitoids are insects that lay their eggs on or in another insect (the host), and the progeny develop by feeding on host tissues. Interactions between parasitoids and their hosts are usually highly intimate (Godfray 1994). For this reason, parasitoids exhibit developmental, physiological and morphological traits that are often highly specialized and correlated with ecophysiological characteristics of their hosts (Price 1972; Vinson and Iwantsch 1980; Jervis and Kidd 1986; Godfray 1994; Harvey and Strand 2002).

Parasitoids are classified according to the temporal production of eggs before and after adult emergence. Synovigenic parasitoids are species that emerge with only a fraction of their potential complement of mature eggs, whereas pro-ovigenic parasitoids emerge with a full egg complement and do not mature additional eggs during adult life (Jervis et al. 2001). The fitness of synovigenic parasitoids is largely dependent on the rate at which eggs can be matured after eclosion, the total number of eggs that can be produced (=potential fecundity), and the number of hosts that are successfully parasitized and that ultimately produced adult wasps (=realized fecundity). Host availability is in turn based on two interacting components, abundance and accessibility, and these parameters are strongly host-stage-dependent. For example, Price (1972) reported significant differences in life history and reproductive traits amongst guilds of parasitoids attacking different stages of the same host species, the sawfly *Neodiprion swainei*. Parasitoids attacking numerous, young larval hosts had high potential fecundities and short life-spans, whereas this situation was reversed for parasitoids attacking more scarce pupal hosts.

Many parasitoids mobilize resources for egg production entirely from tissues carried over from larval feeding (Jervis and Kidd 1986; Ellers 1996; Heimpel and Collier 1996; Ellers et al. 1998; Harvey et al. 2001). Here, the adult parasitoid feeds on sources of carbohydrates, such as floral nectar, which contain sugars but are of low quality in terms of proteins (Boggs 1997). Carbohydrates in adult diet are used primarily for maintenance, and thus reduce the metabolic use of stored lipids for this purpose (Ellers 1996; Ellers et al. 1998, 2000; Ellers and Jervis 2003). Alternatively, in addition to nectar, the adults of many

species of parasitoids also feed on high-quality resources, such as host body fluids and tissues, which are rich in proteins that are utilized directly for egg production (Jervis and Kidd 1986; Rivero and West 2005). Nutrients obtained from host-feeding thus enable the parasitoid to mobilize resources obtained from larval feeding primarily for maintenance purposes.

In parasitoids, as in other insects, the allocation of stored and incoming nutrients to reproduction influences the shape of a species' age-specific fecundity curve (Boggs 1997; Ellers and Jervis 2003). In holometabolous insects, with defined feeding and reproductive stages, differences in the shape of the curve may reflect concomitant differences in the importance of larval and adult feeding to reproduction (Ellers and Jervis 2003). When the quality of adult diet is low, resources obtained from larval feeding may be divided between reproduction and maintenance, and as a consequence the fecundity curve is skewed towards early reproduction (more pro-ovigenic) and reduced longevity (Price 1972; Boggs 1997). In contrast, when the quality of adult diet increases, this may free resources obtained from larva feeding to be used more towards maintenance and resources obtained from adult feeding to be invested more into egg production (Boggs 1997). In this situation, the age-specific fecundity curve is dampened but may be extended over a significant portion of adult life (more synovigenic), and longevity is greatly extended.

This study compares and contrasts host utilization, development, and reproductive strategies in two species of solitary, secondary idiobiont hyperparasitoids that attack fully cocooned (pre)pupae of the same primary parasitoid host. *Cotesia glomerata* L. (Hymenoptera: Braconidae) is a gregarious primary endoparasitoid that attacks young larvae of cabbage white butterflies, including *Pieris brassicae* L. (Lepidoptera: Pieridae). *Lysibia nana* Gravenhorst (Hymenoptera: Ichneumonidae) is a fully winged, sexually reproducing obligate hyperparasitoid that only attacks closely related primary hosts in the braconid subfamily Microgastrinae that pupate in exposed locations, including *C. glomerata*. Adult *L. nana* females do not host-feed, and thus rely on sources of nectar in their habitat. *Gelis agilis* Fabricius (Hymenoptera: Ichneumonidae) is a wingless, asexually reproducing facultative hyperparasitoid of several *Cotesia* species that is also potentially a primary parasitoid of many other hosts in nature. For example, in addition to parasitoid cocoons, *G. agilis* and other *Gelis* species are known to attack such evolutionarily divergent hosts such as moth pupae and even spider egg sacs (Bezant 1956; Schwarz and Boriani 1994; van Baarlen et al. 1996; Cobb and Cobb 2004; Toth and Lucas 2005). In addition to nectar sources, adult *G. agilis* females obtain extra resources by feeding on host fluids.

The main aims of the study are (a) to determine if the larvae of both hyperparasitoids exploit host resources with similar efficiency, (b) to compare daily fecundity schedules (fecundity curves) and lifetime reproductive success of the two species provided with excess numbers of hosts in laboratory experiments, and (c) to compare other reproductive traits, including egg production and size in *L. nana* and *G. agilis*. Based on the results, I argue that option sets for resource exploitation by parasitoid larvae exploiting a given host stage are likely to be limited, resulting in similar patterns for size and development time in hosts of a given mass at parasitism. However, I also suggest that the presence or absence of wings in both hyperparasitoid species may affect the spatial dynamics of their searching patterns. This may account for trade-offs in the allocation of resources to reproduction and longevity in the two species, and may also explain differences in their host ranges.

Methods and materials

Insects

Hosts and parasitoids were maintained at $25 \pm 2^\circ\text{C}$ under a 16:8 h L:D regime. Cultures of *C. glomerata* and *P. brassicae* were obtained from insects reared at Wageningen University (WUR), the Netherlands, and which were originally collected from agricultural fields in the vicinity of the University. All *P. brassicae* larvae used in these experiments had been maintained on *Brassica oleracea* var. *Cyrus* (Brussels sprouts) at WUR. In these experiments, *P. brassicae* larvae were maintained on *B. oleracea* plants that originated from seeds from plants growing along a road near the Institute of Ecology at Driel, the Netherlands.

C. glomerata were reared according to the protocol described in Harvey (2000). Adult female wasps oviposit 10–40 eggs into first (L1) to third (L3) instars of *P. brassicae*. During their development parasitoid, larvae feed primarily on host hemolymph and fat body and emerge from the host caterpillar late during its final instar. After emergence, wasp larvae immediately spin cocoons on the host plant adjacent to the host, which perishes within a few days.

L. nana was originally obtained from cocoons of *C. glomerata* recovered from leaves of *B. napus* growing in a garden plot adjacent to the Institute of Ecology, Heteren, the Netherlands. It is known to attack several closely related gregarious endoparasitoid species in the higher Microgastrinae that pupate in exposed locations on the primary host food-plant, including *C. glomerata*. *G. agilis* was also originally obtained from cocoons of *C. glomerata* placed into the field adjacent to the Institute. Little is known about its biology and ecology (but see van Nouhuys and Hanski 2000; Harvey and Witjes 2005).

Like many ectoparasitic idiobionts, adult females of both hyperparasitoids perforate the host cocoon with their ovipositor and inject permanently paralyzing venom into the prepupa or pupa. Following envenomation, the wasps lay a single egg on the moribund host. After the parasitoid egg hatches, the larva perforates the host cuticle with its mandibles and imbibes hemolymph, but as it grows it begins attacking other tissues indiscriminately and eventually consumes the entire host, pupating within the cocoon of *C. glomerata*. In culture, *L. nana* and *G. agilis* were maintained exclusively on 1–2-day-old pupae of *C. glomerata*. After emergence, hyperparasitoids were kept in large (20 cm diameter) Petri dishes at 10°C . Complete rearing methods of both species are described in Harvey and Witjes (2005).

Experimental protocol

Relationship between host mass and adult hyperparasitoid mass

Larvae of *P. brassicae* were parasitized in the first instar (L1) by females of *C. glomerata* by presenting individual larvae to parasitoids at the end of a brush in plastic vials. Parasitism was ensured by allowing wasps to sting hosts for at least 10 s, which enables a full brood to be laid (Harvey 2000). Parasitized caterpillars were immediately placed in large rearing cages (1 m \times 60 cm \times 60 cm) containing four *B. napus* plants. These were refreshed once every few days as required.

Between 12 and 24 h prior to parasitoid emergence, larvae of *P. brassicae* spin a silken mat on the surface of a leaf or inside the rearing cage. These larvae were collected and

placed individually into Petri dishes (10 cm diameter). Upon larval parasitoid emergence from the host (prior to pupation), separate broods of *C. glomerata* cocoons were collected and separated carefully using a pair of forceps and a cecum. Cocoons of *C. glomerata* within broods were then numbered and weighed individually on a Mettler-Toledo MT5 Electrobalance (accuracy $\pm 1 \mu\text{g}$). Two rows of five cocoons that had been pre-weighed were laid down in a Petri dish and attached to the bottom of the dish with a small drop of honey. A *L. nana* female was introduced into the Petri dish and allowed to forage for 24 h. It was then removed and returned to the main culture. The cocoons were also removed from the dishes and placed in labeled 2-l plastic vials until adult emergence of the hyperparasitoids. Newly emerged wasps were anesthetized using CO_2 and weighed on the Mettler microbalance. Adult wasps were sexed by visually checking for the presence or absence of an ovipositor on the wasps. The same experiment was repeated with *G. agilis*, except that in this case females were offered single rows of five cocoons, and all emerging adults were females. For *L. nana*, $n = 141$ wasps (105 males, 36 females) from 15 broods of *C. glomerata*; for *G. agilis* $n = 14$ wasps from 10 cocoon broods.

Egg production, longevity, and lifetime reproductive success in L. nana and G. agilis

Newly emerged wasps of both species were weighed on the microbalance, placed individually in Petri dishes (12 cm diameter) and provided ad libitum with honey. A small ball of cotton soaked in water was also added to ensure that the honey remained partly in solution (and accessible to the wasps, which cannot imbibe dry honey with their mouthparts). To determine egg loads, separate cohorts of wasps were maintained as described above. Beginning on the day of eclosion, 10 wasps (of *L. nana*) and 5 (of *G. agilis*) were dissected in a drop of water on a glass slide using two pairs of forceps and a cecum, and the number of mature (=ovulated, fully chorionated) eggs in their ovaries counted. For *L. nana*, this process was repeated daily over the first 5 days and then on days 10 and 20 post-eclosion. In *G. agilis*, the same experiment was repeated (as with *L. nana*) except that there were two treatments: in the first, wasps were deprived of hosts, their ovaries removed, and eggs (if any) counted on days 0, 2, 4, 6, 10, 15, and 20 days post-eclosion; in the second, wasps were provided with 10 host cocoons for the first 24 h only post-eclosion and were then dissected from day 2 onwards and the number of eggs counted (as in the control).

Hyperparasitoids were weighed at eclosion and thereafter maintained in Petri dishes (as described above) with honey and water. Beginning 3 days after eclosion, cocoons of *C. glomerata* that were <48-h old (containing young pupae) were presented to individual hyperparasitoids of both species. It was important to evaluate how many cocoons of *C. glomerata* would need to be provided to both hyperparasitoids in order to ensure that cocoon number was not a limiting factor in daily oviposition and reproductive success. This was estimated on the basis of ovary dissections and the results of a previous study (Harvey and Witjes 2005). Moreover, irrespective of host density, pilot experiments revealed adults of *G. agilis* will not parasitize more than three to four cocoons per day. Typically, the wasp kills one or two hosts daily for host-feeding purposes, parasitizes one to four other hosts and ignores other cocoons within a brood of *C. glomerata*. In contrast, *L. nana* does not host-feed and begins to mature eggs on the second to third day after eclosion and, when hosts are unavailable, produces about 10–15 eggs daily for a few days until the ovaries reach their storage capacity (Harvey and Witjes 2005). Based on these criteria, for the lifetime reproductive success experiments *L. nana* ($n = 10$ wasps) was provided continually with 20 cocoons/day until wasp death whereas *G. agilis* ($n = 10$

wasps) was provided with 10 host cocoons/day (until 50 days) and five cocoons/day thereafter until wasp death. At the end of each 24-h period, cocoons were removed and placed in plastic vials with information on the date, wasp species and number written onto adhesive labels on the vials. Data on the fate of all of the cocoons were determined (producing an adult hyperparasitoid, parasitoid, or precocious death). Longevity of *L. nana* and *G. agilis* was also measured by recording the number of days between adult eclosion and death with and without host access. In order to determine if host-feeding also influences longevity in *G. agilis*, separate cohorts of wasps ($n = 10$ for each treatment) were reared from eclosion on the following diets: honey and water, hosts and water, water only, hosts only, and host fluids (hosts were removed from cocoons and mashed using a small spatula, and this was diluted in a small droplet of water and presented to wasps).

Statistical analyses

The relationship between host cocoon mass in *C. glomerata* and adult body mass in *L. nana* and *G. agilis* was compared through regression analyses. Hyperparasitoid longevity was analyzed using two-way ANOVA, with species and host access (with or without hosts) as factors. For *G. agilis*, longevity was compared by means of one-way ANOVA. Multiple comparisons were made by means of Tukey's LSD tests. Mean total fecundity in *L. nana* and *G. agilis* was compared using a Student's *t* test. The relationship between adult body mass and reproductive success was compared through regression analyses.

Results

Adult body size in *L. nana* males ($F_{1,13} = 73.65$, $P < 0.001$) and females ($F_{1,9} = 304.76$, $P < 0.001$), as well as in *G. agilis* females ($F_{1,11} = 45.39$, $P < 0.001$), varied significantly with host size. Host cocoons that were heavier at parasitism produced larger adult hyperparasitoids than smaller cocoons (Fig. 1). The larvae of both species appeared to exploit a given amount of host mass with quite similar efficiency (Fig. 1).

Fully ovulated eggs of the two hyperparasitoids are shown in Fig. 2. Eggs of *L. nana* are considerably smaller than eggs of *G. agilis*, which produces eggs approaching 1 mm in length. Accordingly, maximum egg loads in the two species differed significantly over the course of the first 20 days of adult life. Both species are completely synovigenic, and emerge with no fully matured eggs (Fig. 2b). However, in the absence of hosts, *L. nana* begins maturing eggs soon after eclosion and attains a maximum complement of eggs in the ovaries by about the 5th day post-eclosion (Fig. 2b). In contrast, *G. agilis* produces no eggs unless female wasps are supplied with hosts. Wasps that were supplied with hosts over the first 24 h of adult life produced between one and three mature eggs and this total remained fairly constant over the first 20 days (Fig. 2b).

Hyperparasitoid longevity varied significantly between *L. nana* and *G. agilis* ($F_{1,48} = 62.16$, $P < 0.001$) and with access to hosts or under host-deprivation ($F_{1,48} = 7.05$, $P = 0.011$) but the interaction between these parameters was not significant ($F_{1,48} = 0.03$, $P = 0.86$). Female hyperparasitoids that were provided with hosts had on average significantly shorter life-spans than wasps deprived of hosts, and *G. agilis* lived on average up to 3 weeks longer than *L. nana* (Fig. 3a). In *G. agilis*, there was also a significant difference in hyperparasitoid longevity between different food-host access treatments ($F_{4,52} = 80.60$, $P < 0.001$). Wasps provided with honey and water (with or without hosts) lived consid-

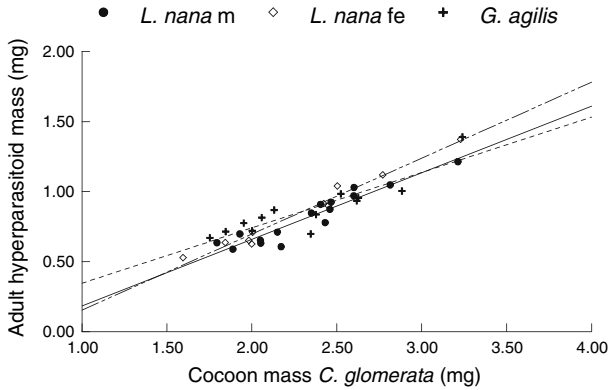


Fig. 1 Relationship between cocoon mass (in mg) of *C. glomerata* and emerging adult male and female mass in *L. nana* and female mass in *G. agilis*. *L. nana* male wasps (closed circles, solid line): $y = 0.49x - 0.33$, $R^2 = 0.85$; *L. nana* female wasps (open diamonds, short- and long-dashed lines): $y = 0.54x - 0.39$, $R^2 = 0.97$; *G. agilis* female wasps (crosses, dashed line): $y = 0.39x - 0.05$, $R^2 = 0.81$. Sample sizes are: *L. nana* males, mean mass from 15 cocoon broods (total of 105 wasps); *L. nana* females, mean mass from 10 cocoon broods (total of 41 wasps); *G. agilis* females, mean mass from 10 cocoon broods (total of 14 wasps)

Fig. 2 (a) Mature, ovulated egg of *G. agilis* (top) and two mature, ovulated eggs of *L. nana* (below). Scale = 1mm. (b) Mature egg loads of adult female *L. nana* (closed diamonds) and *G. agilis* (open circles) at various times over 20-days post-eclosion. Female *G. agilis* that were deprived of hosts produced no eggs (not shown). This species must host-feed to produce eggs, therefore five cocoons were provided to wasps over the first 24 h of adult life (black bar). Line bars represent standard error of the mean. Sample size: 10 wasps/day for *L. nana*, and five wasps/day for *G. agilis*

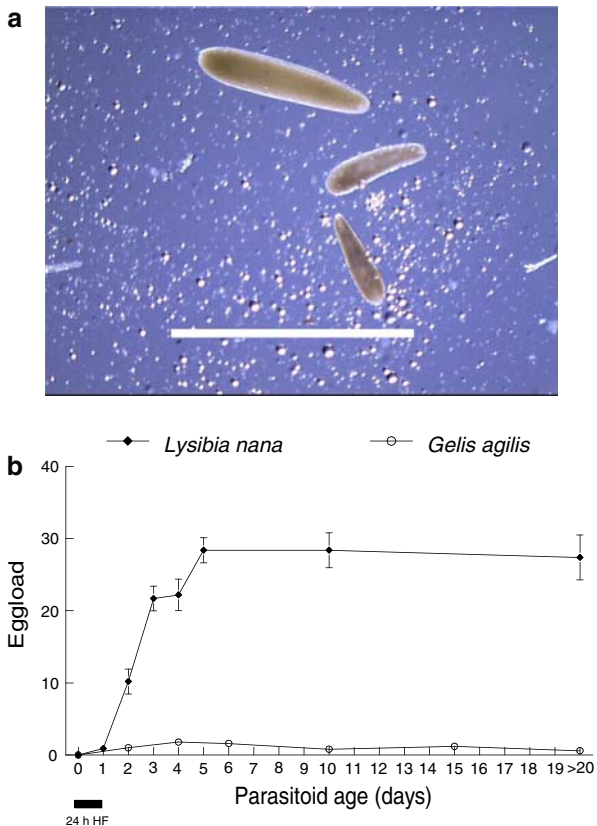
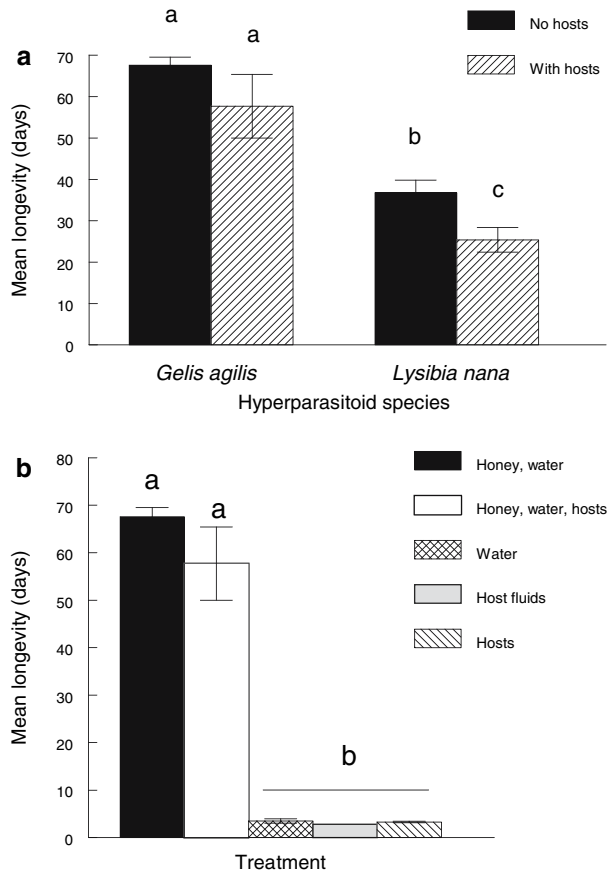


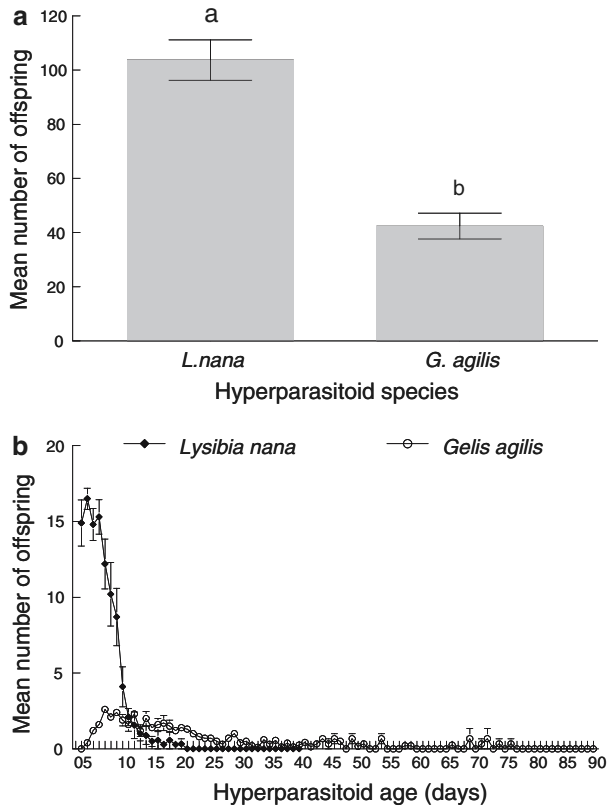
Fig. 3 (a) Mean adult longevity (in days) of female *G. agilis* and *L. nana* when provided with hosts throughout the course of adult life (filled bars) and when deprived of hosts (hatched bars). Bars with the different letters are significantly different ($P < 0.05$, Dunnett's HSD test). Sample sizes (number of wasps): *G. agilis* without hosts = 15, with hosts = 10; *L. nana* without hosts = 19, with hosts = 10. (b) Mean adult longevity (in days) of different cohorts of *G. agilis* under the following food/host access treatments: constant honey and water (black bar), constant honey, water, and hosts (open bar), constant water only (vertical hatched bar), host fluids only (grey bar), and hosts only (angled hatched bar) (partial data repeated from a). Sample sizes: honey, water = 15, all other treatments = 10. Line bars: standard error of the mean



erably longer than wasps provided with only water, hosts, or host fluids in the absence of honey (Fig. 3b). In the case of *G. agilis*, two wasps provided with hosts and honey lived almost 100 days.

Adult body size of *L. nana* and *G. agilis* wasps used in fecundity experiments was not significantly different ($t_{18} = 1.31$, $P = 0.21$). In fact, *G. agilis* wasps (mean = 1.301 mg) were marginally larger than *L. nana* wasps (mean = 1.092 mg). Lifetime reproductive success was, however, significantly higher in *L. nana* than in *G. agilis* ($t_{18} = 6.94$, $P < 0.001$). There was actually little overlap in the minimum number of offspring produced by the least fecund *L. nana* female (70) and the maximum number of offspring produced by the most fecund *G. agilis* female (72). On average, *L. nana* females produced more than twice as many progeny as *G. agilis* females (Fig. 4a). However, the age-specific fecundity curves of the two species also differed markedly. Given unlimited host access, progeny production in *L. nana* was heavily skewed over the first several days, and peaked as early as the second day, declining steadily thereafter. Many wasps experienced fairly long periods of post-reproductive survival, in some instances exceeding the period of oviposition (Fig. 4b). In contrast, progeny production in *G. agilis* gradually increased over the first 4–5 days of host access and then remained fairly constant over the following 2 weeks. Only after this time did daily fecundity begin to decline, although a few wasps were still producing offspring more than 10 weeks after emergence (Fig. 4b).

Fig. 4 (a) Mean lifetime reproductive success of *L. nana* and *G. agilis* provided with constant honey, water, and excess hosts. Sample size = 10 wasps for each species. (b) Daily patterns of progeny production for *L. nana* and *G. agilis* provided with constant honey, water, and excess hosts. Line bars: standard error of the mean. Sample size as in a

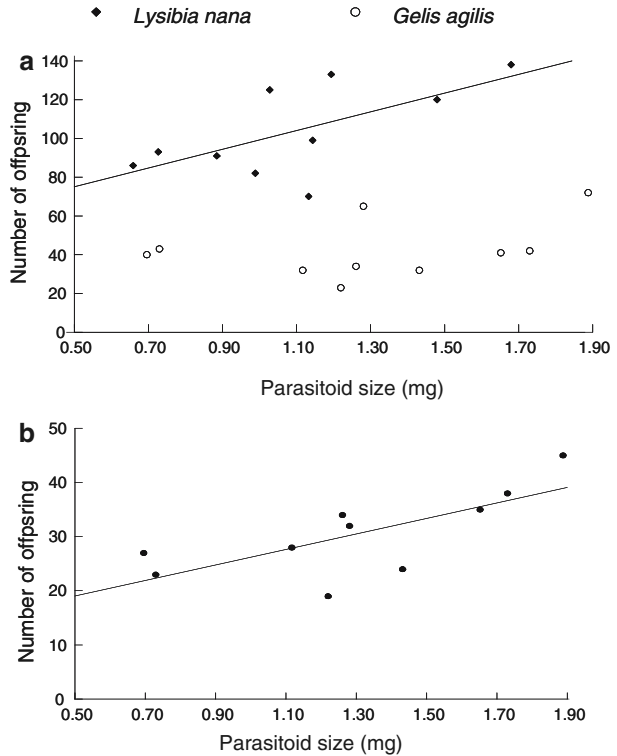


The relationship between adult body size and total progeny production was significant in *L. nana* ($F_{1,8} = 5.72, P < 0.05$) but not in *G. agilis* ($F_{1,8} = 1.26, P > 0.05$). Larger females of *L. nana* were capable of producing more than 130 offspring, whereas small females generally produced less than 100 offspring (Fig. 5a). However, the relationship between body size and progeny production in *G. agilis* was significant over the first 20 days of adult life ($F_{1,8} = 8.73, P = 0.01$; Fig. 5b). This is the period in which *G. agilis* produces most progeny. Longevity in both hyperparasitoids was not influenced by body size with and without hosts: *L. nana* control ($F_{1,17} = 0.73, P > 0.05$); *L. nana* with hosts ($F_{1,8} = 0.02, P > 0.05$); *G. agilis* control ($F_{1,3} = 1.48, P > 0.05$); *G. agilis* with hosts ($F_{1,8} = 2.68, P > 0.05$).

Discussion

In *G. agilis* and *L. nana*, significant convergence was found in some biological traits, whereas in other respects these parasitoids were very different. For a given host (cocoon) mass at parasitism, adults of *L. nana* and *G. agilis* were of approximately the same size. The size of adult hyperparasitoids was correlated with the mass of the host cocoon, although the relationship was somewhat stronger in *L. nana*. Both species exhibited remarkable efficiency in converting host tissues into hyperparasitoid tissues. A previous

Fig. 5 (a) Relationship between adult hyperparasitoid size and lifetime reproductive success in *L. nana* (closed triangles) and *G. agilis* (open circles) provided with constant honey, water, and excess hosts. Regression equation: *L. nana*, $y = 0.01x + 0.20$, $R^2 = 0.42$; *G. agilis*, $y = 0.01x + 0.89$, $R^2 = 0.14$. Regression line provided for *L. nana* data only because this was significant ($P < 0.05$; see ‘‘Results’’). (b) Relationship between adult body size and lifetime reproductive success in *G. agilis* provided with constant honey, water, and excess hosts over the first 20 days of adult life. Regression equation: $y = 14.31x + 11.89$, $R^2 = 0.52$. Sample size as in Fig. 4



study with *L. nana* reported that hyperparasitoid adults emerging from host cocoons of a given mass at parasitism were up to 98% as large as *C. glomerata* adults that had been allowed to develop in cocoons of a comparable size (Harvey et al. 2006). Consequently, hyperparasitoids are likely to be amongst the most efficient organisms in the animal kingdom at utilizing a given amount of food resources (Harvey et al. 2006).

In contrast with development, highly significant interspecific differences were observed in daily patterns of progeny production, lifetime reproductive success, and other biological and reproductive traits in the two hyperparasitoids. When provided constantly with a source of adult nutrition (honey solution), *G. agilis* females lived almost twice as long as *L. nana* females. *G. agilis* is wingless and exhibits ant-like behavior while foraging on the ground, whereas *L. nana* is fully winged and is an efficient flier. Price (1972) suggested that the loss of wings in parasitoid taxa such as *Gelis* spp. is an efficiency measure, allowing the parasitoids to utilize the thoracic cavity to store fat body (used for maintenance) that in winged species is taken up primarily by wing musculature.

Unlike *L. nana*, which does not host-feed and mobilizes metabolic proteins for egg maturation obtained during larval development, *G. agilis* can only initiate oogenesis when proteins are obtained exogenously through destructive host-feeding behavior (Jervis and Kidd 1986). In addition to proteins in host fluids that are mobilized for the production of germinal tissues (eggs), host hemolymph is also known to contain sugars, such as trehalose and sucrose, that slow the metabolic use of fat body that is mobilized for somatic tissues (maintenance) (Jervis and Kidd 1986; Ellers et al. 1998; Ueno 1999; Giron et al. 2002). However, longevity in *G. agilis* was only extended when honey solution was available,

revealing that host fluids play little or no role in metabolic maintenance of this species. Studies with other host-feeding parasitoid species have reported that longevity is extended when female wasps are allowed to feed on both host fluids and honey or sugar solution (Heimpel et al. 1997; Lauziere et al. 2000), whereas in other species there is no apparent benefit of host-feeding on longevity (Giron et al. 2004; Rivero and West 2005). Sources of carbohydrates in the local environment, such as floral nectar, are thus likely to be an important factor in sustaining populations of many host- and non-host-feeding parasitoids (Wäckers 2001).

In *L. nana* (but not *G. agilis*), parasitoid longevity was lower in cohorts of wasps provided with hosts and honey than in wasps that were deprived of hosts. This finding supports the hypothesis of trade-offs between life-history characters, and suggests that there were constraints on the efficiency with which metabolic resources could be acquired and allocated to vital physiological functions in *L. nana* (Reznick 1985). The differing effects of host access on longevity in the two species may be based on the differences in strategies they employ to obtain resources for maintenance and reproduction. This suggests that internal storage sites in *L. nana* are rapidly depleted when resources are allocated to both metabolic activity and reproduction. Alternatively, in *G. agilis* host-feeding enables resources obtained from larval feeding to be used primarily for maintenance and resources obtained from host-feeding to be used for reproduction. Some studies with parasitoids have found evidence of a trade-off between reproduction and survival (Hohmann et al. 1989; Orr and Boethel 1990), whereas others have not (Bai and Smith 1993; Harvey et al. 2001). Thus, the costs of physical activity and reproduction in parasitoids are likely to be association-specific.

Maximum daily progeny production and total reproductive success was much higher in *L. nana* than in *G. agilis*, but temporal patterns of progeny production also differed significantly between the two species. Both species are completely synovigenic, but *L. nana* begins rapidly maturing eggs soon after eclosion. Age-specific fecundity in *L. nana* exhibited a short peak early in life and then declined sharply, whereas the fecundity curve of *G. agilis* was greatly dampened, and offspring were produced over a much longer period of adult life. Irrespective of host (cocoon) availability, *G. agilis* usually only produced two to four progeny per day, which was also reflected in ovary dissections of wasps that were initially allowed to host-feed but subsequently deprived of hosts. On the other hand, over the first few days *L. nana* was able to parasitize more than 15 cocoons per day. In nature, *C. glomerata* produces single broods that typically vary in number between 10 and 40 wasps per brood (Harvey 2000). Therefore, an individual female of *L. nana* is probably able to parasitize a much larger proportion of a single *C. glomerata* brood than is *G. agilis* (Schwarz and Shaw 2000).

These results have demonstrated that, even amongst closely related species attacking a common host type, there may be strong convergence in some evolved characters (e.g., development) and a strong divergence in others (e.g., reproductive biology). In parasitoid larvae, option sets for exploiting host resources are limited by the simple fact that even a slight divergence from a given strategy can result in a significant reduction in fitness or even precocious death (Mackauer and Sequiera 1993). Idiobiont parasitoids such as *L. nana* and *G. agilis* attack resources that are fixed at parasitism and that gradually decline in quality as the host ages. Under these circumstances, the optimal strategy is for the parasitoid larvae to develop at their maximal rate. In contrast, koinobiont parasitoids develop in hosts that continue feeding and growing during much of the interaction. Because host resources are dynamic, the optimal development strategy of the parasitoid depends critically on the host's initial size and on its growth rate, as well as on its susceptibility to other

natural enemies such as insect predators (Harvey and Strand 2002). Consequently, development strategies amongst koinobionts appear to be much more flexible than is the case with idiobionts (Mackauer and Sequeira 1993).

Reproductive strategies in parasitoids represent an adaptive response to a range of selection pressures, in particular host abundance, and accessibility (Price 1972; Pexton and Mayhew 2002). Because it is wingless, *G. agilis* can only exploit a relatively small area during its lifetime. Under these conditions, selection should favor an expansion in the parasitoid's host range, because suitable hosts will be difficult to find. Different species of *Gelis* are known to parasitize a wide variety of arthropod hosts, including moth pupae and spider egg sacs in addition to parasitoid cocoons, supporting this hypothesis (Bezant 1956; van Baarlen et al. 1996). It is therefore quite likely that *G. agilis* switches between various hosts in its habitat, depending on their abundance and accessibility. Because it is a generalist and its hosts are probably hard to find, *G. agilis* has compensated by reducing costly investment in germinal tissue (eggs) for somatic tissue (maintenance) that has resulted in a longer life-span. On the other hand, *L. nana* has evolved a reproductive strategy that is intimately associated with fully cocooned pupae of gregarious parasitoids in the genus *Cotesia* (Schwarz and Shaw 2000). Because it has wings and can fly efficiently, *L. nana* is able to exploit a much larger area than *G. agilis*, a factor that has allowed it to specialize but at the cost of a reduced adult life-span. Consequently, reproduction is more "front-loaded" in *L. nana* than in *G. agilis*, and it is able to mobilize fairly large numbers of eggs in a short time, enabling it to exploit full broods of its host.

Pre-pupae and pupae of *C. glomerata* are attacked by at least five species of secondary hyperparasitoids in the Netherlands (Harvey, unpublished). In addition to differences in host specialization, niche differentiation amongst the various species appears to be influenced by the architectural complexity of the plant as well as on the structure of the surrounding plant community on which *P. brassicae* and *C. glomerata* interact. For example, winged hyperparasitoids like *L. nana* and a closely related species *Acrolyta nens* are much more effective at foraging for host cocoons located higher up on the food plant, whereas wingless species like *G. agilis* are more restricted to lower parts of the plant. A recent study (unpublished) also found that both *A. nens* and *L. nana* emerged from single cocoon broods of *C. glomerata* in plots of *B. nigra* plants. Future experiments with *A. nens* and *L. nana* will hopefully reveal the extent to which the reproductive biologies and ecologies of these hyperparasitoids are convergent or if each species possesses slightly different adaptations that enable both to exploit hosts with equal efficiency in nature.

Acknowledgments The author thanks Leo Koopman and André Gidding of Wageningen University for a constant supply of herbivores and parasitoids; Leontien Witjes and Roel Wagenaar for help with experiments; and Martijn Bezemer for his comments on an earlier draft of the manuscript.

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