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ORIGINAL PAPER

Divergent life history strategies in congeneric hyperparasitoids

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Abstract Life histories can reveal important information on the performance of individuals within their environment and how that affects evolutionary change. Major trait changes, such as trait decay or loss, may lead to pronounced differences in life history strategies when tight correlations between traits exist. Here, we show that three congeneric hyperparasitoids (*Gelis agilis, Gelis acarorum* and *Gelis areator)* that have diverged in wing development and reproductive mode employ markedly different life history strategies. Potential fecundity of *Gelis* sp. varied, with the wingless *G. acarorum* maturing a much higher number of eggs throughout life compared with the other two species. Realized lifetime fecundity, in terms of total offspring number was, however, highest for the winged *G. areator*. The parthenogenic *G. agilis* invests its resources solely in females, whilst the sexually reproducing species both invested heavily in males to reduce competitive pressures for their female offspring. Longevity also differed between species, as did the direction of the reproduction-longevity trade-off, where reproduction is heavily traded off against longevity only in the asexual *G. agilis*. Resting metabolic rates also differed between the winged and wingless species, with the highest metabolic rate observed in the winged *G. areator*. Overall, these geline hyperparasitoids showed considerable divergence in life history strategies, both in terms of timing and investment patterns. Major trait

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changes observed between closely related species, such as the loss of wings and sexual reproduction, may contribute to the divergence in key life history traits.

Keywords *Gelis* · Hymenoptera · Life history theory · Metabolic rate · Reproduction

Introduction

Determining when, how and why organisms attain highest reproductive success is key to understanding how individuals perform within their environment and ultimately how organisms evolve. Life history theory seeks to explain the diversity between organisms in traits such as offspring number, timing of reproduction and longevity, and research on life histories has led to major strides in understanding trait evolution (Gilbert and Manica 2010; Jervis et al. 2012). For instance, a recent study showed that age-related mortality critically affects growth rate and reproductive investment in 20–30 tropical and temperate songbird species (Martin 2015). Life history studies have further provided some of the clearest case studies showing that simultaneous trait optimization may not always be possible (Stearns 1989). Trade-offs frequently exist between major life history traits, such as those between longevity and reproduction (Stearns 1989; Flatt 2011) or offspring number and offspring size (Preziosi et al. 1996; Fox and Czesak 2000; Gibbs et al. 2005). Life history traits and concomitant trade-offs can thus play a key role in directing ecological and evolutionary changes (Stearns 2000).

Trait decay or loss is expected to have major consequences for correlated traits (Lahti et al. 2009), including life histories (Hoffman et al. 2001). The repeated loss of wings in insects is an excellent example where reduced dispersal ability, mediated by wing reduction or absence, increases reproductive output through increased internal resource availability. Major energetic resources that are no longer needed to fuel flight, such as glycogen and fat reserves, can then be allocated towards egg production, as was shown repeatedly in several wing-dimorphic insect species (Denno et al. 1989; King et al. 2011; Clark et al. 2015). Asexuality is another example of trait decay that can severely affect reproductive potential. Sexual reproduction is considered costly, as it requires females to produce both sons and daughters (Lehtonen et al. 2012). In asexually reproducing organisms, more resources should thus be available solely for the production of daughters, allowing for higher reproductive output or larger offspring. Macro-evolutionary adaptations, such as the loss of wings or sexuality, can therefore have major fitness consequences.

Parasitoids are a group of insects that feed and develop on other arthropods during development, but with an adult life stage that is free-living (Godfray 1994). These insects are popular model organisms for studying life histories (Price 1973; Mayhew and Blackburn 1999; Jervis and Ferns 2011), in part due to their immense diversity (Pennacchio and Strand 2006), but also because their life style has led to the evolution of quite unusual life histories (polyembryonic development; production of hydropic or yolk-poor eggs; heteronomous oviposition where males and females develop on different host species; Godfray 1994). Whilst primary parasitoids are common model systems in evolutionary ecology research, hyperparasitoids, i.e. parasitoids that attack other parasitoids, are only rarely studied. This is partly due to the fact that hyperparasitoids are made up of taxonomically difficult groups that require extensive facilities to be studied in the laboratory (Laurenne 2008). Hyperparasitoids play a critical role in ecological communities through top-down effects on lower trophic levels (Harvey et al. 2014, 2015; Gómez-Marco et al. 2015), and hyperparasitoid communities can show high species diversity despite their high positioning within the food chain (Bourchier and Nealis 1992). Little is known, however, about the biology of most hyperparasitoids, in spite of their prevalence and importance within ecological communities.

This study investigates how trait decay can affect key life histories to reveal how macro-evolutionary changes may impact correlated traits on an ecological time scale. We investigate three closely related hyperparasitoids, *Gelis agilis*, *Gelis acarorum* and *Gelis areator* (Hymenoptera: Ichneumonidae) that have diverged in wing development and mode of reproduction. All three species are cosmopolitan with distributions from Scandinavia to Spain (Lei et al. 1997). The gelines are generalists and attack a wide range of hosts, including butterflies, flies and sawflies as primary parasitoids, but gelines also parasitize other parasitoids, including Braconidae and Ichneumonidae (Libert 2010). Despite their ability to develop on numerous hosts, gelines do prefer to lay eggs on cocoons or cocoon-like structures (Shaw 2006), such as those of *Cotesia* sp. (Hymenoptera: Braconidae), and forage in specific parts of the habitat, i.e. trees and bushes for *G. areator* and near the ground for *G. agilis* and *G. acororum* (Shaw 2006; Lei et al. 1997; Harvey et al. 2014). *G. areator* develops fully functional wings, whilst *G. agilis* and *G. acarorum* completely lack wings. *G. areator* and *G. acarorum* are both sexually reproducing species, but *G. agilis* mainly produces females through facultative parthenogenesis (although males are very rarely produced, pers. obs. JAH). We measured potential and realized lifetime fecundity, sex allocation patterns throughout life and longevity to determine life history strategies and concomitant trade-offs. We further measured species-specific resting metabolic rates, a physiological trait that is closely tied to the longevity-reproduction trade-off (Simmons and Bradley 1997; Van Voorhies and Ward 1999; Hulbert et al. 2007). We propose that evolutionary trait transitions, such as the presence/absence of wings and asexual/sexual reproduction, can have correlative effects on life history strategies in closely related species. The large knowledge-base on developmental strategies (Harvey and Witjes 2005; Harvey 2008; Harvey et al. 2011a, 2015), competitive interactions (Harvey et al. 2011b; Visser et al. 2014) and community structure and dynamics in the field (Harvey et al. 2014) of geline hyperparasitoids further allows us to discuss species interactions within their larger insect community.

Materials and methods

Insects

Pieris brassicae (Lepidoptera: Pieridae) and *Cotesia glomerata* were obtained from existing cultures at the University of Wageningen (WUR), the Netherlands that were originally collected from agricultural fields near the University. Rearing conditions for the host *C. glomerata* were similar to those described in Harvey (2000). All gelines were obtained from *C. glomerata* cocoon clutches on a field near the Netherlands Institute of Ecology, Wageningen, the Netherlands in 2011. Females of all three geline species were allowed to host-feed, which is required for egg maturation, and maintained on 1–2 day-old pupae of *C. glomerata*. All experiments were performed at a temperature of 25 °C, a 16:8 L:D regime and a relative humidity of 65 %.

Potential fecundity and longevity without host access

To determine potential fecundity over the lifetime of females with access to honey and water, but without oviposition opportunities, the number of mature, fully chorionated eggs was determined directly after emergence and after 2, 7, 14 and 21 days by dissecting 6–30 females per treatment per species on a glass slide in a drop of water. Egg size was determined by measuring length and width of each egg. When a female contained six or more eggs, length and width of at least five eggs were measured. Both egg size and tibia length were determined using a binocular microscope fitted with an ocular micrometer. Egg volume was then calculated using the formula $V = 4/3\pi Lw^2$ (where L = length and w = width). Tibia length was measured as an estimate of body size (Godfray 1994).

For longevity experiments, individuals were first anesthetized with CO_2 and body mass determined using a microbalance (Mettler-Toledo MT5; accuracy ±1 µg). Each individual was placed singly in a small Petri dish containing honey and water and survival inspected daily. For the asexually reproducing *G. agilis*, longevity was recorded for 10 newly emerged females, while for the sexual species *G. acarorum* and *G. areator* 10 newly emerged individuals of each sex were used.

Realized lifetime fecundity, sex allocation and longevity

Realized lifetime fecundity was determined for 9–11 newly emerged females of each species. Sexually reproducing *G. acarorum* and *G. areator* were allowed access to males during the first 48 h. Clutches containing 25–35 host cocoons were removed and replaced every other day until death of the female, after which longevity was noted. After removal of the female, cocoon clutches were kept in small Petri dishes (6 cm dia.) until development was completed. For all species and for each cocoon clutch the number of hyperparasitoids that emerged was recorded. For sexual species, we further determined sex and sex ratios.

Resting metabolic rate

Within 12 h after emergence, 16 females of the sexually reproducing species were provided with males for mating, as well as honey and water ad libitum. Before experiments, each chamber was cleaned with 70 % alcohol and dried to prevent oxygen-consuming contamination. Resting metabolic rate (RMR) was measured the day after emergence with a closed chamber micro-respiration system (Unisense A/S, Denmark) between 8 am and 8 pm with lights on at a temperature of 25 ± 1 °C. Females were placed singly in small cylindrical chambers (109–169 uL) and allowed to accustom to experimental chambers for 30 min before RMR recordings were started. Individuals typically become inactive within 10 min after a disturbance (placement in experimental chambers or introduction of the sensor, pers. obs. CLL). For each chamber, measurements were taken during 30 min, with a sample recording every second. Obtained values were automatically transformed from mV to µL-O2 using the software package MicOx (Unisense A/S, Denmark). A two-point calibration was done every day prior to experiments using both ambient air (with a 20.9 % oxygen concentration) and pure nitrogen (0 % oxygen concentration). These conditions were already validated for measuring RMR in small insects (Le Lann et al. 2011, 2012, 2014a, b).

For each measurement, the first 10 min were discarded from calculations to allow the sensor to reach equilibrium after introduction into the chamber. Resting metabolic rate in µL O_2 per hour was calculated by determining the slope of O_2 concentrations over time during the remaining 20 min. For each session, the rate of O_2 consumption measured in experimental chambers containing females was corrected for using measurements obtained from a control chamber. As fresh body mass is known to be positively correlated with metabolic rate (Gillooly et al. 2001), females were frozen after measurements were completed and weighed on a microbalance (Metler-Toledo UMT2, sensitivity: 0.1 µg) to estimate mass differences.

Statistical analyses

We used generalized linear models to test for differences between species in egg number, egg volume, body mass, realized lifetime fecundity, longevity with and without host access, and mass-corrected resting metabolic rate. We used a Gaussian error structure for each model, with the exception of tests for realized lifetime fecundity and longevity, for which we used a Quasi-poisson error structure to account for overdispersed data. Species was included as a fixed factor in all models. Age and the interaction between age and species was included as a fixed factor in models on egg number and egg volume and tibia length were included in both models as a covariate. Sex, and the interaction between sex and species was included as a fixed factor in models on body mass and longevity.

To test for differences between species in realized lifetime fecundity and sex ratios with age we used generalized linear mixed models (GLMM) with species and age as fixed factors and female id as a random factor. We used GLMMs with random slopes because they showed a lower Akaike's Information Criterion (AIC) than models with random intercepts. We used a Poisson error structure for tests on realized lifetime fecundity and a Binomial error structure for tests on sex ratios.

Differences in egg number, egg volume and realized lifetime fecundity over time were analyzed by including a quadratic relationship with age. In all cases a model with a nonlinear (quadratic) relationship performed significantly better and had a lower AIC than a model with a linear relationship.

We used likelihood ratio tests to obtain p-values for each factor (Zuur et al. 2009), and multiple comparisons were done using Tukey's Honest Significant Difference (Hsu 1996). All statistical tests were performed using R project version 3.1.0 (R Development Core Team 2014).

Results

Potential fecundity and longevity without host access

Egg number differed significantly between species ($X^2 = 13.52$; $df = 2$; $p < 0.001$), where *G. agilis* maintained the lowest mean number of eggs in the ovaries (Tukey HSD: $p < 0.001$) compared to *G. areator* and *G. acarorum* that did not differ significantly in egg numbers (Tukey HSD: $p = 0.12$; Table 1). Egg numbers further varied significantly throughout life ($X^2 = 193.12$; $df = 2$; $p < 0.001$), and did so differently between species ($X^2 = 9.98$; $df = 2$; $p = 0.04$), despite a joint peak in egg numbers after approximately 14 days (Fig. 1a). Egg volume also differed significantly between the three species ($X^2 = 33.76$; $df = 2$; $p < 0.001$), where age of the female affected egg volume

Table 1 Mean life history and RMR trait values for all species

	G. acarorum	n	*G. agilis*	n	*G. areator*	n
Without host access						
Mean egg no. ± 1SE	3.64 ± 0.38	75	0.54 ± 0.07	103	1.61 ± 0.20	46
Mean egg volume (μm^3) ± 1SE	0.08 ± 0.003	58	0.09 ± 0.003	47	0.13 ± 0.005	35
Mean female mass (mg) ± 1SE	0.92 ± 0.07	10	1.07 ± 0.07	18	1.08 ± 0.03	9
Mean male mass (mg) ± 1SE	0.96 ± 0.05	10	–	–	1.10 ± 0.06	10
Mean female longevity (days) ± 1SE	47.30 ± 5.33	10	65.00 ± 3.56	18	64.78 ± 4.61	9
Mean male longevity (days) ± 1SE	38.80 ± 5.39	10	–	–	38.40 ± 5.87	10
Mean mass-corrected metabolic rate (μL h^{-1} mg^{-1}) ± 1SE	1.73 ± 0.14	17	1.32 ± 0.08	16	3.23 ± 0.34	16
With host access						
Mean female longevity (days) ± 1SE	49.18 ± 2.01	11	42.67 ± 2.86	10	80.20 ± 1.14	10
Mean realized lifetime fecundity ± 1SE	43.55 ± 5.33	11	19.56 ± 2.39	10	83.30 ± 13.39	10
Mean female offspring no. ± 1SE	8.36 ± 4.06	11	19.56 ± 2.39	10	8.10 ± 3.18	10
Mean male offspring no. ± 1SE	35.18 ± 5.79	11	–	10	75.2 ± 12.63	10
Mean sex ratio ± 1SE	0.82 ± 0.08		0 (parthenogenic)		0.88 ± 0.04	
Daily realized fecundity	0,88552257	11	0,458401687	10	1,038653367	10

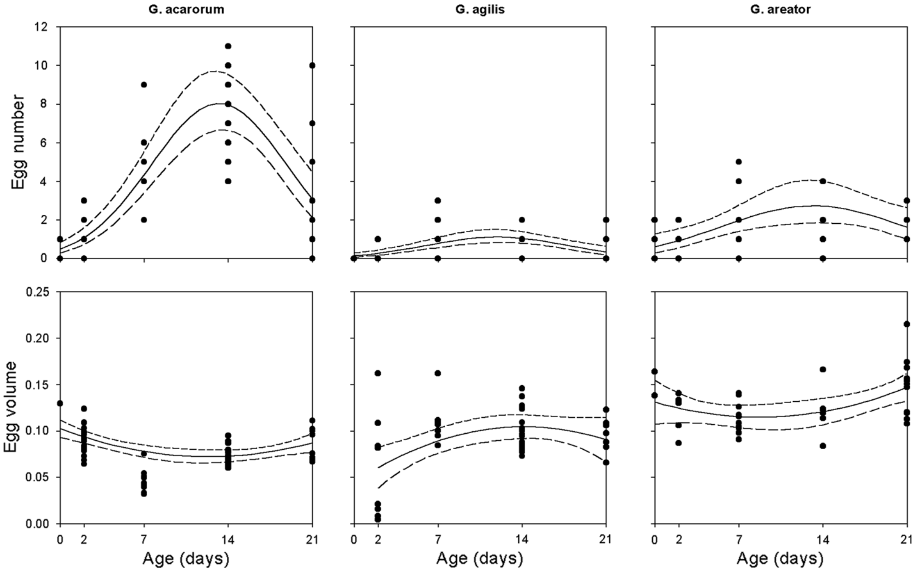


Fig. 1 Model estimates (fit ± 95 % CI) of egg number (*top graphs*) and egg volume (*bottom graphs*) over time

($X^2 = 7.29$; $df = 2$; $p = 0.03$), but differently between species ($X^2 = 33.05$; $df = 4$; $p < 0.001$; Fig. 1b). Body size did not affect egg numbers ($X^2 = 4.00$; $df = 1$; $p = 0.05$) or volume ($X^2 = 1.68$; $df = 2$; $p = 0.20$). Longevity differed significantly between species ($X^2 = 5.17$; $df = 1$; $p = 0.02$), but was similar between the sexes ($X^2 = 1.29$; $df = 1$; $p = 0.26$; Table 1). Body mass differed significantly between females of the different species ($X^2 = 13.39$; $df = 2$; $p < 0.001$), where *G. acarorum* was significantly smaller than *G. agilis* and *G. areator* (Tukey HSD: $p < 0.05$), while the latter two were similar in size (Tukey HSD: $p = 0.70$). Male body mass was similar between the sexually reproducing species ($X^2 = 2.75$; $df = 1$; $p = 0.10$).

Realized lifetime fecundity, sex allocation and longevity

Realized lifetime fecundity, expressed as mean offspring number during life, differed significantly between the three species ($X^2 = 38.73$; $df = 2$; $p < 0.001$; Table 1). Offspring numbers were two to four times higher in *G. areator* compared to *G. acarorum* and *G. agilis*, respectively (Tukey HSD: $p < 0.001$; Table 1). When age of the female was taken into account, there was no more main effect of species ($X^2 = 3.17$; $df = 2$; $p = 0.21$), but female age did affect realized lifetime fecundity ($X^2 = 52.14$; $df = 2$; $p < 0.001$) and there was a significant interaction effect between species and age of the female ($X^2 = 30.01$; $df = 2$; $p < 0.001$; Fig. 2). Sex allocation patterns in the sexually reproducing *G. acarorum* and *G. areator* were heavily biased towards males (Table 1), but sex ratios did not differ between species ($X^2 = 0$; $df = 1$; $p = 0.98$). Age of the female significantly affected sex ratios ($X^2 = 26.93$; $df = 1$; $p < 0.001$), and sex allocation differed with age between species ($X^2 = 17.52$; $df = 1$; $p < 0.001$) (Fig. 3). Host presence was found not to affect longevity ($X^2 = 0.12$; $df = 2$; $p = 0.73$), but species differed significantly in their longevity ($X^2 = 51.19$; $df = 2$; $p < 0.001$). Furthermore, longevity was differently affected between species depending on host presence ($X^2 = 25.77$; $df = 2$; $p < 0.001$; Fig. 4), where longevity was similar (*G. acarorum*, Tukey HSD: $p = 0.98$), longer with host access (*G. areator*, Tukey HSD: $p = 0.02$) or longer without host access (*G. agilis*, Tukey HSD: $p < 0.001$).

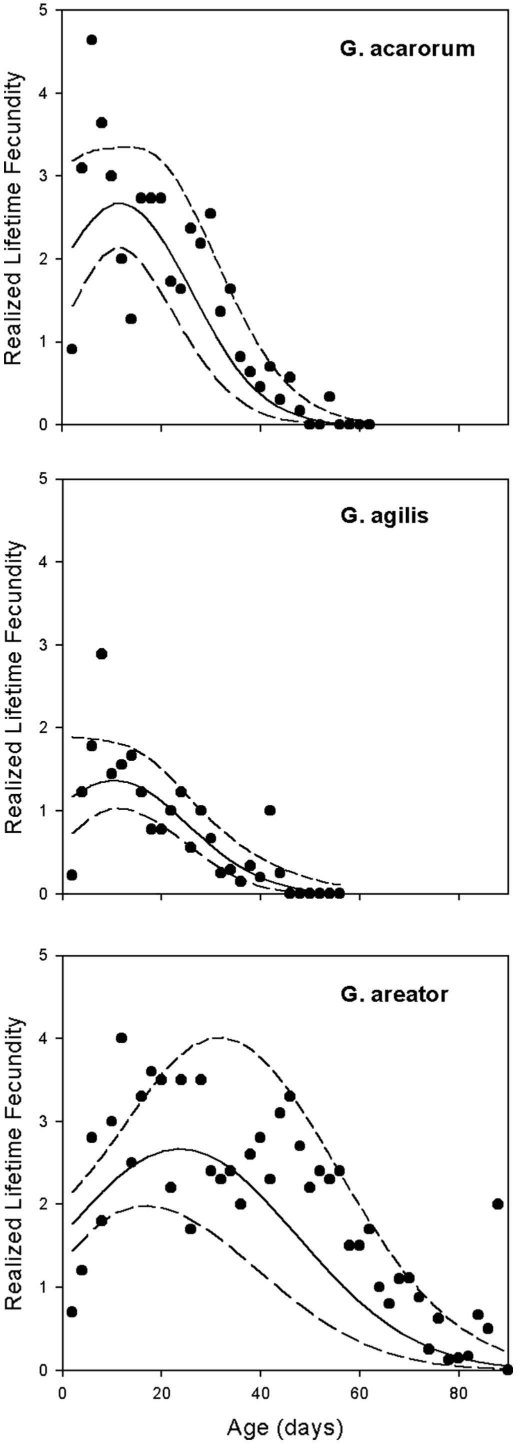
Resting metabolic rate

Mass-corrected RMR differed between species (($X^2 = 42.24$; $df = 2$; $p < 0.001$) with the winged species, *G. areator*, having a higher metabolic rate than both *G. agilis* (Tukey HSD: $p < 0.001$) and *G. acarorum* (Tukey HSD: $p < 0.001$). No difference in RMR was observed between *G. agilis* and *G. acarorum* (Tukey HSD: $p = 0.39$; Table 1).

Discussion

Our study revealed that three congeneric hyperparasitoids all exhibited fecundity schedules that are characteristic of many idiobiont ecotoparasitoids, with eggs being produced in small numbers and being laid over a comparatively long period of adult lifespan (Jervis et al. 2008). However, we also showed that the three *Gelis* species, which have diverged in wing morphology and mode of reproduction, show markedly different reproductive strategies and physiology. The winged *G. areator* attains the highest trait values in terms of realized lifetime fecundity, longevity (for females with access to hosts) and RMR compared to its wingless congeners. *G. agilis* exhibits facultative parthenogenesis, showing severely restricted male production, egg maturation rates and lifetime fecundity. Below, we discuss divergence in reproductive traits, longevity costs on reproduction and postulate how life history divergence may affect these species within their ecological community.

Fig. 2 Model estimates (fit ± 95 % CI) of realized fecundity during life



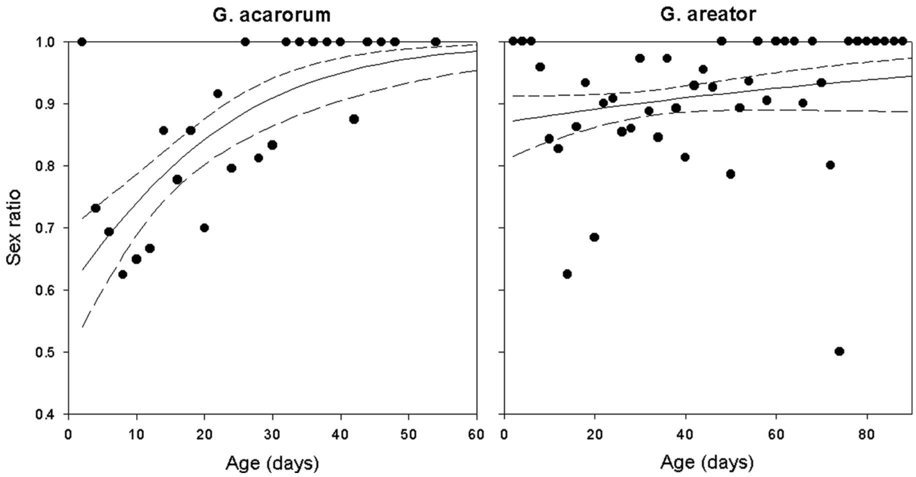
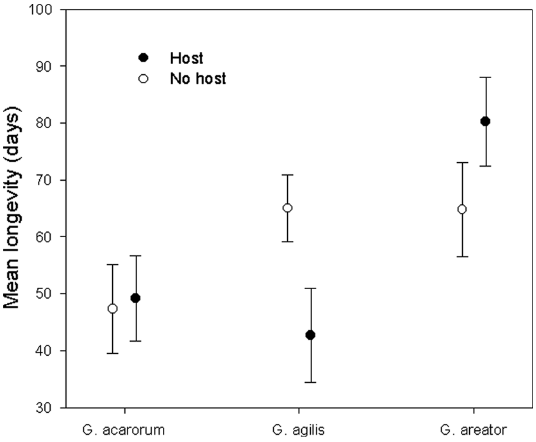


Fig. 3 Model estimates (fit ± 95 % CI) of sex allocation patterns (proportion of males) during life

Fig. 4 Model estimates (fit ± 1SE) of mean longevity (days) with host access (*black circles*) and without host access (*white circles*)



Divergence in reproductive traits

Egg size and number are common metrics for estimating reproductive success and potential fitness, but clear reproductive trade-offs often favour the production of many small eggs or fewer large eggs (Stearns 1989). Trade-offs between egg number and size have been observed in a wide range of animals, including vertebrates (Williams 2001; Kolm et al. 2006; Warne and Charnov 2008), molluscs (Madec 2000) and insects (Preziosi et al. 1996; Gibbs et al. 2005), but this trade-off is not universally found (Schwarzkopf et al. 1999; Timi et al. 2005; Hořák et al. 2008). We found a clear trade-off between egg number and volume for the smallest species, *G. acarorum*, where eggs are high in number but small in size compared to the other gelines. Despite the similar sizes of *G. agilis* and *G. areator*, the latter produces more, larger eggs compared to *G. agilis,* but the number of mature eggs in the ovaries of *G. areator* is less than half of that found in *G. acarorum*. In many insect species egg size further decreases during life (Fox 1993; McIntyre and

Gooding 2000; Giron and Casas 2003), as resources available for allocation towards reproduction become more limiting throughout a female's lifetime. Interestingly, egg volume varied dynamically throughout life in the gelines, but did so differently between species. *G. acarorum* and *G. areator* egg volumes were less when egg numbers in the ovaries peaked, but *G. agilis* produced the largest eggs at times when egg maturation was at a maximum. Dynamic changes in egg volume have also been found in the aphid parasitoid *Aphidius avenae* that produces small, yolk-poor (hydropic) eggs (Le Lann et al. 2012), unlike the large, yolk-rich (anhydropic) eggs produced by the gelines (Jervis and Kidd 1986; Jervis et al. 2001). The strength of the trade-off between egg size and number may direct dynamic changes in egg volume for the two sexual species. Parent-offspring conflict can further lead to different trait optima for egg size, as larger offspring tend to have higher fitness, whilst mothers that reduce provisioning may live longer or prolong successful reproduction (Einum and Fleming 2000; Boivin and Gauvin 2009). However, high egg maturation rates seem to be accompanied by increased egg volume in *G. agilis.* This species takes considerable time to successfully oviposit an egg (a minimum of 30–45 min and as long as 24 h.), and producing larger eggs when egg maturation peaks may increase the chances of offspring survival into adulthood in a species with an extremely low lifetime fecundity.

Under intense female–female competition for host resources, male-biased sex ratios can relieve competitive pressures (Clark 1978; West 2009; Visser et al. 2014). The sexually reproducing gelines indeed showed highly male-biased sex ratios with over 82–88 % of emerged offspring being male, but overall investment in females is only half that of the asexual *G. agilis*, i.e. producing both sexes reduces investment in females. *G. acarorum* increased male investment with age, but the winged *G. areator* showed a constant skewed sex allocation pattern. Parasitoids typically increase male production with age (King 1987), but an overproduction of males compared to females is rarely observed in parasitoids (Hamilton 1967; Charnov et al. 1981; West 2009; Visser et al. 2014). High male-biased sex ratios have also been reported in another species (*Lysibia nana*) within this hyperparasitoid community (Harvey et al. 2011b); hence other hyperparasitoids seem to experience similarly high competitive pressures. Under such conditions, continual male production may increase mating opportunities at larger spatial scales, as is the case for *G. areator* that exploits hosts over a wider area compared to its wingless congeners.

Despite the twofold cost of sexual reproduction, producing both sexes comes with several perks, such as higher genetic variability, reduced accumulation of deleterious mutations and avoidance of competition between relatives (Hurst and Peck 1996). In fact, asexual reproduction in *G. agilis* seems to come at a twofold cost since offspring numbers do not seem to double (resources for the production of sons can be used solely for the production of daughters), but are rather halved in comparison to its congeners. Such decreased reproductive output has also been observed in other asexually reproducing insects (Lamb and Willey 1979; Taylor 1981). Why then would *G. agilis* have switched its reproductive mode to asexual reproduction? Several mechanisms have been proposed that can favour or maintain parthenogenesis, such as the propensity of finding mates and the exploitation of marginal habitats (Kramer and Templeton 2001; Kawecki 2008). Reduced dispersal of wingless *G. agilis* females may indeed limit their ability of finding suitable mates. Exploitation of marginal habitats mainly occurs in species with facultative parthenogenesis, where parthenogens migrate to less favourable environments, but remain geographically close to their sexual conspecifics. *G. agilis* only rarely produces males under laboratory conditions, but further studies in the field are needed to predict which conditions have fuelled the adaptive evolution of parthenogenesis in this species.

Longevity costs on reproduction

The longevity-reproduction trade-off is a classic example of constrained concurrent trait optimization (Stearns 1989; Flatt 2011). Increasing metabolic investment into reproduction shortens longevity in most organisms (Tatar 2010). This can be the result both of high energetic demands for reproduction or increased mortality due to costly behaviours associated with reproduction, such as courtship behaviours (Gems and Riddle 1996) or searching suitable reproductive substrates (Mole and Zera 1993). Shortened longevity due to reproductive investment was indeed observed in *G. agilis*, where females lived ~30 % longer in the absence of hosts for reproduction. Egg numbers are, however, very low in *G. agilis* and energetic investment in eggs is not expected to differ much between the gelines, i.e. all three species produce large yolk-rich (anhydropic) eggs. This species does, however, require considerable time for successful oviposition (>30 min up to 24 h.), which is much longer than that observed in its congeners (<15 min). The cost of reproduction for this species thus likely lies in the energetic requirements of oviposition itself, rather than egg production. Longevity-reproduction trade-offs are not always apparent, however, and several organisms seem to be able to reproduce without the incurring cost on survival (Partridge and Gems 2002). For instance, longevity in the nematode *Caenorhabditis elegans* seems to be unaffected by variation in eggs number (Gems and Riddle 1996) and was even found to increase in a mutant strain despite reproducing (Kenyon 2010). Similarly, longevity remained unaffected by investment in reproduction by *G. acarorum*, whilst *G. areator* lived ~20 % longer when reproducing. All species thus differed in the direction of the longevity-reproduction trade-off. Host-feeding is essential for egg maturation in the Gelinae, even though higher fecundities may be reached when highly nutrient-rich substrates are consumed, such as honey (Harvey et al. 2012). Whereas nutritional resources, particularly proteins, obtained from host-feeding were reported to play a primary role in reproduction (Giron et al. 2002; Rivero and West 2002), our findings suggest that host-feeding may alleviate the cost of reproduction or even increase survival, despite continued investment in reproduction. Exploring how host-feeding affects the large variation in life history trade-offs observed between closely related species could shed more light on the mechanistic basis underlying longevity-reproduction trade-offs.

Resting metabolic rate (RMR) represents another metric for measuring maintenance and is tightly linked to the longevity-reproduction trade-off (Burton et al. 2011). RMR effects on longevity and reproduction can follow one of two distinct directions: Either a low RMR leads to lower maintenance costs, allowing a higher reproductive output (‘compensation hypothesis’), or a high RMR can contribute to increased energy intake for reproduction (‘increased intake hypothesis’)(Boratynski and Koteja 2010). Our findings conform to the latter, as *G. areator* has the highest metabolic rate, but also the greatest longevity and highest realized lifetime fecundity, similar to findings in other animals (Jackson et al. 2001; Boratynski and Koteja 2010). Our results further substantiate reports in other insects that winged species have higher resting metabolic rates compared to wingless species (Reinhold 1999). Indeed the winged *G. areator* has a metabolic rate that is 1.9–2.5 times higher than that of *G. acarorum* and *G. agilis,* respectively. The retention of wings in *G. areator* allows it to cover greater dispersal distances to exploit host resources further away from the natal patch. Moreover, a comparatively higher dispersal potential enables this parasitoid to exploit a larger number of hosts during its lifetime, reflected by its high realized lifetime fecundity. Divergent metabolic rates are thus consistent with the different ecological demands on winged versus wingless species (Reinhold 1999).

Community diversity

In the wild, the community of hyperparasitoids associated with *C. glomerata* contains at least five other, more distantly related, species (Poelman et al. 2012; Harvey et al. 2014). Most gelines are generalists and can attack a variety of hosts either as primary parasitoid, hyperparasitoids or both (facultatively hyperparasitic). Within a dense community, such as the community of insects associated with *Cotesia*, one might wonder why parasitism rates of *C. glomerata* by the gelines remains high when other hosts might be exploited. A previous study on host preference and developmental performance of the three gelines revealed a large variation between species in parasitism success and mortality on different *Cotesia* host species (Harvey et al. 2015). All gelines preferred oviposition on the larger host species *Cotesia rubecula*, but this solitary host species is less abundant and more patchily distributed compared to the gregarious *C. glomerata*. The preference of all three species for larger hosts suggest that each of the gelines is behaviourally more specialized on the same higher quality host species *C. rubecula*. Such behavioural specialization in generalist parasitoids has also been observed in *Nasonia vitripennis,* a species that can attack more than 60 different host species, but which prefers to oviposit on hosts that it can physiologically manipulate (Rivers and Denlinger 1994, 1995). The exploitation of other hosts, such as butterflies, may thus only be a last-resort strategy when more suitable hosts, such as *Cotesia* sp., cannot be found within a considerably time frame during a female’s lifetime.

Two major trait transitions have taken place in the evolutionary history of the hyperparasitoids under study here: the loss of wings and a switch in reproductive mode. These trait transitions have fuelled a reduction in offspring numbers in both wingless species. As a consequence, the winged species *G. areator* is expected to compete with more distantly related hyperparasitoids, and reaches the highest trait values in terms of realized lifetime fecundity, longevity and metabolic rate to exploit a higher number of hosts over a wider area. In contrast, the wingless species are more confined to limiting local resources and compete mainly with each other, while reaching lower overall trait values compared to the winged species. A study concerned with the primary parasitoid *Cotesia melitaearum* and its host revealed differences in species prevalence from those we previously observed in relation to *C. glomerata* (Harvey et al. 2014). In that system *G. agilis* is the dominant geline, whereas *G. acarorum* was only rarely found (Lei et al. 1997). Community composition in terms of available host species and competitors thus seems to vary and is expected to affect life histories differently at a local scale.

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