Variation in longevity between populations of *Asobara persimilis* (Hymenoptera: Braconidae) and *Ganaspis* sp. (Hymenoptera: Figitidae) along a climate gradient

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Intraspecific variation in longevity along a climate gradient is described for the Australian parasitoids *Asobara persimilis* and *Ganaspis* sp. No correlation between longevity and development time is found and in *A. persimilis* differences in longevity are caused by differences in metabolisation rate of lipoprotein reserves, rather than differences in resource allocation to egg production.

*Keywords*: *Asobara persimilis*, *Ganaspis* sp., life history, climate gradient, longevity

Evolution favours organisms that maximise the number of offspring able to survive and reproduce. Shorter developmental time, longer life span and greater fecundity are all attributes that can drastically improve the total number of offspring that an adult produces in its lifetime. The reason that evolution cannot maximise all these traits simultaneously is that resources that are allocated to one trait are no longer available to maximise other traits. Thus, trade-offs are a fundamental aspect of life history evolution.

One of the trade-offs predicted by life history theory is that age at maturity should be correlated with adult lifespan, and this prediction is met within many taxa (Charnov & Berrigan 1990 and references therein). The reason why such a correlation should exist can be summarised as follows: shorter generation times increase fitness expressed as $r$, the intrinsic rate of population increase. Both shorter developmental time and earlier reproduction as adult increase $r$. The costs of reproduction result in a decrease of adult life span with earlier reproduction. Hence, selection for shorter development is likely to result in shorter adult life span. In contrast, longer developmental times can only increase fitness when fecundity increases and/or offspring mortality decreases as a function of age at maturity (Stearns & Crandell 1981, Stearns & Koella 1986, Stearns 1992, Klingenberg & Spence 1997) and the decrease in fitness due to longer development is compensated for. A longer adult lifespan may then be instrumental in realising higher fecundity or better offspring survival. The only plausible mechanism for delayed maturity to result in an increase in fecundity is when fecundity is determined by size (Roff 1981, 1984). Therefore, a correlation between developmental time and adult lifespan can be expected when adult size and fecundity increase with developmental time. This is the case for the examples cited by Charnov & Berrigan (1990): shrimps, fish, snakes, lizards, mammals and birds.

However, there is a growing body of evidence that developmental time and longevity are not always correlated. One can expect to find no correlation between the two (1) if development and longevity are not genetically linked and (2) when an increase in developmental time does not result in a larger adult size and a higher fecundity. Holometabolic insects form an ideal subject to test this hypothesis, because selection regimes are very different for larvae and adults. Also, in holometabolic insects, a longer developmental time does not always result in a larger adult size. Moreover, in insects, size is not always correlated with longevity and fecundity (Klingenberg & Spence 1997). For parasitoids, evidence showing that developmental time and longevity are not correlated comes from a comparative study of 473 species of parasitic Hymenoptera (Blackburn 1991a,b). The same study also found no relation between developmental time and size. Recently, Eijs and van Alphen (1999) compared 5 species of *Leptopilina*, larval parasitoids of drosophilids, and found no correlation. However, species comparisons are not the best method for studying the genetics underlying life history traits. Therefore, we have compared different populations of a single species, *Asobara persimilis* (Hymenoptera: Braconidae), along a climate gradient in eastern
Australia and performed a hybridisation experiment to gain more insight in the relation between development time and longevity in insect parasitoids and the possible reasons why these characters are uncoupled in insect parasitoids.

Asobara persimilis occurs in southeast and eastern Australia. Its known distribution extends from the temperate zone (Adelaide, Melbourne) into the tropics (Cairns) (C. van Achterberg, pers. comm.). The parasitoid attacks larvae of frugivorous Drosophila (Prince 1976). There is a gradual shift in climate along the Australian east coast. In the south (Adelaide), the summers are hot and dry, while the winters are cool and rainy. Average amount of summer rain increases to the east (Melbourne) and keeps on increasing to the north (Sydney, Brisbane, Cairns). Average temperature increases to the north. The shift in climate is likely to result in selection on life history characters along a gradient, as has been shown for one of A. persimilis' hosts, Drosophila melanogaster (James et al. 1997). In the south, the low winter temperatures prevent activity of the parasitoids, which pass the winter in diapause. Up to Brisbane, no parasitoids could be found in August, but July and August records of A. persimilis are available for the Cairns area (C. van Achterberg, pers. comm.). The hot dry summer weather in the south and the hot, humid summers in the north are likely to affect adult life history traits as longevity and timing of reproduction in different ways. It has extensively been shown that parasitoid longevity sharply decreases at high temperatures, probably due to an enlarged use of energy reserves (e.g. McDougall & Mills 1997, Lysyk 1998, Zaviezo & Mills 1999). The hot dry summers in the south probably reduce adult survival and select for rapid early reproduction. Optimal foraging theory predicts that females from populations with shorter longevities superparasitize more readily than females from populations with long adult lifespans (Roitberg et al. 1992, 1993) In the north, summer rainstorms may prevent parasitoids to forage, and a longer adult lifespan would allow a parasitoid to outlive the period of unfavourable weather.

MATERIAL AND METHODS

Asobara persimilis populations were collected at seven sites, two in the Adelaide area, three in the surroundings of Melbourne, one from the vicinity of Sydney and one from the Brisbane region. Cultures were established in the laboratory on D. melanogaster. During the experiments, the wasps were kept at 25°C. For female wasps, we measured the following traits for one strain from Melbourne and one strain collected near Brisbane in Goodna, called "Brisbane strain" below: developmental time (from egg to eclosion as adult), adult longevity without food and with honey as carbohydrate source, number of eggs in the ovarioles at eclosion, number of eggs in the ovarioles after seven days of wasps kept with and without honey, amount of lipoproteins stored at eclosion and after seven days of wasps kept with and without honey (by means of ether extraction, see Ellers 1996), and superparasitism behaviour. Five other strains were collected at McLaren Vale, Waite campus (both in the Adelaide region), Silvan, Yarra Valley (both in the Melbourne region) and Hunter Valley (near Sydney). For these strains, we measured adult longevity without food and with honey.

We also studied three strains of Ganaspis sp. (Hymenoptera: Figitidae). This undescribed species emerged from most of the traps from which we obtained A. persimilis. We kept the Ganaspis strains at 25°C and for female wasps we measured developmental time (from egg to eclosion as adult) and adult longevity without food and with honey.

RESULTS

The populations from Melbourne and Brisbane do not differ significantly in developmental time (one-way ANOVA, df=1, F=2.53, p=0.11). These strains also do not differ in egg load at the day of emergence (one-way ANOVA, df=1, F=0.42, p=0.52) and day seven of their adult life (one-way ANOVA, df=1, F=2.41, p=0.13 without food; df=1, F=0.03, p=0.87 with honey).

Immediately after eclosion, wasps of both strains do not differ in the amount of extracted fat, a measure for the lipoprotein reserves of a parasitoid (one-way ANOVA, df=1, F=0.19, p=0.67). On day seven of adult life, the amount of fat extracted is less than that extracted on the day of emergence in both strains. The decrease in lipoprotein reserves over the first seven days of adult
life is larger in the Melbourne strain than in the Brisbane strain, resulting in a lower egg load of females from the Melbourne strain at day seven (one-way ANOVA, df=1, $F=30.57$, $p<10^{-3}$ without food; $df=1$, $F=26.94$, $p<10^{-3}$ with honey) (Fig. 1).

The difference in lipoprotein reserves is in agreement with the large difference in longevity found between the two populations (one-way ANOVA, $df=3$, $F=27.22$, $p<10^{-6}$ without food; $df=3$, $F=22.57$, $p<10^{-6}$ with honey) (Fig. 2). Females of the Brisbane strain live about twice as long as those of the Melbourne strain. F1 hybrid females have a longevity intermediate to that of the parental strains, suggesting simple genetics underlying this trait.

Figure 1. Amount of fat extracted from females of the Brisbane (white bars) and Melbourne (black bars) strains at day 7 of adult life. A. without food. B. with honey as a carbohydrate source

Figure 2. Adult survival of *A. persimilis* females of the Melbourne (solid line) and Brisbane strains (dotted line) and females of the F1 Hybrids between the strains (— — = Melbourne females x Brisbane males, — — = Brisbane females x Melbourne males). A. without food. B. with honey as a carbohydrate source
Longevity of the five other strains significantly increases across a gradient from Adelaide to Sydney (one-way ANOVA, df=4, F=19.90, p<10^{-6} without food; df=4, F=7.94, p<10^{-5} with honey) (Fig. 3). Hence, *A. persimilis* populations show variation in longevity related to a climate gradient.

Preliminary data obtained for the Melbourne and Brisbane strains of *A. persimilis* show differences confirming predictions from optimal foraging theory as wasps from the shorter-living Melbourne strain superparasitise more often than wasps from the Brisbane strain: 28% vs. 0% superparasitism at a given host and parasitoid density. A comparison of *Ganaspis* sp. populations from Melbourne and from the Brisbane region (Canungra and Samford) shows variation in longevity similar to that found for *A. persimilis* across the same climate gradient. No consistent correlation between development time and longevity was found in the three *Ganaspis* strains tested.

**DISCUSSION**

We have demonstrated that populations of *A. persimilis* differ in adult longevity. For two populations studied in more detail, this difference is not caused by a difference in allocation to egg production and survival, because initial egg loads and egg loads at day seven of adult life did not differ between the strains. Also, lipoprotein reserves at the start of adult life did not differ between these strains, whereas at day seven of adult life lipoprotein reserves of the shorter-living strain were smaller than those of the longer-living strain. Differences in longevity between the strains must therefore be attributed to differences in metabolic rate.

These results are unlike the results of Ellers and van Alphen (1997), who found differences in longevity between *A. tabida* populations from north and Mediterranean Europe. These differences could be attributed to differences in allocation of resources to reproduction and survival, with the Mediterranean population having higher initial egg loads and the northern population, which lived longer, having higher lipoprotein reserves. Ellers and van Alphen (1997) explained these differences as adaptations to the spatial distribution and abundance of hosts.
The lack of differences in allocation to egg production between the two populations of *A. persimilis* suggests that differences in the abundance and the spatial distribution of hosts do not play an important role as a selective agent on longevity in *A. persimilis*. The increase in longevity across a climate gradient found for the populations of *A. persimilis* studied additionally indicates that climate differences play a role. This view is corroborated by the results of a comparison of three *Ganaspis* sp. populations, which show similar variation in longevity across the same climate gradient. The dry hot weather during summer in south Australia most likely reduces expected adult lifespan, and would select for traits that maximise reproduction early in life at the cost of a shorter lifespan. A high level of activity would be such a trait. In the north, summer rainstorms will cause periods that are unfavourable for foraging. Selection for parasitoids that remain inactive during such periods, and by doing so increase their chance of outliving such an unfavourable period, would result in parasitoids with lower activity levels. We will further test these hypotheses by measuring metabolic rates of the studied populations in a respirometer.

The difference in longevity, in the absence of a difference in developmental time between the Melbourne and Brisbane populations, suggest that there is no correlation between adult life span and developmental time in this species. Rather, these traits seem uncoupled. Also, data obtained from the *Ganaspis* strains do not show a consistent correlation between development time and longevity. How uncoupling of developmental time and adult longevity is achieved at a genetic and physiological level is a topic of further research.

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**REFERENCES**


