Life-history evolution in hymenopteran parasitoids : the roles of host and climate

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Chapter 1

General introduction and discussion

Life-history theory

Life-history theory predicts the existence of constraints and trade-offs between traits contributing to the fitness of an organism. Constraints reduce the flexibility in the evolution of particular combinations of traits (Roff 1992). A trade-off means that a trait can only increase in value at a cost to another trait. For instance, natural selection may favor an increased reproductive rate, but this may be impeded by a trade-off between reproduction and survival. Due to this trade-off any increase in reproductive rate will come at a cost to survival rate or vise versa (Roff 1992, Stearns 1992). This trade-off can be studied by measuring traits that are directly related to reproductive rate and survival such as age-specific fecundity, age and size at maturity, size at birth, number of offspring and survival rate. Traits that affect fitness indirectly, such as resource acquisition and allocation, foraging behaviour, stress tolerance, resisting parasite or predator, competitiveness are also considered life history-traits (Jervis et al. 2005; Maeda 2006; Steiner and Pfeiffer 2007). Life-history theory deals with analyzing variation in these traits and investigates relationships between them. The central aim is to establish how variation in life-history traits may lead to variation in fitness of individuals. Life-history theory views organisms from both ecological and evolutionary perspectives (Roff 1992).

Natural selection on life-history traits

Natural selection acts upon fitness-related variation in phenotypes. Given additive genetic variation, trait values that enhance fitness will increase in frequency over time (Fisher 1930). Fitness in general is defined as the ability of individuals to survive and reproduce in a given environment (Brwon 1993). Fitness thus reflects the contribution of that each individual makes to the gene pool of the next generation (King and Standsfield 1990; Daan and Tinbergen 1997; Sober, 2001; Orr 2009). Genetic variation in fitness is the raw material for natural selection without which adaptation can not occur (Orr, 2009). Two different fitness measures are used in evolutionary studies: global fitness and local fitness. Global fitness is the overall fitness of an organism that includes all the interactions between traits contributing to fitness. In other words global fitness is the balance between different fitness components. Global fitness has frequently been

assumed to be identical to lifetime reproductive success (R0) in stable populations or to the intrinsic population growth rate (r) in growing populations (Roff 1981; Charnov and Berrigan 1991; Fox and Wolf 2006). Local fitness is the fitness of each component independently and can be use instead of global fitness only if overall fitness increases with local fitness (Roff 1992).

Life-history traits can vary enormously between and within species. For example, different species of flatfishes may range in body size from 2 cm to 200 cm and in age at maturity from less than one to over 10 years (Roff 1992). Another example is variation in clutch size in birds which ranges from one egg per clutch in albatrosses to nine eggs per clutch for geese species. Some impressive variation in life-history traits at the intraspecific level has also been documented. For example, members of one population of the flatfish *Hippoglossoides platessoides* averaged 25 cm in body length and took 6 years to reach maturity, while in another population the fish measured 60 cm and took over 20 years to reach maturity (Roff 1992). Similarly, age at maturity in the European minnow, a freshwater fish, ranged from one to seven years (Mills 1988). Such variation in life-history traits may be subject to natural selection and result in genetic and phenotypic differences between populations and even speciation when populations have diverged dramatically in the long term. Such continuous spectrum of change in life-history traits is called life-history evolution.

Reproductive success: the main target of selection

In many studies reproductive success has been used to represent global fitness (e.g., Roff 1981; Charnov and Berrigan 1991; Fox and Wolf 2006). Evolution is th result of natural selection favoring individuals with high global fitness. If we equate increase in global fitness with increased reproductive success then the main product of evolution is optimization of reproductive success. Life-history theory predicts a trade-off between reproduction and survival (Roff 1992). This means that the potential increase in reproductive rate in a given environment is limited by the imposed cost on survival rate. As a consequence, a balance between reproduction and survival is inevitable. This trade-off may be observed in nature in different forms, the simplest being a negative relationship between the number of young produced and the parent's survival (Reznik 1985; Roff 1992). It can also be seen as a negative relationship between the number of offspring and the size of the offspring (Williams 1966; Smith and Fretwell 1974; Gustafsson and Suderland 1988; Roff 1992) or between time or resources spent on current versus future reproduction (Godfray 1987; Ackerman and Eadie 2003; Ellers and Jervis 2003, 2004). To maximize reproductive success, organisms must balance reproduction and survival optimally. The question of how individuals maximize reproductive success in a given environment is thus a fundamental question in evolutionary ecology. The maximization of reproductive success is influenced by different factors. The strength and importance of each factor can be determined by the environment. I will discuss some important factors affecting reproductive success in different environments.

Resource acquisition and allocation

One of the main factors influencing reproductive success is resource acquisition and allocation (e.g., de Jong and van Noordwijk 1992; Tanaka 1996). Life-history theory also predicts that resource availability shapes life-history-traits and drives the evolution of organisms (Roff 2002). If resource acquisition and allocation can change the fitness of organisms then it is expected to be subject to natural selection. A considerable number of life-history studies have been devoted to resource acquisition, allocation and the resulting optimal balance between life-history traits (e.g., van Noordwijk and de Jong 1986; Engen and Saether 1994; Worley et al. 2003; Jervis, et al. 2008). Resource acquisition often has been studied as a component of the foraging behaviour of animals. Foraging determines resource intake by the organism. A wide variety of animal foraging strategies has been reported both inter and intraspecifically (Gray and Hodgson 1997; Caldow et al 1999; Jia et al 2002; Cooper 2005). Boggs (1992) suggested that foraging is linked with life-history and must be studied together with resource allocation to provide a better understanding of population dynamics in contrasting environments. Variation in foraging strategies may change the pattern of resource allocation dramatically in different populations or individuals within the same population (Weimerskirch, et al 1997). Resource distribution patterns in the environment and competition between individuals within species also may change foraging strategies and resource intake rates (Sutherland 1996). Efficient foraging strategies may help organisms to overcome the competition between individuals of the same species (Caldow et al 1999). Variation in foraging may affect the fitness of individuals and consequently result in natural selection and potentially the diversification of populations. Many studies reported spatial or temporal partitioning in the foraging patterns of coexisting species under resource limitation (Shargal et al 2000; Hadiprakarsa and Kinnaird 2004). Niche partitioning is the result of long term evolution of traits which allow organisms to exploit distinct ecological niches and allows the coexistence of competitor species in same habitat. For example, differences in the combination of enzymes allows species to prefer different diets (Voytek and Joyce 2009). It is obvious that the presence or absence of a coexisting competitor in different habitats can drive the evolution of populations of the same species in different directions.

Allocation of resources to different traits strongly influences the

fitness of an organism. We have already mentioned that the spatial or temporal distribution of resources influences foraging behaviour and thus resource intake rate (Roff 2002). The availability of resources is a habitat characteristic that may differ between environments. The allocation of limited obtained resources to competing traits can play a fundamental role in fitness of organisms. Many organisms are adapted to a narrow environmental range and may perform poorly in different habitats (Nagy 1970; Fenster and Galloway 2000). Different combinations of trait values may be optimal in different environments. For example, there is evidence for differences in reproduction and survival for birds in different habitats (Clark and Shutler 1999). Habitat specific resource allocation strategies may improve the fitness of individuals. One of the main challenges of evolutionary ecology is to understand the optimal strategies for resource acquisition and allocation. This optimal strategy can vary drastically depending on the habitat and resource distribution patterns. First we need to understand the role of habitat in life-history evolution. A habitat is a combination of biotic and non-biotic factors which form the environment of each organism. Interaction of the organism with both biotic (other species) and abiotic (climate factor and geographical structure) factors can shape its life-history traits. This thesis focuses on the role of hosts as the main biotic factor, and climate as the main abiotic factor in the evolution of life-histories in parasitoids.

Hymenopteran parasitoids

Parasitoids are a group of insects which lay their eggs on or inside the body of preimaginal (and rarely adult-) stages of other insects (egg, larva or pupa) and complete their development by consuming the host tissue, eventually killing their host (Godfray 1994, Quicke 1997). Juvenile parasitoids inhabit a single host from early life to maturity which results in an intimate relationship between parasitoid and host (Godfray 1994). Different groups have been defined within parasitoids, depending on their life style. Idiobionts are a group of parasitoids that start consuming their host immediately after parasitism, while koinobionts allow their host to continue feeding and increase in size. Endoparasitoids define a group of parasitoids that live and feed inside the host body incontrast ectoparasitoids that live and feed externally on the host. Parasitoids have also been categorized based on the stage of the host which they attack for example egg, larval (nymph) or pupal parasitoids (Godfray 1994, Quicke 1997). Parasitoid life styles are predominantly found in two orders of Insecta. The greatest diversity of parasitoids occurs in the Hymenoptera, with a substantial minority in the Diptera. Much smaller numbers are found in other orders, e.g. in the Coleoptera. Parasitoids can in some cases control insect populations and are often used as biological control agents of insect pests on agricultural crops in field. Studies of the cues that parasitoids use to find their host gained them prominence in the scientific study of animal behaviour (Godfray and Shimada 1999). Using hosts- parasitoid as a model system provided an opportunity to test population dynamic models. Godfray (1994) reviewed most of these studies and many new studies have been published since then (Quicke, 1997; Tilman & Kareiva, 1997; Wilson and Hassell 1997; Turchin, 1998; Dieckmann et al., 2000; Ellers et al. 2000b; Schofield et al. 2002; Rivero and West 2002; Lett et al. 2003; Rivero and West 2005; Liu et al 2009). Studies on host-parasitoid relationships have made valuable contributions to evolutionary ecology. Examples include the optimization of foraging strategy according to different host distribution patterns and environmental factors (e. g., Vet et al. 1990; Schofield et al. 2002) and in the role of habitat stochasticity in energy allocation strategy (e. g., Ellers et al. 2000b). Furthermore, comparative studies on host-parasitoid interactions have provided a spectacular evolutionary view of this interaction and the co-evolution of these organisms. Some well known examples of host parasitoid interactions are geographical variation in parasitoid virulence and host defense systems (Kraaijeveld and van Alphen 1994; Kraaijeveld and van Alphen 1995) or superparasitism as an adaptive strategy in parasitoids (Alphen and Visser, 1990; Kraaijeveld et al.,1995). All of these aspects have made parasitoids an excellent model system to study ecology and evolution.

Life-history traits in parasitoids

There is a substantial body of literature on parasitoid life-history (e. g., Price 1973; Blackburn 1991; Godfray 1994; Kraaijeveld & van der Wel, 1994; Jervis 2001; Ellers and Jervis 2003; Jervis et al 2003 Rivero and West 2005). Hymenopteran parasitoids show huge variation in life-history traits. For instance, the ectoparasitic wasp *Sericopimpla sericata* (Ichnieumonidae) measures 12 mm, lives up to 140 days and lays only 30 relatively large eggs (2 mm) in its entire life. By contrast, the endoparasitic wasp *Trioxys complantus* (Braconidae) is only 1.3 mm long, lives 28 days and lays 180 small eggs (0.1 mm) during its lifetime (Mayhew and Blackburn 1999). Astonishing variation in reproductive strategy was also reported for two hyperparasitoids of *Cotesia glomerata*, *Gelis agilis* and *Lysibia nana.* The former has large eggs, long life-span and few progeny per day but performed with similar efficiency as the latter which is reversed in all these traits (Harvey 2008). Although intraspecific variation in life-history traits of parasitoids is much smaller in scale compared to interspecific variation, still considerable life-history variation has been reported among populations of the same species. Variation in reproductive success and allocation to early life reproductive was observed for *Asobara tabida* populations along a geographic cline (Kraaijeveld & van der Wel, 1994). A quantitative genetic study also showed heritable variation in fecundity of the parasitoid *Anagrus delicates* (Cronin and Strong 1996). Studies have shown size dependent variation in life-span and fecundity

of parasitoid individuals (Ellers and Jervis 2003; Jervis et al. 2003; Jervis and Ferns 2004; Thorne, et al. 2006).

Parasitoids should optimize their reproductive strategy by maximizing the number of eggs laid before the end of their life. This means that both time limitation, i.e. coming to the end of life with unlaid eggs left in their body, and egg limitation, i.e. finishing their eggs much earlier than the end of life, could both play a role in parasitoids (Ellers 1998). The optimization of reproduction has been the focus of many life-history studies in parasitoids in both ecological and physiological contexts. Timing of reproduction (age-specific fecundity) is an important component of the reproductive strategy of parasitoids. Parasitoids were initially divided into two groups based on their reproductive strategy. Pro-ovigenic species emerge with all eggs mature, while in synovigenic species, none or only a portion of eggs are mature at emergence (Flanders 1950). Synovigenic parasitoids are able to adjust the timing of egg maturation from early to later in life time. In fact, a continuum of strategies exists between these extremes, which is expressed as the index of ovigeny (Jervis et al. 2001). Timing of egg maturation shows a negative relationship with body size and a positive relation with habitat stochasticity (Ellers 1996; Ellers et al. 2000b; Ellers and Jervis 2003; Jervis et al. 2003; Jervis and Ferns 2004; Thorne, et al. 2006).

Resource allocation in parasitoids has been studied in both ecological and physiological contexts and has been reviewed recently by Jervis et al. (2008). Different nutrients (e.g. sugar, glycogen, lipid and protein) play different roles in locomotion or ovigenesis. Stored lipids are important in both ovigenisis and somatic function in parasitoids (Ellers 1996; Ellers et al. 1998; Pexton and Mayhew 2002; Casas et al. 2005; Rivero and West 2005). The lack of lipogenesis in adult parasitoids results in a key role for lipid allocation. A trade-off in lipid allocation to initial reproduction and fueling soma have been demonstrated both inter and intraspecificly for hymenopteran parasitoids (Ellers and van Alphen 1997; Pexton and Mayhew 2002). The cost of future reproduction on teneral lipid reserve was also shown for synovegenic parasitoids (Ellers et al. 2000b). Plasticity in resource acquisition and utilization, for example through adult host feeding or egg resorption may mask this trade-off (Jervis et al 2001, Jervis and Kidd 1986; Burger et al 2004; Heimpel and Collier 1996). The effect of host feeding on female fecundity varies between parasitoid species (Ueno and Ueno 2009). Resource allocation plays a pivotal role in intertrait correlations because of trade-offs in allocation of resources to different traits. In this thesis, I examine variation in resource allocation in hymenopteran parasitoids in relation to climate and host.

Climate

The ecological and evolutionary effects of climate on life-history traits have taken on a special relevance in the light of recent concerns over climate change (e.g., Stenseth and Mysterud, 2002, Stenseth et al. 2002; Winkler et al. 2002; Stenseth and Mysterud, 2005). A wide range of meteorological factors contribute to form the climate. The strength of each factor may vary between climates. The Islamic Republic of Iran consists of a wide variety of climates. A study on the climatic regions of Iran analyzed the contribution of 27 factors to the variance in climate and identified six as the main climatic factors: temperature, humidity, precipitation, cloudiness, wind and thunder (Masoodian 2003). Among these, temperature and humidity are widely regarded as the most important components of climatic variation (Gorshkov and Makarieva 2002). In life-history studies too, temperature has been mentioned as a key factor affecting the fitness of a wide range of organisms (Roff, 2002). The effect of temperature on life history traits of different organisms has been well documented in many studies (e.g., Johnston and Benneth, 1996; Dahlgaard et al. 2001; Clarke, 2006). The role of temperature on insect life history traits include the increase of some traits with increasing temperature (Nespolo et al. 2007; Stelgenga and Fischer 2007; Karl and Fischer, 2008) or reduction of the traits with increasing temperature during development (Bazzocchi at al. 2003; Karl and Fischer, 2008; Nilssen 1997; Dhileepan at al., 2005; Colinet at al. 2007; Fischer et al. 2003). Climate may affect parasitoid life-history directly or indirectly by altering the life-history traits of the host. Both of these will be addressed in this thesis. Among the climatic factors that will be discussed are frost and drought. Frost can play a crucial role in shaping life-history traits of organisms (Inouye 2000). Dramatic declines in nutrient reserves (mainly in lipid content) under desiccation and cold stress have been documented for insects (Downer and Matthews 1976, Udonsi 1984, Djawdan et al. 1997, Minois and Le Bourg 1999, Colinet et al 2006). In nature, adult hymenopteran parasitoids can obtain carbohydrates from nectar. Carbohydrates and moisture are essential determinants of lifespan for many hymenopteran species (Lewis et al 1998). The availability of food sources in nature may not only affect the longevity of parasitoids but also their fecundity (Hagley and Barber 1992; Olson, D. L. and Nechols 1995). The patterns of nectar availability can be highly diverse in nature due to climate. A lack of a carbohydrate sources in nature can result in starvation of parasitoids (Jones and Jackson 1990; Jervis et al. 1996;Williams and Roane 2007). The evolution of life-history traits in hymenopteran parasitoids is affected by climate in many different ways. It therefore requires broad-scale research to understand the evolutionary aspects of climate and climate change in hymenopteran parasitoids.

Host

The life histories of parasitoids and that of their hosts are intimately linked. Direct host-parasitoid interactions may result in co-evolution between the two species. Second, climate may affect the

host distribution pattern and host quality, which may then affect the parasitoids. An important component of host-parasitoid interactions is the immune system of the host and the ability of parasitoids to suppress it. This has been well studied in hymenopteran parasitoids and their hosts. Encapsulation is a common reaction in insects host to escape parasitism. It operates by aggregation of haemocytes around the parasitoid egg which results in melanization of the egg (Nappi 1975; Rizki and Rizki 1984). *Asobara tabida* populations show geographic variation in their ability to resist encapsulation which is correlated with variation in encapsulation ability of the host, *Drosophila melanogaster* (Kraaijeveld and van Alphen 1994, Kraaijeveld and van Alphen 1995). Interactions between hosts and parasitoids are not limited to the immune system of the host and virulence of the parasitoids. Manipulation of host behaviour by the parasite in such a way that it increases the fitness of parasite has been termed the "*extended phenotype*" (Dawkins 1982). There are many examples in which parasites manipulate their host behaviour in wide range of host, including snails (Miura *et al.* 2006), birds (Holmstad *et al.* 2006) and hymenopteran parasitoids (Brodeur and Vet 1994; Tanaka and Ohsaki 2006; Grosman et. al 2008). Examining variation in the manipulation behaviour of closely related parasitoid species may help to understand its fitness value. The potential effect of climate in shaping these manipulative interactions has never been addressed. Two other important host effects that may be affected by climate are host quality and host distribution pattern. The effect of climate on vegetation and fruit availability may contribute to variation in host quality through differences in food sources and competition. For example, the performance of parasitoids on herbivorous insects has been shown to vary depending on plant cultivars or soil types (Moon et al. 2000; Moreau et al. 2009; Sarfraz et al. 2009). Immature parasitoids are limited to a single host and the amount of resources that they can exploit is thus dependent on the nutrients gained by the host, which in turn is affected by food availability and competition. Host availability in nature is highly dependent on temperature and precipitation. Both temporal and spatial distribution patterns of the host are dictated by climate and are important sources of selection on life history traits of parasitoids. In particular, the stochasticity of the climate has a strong effect on the evolution of life history traits in parasitoids (Ellers et al. 2000b; Ellers and Jervis 2003). In stable climates the probability of finding hosts may be constant in any season, while in more stochastic climates parasitoids may face a lack of hosts at certain times, because of host population crashes. Parasitoids are expected to adapt their life history decisions, such as foraging behaviour, in relation to host distribution pattern (Vos & Vet, 2004; Kraaijeveld & van der Wel, 1994; Kraaijeveld et al., 1995; Dubuffet et al., 2006). Overall, host quality and availability are crucial for parasitoids and are likely to impose strong selection on life-history traits of parasitoids.

Aims and scope the thesis

This thesis explores the relationships between parasitoids, hosts and climate from an evolutionary point of view. I chose hymenopteran parasitoids as a model system. The Hymenoptera are one of the largest orders of Insecta and include the largest group of parasitoids with about 50000 described species (Godfray 1994). An additional motivation for this choice was the role of hymenoteran parasitoid as biological control agents in pest control in agriculture crops. Studying the interplay between parasitoids, hosts and climate may contribute to our understanding of processes involved in the establishment of parasitoids in a new habitat. To study these questions, I adopted a comparative approach. Variation in life-history traits has studied for species or populations from different habitats. First, I looked at closely related species which have evolved from a common ancestor, but occupy different habitats. Second, I studied genetic and life-history trait variation in different populations of a single species. These populations were geographically isolated in contrasting climates.

This thesis examines the following five predictions:

1. Closely related species manipulate their host's behaviour in different ways, depending on their habitat.
2. Different strategies of parasitoid species in spending their limited resource budget result in a lack of correlation between developmental time and life span.
3. The trade-off between initial egg load and lipid reserve is influenced by body size at both the inter- and the intraspecific level.
4. Strong selection on life-history traits of parasitoids induced by climate and host is expected to promote genetic divergence of parasitoid populations along a geographical cline.
5. Natural selection in geographically isolated populations should favour different life history strategies. Variation in life-history traits is thus expected to correlate with climatic factors.

Chapter 2: Closely related parasitoids induce different pupation and foraging responses in *Drosophila* larvae

In this chapter I tested the first hypothesis by comparing pupation site of hosts parasitized by different species of *Asobara* (Braconidae). The central goal of this chapter was to show variation in adaptive host manipulation behaviour by parasitoids. The species originated from highly divergent habitats with very wide differences in climate, host and

competitor species assemblages. The results not only revealed variation in strength of host manipulation but also in the direction of the induced changes. At least for one species (*A. tabida*) the induced change in pupation site was shown to be adaptive for the parasitoid.

Chapter 3: The lack of correlation between developmental time and adult life span in parasitoids: the role of metabolic rate and fat reserves

This chapter explores the relationship between developmental time and life span in presence and absence of food in five species of *Asobara* cultured on *Drosophila melanogaster.* The lack of lipogenesis during adult life in parasitoids places severe constraints on allocation of the limited amount of lipids that can be sequestered from a single host. This is expected to result in different life-history strategies and variation in metabolic rate, lipid storage and lifespan.

Chapter 4: Adult size and early investment in reproduction in five species of *Asobara* parasitoid wasps

Life-history theory predicts a trade-off between initial egg load and lipid content (Roff 1992). Furthermore, large individuals are expected to postpone maturation of more of their eggs than small individuals, while habitat stochasticity should select for higher initial egg loads (Ellers and Jervis 2003). I tested these predictions at both inter- and intraspecific levels for five species of *Asobara*. The results provided strong support for these predictions at both levels.

Chapter 5: Genetic structure of *Leptopilina boulardi* populations from different climatic zones of Iran

I documented genetic variation of 11 populations of *Leptopilina boulardi* along a geographic transect in Iran to test whether populations from different climatic zones had diverged genetically. Nine populations could be divided in groups clustering together based on their zone of origin. One population differed from all others and was probably imported from elsewhere. A montane population was found to be genetically similar to those from the nearby lowlands. Both distance and physical barriers contributed to the genetic structure of these populations.

Chapter 6: Local adaptation in life history traits of *Leptopilina boulardi* populations from different climate zones of Iran

I investigated the energy reserves (lipid, glycogen and sugar) and reproductive effort (egg load and egg size) of 11 populations of *Leptopilina boulardi* originating from contrasting climate zones of Iran. Most traits showed significant divergence according to climate. Two main climatic factors, precipitation and frost, explained significant amounts of the variance in life-history traits. This finding suggests that natural selection on life-history traits imposed by climate can result in rapid evolution of these traits.

General conclusion

The results in chapter two demonstrate significant manipulation of host behaviour by two out of five *Asobara* species affecting both pupation height of the host and foraging behaviour of host larvae. Manipulation of aspects of host behaviour by hymenopteran parasitoids have been reported previously (Brodeur and Vet 1994, Tanaka and Ohsaki 2006; Grosman et al. 2008). However, these studies only demonstrated a host manipulation by a single parasitoid species. Comparison of closely related species originating from different habitats revealed different manipulation strategies when interacting with a common host. Our empirical evidence demonstrated the adaptive value of the induced change by *A. tabida* but not for *A. citri*. As host manipulation by *A. tabida* and *A. citri* occurred in different directions, it is likely that the optimal strategy for host manipulation is species-specific, because these species live in climatically contrasting habitats.

The results of chapter three showed a lack of correlation between developmental time and adult life span of five *Asobara* species. This is consistent with previous findings for hymenopteran parasitoids (Blackburn 1991; Eijs & van Alphen, 1999). The novelty of this chapter is in revealing the role of lipid reserves and metabolic rate in adjusting species-specific life span. Much of the variation could be explained by the habitat of origin of the species. Variation in host distribution pattern results in differences in foraging behaviour among hymenopteran parasitoids (Vos & Vet, 2004; Kraaijeveld & van der Wel, 1994; Kraaijeveld et al., 1995; Dubuffet et al., 2006). It is obvious that different of variation in foraging behaviours require different activity patterns and different metabolic rates. As a consequence of the lack of adult lipogenesis in hymenopteran parasitoids (Ellers 1996; Rivero and West 2002; Giron and Casas 2003; Visser and Ellers 2008) and variation in metabolic rate, parasitoids will vary in lifespan due to exhausting lipid resources at different rates.

In chapter four I show a high initial reproductive effort in smaller *Asobara* species and low initial reproductive effort in larger species. Consistent with this interspecific pattern I found a negative correlation between size and initial reproductive effort on an intraspecific level. These patterns are in agreement with the Ellers and Jervis (2003) model on timing of reproduction in hymenopteran parasitoids. Furthermore, I found a trade-off between initial reproductive effort and lipid reserves in four out of five species, which is consistent with life-history theory (Roff 1992).

In chapter five I established the genetic structure of 11 populations of *Leptopilina boulardi* from different climatic zones of Iran by employing the Amplified Fragment Length Polymorphism (AFLP) technique. Except for an unexpected pattern for one population and an identical genetic structure for another population which is geographically close to the next zone, a clear genetic separation based on geography was observed. This is consistent with the results for AFLP patterns in other insect populations (Reineke et al., 1999; Ravel et al., 2001; Pannebakker et al. 2004; Alamalakala et al. 2009; Tao et al. 2009) and shows that local adaptation to climate is possible.

In the last chapter I found substantial variation in energy reserves (lipid, glycogen and sugar) and reproductive effort of Iranian *L. boulardi* populations. Similarly to genetic structure, the pattern of life-history traits separated populations clearly for most traits. This suggests that divergent natural selection may contribute to the differentiation of populations (Endler, 1986). Most traits showed a correlation with one or both of two climate factors, the number of rainy days and the number of frost days per year. These two climatic factors impose strong selective pressures in the form of drought and frost stress.

To conclude, I suggest that life-history traits of parasitoids are subject to natural selection pressures from both host and climate. These factors are likely to interact through the effect of climate on hosts. The intimate relationship of host and parasitoid and the dependency of parasitoids on their hosts for crucial resources like lipids, result in specific recourse allocation strategies to fit habitat requirements. Resource allocation in parasitoids is species specific and highly diverged among populations.