SEASONAL LIFE-HISTORY ADAPTATION IN THE WATER STRIDER *GERRIS LACUSTRIS*

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Chapter 1

General Introduction

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General Introduction

The components of an individual's life that are closely related to fitness – primarily juvenile and adult survival, development rate, age and size at maturity, age-specific fecundity, offspring size and number, longevity and senescence – are called life-history traits. Due to their linkage to an individual's fitness, selective pressure operates on these traits (Roff, 1992; Stearns, 1992). It is the purpose of life-history theory to explain how an individual's life-history strategy, i.e. the combination and sequence of traits it shows during its life, are shaped by natural selection (Nylin & Gotthardt, 1998) and consequently why we find such a vast variation of patterns of growth, survival and reproduction in nature. Life-history theory suggests that an individual's fitness is maximised in relation to the combination of extrinsic and intrinsic factors that act upon its life. The extrinsic factors are the ecological impacts that vary in space and time and force individuals to adjust their life-histories appropriately. The intrinsic factors are *'trade-offs among live-history traits and lineage-specific constraints on the expression of genetic variation'*, which limit this adjustment (Stearns, 2000). Thus, to explain a life-history strategy observed in an organism, the critical environmental parameters that influence its traits and the major constraints and trade-offs that limit the variation of traits have to be identified.

The environmental influences individuals in natural habitats are exposed to, as well as the theories on life-history adaptations to environmental factors are diverse (Roff, 2002); therefore it is necessary to narrow the subject matter down to the theories that are most meaningful for the type of organism under investigation. This thesis focuses on the life-history strategy adaptations of an annual insects species (with the potential to switch from uni- to multivoltine phenology) living in temperate latitudes. The major constraint these organisms are faced with is the problem of fitting their life-history appropriately to a seasonal environment (Levins, 1969; Tauber *et al.*, 1986; Danks, 1994). The seasonal character of the environment forces poikilothermic organisms (like insects) to pass the climatically adverse part of the season in an appropriately adapted state of diapause. Reproduction, growth and development up to the species-specific diapause state thus have to be completed within the limited period of favourable conditions (Cohen, 1970; Dingle, 1978). The primary problems these organisms have to deal with are (i) to optimally adjust development time to the given season length with respect to the trade-offs connected with development (Roff, 1980) and (ii) to find the optimal switching date between becoming a diapausing individual or producing another generation that has to diapause (Bradford & Roff, 1995, 1997; Roff, 2002). A general overview of the main theories and findings on adaptations of development to seasonality and optimal switching times is given in Chapter 1.1. Chapter 1.2 specifically refers to adaptations of water striders of the family Gerridae, to which the study organism belongs. Further details on the species under investigation, the common pond-skater *Gerris lacustris* (L.) and the study area are given in Chapter 2.

1.1 LIFE-HISTORY ADAPTATIONS TO VARIATIONS IN SEASON LENGTH

The length of the season suitable for growth and reproduction is a critical environmental variable affecting the life-history and especially the voltinism or phenology of poikilothermic organisms like insects (Tauber *et al.,* 1986; Danks, 1994). The body temperature of poikilothermic organisms is closely related to that of the environment. Due to the temperature-dependence of various physiological processes, the life-history of these organisms is strongly shaped by the variation of their thermal environment (Trudgill *et al.*, 2005). Development and growth can only occur in periods where environmental temperature exceeds specific thresholds (Scholander *et al.*, 1953; Pritchard *et al.*, 1996; see below). To avoid lethal temperatures, many poikilothermic organisms have to spend certain periods of their life in an appropriately adjusted stage of diapause (Levins, 1969; Cohen, 1970).

The occurrence of suitable and adverse climatical conditions in biological systems often occurs in seasonal cycles. Although the length of the suitable season is characterised by long-term global predictability, it shows unpredictable variation on a short-term and local scale (e.g. Hoffmann, 1978). Accordingly, an essential feature of poikilothermic organisms is to coordinate their life-cycle and phenology appropriate not only to seasonality, but also to variations in season length (Danks, 1994; Mousseau & Roff, 1989; Roff 2002).

Variations in season length occur on different spatial and also temporal scales (Rowe & Ludwig, 1991). The most obvious variation in the length of the suitable season is observed along geographical clines (e.g. Masaki, 1978; Nylin & Svard, 1991; Blanckenhorn & Fairbairn, 1995; Billerbeck *et al.*, 2000); along a latitudinal gradient, season length generally decreases due to declining temperatures. Differences in the season available for development also can be found on more local scales, e.g. between habitats situated closely to each other, but differing in climatic conditions (Fairbairn, 1984, 1985; Blanckenhorn, 1991). Furthermore, the length of the time available for development can even vary within populations, e.g. due to climatic differences between consecutive years, or due to individual differences in oviposition time. The latter results in a decrease in the time horizon for individuals hatching later in the year (Roff, 2002; Stoks *et al.*, 2005).

The variability of the environment acts as a strong selective pressure as reproduction or development up to the appropriate stage for diapause has to be completed until the end of the season. Thus, the questions how individuals adapt their life-history to such variations in season length, and whether these adaptations are due to phenotypic plasticity or genetic differentiation have gained considerable interest of empirical (e.g. Mousseau & Roff, 1989; Blanckenhorn & Fairbairn, 1995; Bradford & Roff, 1995; Berner *et al.*, 2004) and theoretical research (e.g. Roff, 1980; Abrams *et al.*, 1996).

When investigating adaptations to seasonality, it is essential to consider the appropriate scale for measuring the length of the season. For poikilothermic organisms it is not time, but rather the amount of thermal energy that accumulates throughout the season, which limits the length of the period suitable for development (Van Straalen, 1983). Invertebrates usually need to accumulate a specific amount of thermal energy to develop from one developmental stage in their life to another. A measure for the thermal requirement of development is the physiological time, i.e. the number of degree-days above the lower developmental threshold accumulated during development (Taylor, 1981; Danks, 1994; Roff, 2002; see Box 1). The latter is considered to be a constant which is species-specific (e.g. Honek, 1996a, b, 1999), and can vary in response to extrinsic limitations like food availability (e.g. Larsen *et al.,* 1990). Information on thermal constants of species development allows predicting life-history processes, such as the duration of development, the timing of reproduction, or the number of generations in a season (Trudgill *et al.,* 2005). Therefore they have widely been used in agriculture for prediction of optimal planting and harvesting time (e.g. Fisher & Lieth, 2000), and also in pest management to generate phenology models or to calculate optimal spraying time (e.g. Riedl & Croft, 1978; Rock & Shaffer, 1983). However, a recent demand is that the concept of physiological time should be used in a much wider ecological context (Trudgill *et al.*, 2005), e.g. to detect variations in thermal constants or relative rates of growth between individuals. Thus, the concept of physiological time may be a basis for characterising adaptations in life-history strategies.

Whenever individuals need to adjust their development or life-cycle to a limited season, it is necessary to detect environmental cues that provide information on the length of the remaining time (or energetic) horizon (Danks, 1994). Furthermore, individuals should be able to respond to such cues with a plastic reaction of life-history traits. In insects living in temperate latitudes, the most relevant environmental signal presumably is the photoperiod, i.e. the ratio of daylight to darkness (Tauber *et al.*, 1986; Saunders, 1987; Nylin & Gotthard, 1998). Adjustments of life-history traits concerning adaptation to season length in response to changes in photoperiod have been shown for many insect species (e.g. *lepidopterans*: Nylin, 1992; Nylin *et al.*, 1989; *heteropterans*: Köpfli *et al.*, 1987; Vepsäläinen, 1974b; *zygopterans*: Johansson &

Rowe, 1999; Strobbe & Stoks, 2004 or *orthopterans*: Masaki, 1967; Carriere *et al.*, 1996).

Box 1 Physiological time and the thermal constant *k*

The amount of thermal energy an individual accumulated during a certain time is usually called the physiological time. The thermal constant k (unit degree-days [°d]) is a measure for the thermal energy required to complete a specific developmental process (e.g. larval development). It is calculated as the temperature T (in °C) that accumulates above the specified lower threshold temperature t_0 during the development time D (in days; Allen, 1976):

$$k = \int_0^D (T - t_0)dt$$

or

$$k = D(T - t_0) \text{ ; when } T = \text{const. \& } T > t_0$$

When development occurs within the range of the species-specific lower developmental threshold t_0 and an upper temperature limit t_u, the relationship between the reciprocal of the development time D of the process under study (= development rate) and the environmental temperature T is usually assumed to be linear (linear degree-day model; Briere *et al.*, 1999):

$$\frac{1}{D} = -\frac{t_0}{k} + \frac{1}{k}T$$

The linear degree-day model offers a method for estimating the thermal constant k as well as the lower developmental threshold t_0 from the regression line of the development rate ($y = 1/D$) on the environmental temperature ($x = T$). Here, t_0 is the intercept with the x-axis, while k is the reciprocal of the slope of the regression (Garcia-Huidobro *et al.*, 1982; Trudgill *et al.*, 2005).

The length of the season constrains the time available for an individual's development (Roff, 2002). Individuals should therefore adjust their development to changes in season length (reviewed in Nylin & Gotthard, 1998). A common assumption of life-history theory is that under increasing time constraint, individuals should fasten development to ensure the completion of development up to the appropriate diapause stage before environmental conditions become unfavourable (Abrams *et al.*, 1996; Roff, 2002). Development can be fastened and development time shortened. However, this can lead to a decrease in body size, as body size and development time are often positively correlated (Roff, 1981). Various empirical studies show a decrease in body size in species exposed to declining season length along latitudinal clines (e.g. Nylin & Svard, 1991; Blanckenhorn

& Fairbairn, 1995; Mousseau, 2000). Body size is assumed to be closely related to fitness-relevant traits (Roff, 1992; Stearns, 1992). Although there are counterexamples (Klingenberg & Spence, 1997), many studies confirm a positive correlation between body size and fecundity in insects e.g. (Honek, 1993; Preziosi *et al.*, 1996; Sopow & Quiring, 1998). Thus, life-history theory postulates that the decrease in body size caused by shortened development times should be minimised by speeding up development rate (Stearns, 1992; Abrams *et al.*, 1996; Roff 2002). Several recent studies indeed found acceleration of development in individuals under time stress at the between population level (Billerbeck *et al.*, 2000; Berner & Blanckenhorn, 2006) as well as within populations (Johansson & Rowe 1999; Strobbe & Stoks, 2004; Stoks *et al.*, 2005). However, most of these studies simultaneously report severe costs of fastened development. These costs primarily result from the increased foraging rate of rapidly growing individuals. An increase in foraging rate is positively related with predation risk (Houston *et al.*, 1993; Gotthard, 2000; Lankford *et al.*, 2001; Metcalfe & Monaghan, 2001). Because of this sensitivity of fitness related traits to variations in development time and rate, these two parameters should only be modified when individuals are forced to react on extrinsic limitations of resources, like time (Stearns, 1992; Arendt, 1997; Roff, 2002).

According to the shortened development observed under decreasing season length, an increase in the time horizon for development is often associated with prolonged development time and increased body size (Masaki, 1978; Brennan & Fairbairn, 1995). However, there is no simple proportionality between development and season length. In climatical transition zones where time and thermal energy available per season is sufficient for the development of more than one generation, there may even occur a switch in the reproductive strategy of individuals, i.e. from diapause to direct reproduction (Cohen, 1970). This results in a change in the life-cycle strategy from uni- to bivoltinism. When switching from uni- to bivoltinism (i.e. when increasing the number of generations per season), the thermal energy available for the development of each generation is smaller than in univoltine populations. Thus, life history theory predicts that in transition zones individuals from bivoltine populations should develop faster and mature at a smaller size than in univoltine populations (Roff, 1980). Development time and body size of the individuals from the populations with bivoltine life-cycles should increase towards areas with longer season length. This so called 'saw-tooth' pattern in body size along seasonal clines has been confirmed in several studies on insects (Masaki, 1978; Mousseau & Roff, 1989; Nylin & Svard, 1991; but see Blanckenhorn & Fairbairn, 1995 and Chapter 1.2).

Box 2 Measures of fitness

The evolution of life-history traits is investigated by the use of optimization-models, based on the assumption that selection maximises direct individual fitness (Stearns, 1992). However, up to now there is no general measure of fitness (Charlesworth, 1994). Commonly used measures of fitness are separated into 'local' measures that *assume that maximization of a fitness component will also maximize the overall fitness* and 'global' measures *that involve the interaction of all life-history components* (Roff, 1992). Evolutionary ecologists assume that selection primarily acts through maximization of global measurements (Stearns, 1992; Charlesworth, 1994). A typical global measure of fitness is the finite rate of increase λ of population size N during time t (see Formula 2.1).

$$N_t = N_0 \cdot \lambda^t \quad (2.1)$$

In age-structured populations λ can be obtained from equation 2.2:

$$\sum_{x=1}^{\omega} \lambda^{-x} l_x m_x dx = 1 \quad (2.2)$$

In stationary populations ($\lambda \approx 1$), the global measurement of fitness is the net reproductive rate R_0, which is the expected number of (female) offspring of a female during her life span (x=1..ω)

$$R_0 = \sum_{x=1}^{\omega} l_x m_x dx \approx 1 \quad (2.3)$$

Both formulas contain the product of age (x)-specific survival (l_x) and fecundity (m_x). However, the appropriate use of this measure of fitness depends on density-dependence of population regulation, frequency dependence of selection and on the variability of the environment (Roff, 1992). In a density-independent and constant environment where little year-to-year variance in the finite rate of increase is expected, the arithmetic mean of this variable is proposed to be an adequate measure of fitness (Charlesworth, 1994):

$$\text{arithmetic mean: } \frac{\sum_{i=1}^{i=t} \lambda_i}{t} \quad (2.4)$$

Contrary, in spatially and temporally uncertain environments, e.g. when season length varies between years and all individuals of the population are synchronously affected by these fluctuations, the geometric mean of the intrinsic rate of increase is suggested to be maximised by selection (Cohen, 1966; Gillespie, 1977).

$$\text{geometric mean: } \sqrt[t]{\prod_{i=1}^{i=t} \lambda_i} \quad (2.5)$$

An increase in the geometric mean results from reduced variance in the finite rate of increase between years. To avoid severe reduction of population size in unfavourable years, selection will favour a strategy that minimises variance in the finite rate of increase in variable environments (Lacey *et al.*, 1983).

As the offspring of the direct reproducing generation of bivoltine populations need to develop up to the appropriate diapause stage within the limited remaining season, the optimal timing of a switch between developing into a direct reproducing and a diapausing individual is essential (e.g. Taylor & Spalding, 1988). This switch should ideally occur when the fitness of a direct reproducing individual falls below that of a diapausing individual (Cohen, 1970). However, individuals never exactly know how much time they will have for development in a specific season. Although insects have developed photoperiod-sensing systems to get information about the remaining season length (Saunders, 1987), they are not able to exactly forecast the remaining thermal energy due to the short-term variability of season length. Consequently, a strategy of diapause timing should evolve that maximizes the long-term fitness in a variable environment (Box 2).

Strategies known as 'bet hedging' or 'spreading of risk', e.g. like the production of phenotypically diverse offspring (i.e. gradually changing between non-diapause and diapause individuals) to ensure that at least some of the offspring will reproduce under the given (uncertain) environmental conditions, have been shown to allow an increase of the long-term fitness by maximizing the geometric mean of the finite rate of increase (Box 2; Seger & Brockmann, 1987; Philippi & Seger, 1989; Frank & Slatkin, 1990).

1.2 ADAPTATIONS OF WATER STRIDERS TO SEASONALITY

Northern temperate water strider species of the family Gerridae are suitable objects for studying adaptations to seasonality as they occur in seasonal habitats along considerable geographical clines (Vepsäläinen, 1973a; Andersen, 1982). They inhabit different types of environment (Fairbairn, 1985; Spence 1989; Guthrie, 1989) and females oviposit eggs for a time span of several weeks (Andersen, 1982; Kaitala, 1988; Harada, 1992), leading to differences in the time horizon for development between offspring within populations.

Investigations on adaptive potential of species belonging to the Gerridae in response to differences in season length have been conducted along seasonal clines (Blanckenhorn & Fairbairn, 1995) and between nearby habitats with differing climatical conditions (Fairbairn, 1984, 1985; Blanckenhorn, 1991). These studies showed that in accordance with the assumptions of life-history theory (e.g. Mousseau & Roff, 1989), water strider populations (of *Aquarius remigis* Say) separated by extended geographical distances adapt to an increase in season length by extending development and growing larger (Blanckenhorn & Fairbairn, 1995). The same adaptation could be found in populations inhabiting streams situated close to each other, but differing highly in temperature and thus in thermal energy available during the season (Blanckenhorn, 1991). *Aquarius remigis* also was found to switch from uni- to bivoltine life cycles in response to increasing habitat temperatures along the macro-geographical scale as well as between two nearby habitats (Fairbairn, 1985). A switch from uni- to multivoltinism under favourable climatical conditions has been shown for several other water strider species as well (Vepsäläinen, 1978; Köpfli *et al,*. 1987; Spence, 1989). The most important environmental cue triggering this switch is the photoperiod larvae encounter during their development. While developing under critical long-day conditions induces direct reproduction and multivoltinism, short-day conditions induce diapause (Vepsäläinen, 1974b; Köpfli *et al.*, 1987). However, the larval instars sensitive to photoperiod and the critical length of photoperiod differ between species and latitude, and some species or individuals do not react to photoperiod at all (Köpfli *et al.*, 1987; Spence, 1989).

Studies investigating either the reaction of populations living in different environments to photoperiod, or their development time, growth rate and body size in response to common environmental conditions, furthermore showed a rapid genetic differentiation due to natural selection in water striders (Blanckenhorn, 1991; Blanckenhorn & Fairbairn, 1995). In contrast, the ability to react with phenotypic plasticity to variations in season length by individuals with a common genetic background has been less investigated (Chapter 3).

As the direct reproducing individuals do not have to diapause before reproduction, a switch from a uni- to a multivoltine life-cycle is advantageous. However, the increase in generation number within a season increases the time constraint on each generation (Roff, 2002). According to the sawtooth-cline pattern in body size predicted by Roff (1980, see above), individuals of populations in transition zones should thus shorten development time and mature with a smaller body size when switching to a multivoltine phenology. A saw-tooth cline in body size was found in natural populations of *A. remigis* along a latitudinal cline in eastern North America (Brennan, 1993). In laboratory rearings of individuals collected from populations along this gradient (Blanckenhorn & Fairbairn, 1995), direct reproducing individuals in the transition zone did not reduce body size, but accelerated development rate, allowing to reach 'normal' body size in less time. However, in many laboratory studies investigating adaptations to variations in season length, food intake of individuals is not controlled. Considering the fact that (i) the development of (not only) water striders depends strongly on feeding rate (Blanckenhorn, 1994), (ii) natural water striders are assumed to be highly food limited (Järvinen & Vepsäläinen, 1976; Vepsäläinen, 1978; Fairbairn, 1984), and (iii) the increase of development rate carries fitness costs due to the higher energy needs (Johansson & Rowe, 1999; see above), the question arises whether in natural systems there would be a trade-off between an increase in generation number and other life-history traits (e.g. dispersal ability) as predicted by life-history theory (Chapter 4). A first step to answer this question is to investigate whether a limitation of food really limits the ability to accelerate development in water striders (Chapter 5). To detect the possible trade-offs that are connected with an increase in the number of generations, it would furthermore be helpful to take into account those life-history traits that are organised seasonally and that differ between uni- and multivoltine populations, respectively.

The most obvious life-history variation that accompanies the change in voltinism in several Northern European water strider species is a seasonal wing dimorphism (Andersen, 1973; Vepsäläinen, 1978; Andersen, 2000). Water striders in general exhibit a great variability in wing dimorphism – ranging from fully-winged, seasonal or permanent dimorphic to completely wingless species (Andersen, 1982, 2000). A remarkable number of empirical (e.g. Zera *et al.*, 1983; Zera, 1984; Fairbairn, 1986, 1987; Kaitala, 1987, 1988; Spence, 1989; Kaitala & Hulden, 1990; Spence, 2000) and theoretical (e.g. Järvinen & Vepsäläinen, 1976; Vepsäläinen, 1978; Vepsäläinen *et al.*, 1985; Kaitala *et al.*, 1989) studies tried to analyse the adaptive significance of wing dimorphism in water striders. The maintenance of wing dimorphism in water striders is assumed to be due to the balanced fitness advantages between the two wing-morphs. Long-winged individuals benefit from their flight ability; they are able to disperse between temporary habitats, to fly between reproductive and terrestrial diapause sites, or to use bet-hedging strategies by distributing offspring among different habitats (Kaitala & Hulden, 1990; Spence, 2000). In contrast, the short-winged morph reaches reproductive maturity earlier and, in some species, has a higher reproductive rate than its long-winged counterpart (Andersen, 1973; Vepsäläinen, 1978; Zera, 1984; Spence, 1989; Harada, 1998). Thus, individuals with reduced wings have a selective advantage within stable habitats. Phylogenetic studies comparing the stability of habitats of various water strider species with their patterns of flight ability confirm this assumption (Andersen, 2000). However, while the general maintenance of wing dimorphisms seems to be clear, the adaptive significance of a seasonal wing dimorphism in water striders is less understood, and was only investigated in few empirical studies (Landin & Vepsäläinen, 1977; Kaitala & Hulden, 1990; Spence, 2000). In temperate Europe, seasonal dimorphism primarily occurs in *Gerris* species that inhabit lentic and thus more or less temporary habitats (Andersen, 2000). The diapausing generation of these species normally has a high fraction of long-winged individuals. They have to escape habitat deterioration and to fly between diapause- and reproduction sites (Landin & Vepsäläinen, 1977). The directly reproducing generation, on the other hand, appears in bivoltine populations in midsummer and has a high proportion of the short-winged morph (Andersen, 1982; Hauser, 1982; Vepsäläinen, 1978). The mechanism determining wing length is due to a combination of genetic and environmental factors (Zera *et al.*, 1983;

Selvanayagam & Rao, 1986), and the strong association between long-wingedness and diapause on the one hand, and short-wingedness and direct reproduction on the other hand, presumably is caused by the fact that like the determination of voltinism, the induction of the wing morph is affected by photoperiod (Vepsäläinen, 1971; Vepsäläinen, 1973a). However, the question remains why flight ability is reduced in a generation appearing in midsummer, and thus at a time where the risk of the drying up of habitats is extremely high in temperate Europe.

Studies on fitness differences between the two wing morphs showed that in several water strider species the short-winged morph has a clear temporal advantage compared to its long-winged counterpart, due to higher speed of development or a higher reproductive rate. In these species, larval (Zera, 1984), teneral (Andersen, 1973) and/or prae-ovipositional period (Zera, 1984; Spence, 1989; Harada, 1998) of the short-winged morph is shorter than in the long-winged morph. Furthermore, short-winged individuals can have higher rates of egg production at the beginning of the reproductive period (Spence, 1989). These advantages may result from the fact that no flight apparatus has to be constructed in the short-winged morph during juvenile development, and that flight muscles do not have to be developed in the teneral period (Andersen, 1973). The faster development of the short-winged morph has been proposed to be of selective advantage in the midsummer generation. Their offspring avoid cannibalism and unfavourable environmental conditions in the late season (Järvinen & Vepsäläinen, 1976). However, selective pressures favouring long-wingedness also act on water strider populations during summer. Habitat instability (Andersen, 2000) may force individuals to new habitats and unpredictable predator and parasitoid pressures (Spence, 1983; 1986a, b; Zimmermann & Spence, 1989) may favour individuals that can leave an infested place. Thus, it remains unclear if short-wingedness is more favoured in the midsummer generation than longwingedness.

Considering the temporal constraint on bivoltine populations in transition zones, i.e. in regions where thermal time just allows a switch from uni- to bivoltinism, the reduction of wings in the direct breeding generation may result from a trade-off between increasing generation number and being flight capable throughout the season. If this is the case, the thermal energy (degree-days) actually available in habitats where bivoltine populations with short-winged midsummer generations appear should constrain development of two long-winged generations (Chapter 4). This furthermore makes it obvious that – especially in transition zones - individuals are faced with the problem of deciding whether to develop into a (short-winged) direct reproducing or a (long-winged) diapausing individual. Physiological time needed for successful development varies between individuals, and the remaining thermal energy available for development depends on the oviposition date of an individual within the season and furthermore varies from year to year. Thus, the optimal switching date between a uni- and bivoltine strategy can not be predicted until a suitable measure of fitness is provided that accounts for all relevant traits spending thermal energy during an individual's life time. So far, such a measure of fitness has been specified for crickets, for example (Bradford & Roff, 1997), but not for waterstriders (Chapter 6).

1.3 OUTLINE OF THE THESIS

This thesis investigates the flexible adjustment of life history traits in response to variations in season length and the major constraints and trade- offs that limit this flexibility in a water strider, the common pond skater *Gerris lacustris* (Heteroptera: Gerridae).

Gerris lacustris shows a switch from uni- to bivoltine life-cycles accompanied by a seasonal wing dimorphism along a north-south gradient in Europe (Vepsäläinen, 1978). The differences in its life-history strategy have been shown by comparative studies on populations occurring over substantial distances along this latitudinal cline. In contrast, the life history variability between individuals living on a very local scale (i.e. with a common genetic background) but under different natural environmental conditions has rarely been investigated, so far. Consequently, the ability to adjust voltinism solely by phenotypic flexibility to environmental conditions is investigated in field- as well as laboratory studies in Chapter 3. The study focuses on individuals occurring in two different environments (shaded forest- vs sun exposed field-ponds) on a spatial scale too small to allow local genetic differentiation between populations. In Chapter 4 it is investigated whether the switch in voltinism and the differences in wing morph pattern observed between populations inhabiting field- and forest-ponds (see Chapter 3) are influenced by a constraint in thermal energy available throughout the season in these two habitat types. Life-history theory predicts that constraints in season length or thermal energy, respectively, should be compensated by accelerating development. However, limitations of food - a situation that water striders are likely to experience in natural habitats - are assumed to prevent the acceleration of development. In Chapter 5 the hypothesis is tested whether *within* populations larvae of *G. lacustris* are able to react on environmental signals indicating that the end of the season draws closer (i.e. photoperiod) with a reduction in the thermal energy required for development, and whether a limitation in food supply confines this phenotypic flexibility. In addition, the influence of food limitation on the development of wings is discussed.

Chapters 3 to 5 provide various field- and laboratory data and statistical analyses of different traits of the life history of *G. lacustris*. However, the potential evolutionary relevance of the considered traits can only be discussed against the background of plausible but local measures of fitness (see Chapter 1.1 and Box 2). The optimal reproductive strategy and its quantitative temporal response as well as the effects of (possibly unexpected) interactions between the traits and environmental variation can not be predicted until the complete life cycle of an individual has been specified in a more formal way. In Chapter 6 we present a mathematical model of the life cycle of *G. lacustris* using field- and laboratory data of growth, survival and reproduction. We have analysed the expected transition between uni- and bivoltine reproduction in dependence of predictable life history traits like mortality and development time and unpredictable heterogeneity of season length. The relative relevance of these factors is discussed based on the grade of accordance between theoretical predictions and the outcome of corresponding field experiments.

Chapter 2

Species and Study Area

Chapter 2

Species and Study Area

2.1 THE COMMON POND-SKATER *GERRIS LACUSTRIS*

Figure 2.1: The common pond skater *Gerris lacustris* (L.).

Water striders of the genus *Gerris* are suitable objects for investigating adaptation of life-history to seasonality because they frequently occur in variable habitats along seasonal clines. A species that has gained considerable attention because of its phenotypic flexibility in voltinism and wing phenology is the common pond skater *Gerris lacustris* L. (Heteroptera: Gerromorpha; Fig. 2.1; Poisson, 1924; Larsen, 1950; Andersen, 1973; Vepsäläinen & Krajewski, 1974; Spott & Bartels, 1997). This species inhabits the cool water-bodies near the Arctic Circle in northern Finland (~ 65.5°N; Vepsäläinen, 1974a) but also occurs in northern Africa and throughout the Caucasus (Lindberg, 1948). Beside its wide distribution, *G. lacustris* is one of the most abundant water strider species among the Gerridae within Europe. In Germany eleven other species of the family Gerridae occur (Hoffmann & Melber, 2003).

One of the major reasons for the wide distribution of the common pond-skater presumably is its modesty concerning its habitat preferences. *G. lacustris* is found on small lakes and ponds, but also on ditches and backwaters. It inhabits (semi-) permanent but also temporary habitats, the latter especially south of Finland (Vepsäläinen & Krajewski, 1974). In addition, it is the most pollution tolerant water strider species in Europe (Guthrie, 1989). Preferably, its habitats are semi-open, have firm and well raised banks and are covered with vegetation for hiding, resting and oviposition, at least in the littoral zone (Vepsäläinen, 1973a). Furthermore, *G. lacustris* shows a preference for shaded habitats and often occurs in water-bodies under trees (Brinkhurst, 1959). The latter fact makes *G. lacustris* an ideal object for studying life history adaptation at small spatial scales, as it is the only water strider species abundant in both, warm sun-exposed and cool, shaded habitats within the study area (see Chapter 2.2). Further water strider species occurring in the sun-exposed habitats within the study area are *Gerris paludum, Gerris thoracicus, Gerris odontogaster* and *Gerris argentatus,* but all of them are at best found sporadically in the shaded habitats. Within its habitats, *G. lacustris* typically forms large populations with up to ten individuals per m², but small populations mixed with other *Gerris* species can also be found (Vepsäläinen, 1973a). Individuals of *G. lacustris* are not randomly distributed on the water surface. While foraging adults spend much time on the open water, larvae are primarily found in the vegetation of the littoral zone (Nummelin *et al.*, 1984; Vepsäläinen & Nummelin, 1986).

In northern Finland, *G. lacustris* is primarily univoltine while it becomes bivoltine further to the south (Vepsäläinen, 1974a, 1978). Imagos usually overwinter in the vegetation far away from the breeding water-bodies (Kaitala & Hulden, 1990). In spring overwintered individuals recolonise the water-bodies for reproduction. The length of the reproductive season depends on the latitude (northern Finland: June – September, Vepsäläinen, 1974a; Austria: April – October, Hauser, 1982). Long-winged individuals of *G. lacustris* repopulate the water-bodies in spring by dispersal flights (Landin & Vepsäläinen, 1977; Kaitala & Hulden, 1990). During this time they show strong phototaxis, presumably because they locate water-bodies by the reflections from their surface (Landin & Vepsäläinen, 1977; Harada, 1991). When the water-bodies are relatively close to each other, spring dispersal flights lead to a mixing of individuals born in different ponds and thus, to high gene flow between local populations (Varvio-Aho *et al.*, 1979; Varvio-Aho & Pamilo 1979, 1980, 1981).

European *Gerris* species are assumed to hibernate in a state of reproductive immaturity (Andersen, 1973). Ovaries of the overwintered females are not fully developed until they colonize a habitat. Short-winged individuals of *G. lacustris* which overwinter close to the breeding pond, generally appear earlier on the water-bodies and start reproduction earlier in the season than their long-winged conspecifics (Vepsäläinen, 1974a). After gaining reproductive maturity, females lay eggs continuously during their remaining life-time (Andersen, 1973). Eggs are attached to the vegetation (Fig. 2.2) slightly below the water surface. Dependent on environmental temperature the development of eggs and the following five larval instars lasts between 30 and 50 days under natural conditions (Vepsäläinen, 1974b).

Figure 2.2: Eggs of the common pond skater *Gerris lacustris.*

Adults moulting from the larvae show phenotypic plasticity in two major live-history traits. First, they can develop into individuals that overwinter before reproduction.This decision would necessarily result in a univoltine life-cycle. Or they can produce offspring in the same season which then form the next hibernating generation. The latter leads to a bivoltine life-cycle (see Chapter 3, Fig. 3.6). Second, the adults can either be fully winged and able to fly or have shortened wings with undeveloped flight muscles (Fig. 2.3). Wing morph and life-cycle strategy of the adults are determined by a combination of genetical and environmental factors (Vepsäläinen, 1974b; Zera *et al*., 1983). The most important environmental trigger is the photoperiod larvae experience during specific stages of their development (see also Chapter 1.2). Under critical long-day conditions, larvae sensitive to photoperiod develop into directly reproducing individuals (= "midsummer generation") while under short-day conditions the hibernating "winter generation" develops (Köpfli *et al*., 1987). The wing status of adults is basically determined by genetic mechanisms, but environmental cues, like temperature and photoperiod influence wing development, too (Vepsäläinen, 1974b; Zera *et al*., 1983; Harada & Taneda, 1989). As a consequence, in *G. lacustris* the "midsummer generation" predominantly is short-winged, while the "winter generation" is mostly long-winged (Vepsäläinen, 1978; Andersen, 1982). However, while in other *Gerris* species this dimorphism is strictly seasonal, *G. lacustris* actually is a species with permanent dimorphism, as both morphs can potentially occur in both generations (Köpfli *et al*., 1987).

Figure 2.3: Short-winged (a.) and long-winged (b.) morph of *G. lacustris.*

In *G. lacustris* females of the midsummer generation can be distinguished from the winter generation females by the pigmentation of their thoracic venter (Fig. 2.4; Andersen, 1973). While direct reproducing females of the midsummer generation show a reduced pigmentation of the ventral surface (Fig. 2.4a), diapausing females develop into the normal, dark-colour morph (Fig. 2.4b). Beside its wing dimorphism and ventral coloration, *G. lacustris* is morphologically characterised by its body size (8-10mm) and the specific coloration of the pale femur of the foreleg – a black band on the front and the back, each running from tip to the middle (Guthrie, 1989).

Figure 2.4: Pale ventered (a.) and dark ventered (b.) female of *G. lacustris.*

2.3 STUDY AREA

All field studies were conducted in a system of 65 ponds in the surrounding of *Fabrikschleichach*, a village in northern Bavaria, Germany (49°55′N, 10°33′E, ~ 400m above sea level, Fig. 2.5). *Fabrikschleichach* is located in the northern part of the *Steigerwald*, a densely wooded low mountain range which rises up to ~ 500 meters above sea level. Due to its altitude the *Steigerwald* has a high mean annual precipitation of about 750-800 mm and a mean annual average temperature of 6-7 °C, which is about 1 °C lower than that of the surrounding landscapes of lower elevation. The whole area is located in a transition zone between oceanic and continental climate.

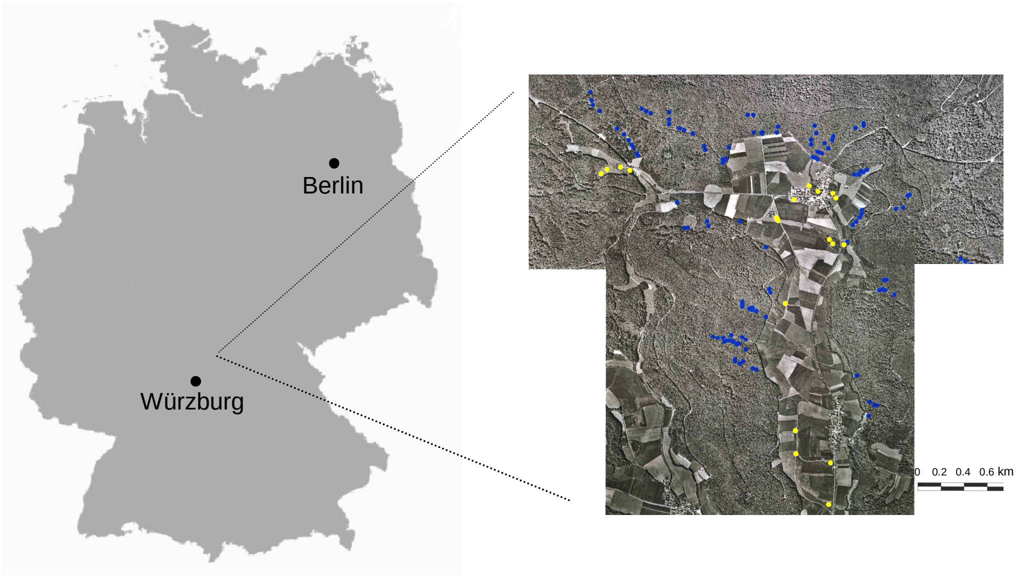

Figure 2.5: Study site with field (•) - and forest (•) -ponds in the surrounding of the village of Fabrikschleichach, located in the center of the Steigerwald, Northern Bavaria, Germany (arial view).

Figure 2.6: Arial view of the study site, the village of *Fabrikschleichach* with surrounding agricultural and forested areas.

The study ponds are distributed over an area of 3.5 x 3 km (Fig. 2.5 and 2.6). 14 of these ponds, referred to as "field-ponds", are located within fields or meadows outside the forest. They have been installed by the municipality to serve as stabilization ponds, rain storage reservoirs or for fish farming. The other 51 ponds are located within the forest (referred to as "forest-ponds") and have been installed by the forestry office Eltmann over the last 20 years. The dominant tree composition in the local forest consists of oak, hornbeam and beech with small patches of coniferous trees.

Figure 2.7: Pond after rainfall (a.); the same pond drying up a few weeks later (b.).

Most of the ponds investigated are temporary. They are all rather flat, i.e. less than 1m deep and the majority of the ponds are small in size. About 80% of the forest-ponds do not exceed 100 m², only few of them reach sizes up to 400 m². Although some of the field- ponds are rather large with sizes between 1300 and 3200m², more than half of them are smaller than 100 m² as well. Due to their small size and depth, they are quickly filled by water from snow-melt or rainfall, but in summer, they have a high risk of desiccation (Williams, 1987). Few of the ponds have inflow from brooks which often also dry up during summer. In fact, during the extremely dry season 2003 more than 50 % of the forest- and field-ponds – even the larger ones - that were water bearing at the beginning of the season dried up until the middle of August (Fig. 2.7).

Figure 2.8: Typical vegetation of field (a.)- and forest (b.)- ponds.

Vegetation in the ponds depends strongly on sun exposure. All of the sun exposed field-ponds have a dense submerse and emergent vegetation mainly of algae, Graminales and/or reed, at least at the littoral zone (Fig. 2.8a). In the shaded forest-ponds the vegetation is very different. Completely shaded ponds mostly lack vegetation but material like leaves or branches from surrounding trees often supplies shelter or oviposition sites. Whenever sun reaches the water surface much more vegetation, especially duckweed, covers the ponds (Fig. 2.8b).

Because of their small size forest-ponds are strongly shaded by the surrounding trees. Only the water surface of bigger ponds or those lying in glades also have sun exposed areas. In contrast, field-ponds are almost completely exposed to the sun (Fig. 2.9a, b). The differences in insolation lead to strong temperature differences between the forest- and field-ponds. Throughout the season 2004 the mean daily temperature of the water surface, measured in the littoral zone at the south side of 11 field- and 18- forest ponds, was about 2.6 °C lower in the canopied forest-ponds (13.6 ± 3.2 °C) than in the sun-exposed field-ponds (16.2 ± 3.6 °C, see Fig. 4.1). This temperature difference greatly affects the thermal energy available for development that accumulates throughout the season (see Chapter 4, Fig 3.4).

Figure 2.9: Field-pond (a.) and forest-pond (b.) within the study area

Chapter 3

Variability in the life history of the water strider *Gerris lacustris* (Heteroptera: Gerridae) across small spatial scales

Chapter 3

Variability in the life history of the water strider *Gerris lacustris* (Heteroptera: Gerridae) across small spatial scales

with Hans Joachim Poethke

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Abstract. 1. Variability in life history traits of the common pond skater *Gerris lacustris* (L.) (Heteroptera: Gerridae) was investigated on a small geographical scale in Bavaria, Germany (~ 49°N). In an area of approximately 3.5 x 3.0 km, voltinism and wing length data of *G. lacustris* were recorded from 65 ponds located either in an open field or surrounded by forest.

2. Life history differed significantly between populations in the two habitat types. *Gerris lacustris* showed a bivoltine life-cycle in most of the field-ponds with a high proportion of long-winged individuals in the diapause generation and a strong increase of the short-winged morph in the midsummer generation. In contrast, almost all populations inhabiting forest-ponds were univoltine. Only few forest-populations produced some second generation larvae. The long-winged morph dominated during the whole season in forest-ponds.

3. The appearance of first-instar larvae was delayed by 3-4 weeks in forest- compared to field-ponds. Presumably, low temperatures lead to this reduction in the developmental rate of eggs and larvae. Consequently, "field larvae" of the first generation developed under increasing daylight conditions (triggering direct reproduction and brachyptery) but "forest larvae" developed under a shortening photoperiod (triggering diapause and long-wingedness).

4. Offspring raised from "forest-parents" in the laboratory showed the same variability in life history when reared in a "cool" (16.9 ± 2.4 °C) or warm (23.1 ± 1.8 °C) temperature regime.

5. Given the small spatial scale of the study it is concluded that the variability in the life history of *G. lacustris* has a strong phenotypic component.

3.1 INTRODUCTION

Life history theory predicts variations in life history traits among organisms occurring along geographical clines or in environmentally variable habitats (Roff, 1980; Nylin & Gotthard, 1998). Responding with phenotypic variation to environmental cues, like photoperiod or temperature, is essential to adjust life history to the given environmental conditions (Tauber *et al.*, 1986; Danks, 1994).

Water striders (Heteroptera: Gerridae) show high intraspecific variation in life history traits (Kaitala, 1987; Spence, 1989; Blanckenhorn, 1994; Harada, 1998). The variability in voltinism (Vepsäläinen, 1978; Hauser, 1982; Blanckenhorn & Fairbairn, 1995) and alary polymorphism (Harada & Taneda, 1989; Kaitala & Dingle, 1992; Ahlroth *et al.,* 1999) has been described in several studies. The variation in water strider life history mainly results from the correlation between life-cycle and wing length pattern with seasonal length and the stability of habitat. In general, water striders are univoltine in northern latitudes with adults diapausing in winter (diapause generation). Several laboratory and field studies have shown that the life-cycle of many European *Gerris* species changes to bi- or multivoltinism under warmer climatic conditions (Andersen, 1973; Köpfli *et al.,* 1987; Ahlroth *et al.,* 1999). In bivoltine populations the offspring of the diapause generation develop into directly reproducing imagos (midsummer generation) that produce a second, diapause generation before they die in late autumn (Vepsäläinen, 1974a). The voltinism in a population is determined during the development of the individuals of the first generation. The critical factor triggering diapause or direct reproduction is the photoperiod experienced by larvae not older than the fourth instar (Vepsäläinen, 1978; Hauser, 1982). Under lengthening daylight the larvae will develop into a directly reproducing midsummer generation, otherwise diapausing imagos develop (Vepsäläinen, 1974a). Critical daylength and photoperiodic response differ between *Gerris* species (Köpfli *et al.,* 1987).

In wing dimorphic water strider species the photoperiod also strongly influences the determination of the wing morph (Vepsäläinen, 1978). Development under increasing daylength induces short-wingedness while the long-winged morph is preferentially produced under decreasing photoperiod. Thus, intraspecific variation in voltinism is accompanied by seasonal alary polymorphism with a higher proportion of short-winged individuals in the midsummer generation than in the diapause generation (Andersen, 1973; Harada & Taneda, 1989). However, the determination of wing morph has also a genetic component (Zera *et al.*, 1983) and is presumably influenced by further environmental conditions, like temperature during development (Vepsäläinen, 1978).

Various studies have been conducted to clarify the effect of environmental cues on life history variations in water strider species (e.g. Spence *et al.*, 1980; Köpfli *et al.*, 1987, Park, 1988; Inoue & Harada, 1997). Variation in life history traits can either be the sole consequence of phenotypic reactions to varying environmental cues or can also be the result of genetically determined differences in the reaction norm among the populations under investigation. Consequently, variations observed under different environmental treatments can solely be assigned to phenotypic plasticity only when there are no differences in the genetic background of the tested individuals, a precondition not clearly fulfilled in any of the studies mentioned above. Several researchers tried to differentiate between the environmental and the genetic contribution to the life history differences among populations of water striders. Rearing offspring from populations connected by at best weak gene flow (Blanckenhorn, 1991; Blanckenhorn & Fairbairn, 1995; Ahlroth *et al.*, 1999) under similar environmental conditions invariably showed that variations in the investigated traits between populations are at least in part heritable. These studies suggest a rapid genetic adaptation of water strider populations to changing local conditions, e.g. along latitudinal clines. However, few studies focus on life history variability between individuals with a common genetic background but living under different natural environmental conditions. In a rather singular observation Hauser (1982) observed a local population of *G. lacustris* changing its life-cycle from univoltinism to partial bivoltinism in two consecutive years in Austria, presumably due to different weather conditions.

In the study presented here the variability in life history traits among 65 populations of the common pond skater *G. lacustris* (L.) separated by very small distances was investigated in the field. *Gerris lacustris* is a common inhabitant of lentic waters in Europe. Populations of *G. lacustris* are univoltine at the northern edge of the species´ distribution (Arctic Circle, ~65.6° N), but show bivoltinism further to the south (e.g. Poland ~52° N, Hungary, ~ 47° N, Vepsäläinen, 1978) with a transition zone in southern Finland. Bivoltine populations express permanent wing dimorphism. The fraction of long-winged individuals in the diapausing generation increases from north to south, possibly as habitat stability decreases in warmer regions due to an increased desiccation risk (Vepsäläinen & Krajewski, 1974). In contrast to the diapausing generation, the directly reproducing individuals that occur in midsummer in warmer regions are mostly short-winged (Hauser, 1982). Differences in life-cycle and wing polymorphism of *G. lacustris* can be seen in population comparisons over substantial distances along a latitudinal cline (Vepsäläinen, 1974a, b; Vepsäläinen & Krajewski, 1974; Hauser, 1982; Köpfli *et al.*, 1987; Spott & Bartels, 1997). In this paper the life history of *G. lacustris* occurring in two different environments (canopied forest- vs sun exposed field-ponds) is compared over a very small spatial scale. Specifically, data on the number of generations per season and wing length pattern of populations of *G. lacustris* in a system of ponds scattered over an area of approximately 3.5 x 3 km was collected. Because of the extreme nearness of the habitats and the flight ability of the diapause generation local genetic differentiation is highly unlikely. Thus, observed life history differences may primarily be due to phenotypic plasticity. In addition, to investigate the phenotypic flexibility of local populations offspring of parents collected from a forest-pond were reared in two different temperature treatments.

3.2 METHODS

The study was carried out on 65 ephemeral ponds in the *Steigerwald*, a beech forest in southern Germany (49°55′N, 10°33′E, ~400m above sea level). The ponds are distributed over an area of 3.5 x 3 km in the open field and forested areas around the village of *Fabrikschleichach* (Fig. 3.1).

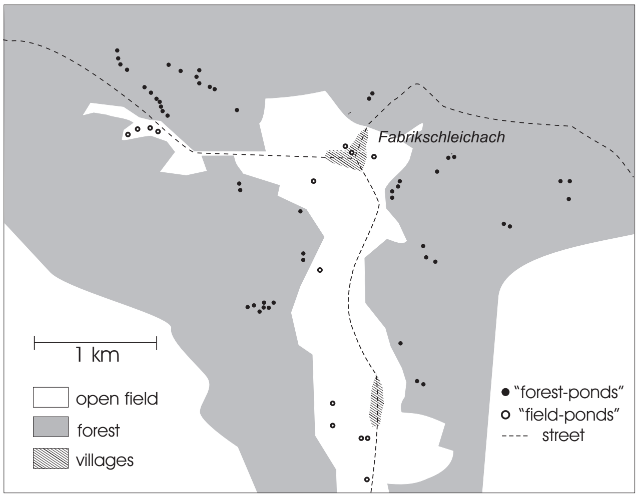

Figure 3.1: Map of the study area in the surrounding of the village of *Fabrikschleichach*, located in the center of the Steigerwald, Northern Bavaria, Germany.

The majority of the ponds were installed by the forestry office during the last twenty years. Most of them are less than 100 m^2 in size and in part subject to desiccation during dry summers. Ponds completely surrounded by a band of trees at least 10m wide were classified as "forest- ponds". Ponds with less than 25% of the edge encompassed by trees or shrubs were identified as "field-ponds". To detect temperature differences caused by differences in sun exposure between these two types of habitat the surface temperature of 11 field- and 18 forest-ponds was measured from 1 April to 12 September 2004 hourly by a thermo-logger (Dallas Semiconductor, Dallas, Texas, DS1921L-

F51). The thermo-loggers were placed in the middle of a piece of styrofoam (4x4cm) which was floating on the water surface. It was attached to a bamboo stick in the littoral zone at the south side of the ponds. A piece of plastic foil shaded the loggers against direct sunlight. Mean daily temperatures of field- and forest-ponds were calculated from the temperature measurements.

3.2.1 Wing length pattern and life-cycles of reference populations and reared individuals

Wing length and voltinism of *G. lacustris* populations were recorded weekly from April to October 2003 on two ponds ("reference-ponds"), one located in the field (~110 m^2) and the other in the forest (~ 80 m^2). The incidence of imagos and larvae was determined by thoroughly screening the water surface. Whenever imagos were present, twenty of them were collected with a long-handled aquatic net by selective sweeps from the edge of the pond. Because of the small size of the ponds usually the whole water surface was accessible. The fraction of the long-winged morph among the collected individuals was determined. Newly moulted individuals are always pale ventrally. All males and the reproductively immature diapause females develop into dark-colour-morphs within a few days, but directly reproducing, nondiapause females develop into light-colour morphs (Andersen, 1973). Thus, the reproductive stage and the generation to which females belong (midsummer or diapause) were deduced from the pigmentation of their ventral surface (Vepsäläinen, 1974a, 1978; Hauser, 1982). The ventral coloration and sex of the twenty individuals were noted.

Within population life-history data were obtained using offspring of the P (parental)-generation from the reference forest-pond that were raised under two different temperature treatments. Adult individuals were caught after diapause on 22 April and kept individually for 10 days to ensure that females oviposited any eggs fertilised previous to capture. Thereafter, seven long-winged (LW) and seven short-winged (SW) females were paired with males of the same wing status in water-filled plastic boxes (25 x 15 x 8 cm). Pieces of styrofoam (3 x 1 cm) were added as oviposition sites. On 9 May all females had started to lay eggs. From this day on all freshly laid eggs were removed each day for a period of 14 days. The newly deposited eggs of each field-collected pair were divided into two lots, marked with the oviposition date and transferred to separate glass containers (20 x 30 x 20cm) filled with 10 litres of water. For each of the 14 pairs, one lot of eggs was raised in a heated and the other in an unheated rearing container. The 28 containers were placed outdoors in seven rows on sandy soil protected from direct sunlight and wind by a tarpaulin open towards the western side. Thus, eggs of the two groups were reared under quasi-natural conditions. Every second container was heated with an automatic heater (Sacem, Bluetherm, 25 W) to a mean daily surface temperature of 23.1 ± 1.8 °C. Mean water temperature in the unheated treatment was 16.9 ± 2.4 °C during the course of the investigation. The containers were checked daily for freshly hatched larvae, which remained in the containers and were fed with *Drosophila spp. ad libitum*. Larval development was observed for each cohort of larvae until final moult or death of the individuals. Moulting date, sex and wing morph of newly moulted adults in the two temperature treatments were recorded.

3.2.2 Wing length pattern of field- and forest-populations

To collect representative information on wing length of populations of *G. lacustris* inhabiting field- and forest-ponds, the morphological status of individuals was sampled three times during the season at each accessible pond in the study site bearing water at the time of data collection. Because of the extreme warmth and drought in summer 2003, many of the ponds dried up over the course of the season; consequently sample size shrunk from 65 ponds in the first to 25 ponds in the last sample. Twenty individuals were collected from each pond and their wing status, sex, and ventral coloration were determined. The aim was to determine the fraction of long-winged individuals of the P-, F1- and (potential) F2-generations, consequently dates of these three investigations were chosen according to the developmental status of the two reference populations. The first collection took place between the 19-21 May when none of the two reference populations had newly moulted pale-ventered imagos indicating that only individuals of the overwintered parental generation were present at this time. The second sample was collected between 14-16 July. At this time both reference ponds had undergone a period where the dark ventered imagos of the P-generation had vanished and newly moulted imagos had appeared, thus only the F1-generation was present. The final sample was taken between 25-27 August after a strong decline in the amount of pale-ventered imagos on the field-pond (forest-population produced only a small number of pale-ventered imagos). Additionally, data collected with the same method from 11-14 July 2002 were available. Kruskal-Wallis H-Test was used to test for differences in the proportion of long-winged individuals during the season within the two types of habitat. For each of the three sampling dates the proportion of the long-winged morph of field- and forest- ponds was compared by a Mann-Whitney U-test. All statistics were calculated with R 2.0.0 for Windows.

3.2.3 Population dynamics and voltinism of field- and forest- populations

In order to investigate if there are differences in the voltinism of *G. lacustris* populations in the field relative to the forest, the appearence of first instar larvae was recorded througout the season 2004. On 11 field- and 18 forest-ponds the incidence of first-instar larvae was examined weekly between 4 May and 21 September. When larvae appeared for the first time on a pond, their relative density was measured every second day by placing eight frames of a wire quadrat (20x20cm) evenly distributed along the littoral line of the whole pond. Unlike adults that inhabit the open water surface, newly moulted larvae of *G. lacustris* are predominantly found in the littoral zone (Nummelin *et al.*, 1984; Vepsäläinen & Nummelin, 1986). As the wire-frames were submerged and kept some millimeters below the pond surface by styrofoam cubes (at the four corners of the frames) larvae could pass the edge of the frames undisturbed. Ten minutes after placing the frames under the water-surface the number of larvae in the frames were counted. The mean number of first-instar larvae per frame was determined and used as measurement of the average density of first-instar larvae. The procedure was repeated on every pond until the peak of density of first-instar larvae declined for at least two consecutive recordings. From this date on the incidence of first-instar larvae was again examined on a weekly basis. About six weeks after the first peak in the abundance of first-instar larvae they had disappeared on all ponds. At the moment of first appearance of the second generation of first-instar larvae, density estimates were again performed every second day. The procedure was repeated on all ponds that produced a second generation. The time of the peaks of density of first-instar larvae (measured in Julian days) and the number of larvae per frame at this moulting peak were compared between field- and forest-ponds with a Mann-Whitney U-Test. The analysis was done separately for the F1-and F2- generation. As one field- and one forest-pond dried up during summer, only 10 field- respectively 17 forest-ponds were included in the analysis.

3.3 RESULTS

Temperature of the water surface differed clearly between field- and forest-ponds. The measurement of the surface temperature of the two different types of habitat showed that during the reproductive season 2004 mean daily temperature on field-ponds (16.2+-3.6 °C) was about 2.6 °C higher than on forest-ponds (13.6+-3.2 °C).

3.3.1 Wing length pattern and life-cycle of reference populations and reared individuals

In the reference field-population, long-winged imagos dominated in the early and late season and showed a clear decline in midsummer (Fig. 3.2a). The females of the short-winged individuals appearing during midsummer were mostly pale-ventered. The appearance and strong increase of pale-ventered individuals started with the decline of the long-winged overwintered individuals and ended when the long-winged F2-adults had appeared at the end of the season.

In contrast to the field-pond, no short-winged midsummer generation was found in the forest-population. As in the field-pond, the fraction of long-winged imagos dominated in the overwintered P-generation, but it did not decline with the appearence of pale-ventered individuals in midsummer (Fig. 3.2b). However, there was a decline in the proportion of long-winged individuals towards the end of the season.

Moulting period of the 68 individuals that grew up until final moult in the unheated treatment started two weeks after midsummer and ended on 10 August. Almost all of these individuals (97 %) were long-winged. In contrast, all of the 41 individuals developing in the heated treatment had finished their development at latest two weeks after summer solstice. Only 22% of the adults moulting in the heated treatment developed into the long-winged morph.

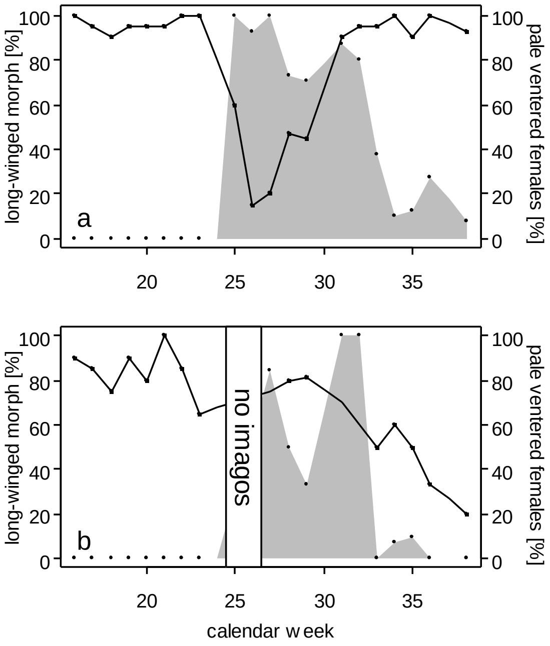

Figure 3.2: Seasonal changes in the fraction of long-winged individuals (solid dots and line) and females with pale venter (open dots and grey shaded area) on a pond surrounded by (a) field and (b) forest.

3.3.2 Wing length pattern of field- and forest-populations

The change in the fraction of long-winged individuals on all field- and forest-ponds during the season is in accordance with the pattern observed on the two reference populations (Fig. 3.3a, b, c). The field populations had an equally large proportion of the long-winged morph in May and August (Mann-Whitney *U*-test, n = 16, *U* = 22, *P* = 0.195) but significantly less long-winged individuals in July (n = 19, Kruskal-Wallis test, $\chi^2{}_2 = 9.2$, *P* = 0.01). In contrast, the forest-populations showed no significant decline in the fraction of long-winged individuals in July compared to May (n = 80, Mann-Whitney *U*-test, *U* = 616, *P* = 0.21). However, at the end of the season the fraction of long-winged *G. lacustris* on forest-ponds was significantly smaller than in May and July (n = 103, Kruskal-Wallis test, $\chi^2_2 = 16.2$, *P* < 0.001). The difference in the fraction of long-winged individuals between field- and forest-populations in spring (May) and midsummer (July) was highly significant (May: n = 65, Mann-Whitney *U*-test, *U* = 248, *P* < 0.05; July: n = 32, Mann-Whitney *U*-test, *U* = 0, *P* = 0.005) but not in August (n = 25, Mann-Whitney *U*-test, *U* = 6.5, *P* < 0.107). The records on wing length pattern collected in July 2002 on eight field- and eight forest-ponds are in accordance with the results of July 2003 (n = 18, Mann-Whitney *U*-test, *U* = 9, *P* = 0.004, see Fig. 3.3b).

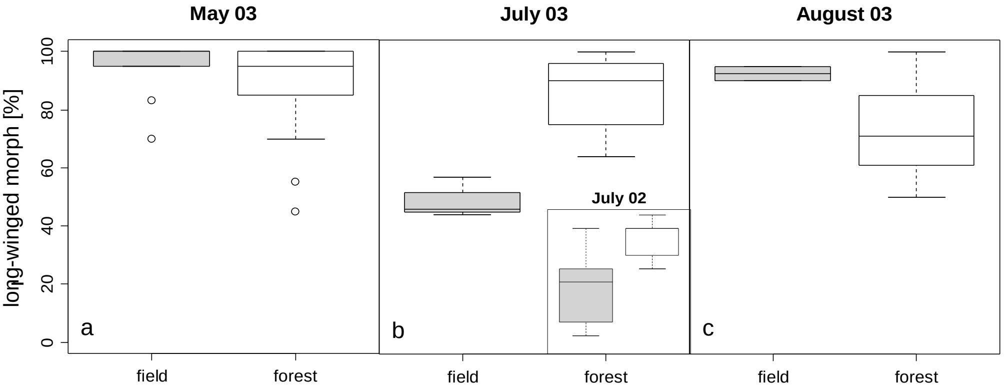

Figure 3.3: Boxplot of proportion of long-winged individuals on ponds surrounded by field (grey) or forest (white) at three dates of investigation, (a) May 2003, (b) July 2003 and (c) August 2003. Results of the summer 2002 are added as inlet in b. Boxes indicate the 25 to 75% interquartile range, whiskers indicate the minimum and maximum data values up to a maximum of 1.5 times the inter-quartile range and circles represent outliers.

2.3.3 Population dynamics and voltinism of field- and forest-populations

Eight field-populations developed two clear peaks in the abundance of first-instar larvae. The median date of the first peak was 26 May, the second peak occurred about eleven weeks later with a median at 11 August (Fig. 3.4). In the forest two peaks of first-instar larvae only appeared in three out of 17 populations. Both peaks had a significant temporal delay of 3 - 4 weeks relative to the corresponding peaks in the field-populations (first peak June 20th: Mann-Whitney *U*-test, Julian days, $U = 0$, $P < 0.001$; second peak August 29th: Mann-Whitney *U*-test, Julian days, $U = 0$, $P = 0.012$). Mean distance between the peaks in the forest-populations was ten weeks.

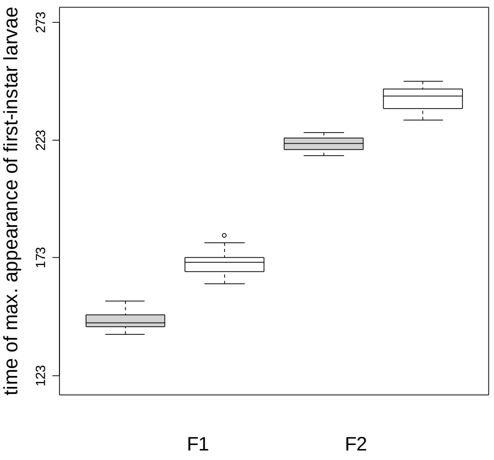

Figure 3.4: Boxplot of time (in Julian days, starting from January 1st, 2004) of moulting peaks of first-instar larvae during the season on field (grey)- and forest (white)-ponds ranges from May 3rd (day 123) to September 30th (day 173).

The three forest populations that produced a second generation had only about 10% of the maximum number of first-instar larvae in the second peak than the field populations (Fig. 3.5, Mann-Whitney *U*-test, $U = 0$, $P = 0.012$).

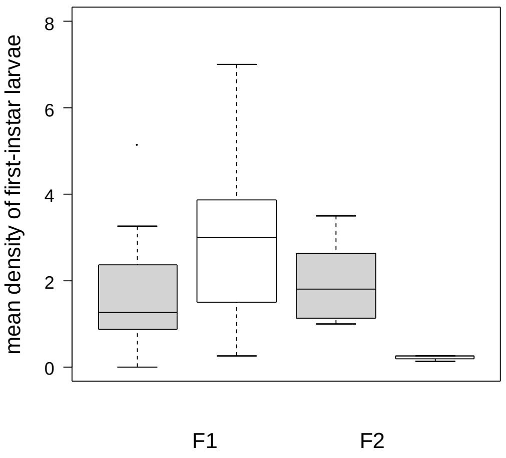

Figure 3.5: Boxplot of mean density of first-instar larvae per frame (see methods for explanation) at the moulting peak of F1- and F2- larvae in field (grey)- and forest (white)-populations.

3.4 DISCUSSION

The results of this study clearly demonstrate that *Gerris lacustris* has different phenologies in warm open environments versus cooler canopied habitats. The investigation on the occurence of first-instar larvae during the season showed that populations of *G. lacustris* were dominantly bivoltine on field-ponds while forest-populations were mostly univoltine. In the field the first peak of first-instar larvae was on 26 May. Larval development of *G. lacustris* lasts between 24-30 days (Poisson, 1924; Larsen, 1950). Thus, most larvae reached the fourth instar before summer solstice. As this is the last instar sensitive to photoperiod they developed into directly reproducing individuals. The second peak of first-instar larvae in field populations occurred approximately eleven weeks after the first one. This temporal appearance of the first and second generation is in accordance with the bivoltine life-cycles found in the studies from Poland (Vepsäläinen & Krajewski, 1974). In contrast, the first peak of larvae on the forest-ponds occurred about four weeks later than in the field. Considering the duration of larval developmental time, the juveniles on forest-ponds reached their fourth instar after midsummer and thus developed into diapausing individuals. This assumption is supported by the observation that only one new generation appeared on most of the forest-ponds and that the density of larvae of the second generation that appeared on a few forest-ponds at the end of August was much lower than on the field-ponds. The threshold for the change from uni- to bivoltinism appears to be approximately the same in climatically very different regions (Vepsäläinen, 1978).

The difference in voltinism between the two habitat types is also reflected in the pattern of wing dimorphism observed during the season on field- and forest-ponds. The appearence of a substantial fraction of short-winged midsummer individuals was only recorded on the field-ponds (Fig. 3.3). In forest-populations the long-winged morph dominated throughout the season. However, there was a gradual decline in the fraction of long-winged individuals towards the end of the season.

From the detailed observations of our reference populations and other studies (Andersen, 1973; Vepsäläinen & Krajewski, 1974; Vepsäläinen, 1978), the typical temporal course of the incidence and relative abundance of different wing morphs in bivoltine and univoltine populations of *G. lacustris* (Fig. 3.6) can be derived. The fraction of the long-winged morph observed on the two types of habitat at the three dates of investigation corresponds with either a uni- or a bivoltine life cycle. Comparing the fraction of the long-winged morph of the two different life-cycles with those observed in these field sites suggests that field-populations were dominantly bivoltine. In contrast, the fraction of long-winged individuals in the forest-ponds indicates a predominantly univoltine life-cycle.

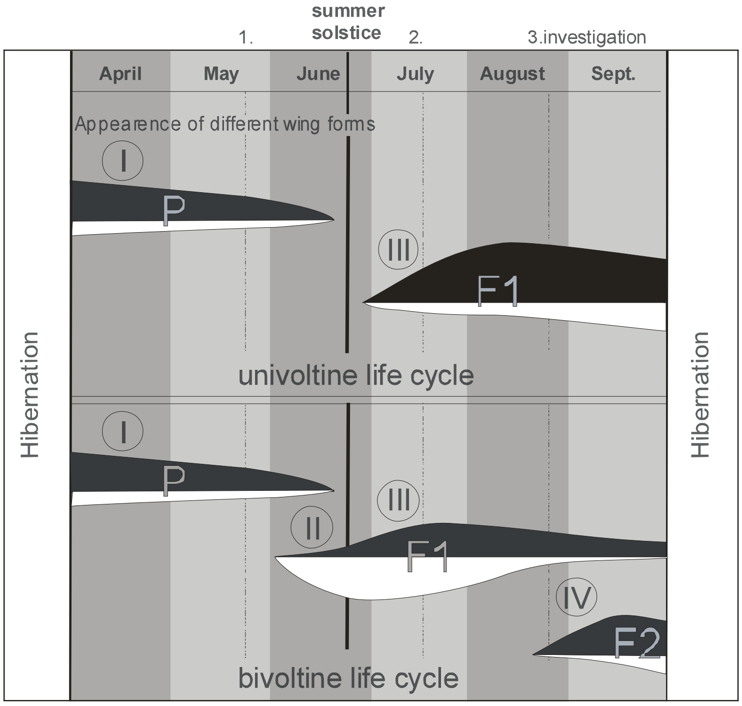

Figure 3.6: Occurrence of long-winged (black) and short-winged (white) wing morphs in a typically bivoltine and univoltine population of *G. lacustris* (summarised from data in this paper and Andersen, 1973; Vepsäläinen & Krajewski, 1974; Vepsäläinen, 1978). Summer solstice (solid line) as well as the dates of the three investigations of all ponds (dotted lines) are marked; I - overwintered parental generation; II - appearance of the first F1-adults, short-winged when moulting before summer solstice; III - increase of the fraction of long-winged F1-adults after summer solstice; IV - appearance of F2-adults, early moulting individuals are long-winged, late ones are brachyterous.

However, the significant differences in the fraction of long-winged individuals between the field- and forest-ponds at the third date of investigation – caused by the strong decline in the fraction of the long-winged morph in the forest - needs further explanation. Vepsäläinen (1978) argued that the determination of wing morph in *Gerris* is due to a combination of photoperiod and temperature. In general, shortening daylength induces long wings but when temperature falls below a certain threshold (at the end of the season) short-winged imagos develop. This hypothesis is supported by several studies that showed that the fraction of short-winged individuals moulting from larvae increases strongly at the end of the season (Andersen, 1973; Vepsäläinen & Krajewski, 1974). This shift is presumably due to the shorter time short-winged individuals need to complete teneral development (Andersen, 1973). Thus, the chance to attain cold-hardiness before climatic conditions become too severe is increased in the short-winged morph (Vepsäläinen, 1974a). As the forest-ponds in this study were approximatley 2.6 °C cooler than the ponds in the field it is suggested that the threshold for short-wingness was reached earlier in the season and thus may have led to a stronger increase in the fraction of short-winged individuals in the forest-populations.

The temperature difference between the water surfaces of field- and forest-ponds presumably is also the major cause for the relative delay in developmental time of eggs and larvae of *G. lacustris* on forest-ponds and thus, for the differences in voltinism. Fairbairn (1985) also found a shift from univoltinism to partial bivoltinism between two closely situated populations due to differences in habitat temperature but for the largely wingless *G. remigis* (Say). In contrast, populations of the highly mobile *Limnoporus notabilis* (Drake & Hottes) did not differ in life history when situated less than 10 km apart (Fairbairn, 1984). However, the environmental differences between the investigated habitats probably were not as drastic as in our study. The rearing of offspring from a single forest-population in two temperature treatments shows that the observed variation in life history traits of *G. lacustris* can solely be induced by temperature differences. Furthermore, the laboratory rearing confirms the assumption that this species expresses an extreme variability in life history even among individuals with a common genetic background. This allows the common pond skater *G. lacustris* to flexibly respond to both, the temporal as well as the spatial variability of environmental conditions it is likely to experience.

Chapter 4

Alternative life-histories in the water strider *Gerris lacustris*: temporal constraint on wing morph and voltinism

Chapter 4

Alternative life-histories in the water strider *Gerris lacustris*: temporal constraint on wing morph and voltinism

with Sabine Gerstner and Hans Joachim Poethke

SUBMITTED TO ENTOMOLOGIA EXPERIMENTALIS ET APPLICATA

Abstract 1. The wing dimorphic water strider *Gerris lacustris* L. (Heteroptera: Gerridae) switches to a bivoltine life-cycle under favorable climatic conditions. The switch in voltinism is accompanied by a reduction of wing development in the directly reproducing midsummer generation while the diapausing generation has a high fraction of long winged individuals. We investigated if the thermal energy available in natural habitats constrains the combination of developmental pathway and wing morph.

2. Offspring of *G. lacustris* were reared under quasi natural conditions in two different temperature regimes to determine the thermal constant *k* [°d] (i.e. the physiological time of development) in either wing morph. The thermal constant for egg-to-adult development of the short-winged morph was about 20% less than in the long-winged morph.

3. Based on the results from the outdoor laboratory we calculated the total physiological time necessary to complete the different possible combinations of wing morph pattern and voltinism. Comparison of these estimates with the thermal energy actually available during the reproductive season 2004 for different natural habitats (sun-exposed field- and shaded forest-ponds) suggests that voltinism as well as wing morph pattern is strongly limited by the thermal energy available in these habitats. On forest-ponds only univoltine life-cycles were possible while on field-ponds temperatures allowed bivoltine life-cycles. However, only the eggs laid at the very beginning of the season had the potential to accumulate enough thermal energy to complete a bivoltine life- cycle with both generations long-winged.

4. We conclude that thermal energy is the main environmental constraint limiting voltinism of populations in the two habitat types. Furthermore, the available thermal energy also seems to influence the determination of the seasonal wing pattern in *G. lacustris*.

4.1 INTRODUCTION

Due to temperature-dependent development, poikilothermic organisms, like insects, adapt their life history to seasonal climates (Tauber *et al.*, 1986). Reproduction and growth must be completed within a limited time and the unfavourable period has to be spent in an appropriately adapted stage of development (Roff, 2002). To complete developmental stages, poikilothermic organisms need to accumulate specific amounts of heat, the thermal constant *k* (Taylor, 1981; Pruess, 1983; Danks, 1987; Howell & Neven, 2000; Trudgill *et al.*, 2005). As a consequence, a plastic reaction to environmental cues that provide information on the time or thermal energy left for development is an essential feature of life history strategies among insects living in seasonal habitats, especially when hatching date or season length is variable (Danks, 1994; Abrams *et al.*, 1996). Common responses to environmental signals that indicate the end of the favourable season, e.g. decreasing photoperiod, are an increase in growth rate and/or shortening of development time (for a review see: Nylin & Gotthard, 1998; Roff, 2002). This reaction allows individuals hatching later in the year to complete development before the season becomes unfavourable. On the other hand, individuals developing early in the season under conditions indicating that thermal energy available per season is sufficient for the development of more than one generation may switch their reproductive strategy from uni- to bivoltinism (Cohen, 1970). An increase in generation number within a season increases the time constraint on each generation as thermal energy available for the development of each generation is smaller in bi- than in univoltine populations (Roff, 1980).

The wing-dimorphic common pond skater *Gerris lacustris* L. switches from uni- to bivoltinism along a north-south gradient in Europe (Vepsäläinen, 1974a). The change in voltinism in *G. lacustris* is accompanied by a seasonal pattern of wing dimorphism, with a high fraction of long-winged individuals in the diapausing generation and a strong increase of adults with reduced wings in the directly reproducing midsummer generation (Vepsäläinen & Krajewski, 1974; Hauser, 1982). The developmental pathway and the wing morph type is determined by a combination of genetic and environmental factors (Vepsäläinen, 1974b), whereas the main environmental cue is the photoperiod. In individuals sensitive to photoperiod, long-day conditions during critical stages of larval development induce direct reproduction, which is strongly associated with short-wingedness. Under short-day conditions flight capable diapausing individuals develop (Köpfli *et al.*, 1987).

The pattern of wing dimorphism in water striders is suggested to result from the different selective pressures acting on the two wing morphs. Long-winged individuals primarily benefit from the ability to disperse in spatially or temporally heterogeneous environments and to fly between aquatic reproductive and terrestrial diapause sites in spring and autumn (Kaitala & Hulden, 1990; Spence, 2000). The short-winged morph of *G. lacustris* is unable to fly, as flight muscles are undeveloped in individuals with reduced wings (Darnhover-Demar, 1969; Andersen 1973). Individuals with reduced wings have been shown to reach reproductive maturity earlier than the flight capable morph, due to a reduced larval or teneral development time (Andersen, 1973; Zera, 1984) and/or a shorter preovipositional period (Spence, 1989; Harada, 1998). Offspring of the flightless morph thus experience advantages of early development, like avoidance of cannibalism or an increased chance of reaching maturity before environmental conditions become adverse (Järvinen & Vepsäläinen, 1976). Therefore, the short-winged morph has a reproductive advantage, but reduction of wings should only occur when habitat changes are more or less predictable (Andersen, 2000).

The length of the season suitable for development and reproduction in temperate regions, where life-cycle of *G. lacustris* switches from uni- to bivoltinism, is characterised by long-term predictability (Hoffmann, 1978). However, *G. lacustris* experiences short-term unpredictability of habitat, as this species inhabits temporal water bodies (Vepsäläinen 1974; Vepsäläinen & Krajewski, 1974) which have a high risk of dry down during summer months in temperate regions (Williams, 1987). The reduction of wings in the direct breeding generation appearing in midsummer, i.e. in a stochastic environment, thus indicates a strong selective pressure on fast development up to reproductive maturity. Considering the constraint of thermal energy on populations switching to bivoltinism in transition zones, shortened developmental time and the resulting early reproduction may allow a bivoltine life cycle in habitats where a strategy with two long-winged generations would fail.

For the seasonally dimorphic common pond skater *Gerris lacustris* we determined the thermal constant of development for the short- and long-winged morph. We use combined results from laboratory and field studies to investigate if patterns of voltinism and wing morph, occurring in natural populations under different environmental conditions are restricted by the available thermal conditions.

4.2 MATERIALS AND METHODS

4.2.1 Effects of temperature on developmental time of eggs and larvae

Overwintered adults of *G. lacustris* (14 ♀ and 14 ♂) were collected at the beginning of the reproductive season (22th April) 2004 from a pond in the forests surrounding the village of Fabrikschleichach (49°55′N, 10°33′E), Bavaria, Germany. The males and females were first kept separately for 10 days and then paired in plastic boxes (25 x 15 x 8 cm), filled with water to a depth of 3 cm. The adults were fed with an unlimited supply of *Drosophila spp.* Pieces of styrofoam (3 x 1 cm) were put into each plastic box for resting and egg deposition. From 9 May onwards styrofoam pieces containing newly deposited eggs batches were removed daily from the plastic boxes for a period of twelve days and replaced. Within this period about every fourth day styrofoam pieces and the newly deposited batches of eggs on it were divided into two lots. The styrofoam pieces were marked with the oviposition date and for each of the 14 pairs, half of the lots were transferred in a heated and the others in an unheated rearing container. Thus, for each pair of parents three "cohorts" of offspring differing in their day of oviposition by at least 4 days were raised in each temperature regime. Therefore, 28 glass containers (20 x 30 x 20cm) filled with 10 litres of water each were placed in an outdoor laboratory in seven rows of four containers each on sandy soil. Containers were protected from direct sunlight and wind by a plastic foil open towards the west and every second container was heated with an automatic heater (Sacem, Bluetherm, 25 W). Temperature of six heated and six unheated rearing containers was recorded just under the water surface by temperature loggers (Dallas semiconductor, Dallas, Texas, DS1921L-F51) half-hourly throughout the course of the investigation. The mean temperature difference between the two temperature regimes (heated vs. unheated) was 6.21 ± 0.98 °C. Water temperature of both treatments fluctuated synchronously with outdoor temperature (Fig. 4.1). Hatching dates were measured daily by controlling eggs on the styrofoam pieces for eclosion and counting the number of newly hatched first-instar larvae in the containers. Development of the larvae, which remained in the rearing containers, was recorded from the day of eclosion until final moult or death. Sex and wing morph of newly moulted adults were noticed.

From the individuals that developed up to the final moult, nine short-winged (= SW) and nine long-winged (= LW) females were paired in plastic boxes with males of the same morph type after eclosion, to measure differences in the length of teneral development of the two morphs. The pairs were kept outdoors under unheated conditions. Time between final moult and beginning of oviposition was noted and surface water temperature was measured half-hourly by thermo-loggers.

For statistical analysis mean ± SD of the developmental time *D* (in days) of eggs and larvae in the two different temperature regimes was calculated separately for each pair of parents. Developmental times of eggs and larvae in heated and unheated containers were than compared with a Wilcoxon signed rank-test. For the comparison of the developmental time of larvae developing either into short- or long-winged individuals the same method was applied.

From the half-hourly temperature measurements, the mean daily temperature every egg and larvae was exposed to from 12.00a.m. of oviposition (eclosion) day until 12.00a.m. of the day of eclosion (final moult) was determined. Based on this data, the mean daily incubation temperatures *T* (needed for the calculation of the lower developmental threshold t_0) of eggs and larvae of each pair of parents were calculated.

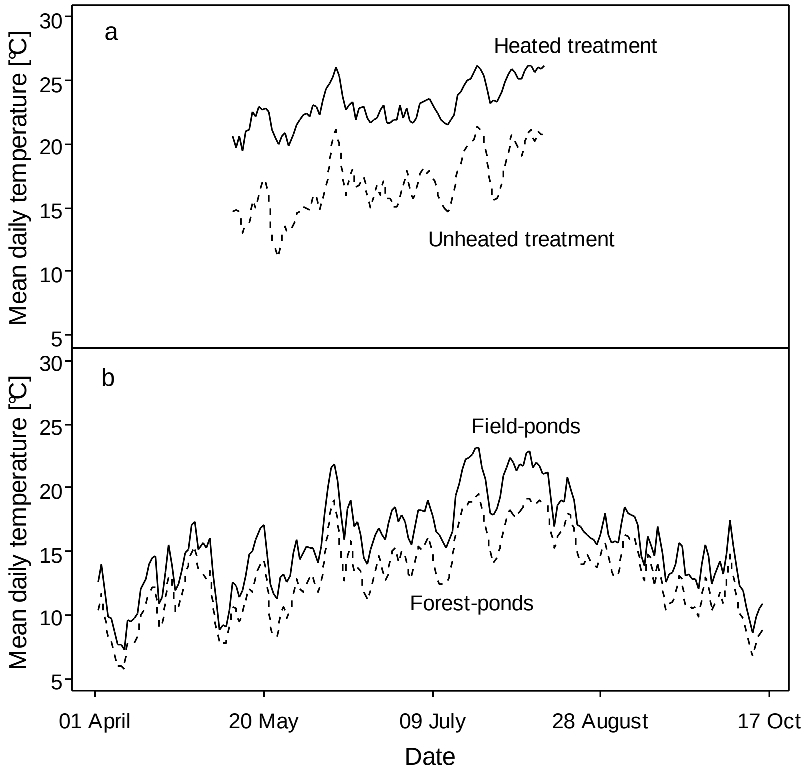

Figure 4.1: Mean daily temperature of the water surface of (a) the two rearing regimes in the outdoor laboratory throughout the investigation and (b) the 10 field– respectively 18 forest-ponds over the course of the season

4.2.2 Estimation of lower developmental threshold t_0 and thermal constant k

In poikilothermic organisms the developmental rate is assumed to depend on temperature in a way that the product of the duration of development *D* (days) and the incubation temperature *T* (degrees) above the species-specific lower developmental threshold t_0 is a constant *k* (degree-days). Thus, a specific number of degree-days, the so called thermal constant *k* (or physiological time [°d]) is required for an individual to complete development (e.g. Pruess, 1983). In this study, the lower developmental threshold t_0 and the thermal constant *k* of development for eggs were determined using the line-fitting method of Ikemoto and Takai (2000): $D*T = k + t_0D$ (where D is the duration of development, T the incubation temperature, t_0 the lower developmental threshold and k the thermal constant). Their model is an extended version of the linear degree-day model (e.g. Campell *et al.*, 1974; Briére *et al.*, 1999), which is based on the assumption that the rate of development (1/D) increases linearly with incubation temperature T in the range of temperature usually experienced. To account for possible differences in lower developmental threshold and/or thermal constant between individuals developing into short- and long-winged individuals we used an Analysis of Covariance based on the regression model of Ikemoto and Takai (2000) for the calculation of t_0 and k of larval development with wing morph as grouping factor.

The thermal constant needed to complete teneral development was determined by calculating the mean degree-days above the lower developmental threshold from final moult until beginning of oviposition. All statistical tests were performed with the statistical package R 2.0.0 for Windows.

4.2.3 Temporal constraint on voltinism and wing dimorphism on field- and forest- ponds

Based on the information on values of the thermal constant k necessary for egg, larval and teneral development of short- and long-winged individuals, respectively, the total sum of degree-days needed for *G. lacustris* to complete uni- and bivoltine life-cycles with different combinations of short- and long-winged morphs in the F1- and F2- generation was calculated.

We compared the total number of degree-days needed to complete different life-history strategies with the degree-days available in various natural systems distributed over an area of 3.5 x 3 km and located around the village of *Fabrikschleichach* (49°55'N, 10°33'E). Natural surface temperatures were recorded hourly with thermo-loggers from the 1 April to the 15 October 2004 from 10 field-ponds (i.e. ponds with less than 25% of the edge encompassed by trees or shrubs) and 18 forest- ponds (i.e. ponds completely surrounded by a band of trees at least 10m wide). The loggers were placed in the middle of a piece of styrofoam (4 x 4cm) and protected from direct sunlight by a cap of plastic foil. Each logger assembly was further buoyed by 4 styrofoam floats, one at each corner. The recording system was attached to the litoral zone at the south side of the ponds, the preferred habitat of larvae (Nummelin *et al.*, 1984; Vepsäläinen & Nummelin, 1986). Mean daily temperature of each pond was calculated separately and then used to estimate mean ± SD of daily temperatures of field and forest-ponds.

To calculate the mean degree- days available for development and reproduction in the two types of habitat over the reproductive season, for each day j the mean ± SD of the temperature above t_0 accumulated up to this day was determined separately for field- and forest- ponds:

$$k_{field/forest} = \sum_{j=1April}^{j=15October} T_{field\,/\,forest,\,j} - t_0$$

4.3 RESULTS

4.3.1 Developmental time of eggs and larvae

Developmental time of eggs as well as of larvae of *G. lacustris* was substantially shorter in the heated than in the unheated containers (Fig. 4.2a, b). Eggs in the heated containers developed twice as fast as those in the unheated treatment (11 vs. 22 days, n = 14 (container means), Wilcoxon signed rank test, V = 0, p < 0.001). Larval developmental time also differed significantly between the two temperature treatments (n = 14 (container means), Wilcoxon signed rank test, V = 0, p < 0.001). The larvae that developed up to the final moult in the unheated treatment needed at least 1.6 times as long (median of 47.8 days) as those developing in the heated ones (median of 27.2 days).

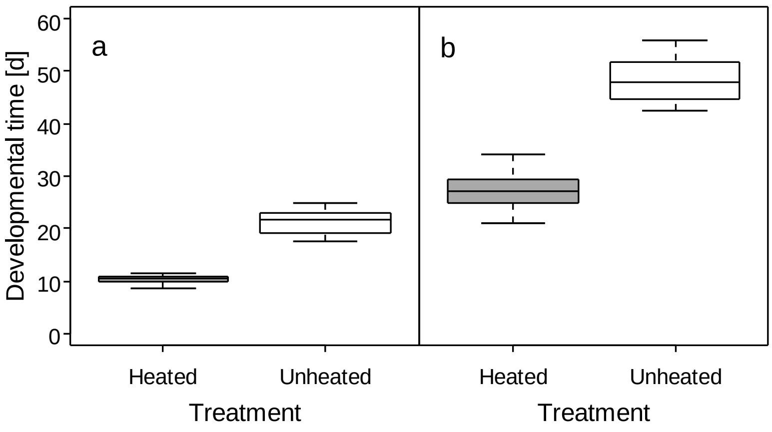

Figure 4.2: Box-plot of developmental time of (a) eggs and (b) larvae in the two temperature regimes. 568 eggs (221 in the heated and 365 in the unheated treatment) and 132 larvae (81 in the heated and 51 in the unheated treatment due to mortality differences) from 14 females (= 14 container means at maximum) were included.

On average, 30.14 ± 9.46 (mean ± sd) eggs were transferred into each of the unheated and 23.71 ± 8.31 eggs into each of the heated containers. 81 individuals developed up to the adult stage in the unheated treatment and 51 individuals survived in the heated temperature regime. Larval mortality did not differ significantly between the two temperate treatments (chi^2-test, χ^2 = 1.21, p = 0.289), but was slightly higher in the heated containers (84.6 % vs. 80.8 %). In the unheated temperature regime 96% of the individuals developed into the long-winged morph, while only 46% in the heated treatment developed full wings. This difference was significant (chi^2 - test, χ^2 = 47.81, p < 0.001). Analysis of the developmental time of the two different morphs developing in the heated containers showed that the developmental time of the short-winged morph was highly reduced relative to the long-winged morph (Fig. 4.3, Wilcoxon signed rank test, n = 11 (container means), V = 65, p = 0.005).

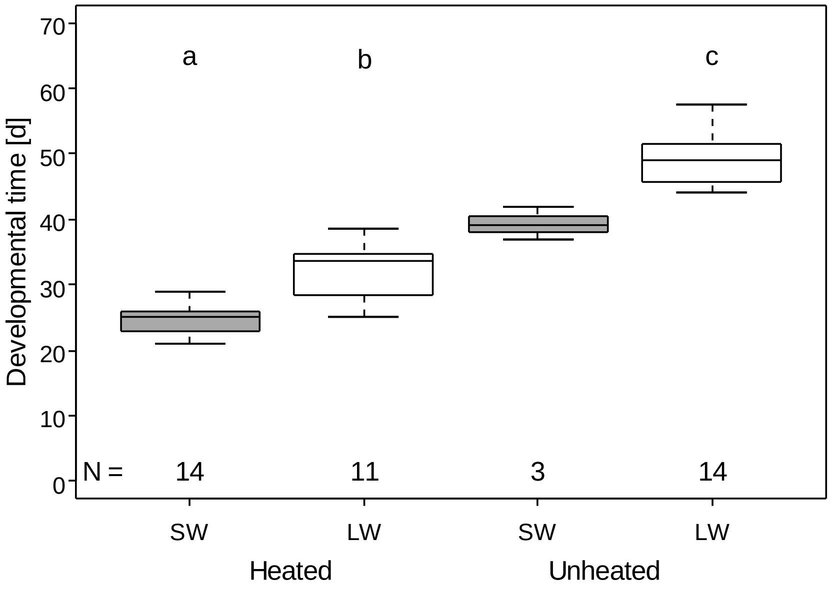

Figure 4.3 Box-plot of the time larvae needed to develop into either long-winged (LW) or short-winged (SW) individuals for each of the two temperature regimes. Different letters indicate significant differences (p < 0.01, Wilcoxon signed rank test, see results) between treatments.

4.3.2 Estimation of lower developmental threshold t_0 and thermal constant k

Lower developmental threshold for egg development was 10.23 ± 0.45 °C and the thermal constant for egg-to-larvae development was 90 ± 7.53 °d above t_0 (r^2=0.9; Table 4.1).

Table 4.1: Lower developmental threshold t_0 , thermal constant k and regression coefficient r^2 for eggs and for larvae developing into short- and long-winged individuals of *G. lacustris*.

	Eggs	SW- larvae	LW- larvae	Difference between SW-and LW- larvae
$t_0 \pm$ SE [°C]	10.23 ± 0.45	9.78 ± 0.92	9.78 ± 0.92	NS
$k \pm$ SE [°d]	90 ± 7.59	299.52 ± 19.44	355.54 ± 38.59	**[a]
r^2	0.9523	0.8844	0.8844	

[a] ANCOVA (d.f. = 37, F = 141.5, p < 0.001)

Analysis of covariance shows that there is no significant difference in the lower developmental threshold t_0, of larvae developing into short- or long-winged adults (t_0 = 9.78 ± 0.92, p = 0.940) whereas the thermal constant *k*, for development is significantly larger (~ 1.2x) for individuals developing into the long-winged morph (see Table 4.1).

Eight of the nine short-winged females paired after final moult started to lay eggs after a teneral period of 59.11 ± 12.55 °d above the lower developmental threshold, but only one of the nine long-winged females became reproductively mature. The rest were diapausing individuals that could be distinguished from direct reproducing females by the dark pigmentation of the ventral thorax after hardening of the cuticle (Andersen, 1973). The thermal constant for teneral development could thus not be estimated for long-winged individuals. According to literature data showing that long-winged individuals accumulated at least twice the number of degree-days compared to the short-winged morph for teneral development (Andersen 1973, Harada 1998), we assume a value of 118 °d for further calculations (see also discussion).

4.3.3 Temporal constraint on voltinism and wing morphism on field- and forest-ponds

In Table 4.2 we have compiled the sum of degree-days individuals of *G. lacustris* need to complete uni- and bivoltine life-cycles with different combinations of short- and long-winged morphs in the F1- and F2- generation.

Table 4.2: Estimated thermal constant *k* [°d] necessary to complete uni- or bivoltine life-cycles with different combinations of wing morph pattern (long-winged = LW, short-winged = SW).

Strategy	Thermal constant *k* [°d] of developmental stages						$\sum k$[°d]
	Egg	Larvae	Teneral[a]	Egg	Larvae	Teneral	
F1 LW-F2 LW	90	366	118	90	366	118	1148
F1 LW-F2 SW	90	366	118	90	299	59	1022
F1 SW-F2 LW	90	299	59	90	366	118	1022
F1 SW-F2 SW	90	299	59	90	299	59	896
F1 LW	90	366	118	-	-	-	574
F1 SW	90	299	59	-	-	-	448

[a] The teneral stage is the development between final moult and achievement of reproductive maturity respectively cold-hardiness

The thermal constants necessary to complete different strategies were compared to the actual amount of thermal energy that accumulated during the season in the two types of habitat, i.e. field- and forest-ponds (Figure 4.4).

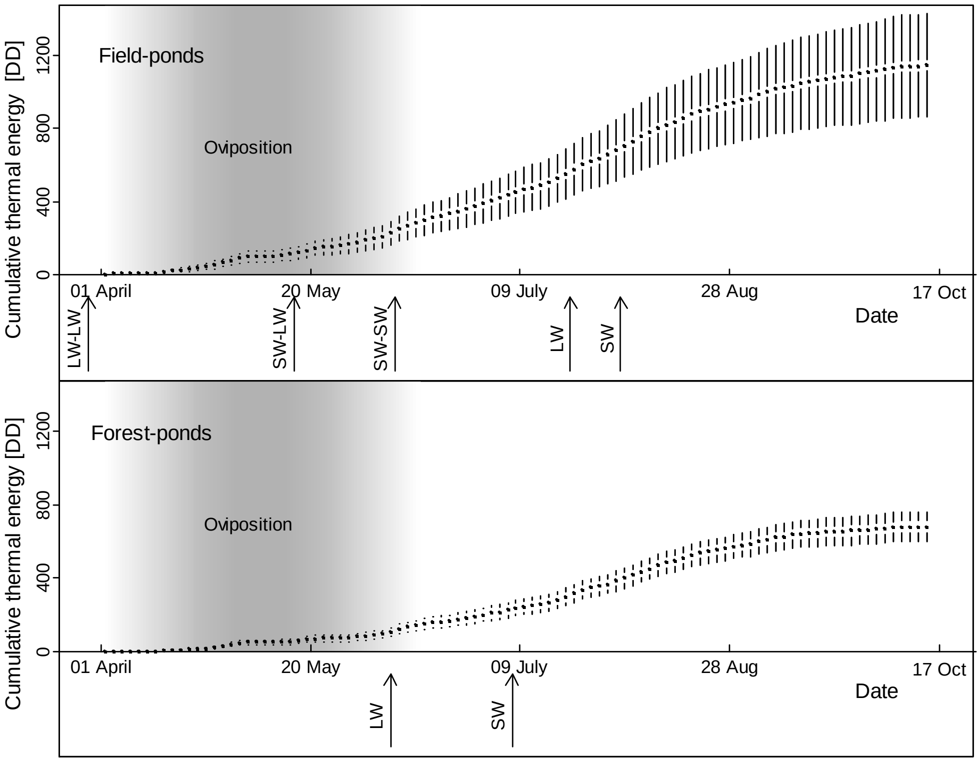

Figure 4.4.: Mean ± SD of the thermal energy [°d] above the lower developmental threshold t_0 that accumulated over the course of the season for field- (a.) and forest- (b.) ponds. Oviposition period of the parental generation is indicated in grey. The arrows mark the final dates before an egg must be laid so that a specific life-history strategy can be completed until the end of the growing season.

In general, mean daily temperatures were about 2.54 ± 0.69 °C lower on forest- ponds than those located in the fields (Fig. 4.1). As a consequence, the degree-days that accumulated during the reproductive season on forest-ponds were about ~ 40% less than on field-ponds. The arrows in Fig. 4 a, b indicate the latest possible oviposition dates for progeny to accumulate enough degree-days to complete one of these strategies during the rest of the reproductive season. It becomes obvious that only univoltine life- cycles are possible on forest-ponds while on the field-ponds temperatures are such that two generations are possible. As shown in Fig. 4a, wing morph of the direct breeding generation is also crucial to an effective bivoltine strategy. Comparing the positions of the arrows with the time of oviposition of the parental generation shows that only F1-eggs laid extremely early in the season or on especially warm ponds would be able to complete a bivoltine life- cycle with both generations long-winged while most of the eggs only have the time to complete a LW-SW/SW-LW or SW-SW life-cycle.

4.4 DISCUSSION

Our rearing study on *G. lacustris* shows a clear difference in the larval developmental time of long- and short-winged individuals. Prolonged larval development of the long-winged morph of *G. lacustris* was already observed by Poisson (1924) and Guthrie (1959) but could not be confirmed by Andersen (1973) and Vepsäläinen (1973). The lower developmental threshold t_0 of total larval development was about 10 °C for larvae of both morph types. This is within the range of t_0-values found for *G. paludum insularis* (9.4 – 12.7 °C, Park, 1988) and (slightly) higher than most of the values found by Spence *et al.* (1980) who determined t_0 separately for different larval stages of *Gerris* species occurring in British Columbia (~3.8 – ~12.5 °C). Base temperatures and thermal constants underlie adaptation to local environmental conditions (Blanckenhorn, 1991) and thus, vary between species and populations (Honek, 1996). Although the developmental threshold t_0 was equal for both wing morphs, long-winged individuals resumed about 20% more degree-days than did the short-winged individuals to complete larval development. This difference in thermal constant for egg-to-adult development may arise in the last larval instar when the histogenesis of the flight muscles and their tracheal supply and the formation of the wings are enhanced in the potential long-winged morph while wing muscle development is stopped in the short-winged morph (Andersen, 1973). The thermal constant k for egg plus larval development of the long-winged morph was about 445 degree-days. This value is lower than that found for *G. paludum* (500 °d; Park, 1988), a long-winged species, which is about 1/3 larger than *G. lacustris* (Guthrie, 1989). This suggests that size differences between the two wing morphs also contribute to the differences in the requirements of thermal energy as long-winged individuals are larger than short-winged ones (Vepsäläinen, 1973).

The thermal constant *k* of teneral development, i.e. period between final moult and beginning of oviposition, could only be determined for the short-winged morph (~59 °d) as only a single long-winged female reproduced directly in the outdoor laboratory. Andersen (1973) describes a teneral period of 11 days at 26 °C for long-winged females of *G. lacustris* corresponding to approximately 170 °d above the lower developmental threshold. In a study of Harada (1998) the preoviposition period of long-winged females of *Aquarius paludum amamiensis* (Miyamoto) also lasted 2-3 times longer than in the short-winged morph. According to these studies, we assumed twice the amount of degree-days for teneral development of long-winged individuals of *G. lacustris* (~118 °d). Thus, our assumption presumably does not overestimate the real thermal constant of teneral development of long-winged individuals. However, Spence (1989) found significantly longer preovipositional periods in long- compared to short-winged individuals of *G. buenoi* and *G. pingreensis*, but the differences in the length of this period between the two wing morphs were less profound.

Comparing the thermal constant of egg-to-adult plus teneral development between the two wing morphs (Table 4.2, 574 °d vs. 448 °d) makes clear that requirements of thermal energy to complete development up to reproductive maturity in *G. lacustris* are substantially higher in long-winged than in short-winged individuals. This finding confirms the temporal advantage of the short-winged morph that has already been shown for other water strider species (Zera, 1984; Spence, 1989; Harada, 1998) and suggests that not only voltinism but also wing length pattern may be restricted by ambient temperatures in natural habitats. In Fig. 4.4 the total effective temperature necessary to complete different life-cycle strategies were compared with the actual total effective temperature available in different natural systems. Evidently, in the cooler forest-ponds accumulation of degree-days during the season was sufficient for only one generation to grow up before winter. In contrast, in the warmer field-ponds enough degree- days were available to complete a bivoltine life-cycle. However, while most of the (univoltine) individuals growing up on forest-ponds would have acquired enough thermal energy to become long-winged the surplus of degree-days on field-ponds only allows a short-winged generation in addition to the long-winged diapausing individuals. Considering this constraint in thermal energy, the directly reproducing generation of bivoltine populations of *G. lacustris* on field-ponds in this region is predicted to be primarily short-winged. The predicted patterns of wing morph and voltinism are in congruence with those actually found for *G. lacustris* on the field- and forest-ponds in nature. In a field study (Pfenning & Poethke, 2006) most populations of *G. lacustris* were univoltine with a high fraction of long-winged individuals on forest-ponds, but field-populations generally were bivoltine with high numbers of short-winged individuals in the midsummer generation. The reduction of wings in the directly reproducing midsummer generation is also observed in other bivoltine populations of *G. lacustris* in central Europe (Vepsäläinen & Krajewski, 1974; Hauser, 1982)

Our results suggest that not only voltinism but also the seasonal wing dimorphism of *G. lacustris* in temperate regions may be influenced by the variation of thermal energy available in natural habitats. It seems that the reduction of the thermal constant k needed to develop into a short-winged morph allows bivoltinism and thus the production of offspring under environmental conditions where a LW-LW life-cycle would fail. The advantage of an increase of the number of generations per year under favourable conditions is obviously the multiplication of overwintering offspring (Järvinen & Vepsäläinen, 1976). However, *G. lacustris* lives in a spatially and temporally heterogeneous environment. The range of its habitat preference includes temporary instable water bodies like ephemeral ponds and the length of the season suitable for development and reproduction varies between years. Thus, this species also experiences environmental factors that select against short-wingedness in the midsummer generation or against direct reproduction itself. The reduction of wings prevents escaping habitat deterioration and natural enemies or spreading offspring between different reproductive sites (Spence, 2000) and the production of a directly reproducing generation increases the risk for the next diapausing generation to not become adult before winter. The fact that the midsummer generation of *G. lacustris* is not exclusively short-winged (Vepsäläinen & Krajewski, 1974; Vepsäläinen, 1978; Hauser, 1982) and that in some populations, direct reproduction can only be induced in a part of the offspring of the overwintered generation (Köpfli *et al.*, 1987) presumably reflect adjustments to this environmental heterogeneity. Together with the results of this paper they show the high flexibility of *G. lacustris* to adjust life-cycle and wing morph pattern to the variability of the environment this species encounters.

CHAPTER 5

Dealing with time constraints on development: the effect of food availability

Chapter 5

Dealing with time constraints on development: the effect of food availability

with Hans Joachim Poethke and Thomas Hovestadt

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Abstract. 1. Life-history theory predicts that organisms should speed up development in response to time constraints. However, acceleration of development carries energetic costs that have to be compensated, e.g. by an increase in foraging rate. For the wing dimorphic water strider *Gerris lacustris* (L.) the hypothesis was tested that the adjustment of development to time constraints is limited by the availability of food resources.

2. Six cohorts of larvae hatched at increasingly late moments in the season were reared under two feeding regimes. For each cohort and experimental group the physiological time (in degree-days) of larval development was estimated.

3. In both, high- and low-food groups, there was a significant reduction of physiological time for development towards the end of the season. Furthermore, within cohorts, physiological development time was always lower in the high- compared to the low-food group. However, there was no significant interaction effect between food treatment and cohort.

4. The results demonstrate that *G. lacustris* has the flexibility to adjust development to time constraints. In addition, 20% of the 'low-food individuals' developed into the short-winged morph, while all of the 'high-food individuals' became long-winged. The limitation of food may thus lead to a reduced allocation of energy into the development of the flight apparatus. This may explain the strong increase in short-wingedness at the end of the season in natural populations, which are highly food limited.

5.1 INTRODUCTION

Insects living in seasonal habitats generally complete growth and reproduction within the favourable season while they spent the unfavourable period in a state of diapause. Such a life history requires the completion of development up to the stage capable of diapause within a limited season (Cohen, 1970; Danks, 1994). Thus, when the length of the season decreases, life- history theory predicts a fastening of development to ensure the completion of development before environmental conditions become adverse (Roff, 1980, 2002; Abrams *et al.*, 1996).

A quicker development – often accompanied by a reduced size at maturity – in response to a shortened season length has been shown in several insect species occurring along extended latitudinal clines (*crickets*: Masaki, 1978; *butterflies*: Nylin & Svard, 1991; *water striders*: Blanckenhorn & Fairbairn, 1995) but also at a smaller scale along an altitudinal gradient (Berner *et al.*, 2004) or between habitats differing in temperature (Blanckenhorn, 1991). In most of these studies the differences in development were at least found to be partly due to genetic adaptation, presumably because of the separation of the investigated populations. However, time constraints on development can also vary *within* populations or between individuals with a common genetic background, e.g. when oviposition and hatching time of organisms varies within a season (Roff, 2002). Larvae hatching later in the year have less time for development. However, individuals will only survive when they reach the species-specific diapause stage before winter and genotypes able to react with a plastic reaction of development to the experienced limitation in season length will consequently be favoured (Nylin & Gotthard, 1998).

An acceleration of development in response to a decreasing time horizon has been reported for several insect species, e.g. butterflies (Nylin *et al.*, 1989; Nylin, 1992; Leimar, 1996), crickets (Carriere *et al.*, 1996), and damselflies (Johansson & Rowe, 1999; Strobbe & Stoks, 2004). However, an increasing number of studies report fitness costs of such acceleration (Houston *et al.*, 1993; Gotthard, 2000; Lankford *et al.*, 2001). These costs mainly result from the higher energetic needs of fast developing larvae that have to be compensated by an increase in foraging activity, which is positively correlated with predation risk (Werner & Anholt, 1993; Stoks *et al.*, 2005). Consequently, many laboratory studies that investigate the adjustment of development to time constraints have been criticized because food supply was always super-abundant and thus not controlled. Under natural conditions, an acceleration of development may be limited, for example by the availability of food resources or the increased predation risk on foraging individuals (Leimar, 1996; Johansson & Rowe, 1999).

Northern European temperate water strider species of the genus *Gerris* (Heteroptera: Gerridae) inhabit seasonal habitats occurring along extended latitudinal clines (from Southern Europe up to the Arctic Circle) and in different environments (e.g. Vepsäläinen, 1974a; Andersen, 1982; Guthrie, 1989). The oviposition process and hatching period of larvae belonging to the diapausing generation - that have to reach adulthood before winter - typically spans several weeks (Andersen, 1982). This leads to strong variations in the time horizon for development. Thus, water striders are forced to adapt their development to decreasing season length across, as well as within, populations. Adaptations in life history traits concerning development have primarily been described for different water strider species on the scale of geographical clines (Blanckenhorn & Fairbairn, 1995) and diverging habitat types (Fairbairn 1984, 1985; Blanckenhorn, 1991).

This study investigated whether larvae of the common pond skater *Gerris lacustris* from the same population are able to react with a reduction of the physiological time of development to environmental signals indicating that the end of the season draws closer (i.e. photoperiod). Furthermore, it was tested whether limiting food supply reduces this phenotypic flexibility, because natural water strider populations are assumed to be strongly food limited (Järvinen & Vepsäläinen, 1976; Vepsäläinen, 1978; Fairbairn, 1984) and food supply has been shown to influence development time of water striders (Blanckenhorn; 1994). In addition, the development of wings and the larval mortality in dependence of the time- and food- constraints experienced by the larvae were recorded.

5.2 MATERIAL AND METHODS

5.2.1 Rearing experiment

Six cohorts of 40 individuals of *G. lacustris* were raised under two feeding regimes in an outdoor laboratory to determine the physiological time (in degree-days [°d]) of larval development. The first cohort of first-instar larvae was brought to the lab about four weeks after summer solstice (24 July 2005) to ensure that individuals were clearly responding to the decreasing photoperiod. Five further larval cohorts were collected every 5th day. The first-instar larvae of the diapausing-generation were collected in the littoral zone of a pond in the surrounding of Fabrikschleichach, Germany (49°55′N, 10°33′E). Individuals were transferred into plastic boxes (8 x 8 x 5 cm) that were filled with 2 cm of water. For logistic reasons it was not possible to raise each individual separately; instead always two individuals were kept in one box.

The boxes were placed in an outdoor laboratory, which protected the larvae from rain and direct sunlight, but provided the natural photoperiod and temperature conditions of a shaded habitat. The twenty boxes were randomly assigned to a "high food" and a "low food" group fed according to two differing feeding regimes. Food provisioning of the two groups was elevated every twelve days to account for the increasing size of larvae: first, each box of the low food group was provided with 8, then with 12, 16, 24 and in the final period with 48 individuals of *Drosophila spp*. Individuals belonging to the high food group were provided with three times the number of *Drosophila* and given 24, 36, 48, 72 and finally 144 individual *Drosophila*. *Drosophila* flies were supplied as a whole, and the total number of flies listed above was supplied evenly distributed over the 12 day period. Each of the six cohorts started with the feeding regime described above. The plastic boxes were covered with gauze to prevent larvae from escaping and to exclude influx of additional food items. Water temperature of every cohort was measured hourly by thermo loggers (Dallas Semiconductor, DS1921L-F51) placed on the base of two plastic boxes of each cohort. Each day it was recorded whether larvae had moulted or died. The date of change in larval stages of every individual and the wing status and sex of individuals that had become adult was noted individually.

5.2.2 Effect of feeding and hatching time on development

After the experiment, for each individual the degree-days [°d] accumulated up to each change in larval instar were determined from the mean hourly temperature provided by the thermo logger measurements. As the cohorts were started with first-instar larvae with unknown date of hatching, the physiological time [°d] only refers to the larval instars II-V. Physiological time for each developmental stage was calculated separately for each individual by summing the degree-days above the species-specific lower developmental threshold of 10 °C (Pfenning *et al.*, subm.) that accumulated between two moults (starting and ending at 12:00 a.m).

The physiological time [°d] was the response value indicating a potential change in the larval development. A decrease in physiological development time is expected to occur in individuals (cohorts) hatching later in the year in response to the approaching end of the season. However, the ability to shorten physiological development time could be reduced in the low food compared to the high food group as limitation of food resources prolongs larval development of water striders (Blanckenhorn, 1994); this should appear as a significant interaction effect between feeding regime and cohort in the statistical analysis. To achieve optimal linearization, data on physiological development time, i.e. degree-days [°d], were cube-root transformed. Change in cube-root transformed degree-days was then analyzed by repeated-measures ANCOVA with feeding regime as a main factor, cohort number as covariate, and larval stage as within-subjects factor. The moments of cohort initiation ranged from day 0 (July, 24th) to 25 (August, 18th). Only individuals that developed up to the adult stage were included into this statistical analysis.

4.2.3 Mortality and wing phenology

For each cohort and each feeding regime, larval mortality rate was calculated separately for the different larval instars as well as for overall larval development. It was investigated whether there was an effect of the feeding regime on larval mortality of the six cohorts using a chi-squared test, and whether the hatching date of the cohorts was related to mortality using Pearson’s product moment correlation. Furthermore, a difference in the proportion of individuals developing into the long-winged morph between the two different feeding groups was tested using a Fishers` exact test. All statistical analyses were performed with the statistical package R 2.0.0 for Windows (www.r-project.org).

5.3 RESULTS

5.3.1 Effect of feeding regime and hatching time on development

Physiological development time depended strongly on larval stage (Table 5.1), with older instars accumulating more degree-days. Furthermore, the repeated-measures ANCOVA on the physiological development time of larval stages showed a significant effect of both, food treatment and cohort, i.e. time of hatching, on physiological development time (Table 5.1). However, contrary to predictions a significant interaction effect between these two factors did not emerge (repeated measures ANCOVA, Mean squares = 0.008, d.f. = 1, F = 1.06, P = 0.313, n.s.).

Except for juvenile instar II, all instars decreased physiological development time with increasing hatching date/cohort number (Table 5.2). In general, high food individuals accumulated less thermal energy per larval instar than low food individuals (Fig. 5.1). On average, individuals of the low food group required 1.14 times the physiological time (273.29 ± 15.40 °d) for development from larval instar II to final moult compared to the high food individuals (241.54 ± 17.97 °d).

Table 5.1: Repeated measures ANCOVA for physiological development time [°d] of larval instar two to five as function of food treatment (high vs. low) and cohort (i.e. hatching time).

Source	MS	d.f.	F	*P*
Within subjects				
Instar	0.857	3	69.63	0.000
Error	0.12	81		
Between subjects				
Cohort	0.207	1	28.53	0.000
Food	0.034	1	4.625	0.041
Error	0.007	27		

Sphericity assumed, (Mauchly's test of sphericity, Mauchly-W = 0.746, d.f. = 5, *P* = 0.184);
MS = mean squares

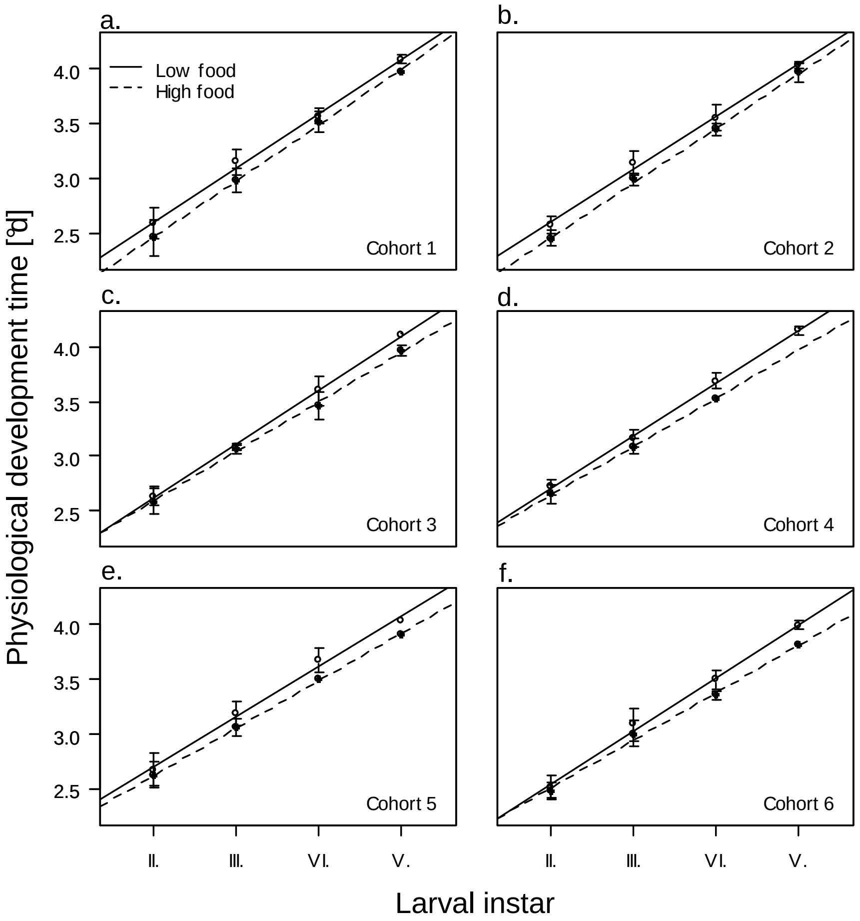

Figure 5.1: Plot of the mean ± sd of cumulative, cube-root transformed physiological development time [°d] against the larval stage (II.-V.). Separate lines are given for each of the six cohorts (a.-f.) of the two food regimes.

Table 5.2: Parameter estimates from repeated measures ANCOVA (Table 5.1) for the effects of food treatment (high vs. low) and cohort (hatching time) on the physiological time of larval development. Parameters give slope for the covariate "cohort" (i.e. time of hatching) and change in intercept of low food treatment compared to high food treatment. Estimates are given separately for the four larval stages included in the experiment.

Instar	Parameter	B ± SE	*P*
II	Cohort (slope)	0.014 ± 0.013	0.287
	Food (factor)	0.122 ± 0.049	0.018
III	Cohort (slope)	- 0.027 ± 0.011	0.017
	Food (factor)	0.084 ± 0.039	0.041
IV	Cohort (slope)	-0.010 ± 0.011	0.384
	Food (factor)	0.071 ± 0.040	0.089
V	Cohort (slope)	-0.017 ± 0.011	0.116
	Food (factor)	0.086 ± 0.039	0.036

5.3.2 Mortality and phenology

From the 240 first-instar individuals 30 survived up to the final molt (low food: n = 21; high food: n = 9). Within each feeding regime, larval mortality was strongly dependent on larval instar (high food: χ^2_{15}= 75.95, $P <$ 0.001; low food: χ^2_{15} = 123.78, $P < 0.01$) and increased with increasing instar (Fig. 5.2). The total larval mortality rate of the different cohorts was not correlated with the hatching time (Pearsons product-moment correlation, high food: R = 0.28, d.f. = 4, $P = 0.59$; low food: R = 0.62, d.f. = 4, $P = 0.18$). The feeding regime also had no significant effect on total mortality (χ^2_5 = 3.57, $P =$ 0.6124).

Because of the high mortality during the fourth and fifth larval instar, wing status of the adult could only be tested in relation to feeding regime and not in relation to hatching time. In the low food group 19.05% of the individuals developed into the short-winged morph. Contrary, none of the larvae developing in the high food group became short-winged. However, this difference was not significant (Fisher's exact, 0% vs. 19.05% short-winged individuals in the high vs. low food treatment, $P = 0.28$).

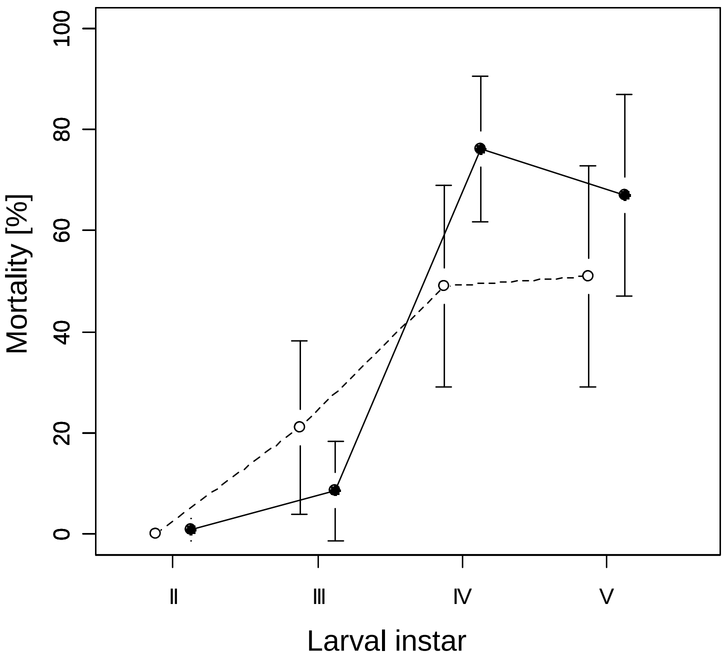

Figure 5.3: Mean and standard deviation of the larval mortality during the different larval instars for the two feeding regimes (High-food: solid line and dots, Low–food: dashed line and circles)

5.4 DISCUSSION

The rearing of larvae under natural light conditions showed that, independent of hatching time, individuals in the high food group developed faster than their low food counterparts. Obviously, higher food resources allowed larvae to reach the critical body size for initiation of moulting cycles within shorter periods of time. This result confirms the constraint of food resources on the development speed of water striders shown in earlier studies, for example for the water strider *Aquarius remigis* (Say) (Blanckenhorn, 1994); in this species, low food conditions led to an increase in development time (measured in terms of days) and a decrease in body size.

Furthermore, the experiment showed that both, individuals of the high and low food groups needed to accumulate significantly less degree-hours to complete larval development when hatching and developing later in the season compared to those that hatched earlier in the season. Thus, the larvae of *G. lacustris* obviously have the ability to respond to the decrease in season length by speeding up their development. As in many other insects (reviewed in Nylin & Gotthard, 1998), the main cue telling the developing larvae that the end of the season draws closer presumably is the declining day length. The photoperiodic sensitivity of water striders has been confirmed in several studies on the determination of wing length and diapause in this genus (Vepsäläinen, 1978; Köpfli *et al.*, 1987; Inoue & Harada, 1997). A shortening of developmental time in response to a declining season length (i.e. shortened photoperiod), has been shown for other species at a population level (Johansson & Rowe, 1999; Johansson *et al.*, 2001; Stoks *et al.*, 2005). In these studies the shortened developmental time was accompanied by an increase in growth rate. Accelerated growth allows compensation for the reduction in body size caused by the shortening of development time (Stearns, 1992). Even though not measured, this was presumably also the case for the larvae of *G. lacustris* developing at the end of the season. In fact, such an increase in growth rate appears to be necessary as in many insects, such as Heteropterans, the moulting cycle is initiated only when an individual reaches a critical threshold body size (Nijhout, 1979, 1994; Davidovitz *et al.*, 2003). The primary mechanism underlying acceleration of growth in the studies mentioned above was an increased energy intake mediated by higher foraging rates (and risk-taking behaviour) of individuals developing under a decreasing time horizon. In addition, an increase in growth *efficiency* under time constraints was observed within a population of the damselfly *Lestes sponsa* (Stoks *et al.*, 2005). This requires morphological or physiological plasticity, which has also been shown to explain growth variation between populations of the Atlantic silverside (Billerbeck *et al.*, 2000).

The ability to adjust physiological time was not reduced in the low food individuals of *G. lacustris* in this study. This finding is in contrast to expectation and to the results of several other studies. De Block & Stoks (2005) report a shortening of development under time constraints in individuals reared at high food compared to those reared at low food conditions in the damselfly *Lestes viridis*. Comparable trends also have been shown in a study on the yellow dung fly which increased growth rate under high food, but not low food, conditions towards the end of the season (Blanckenhorn, 1998). Eventually, two reasons may explain why the larvae of *G. lacustris* in the study presented here were able to accelerate development in late cohorts despite low food conditions. First, although physiological development time of low food individuals was prolonged, food supply possibly was still high enough to allow more than a minimum development rate. The fact that larval mortality rates showed no significant difference between the high- and low- food group supports this interpretation. In fact, mortality was even higher in the high food group, eventually as a consequence of the high quantities of *Drosophila* debris attracting bacteria, parasites or fungi. In general, larval mortality was high, but this has been found in other studies on *Gerris* in captivity (Park, 1988). Second, individuals may increase development by facultatively forgoing the development of morphological structures that otherwise increase fitness. In *G.*

lacustris the diapausing generation generally is long-winged in Central Europe, presumably because of fitness advantages incurred by the flight-capable morph that has to fly to and from diapausing sites (Vepsäläinen, 1978), but in natural populations the proportion of individuals developing into the short-winged morph increases strongly towards the very end of the season (Andersen, 1982; Hauser, 1982; Pfenning & Poethke, 2006). In some water strider species the short-winged morph develops faster than its long-winged counterpart (Zera, 1984; Pfenning *et al.*, subm.), presumably as they do not develop flight muscles. Strobbe & Stoks (2004) showed that individuals of a damselfly reduced body mass at emergence but not body size. Thus, the reduction of the flight apparatus may allow individuals to reach the critical body size for initiation of the moulting cycle in less time. The switch in wing morph of individuals moulting at the very end of the season may therefore be the morphological 'cost' of the adaptive reaction of development to a strong time and food constraint. Trade-offs between nutritional deficits during development and fitness of the adults have been shown in numerous species (reviewed in Metcalfe & Monaghan, 2001) and in fish species muscles were less developed at a given size in fast compared to slow growing individuals (Valente *et al.*, 1999). In the study presented here, twenty percent of the individuals reared in the low food group developed short wings, whereas high food larvae all became long winged; however, this difference was not significant due to the small sample sizes caused by high larval mortality in the last two larval stages. As the proportion of individuals moulting into the short-winged morph was lower in the experiment compared to observations in natural populations, food supply in the low food group may still have been higher than in natural habitats.

This study demonstrates the phenotypic ability of the common pond skater *G. lacustris* to adjust development to time constraints. The finding that under limited food provision more larvae tended to develop into the short-winged morph than under high- food conditions implies that there may be a trade-off between the allocation of energy into the acceleration of growth rate and the histogenesis of flight muscles and wings. The observed plastic reaction of development in response to increasing time constraint is in accordance with the assumption of the life-history theory that acceleration of development, or shortening of development time, should only occur when individuals are forced to react on extrinsic limitations of resources, due to trade-offs with other fitness-relevant traits, like body size or predation risk (Stearns, 1992; Arendt, 1997; Roff, 2002).

Chapter 6

The annual reproductive pattern of the water strider *Gerris lacustris* in variable environments

Chapter 6

The annual reproductive pattern of the water strider *Gerris lacustris* in variable environments

with Oliver Mitesser and Hans Joachim Poethke

IN PREP

Abstract. 1. Eggs laid by over-wintering females of the water strider *Gerris lacustris* may either develop into individuals that reproduce in the same year or into individuals that over-winter and postpone reproduction to the following year. The development of an egg strongly depends on the time it is laid, but there is no distinct switch from early laid eggs developing into directly reproducing individuals to later laid eggs developing into diapausing individuals. Over a time span of nearly two month we observe a gradual change in the odds to develop as either type.

2. We ask whether this behaviour is a type of bet hedging that can be explained as an adaptation to inter-annual variations in environmental temperature (thermal energy available for development) or whether it is a consequence of unpredictable inter-individual differences in development rates (i.e. in physiological time of development).

3. We compare the width of the observed transition zone with predictions of mathematical models based on (i) inter-individual variance of developmental rates (observed under controlled conditions) and (ii) a bet-hedging model based on long term data of environmental temperatures.

4. Our results clearly show, that predictions from the bet-hedging model readily explain the broad transition zone while individual differences in development rates are not sufficient to create the observed width of the transition zone between both developmental types.

6.1 INTRODUCTION

A major life history decision of insects living in temperate regions where suitable and adverse climatic conditions occur in seasonal periodic cycles is whether to reproduce within the same season, or to diapause before reproduction (Danks, 1994; Roff, 2002). Diapause allows individuals to survive periods of unfavourable environmental conditions, mostly characterised by extreme temperatures (Danks, 1987; Caceres, 1997); thus, diapause is an obligatory part of the life of individuals being oviposited close to the end of the season, i.e. usually the second generation individuals of bivoltine populations (Tauber *et al.*, 1986). Contrary, individuals of the first generation produced by the hibernated generation have to decide whether to reproduce directly or after diapause.

When individuals of the first generation would be able to exactly predict the remaining time in relation to their own and their offspring's development, they should switch to diapause as soon as there is less time remaining than required for a bivoltine life-cycle (Cohen, 1970). Consequently, the switch between the two strategies should be abrupt. However, several empirical studies show that the switch between direct reproduction and diapause is gradual (e.g. crickets, Bradford & Roff, 1997).

Water striders of the species *Gerris lacustris* show partially bivoltine life-cycles in suitable habitats in Central Europe (Vepsäläinen & Krajewski, 1974; Vepsäläinen, 1978; Hauser, 1982). According to Vepsäläinens (1978) general model of diapause induction in gerrids, it is determined during the larval phase of the first generation individuals, whether individuals develop into directly reproducing or diapausing individuals. Individuals that develop up to the 5th larval instar before summer solstice encounter long-day conditions during the critical stage sensitive to photoperiod, which is assumed to be the 4th. These individuals should become direct reproducing individuals. Later developing larvae go to diapause and postpone reproduction to the next year. In *G. lacustris* the reproductive strategy is closely associated with a wing dimorphism (Vepsäläinen, 1974b). While the direct breeders are more often short-winged, a high proportion of the diapausing individuals is long-winged (Vepsäläinen & Krajewski, 1974). Short-winged individuals seem to have a reproductive advantage compared to their long-winged counterpart (Andersen, 1973). On the other hand flightlessness is associated with severe costs as the short-winged morph can not escape habitat deterioration or fly to appropriate diapause sites in winter (Vepsäläinen, 1978). However, the larval stage sensitive to and the amount of individuals reacting on photoperiod vary between species and even within species but between latitudes. Thus, the general model of Vepsäläinen (1978) does obviously not sufficiently explain diapause induction in *Gerris* (Köpfli *et al.*, 1987; Spence, 1989).

In a laboratory study described in this paper we found a gradual switch between production of eggs that will become directly reproducing and diapausing individuals in *G. lacustris*. The most likely cause for such a gradual switch, characterised by a broad phase of simultaneous production of eggs that will develop into directly reproducing individuals and eggs that will become diapausing individuals is the intrinsic variation of development time between individuals (Philippi & Seger, 1989; Hopper, 1999). There is always some variability in the developmental speed of individuals. Thus, eggs laid at the same day will reach the 5th instar at different times. Consequently there will be a certain period where eggs laid on the same day will choose different developmental paths later on.

Risk spreading theory offers another important mechanism that may explain the observed gradual switch. European *Gerris* species live in seasonal environments where environmental conditions like season length and thermal energy available for development vary between years. Due to this short-term variability of the environment organisms can not predict the remaining time for development exactly. In populations living in such temporally uncertain environments, 'risk-spreading'- diapause strategies like the gradual increase in the production of diapausing offspring, may ensure that independent of environmental conditions at least some of the offspring will reach maturity (Philippi & Seger, 1989). However, there is a controversial discussion whether gradual declines in diapause strategy can be explained by risk-spreading or rather always depend on constraints like variance in developmental time (Hopper, 1999).

In this study we quantify the gradual transition between the production of directly reproducing and diapausing individuals. We compare the width of the observed transition zone with predictions of two modelling approaches. The first one is based on the inter-individual variance of developmental rates (observed under controlled conditions) while the other is a fitness analysis based on long term fluctuation in environmental temperatures.

6.2 METHODS

6.2.1 Diapause strategy of Gerris lacustris

Reproductive strategies of *G. lacustris* individuals were determined in a laboratory study. Individuals of *G. lacustris* were reared under quasi-natural conditions from eggs laid by 14 field-caught, overwintered females (for details of the rearing method see Pfenning & Poethke, 2006). The development of (N = 46) individuals hatching from egg batches laid between 9 Mai and 8 June was followed from hatching until adulthood. Wing status, ventral coloration, and sex of adults were recorded. Directly reproducing females are characterised by a pale pigmentation of their ventral thorax (Andersen, 1973) and can easily be distinguished from diapausing individuals. Thus, ventral coloration was used to determine the reproductive state of females. As males do not show this striking dimorphism of ventral coloration we used the strong association between wing status and developmental pathway to determine the reproductive status of males. For each day of the rearing experiment we recorded the proportion of eggs laid on that day that developed into the pale-ventered or short-winged (males) morph. The influence of the oviposition date on the fraction of individuals developing into directly reproducing males or females was subsequently analysed by a logistic regression.

6.2.2 Inter-individual variability of development

A simple rule of thumb was suggested by Vepsäläinen (1978) for predicting the reproductive strategy of the waterstrider *G. lacustris*: If an individual has reached the 5th larval instar before summers solicit, it will develop into a directly reproducing short-winged adult. For every day (*d*) during the season this behavioural rule implies that a certain proportion (*p(d)*) of the currently laid eggs will develop into directly reproducing individuals. This is a consequence of the different developmental rates of the individuals and the corresponding development time the individuals need to reach the 5th larval instar. The adequate quantity describing the time spans of development is the physiological time, i.e. the amount of thermal energy [°d] above the lower developmental threshold accumulated during development (Trudgill *et al.*, 2005). As rates of developmental processes are usually assumed to be normally distributed, we model the distribution $\Phi(T, m_{5th}, \sigma_{5th})$ of the physiological time T required for development up to the 5th larval instar as an inverse normal distribution characterised by the mean development rate and the corresponding variance (m_{5th}: mean development rate until an individual has reached its 5th instar, σ_{5th}: corresponding standard deviation; see Sharpe *et al.*, 1977).

To determine the proportion of directly reproducing individuals (*p(d)*) we calculate the fraction of eggs (layed on day *d*), which need less thermal energy for reaching their 5th larval instar than available from day *d* until summer solicit. If $T_R(d)$ is the remaining thermal energy available from day *d* until the end of the season, then the thermal energy available for an egg layed on day *d* until summer solicit (*SS*) can be expressed by $T_R(d) - T_R(SS)$. We assume that the physiological time required for development is distributed randomly with distribution density Φ. Thus, the proportion *p(d)* can be calculated as

$$p(d) = \int_{0}^{T_R(d)-T_R(SS)} \Phi(T, m_{5th}, \sigma_{5th})dT \text{ (for } d = 1, .., \text{SS)} \qquad (6.1)$$

To evaluate this expression we have to calculate 1) the remaining thermal energy for each day (*d*) of the year under consideration, 2) the mean (m_{5th}) and 3) the standard deviation (σ_{5th}) of the development rate until the 5th instar is reached (see Appendix 2 for parameter estimation).

6.2.3 Fitness model: Calculating fitness for diapause and directly reproduction strategies

The second approach analyses the question, if the gradual transition from the production of directly reproducing to that of diapausing individuals may be explained as a fitness maximising strategy. Expected fitness of individuals that choose to reproduce directly $F_{rep}(d)$ or to diapause $F_{dia}(d)$ depends on the day *d*, when the corresponding egg is laid. To determine the fitness values $F_{rep}(d)$ and $F_{dia}(d)$ we used a model developed by Bradford and Roff (1997) respectively Cohen (1970) and Levins (1968, 1969), see Appendix 1. It is based on estimates of the life history parameters of *G. lacustris*. Larval mortality μ_l (per °d), adult mortality μ_a (per °d), development rates m_{sw} and m_{lw} of short and long winged individuals and the timing of reproduction were estimated from field data. Additionally, we considered fitness reduction φ of short winged compared to long winged individuals and the additional mortality risk of short-winged direct reproducing individuals due to pond drying in summer (μ_d). As the parameters φ and μ_d could not be estimated from field data, their influence on the strategy transition had to be analysed in a sensitivity analysis for a wide range of values (see Table 6.1).

As long as environmental variations are predictable (e.g. fixed season length) switching between a diapause strategy and direct reproduction should always be realised as a dichotomous transition exactly when $F_{dia}(d) = F_{rep}(d)$ (Bradford and Roff, 1997). If the season length varies randomly individuals can not predict the currently remaining season length and the remaining thermal energy available on day *d*. In this case mixed strategies (consisting of a specific fraction *p(d)* of directly reproducing eggs and a complementary fraction 1 - *p(d)* of diapause eggs) might be the solution of the fitness optimisation problem. For a given remaining T_R the fitness function on day *d* has the more general form

$$\tilde{F}(d, p, T_R) = p(d)\tilde{F}_{dia}(d, T_R) + (1 - p(d))\tilde{F}_{rep}(d, T_R) \qquad (6.2)$$

Note that in stochastic environments fitness ($\tilde{F}$) must be considered as a function of both the egg laying day (*d*) and the remaining thermal energy (T_R). Both quantities are no longer linked by a unique correlation function as in the deterministic case. However the probability distribution of possible remaining thermal energy $\Psi(T_R, m_d, \sigma_d)$ still depends on the day (*d*) under consideration. We assume $\Psi(T_R, m_d, \sigma_d)$ to be normally distributed with mean (m_d) and variance (σ_d^2) depending on day d under consideration. When all individuals are exposed to identical environmental variations between years, then long term mean fitness ($\tilde{F}(d, p)$) of the phenotype choosing a specific strategy (*p(d)*) must be calculated as the geometric mean of single year fitness values $\tilde{F}(d, p, T_R)$ with a specific season length. As a log-transformation does not change the position of the maximum but simplifies calculations, geometric mean is usually replaced by its logarithm, so that averaging over different years can be obtained by integration

$$\ln(\tilde{F}(d, p)) = \int \Psi(T_R, m_d, \sigma_d) \ln(\tilde{F}(d, p, T_R)) dT_R \qquad (6.3)$$

Numerical maximisation of this expression determines the optimal switching strategy *p(d)*.

We are mainly interested in the transition zone, where 0 < *p(d)* < 1. To characterise the transition zone by a single value, we choose the odds-ratio *OR* from a logistic regression curve fitted to the transition function. The odds-ratio specifies the change in the odds of being an individual with direct reproduction when the independent variable (laying day) changes by one unit:

$$OR = \frac{p(d) / (1 - p(d))}{p(d+1) / (1 - p(d+1))} .$$

The odds-ratio *OR* can be calculated from the logistic regression parameters and is constant along the complete logistic regression curve although the slope changes (Hosmer & Lemeshow, 2000). High values of *OR* indicate a steep transition and a narrow transition zone while low values represent a wide transition zone.

6.3 RESULTS

From the eggs laid by female water striders between 10 May and 8 June at the beginning of the season 2004 in the outdoor laboratory, directly reproducing and diapausing individuals developed in gradually changing proportions. The fraction of eggs that will develop to directly reproducing adults showed a clear gradual decline (Fig. 6.1) with increasing laying date. While all of the eggs laid at the beginning of the experiment developed into the short-winged morph, this fraction continuously decreased during the experiment. The decline started on day 20 and ended on day 80 (since 1. April) with a median at day 52 (Fig. 6.1).

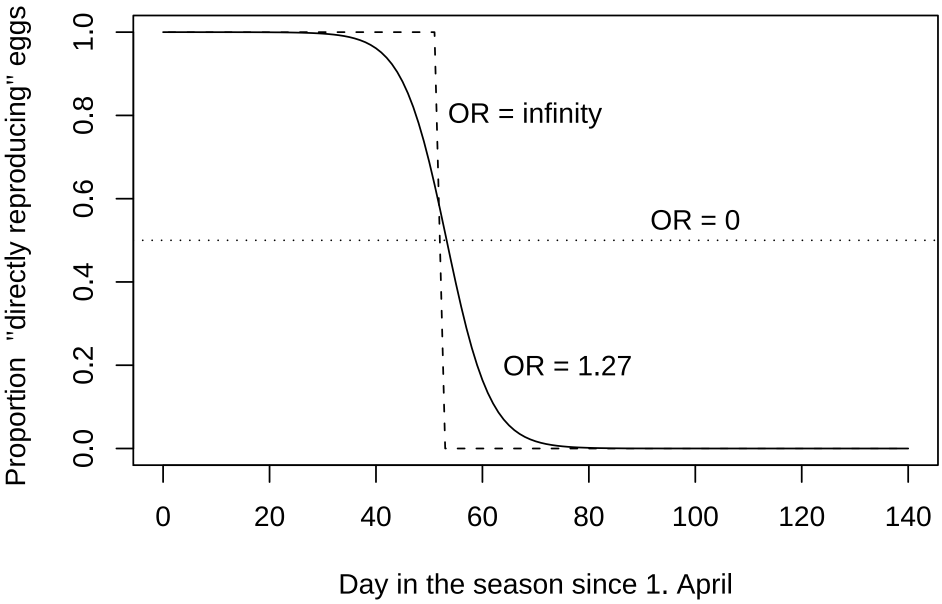

Figure 6.1: Proportion of individuals developing into short-winged, directly reproducing individuals from eggs laid at different dates within the season. The solid line represents the logistic regression model fitted to the data (*OR* = 1.27; n = 46). Data are from laboratory rearings. Two additional curves (dotted lines) illustrate extreme values of the odds-ratio (*OR* = 0 and *OR* = infinity).

The physiological time necessary for development of *G. lacustris* from the egg state up to the 5th larval state varies between individuals. Unfortunately the physiological time could not be estimated from a single sample, but must be calculated statistically from a combination of two samples (see Appendix 2 for parameter estimation). These calculations give an estimation of mean and variance of physiological development rate and the corresponding confidence intervals: mean = 0.0034 1/°d (95% confidence interval: [0.0033; 0.0035]) and var = 1.1E-07 (95% confidence interval: [5.9E-08; 1.8E-07]). The average number of degree-days necessary for the development from eggs to 5th instar individuals was 290 °d (95% confidence interval: [283; 299]) (Fig. 6.2). The physiological time of development up to the 5th instar presumably is independent of wing morph type, as flight muscles develop not before the 5th larval instar (Andersen, 1973).

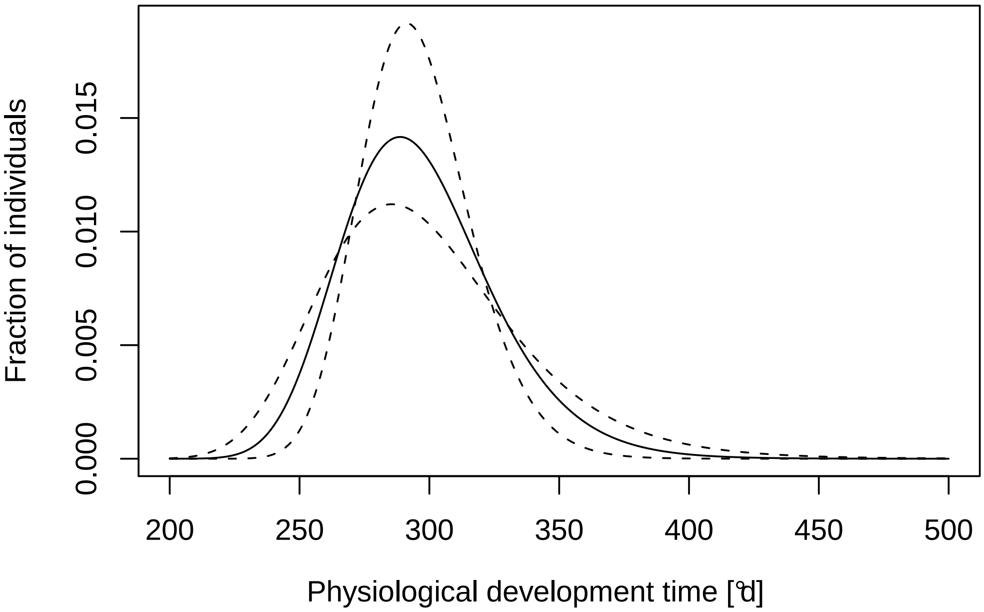

Figure 6.2: Distribution of physiological development times (in degree-days above the lower developmental threshold of 10 °C) for the development from oviposition up to the 5th istar (*n* = 422 for egg to larva development and *n* = 30 for 1st to 5th larval instar). As the physiological time could not be estimated from a single sample, but had to be calculated from a statistical combination of two samples (see Appendix 2 for parameter estimation), we can give only an estimation of mean and variance of physiological development rate. Here we show the mean (solid line) and two extreme distribution functions (broken lines) based the estimation of the mean development rate (0.0034 1/°d) and the confidence interval of the variance: [5.9E-08; 1.1E-07; 1.8E-07].

For *G. lacustris* a season lasts approximately from 01 April until 31 October. The variation of the thermal energy available for development and reproduction during this phase varies between years (see Fig. 6.3, the distribution of available thermal energy for an egg laid on the 1st of April). The calculation of the environmental variability refers to above ground data from weather station Hassfurt for the time interval from 1992 to 2004. Fig. 6.3 shows that on average 1255 ± 85 °d accumulate throughout a season.

We used both, the inter-individual variation of physiological development time (Fig. 6.2) as well as the random variation of season length (Fig. 6.3) to predict the shape of the gradual transition between the production of direct and delayed reproducing individuals. Figure 6.4 provides the comparison of the odds-ratios (indicating the slope of the transition zone) observed in the laboratory and predicted by the behavioural as well as by the fitness model. Both, laboratory observations and the fitness model yield comparatively low odds-ratios (i.e. a broad transition zone) and a small error range, while the odds-ratio resulting from the behavioural model (as well as the corresponding error bars) is rather high (i.e. narrow transition zone). Thus, only the prediction based on seasonal variability (*OR* = 1.36 [1.33; 1.46]) is in accordance with the field observations (*OR* = 1.27 [1.18; 1.37]). Odds-ratio estimates based on variable development rates are too high (*OR* = 1.65 [1.47; 1.88]) and the corresponding transition zone is too small. The gradual transition between the production of direct and delayed reproducing individuals is unlikely to be explained by inter-individual variation of physiological development time alone.

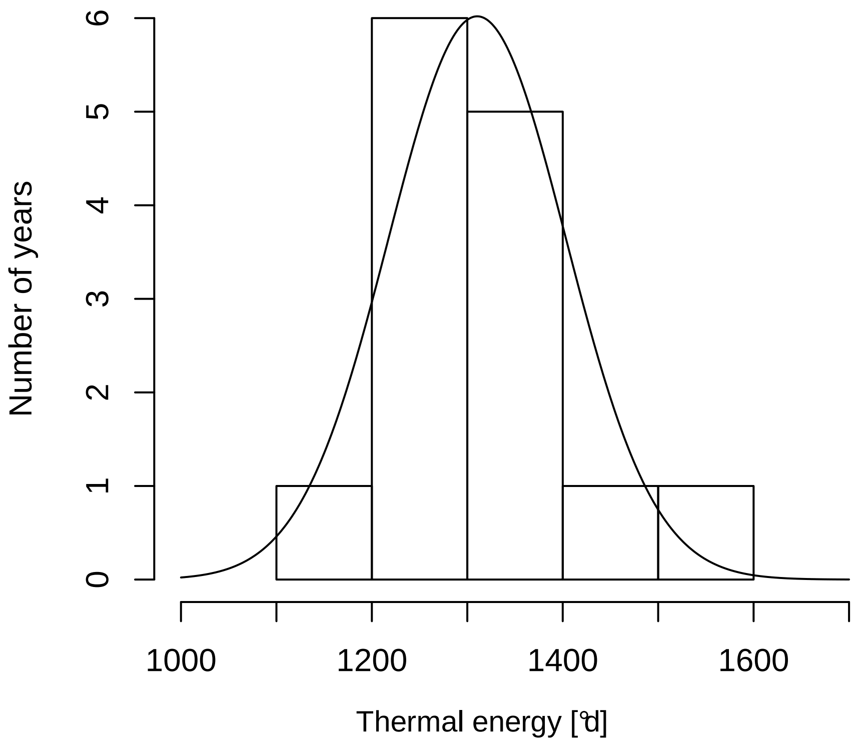

Figure 6.3: Distribution of the thermal energy (in degree-days above the lower developmental threshold of 10 °C) remaining for the development and reproduction of an individual at the beginning of the season. Mean and sd have been calculated from the adjusted temperature data from 1992 – 2005 (n = 14) of the weather station *Hassfurt* (see methods for details).

Estimation errors of the predicted *OR* in a) the behavioural model, b) field observation of the strategy transition zone, and c) the fitness model (error bars in Fig. 6.4) result from: a) the uncertainty of mean and variance estimation (95% confidence interval of both) in the behavioural model due to finite sample size and statistical combination of two samples, b) the finite sample size in field observations, and 3) the uncertainty in parameter estimation (fitness model, see Table 6.1).

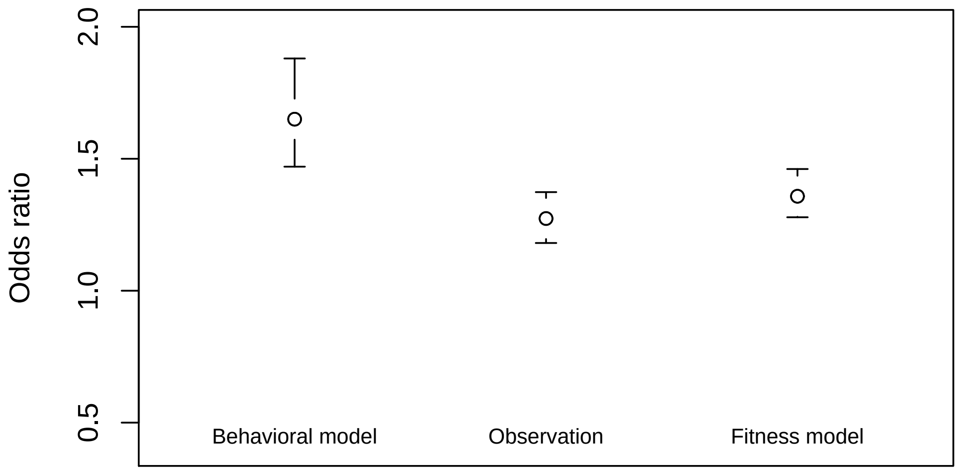

Figure 6.4: Odds-ratio as observed and predicted by the behavioural and the fitness model. Error bars of the predicted OR result from: 1) uncertainty of mean and variance estimation (95% confidence interval of both) in the behavioural model, 2) sample size (field observation), and 3) uncertainty in parameter estimation (fitness model, see Table 6.1).

A detailed analysis revealed that the width of the error bars in the fitness model results mainly from the parameters φ and μ_d. As we can not give a precise estimation of fitness reduction due to wing state and mortality due to pond drying, we had to consider a wide range of the corresponding factors (see Table 6.1). However, this did not result in a wide estimation range. Both errors from field estimation and the fitness model are comparably low. Thus, we can conclude that reproductive timing is mainly determined by the major time constant of the system, i.e. the mean development time of the individuals.

6.4 DISCUSSION

A thorough comparison of the shapes of the diapause curves shows that the behavioural model is not able to explain the diapause response function observed in the laboratory which is characterised by a much broader transition zone. Obviously, inter-individual variation in development time does not sufficiently explain the graded response observed in the laboratory population. Variance in development time might be higher under natural conditions due to variations in extrinsic parameters like food availability (Blanckenhorn, 2006), temperature (Spence *et al.*, 1980) or concurrence. However, this does not alter the fact that the observed shape of the transition zone can not be explained by the observed variation in development time. Other mechanisms are required to provide a sufficient explanation for the width of the transition from the production of direct reproducing to that of diapausing individuals. Hopper (1999) has suggested to emphasise the analysis of simple mechanisms that are often neglected as possible explanations of behavioural transition. However, at least in this case such an explanation is not sufficient.

Contrary to the small graded diapause response predicted by the behavioural model, the shape of the response curve predicted by the fitness model, considering long term variation in climate, was very similar to the gradual decline in the reproductive strategy observed in the laboratory. Thus, a bet-hatching strategy is a possible explanation for the broadness of the diapause response curve, i.e. an (evolutionary) adaptation to the variance in year-to-year weather conditions. Thermal energy available for development during the 14 years considered varied up to ~30% between years (Fig. 6.3). This high variation points to the unpredictability of available thermal energy and consequently, the relevance of strategies ensuring that at least part of the population will reach the adequate stage for diapause, i.e. adulthood, before environmental conditions become adverse.

Two findings on diapause induction in different water strider species might provide possible additional mechanisms that influence the shape of the diapause response curve. On the one hand several studies showed that part of the offspring of females from the same populations seemed not to be sensitive to photoperiod and developed into diapausing individuals obligatory (e.g. Vepsäläinen, 1974b; Köpfli *et al.*, 1987; Spence, 1989). On the other hand, in some of these studies, the last instar sensitive to photoperiod varied between individuals; a phenomenon that normally is found between populations of insects occurring in different latitudes (Danks, 1987). A variation in the critical stage for diapause induction between individuals of the same population clearly would broaden the gradual transition between the production of direct and delayed reproducing individuals.

However, the exact time period of diapause induction and the decisive day length is known only for very few species (Inoue & Harada, 1997). To verify the result of our fitness model the mechanism of diapause induction in *G. lacustris* should be investigated in detail. We suggest to determine the last larval instar sensitive to photoperiod by determining when long- and short winged individuals start to differ in their physiological time of development, as we found clear differences in the distribution of degree-days accumulated by these two wing morphs during development (Pfenning *et al.*, subm.). Primarily, this method will determine the stage where wing form is determined. However, due to the close association between wing form and reproduction in *G. lacustris*, wing morph type and developmental pathway presumably are determined at the same time in this species.

The result of our study contrasts the finding of Bradford and Roff (1997) where a fitness model did not fully explain the shape of the diapause response of the partially bivoltine cricket *Allonemobius socius*. However, to conclude that the observed gradual decline in the production of eggs that develop into directly reproducing and diapausing individuals is necessarily due to a risk-spreading strategy, further studies have to be conducted. This analysis can just characterise risk-spreading as a sufficient mechanism to explain the behavioural transition. Although there are studies showing that the long- and short-winged morphs of the summer generation do not necessarily differ genetically (Vepsäläinen, 1978), further genetic studies should follow. The latter is important to find out whether larvae with different sensitivity to photoperiod differ in their genotype. Only pure phenotypic variation would support the assumption of a stable risk-spreading strategy (Hopper, 1999). Another possibility to e.g. investigate whether there are costs that select for risk-spreading would be the measurement of fitness effects of risk-spreading compared to non risk-spreading genotypes. Furthermore, the reproductive strategy of further populations of *G. lacustris* e.g. occurring along a gradient of variation in environments could be determined and compared. An increase in environmental stability should reduce the need for a temporal risk-spreading strategy.

6.5 APPENDIX 1: FITNESS CALCULATION

Due to their wing morph and voltinism eggs of the water strider *Gerris lacustris* potentially can perform four possible life-cycle strategies: 1) diapause as long-winged adults, 2) diapause as short-winged adults, 3) direct reproduction as long-winged adults and 4) direct reproduction as short-winged adults. Strategy 3 is rarely observed in natural populations. One possible reason explaining this is the fact that directly reproducing individuals should start reproduction as soon as possible to ensure that their offspring become adult before the end of the season. As developmental (Zera, 1984; Pfenning *et al.*, subm.) and preovipositional (Andersen, 1973; Spence, 1989) time of long-winged individuals is prolonged compared to their short-winged counterparts, it might be too risky to develop wings as direct reproducing individual. (This can also be shown with an extended version of our fitness model.) Our goal is to compare the fitness of the two main strategies "diapause" (1 and 2) and "direct reproduction" (4). As water striders hibernate as adults fitness of each of both main strategies is measured as the number of adults developing and surviving up to the beginning of diapause.

Fitness of strategy "diapause": Both for a long-winged and a short-winged, diapausing individual oviposited at day *d* in the season fitness depends on the relation between physiological time T required for development from egg to adult and thermal energy T_R available in the rest of the season. The latter accounts for the fact that an individual may not become adult before winter if the egg is laid too late in the season. In addition the individuals suffer from larval mortality with rate μ_l (per unit of consumed physiological time). Depending on the remaining thermal energy T_R for the development, a long-winged individual or a short-winged individual with a fitness reduced by factor φ will develop:

When short-winged the fitness $\tilde{F}_{dia}(d,T_R)$ of a diapause individual is

$$\tilde{F}_{dia,sw}(d,T_R) = \tilde{F}_{dia,sw}(T_R) = \varphi \int_0^{T_R} e^{-\mu_l T}\Phi(T,m_{sw},\sigma_{sw})dT \qquad \text{(A 6.1a)}$$

for a long-winged individual it is

$$\tilde{F}_{dia,lw}(d,T_R) = \tilde{F}_{dia,lw}(T_R) = \int_0^{T_R} e^{-\mu_l T}\Phi(T,m_{lw},\sigma_{lw})dT \qquad \text{(A 6.1b)}$$

Note that these expressions only implicitly depend on day d. In a deterministic scenario T_R is fully determined by d ($T_R = T_R(d)$) and for stochastic environments d determines a probability distribution of possible remaining thermal energy. As we do not focus on the potential transition between long- and short-winged phenotypes within the diapause strategy, we assume that the phenotype with the higher fitness value will develop at each day d during the season and calculate diapause fitness as

$$\tilde{F}_{dia}(d,T_R) = \max\{\tilde{F}_{dia,sw}(d,T_R), \tilde{F}_{dia,lw}(d,T_R)\} \qquad \text{(A 6.1c)}$$

Fitness of strategy "direct reproduction": For a specific short-winged direct reproducing individual (with development time T and oviposition day d) we calculate its fitness $F_{rep}(d, T)$ as the product of its egg-to-adult mortality exp(μ_l T) and the number of its offspring that become adult until the end of the season (= $F(d,T)$):

$$F_{rep}(d,T) = e^{\mu_l T} \cdot F(d,T) \qquad \text{(A 6.2a)}$$

Mean fitness (with respect to different physiological time sums T required by different individuals) can be calculated by averaging over all possible development times T of the mother.

$$\tilde{F}_{rep}(d,T_R) = \int_0^{T_R} \Phi(T,m_{sw},\sigma_{sw})\, e^{\mu_l T} F(d,T)dT \qquad \text{(A 6.2b)}$$

The number of offspring that become adult before winter (*F(d,T)*) depends on three factors. First, the fecundity rate *Fec(x)* of the mother with respect to the accumulated physiological time *x* since maturity. Second, the mortality rate a directly reproducing adult is exposed to during its life-time. This parameter consists of two factors $(\mu_a + \mu_d)$, the intrinsic adult mortality rate and mortality due to pond drying. Third, the fitness $F_0(x,d)$ of the second generation offspring with parent oviposited on day *d*. Both fecundity *Fec(x)* and offspring fitness $F_0(x,d)$ depend on the physiological time *x* accumulated by the reproducing individual from its maturity (*x* = 0) until the end of the season. As T_R day degrees remain when the individual is born and further *T* day degrees are consumed for the development from egg to adult, an amount of T_R - *T* day degrees is left for the individual's own reproduction (upper limit of integration).

$$F(d,T) = \int_0^{T_R - T} e^{-(\mu_a + \mu_d)x} Fec(x) \cdot F_0(x,d) dx \qquad \text{(A 6.2c)}$$

How does second-generation offspring fitness $F_0(x,d)$ depend on accumulated physiological time *T* of the mother? When a parental individual (oviposited on day *d* itself) has accumulated *x* day degrees, the currently produced offspring have $y = T_R - T - x$ day degrees left for their development. Thus

$$F_0(x,d) = \tilde{F}_{dia}(y) = \tilde{F}_{dia}(T_R\text{-}T\text{-}x) \qquad \text{(A 6.2d)}$$

The fecundity rate *Fec(x)* of a directly reproducing individual during its lifetime (measured per degree-days) was calculated from laboratory data (see Appendix 2 for parameter estimation).

6.6 APPENDIX 2: PARAMETER ESTIMATION

6.6.1 The environment

According to our own observations and literature data from Denmark (Andersen, 1973), Poland (Vepsäläinen & Krajewski, 1974) and Austria (Hauser, 1982) the reproductive season almost never exceeds the interval from 1 April to 31 October (= 214 days). The seasonal course of the thermal energy available during the season length was estimated from temperature data of 14 years (1992-2005) of the weather station *Hassfurt* (15 km apart from the study area). Data from both, 10 field ponds investigated in 2004 (for details see

Pfenning & Poethke, 2006) and the weather station in 2004 were used to calculate linear regression coefficients of the relationship between the mean daily above ground temperatures measured at the weather station and the mean daily water surface temperatures on field-ponds in the study area. Then each day *d* of any season could be characterised by the cumulative thermal energy ($T_R(d)$) left for the remaining (future) part of the season after day *d*. Mean (m_d) and variance (σ_d^2) of the remaining physiological temperature T_R [°d] were calculated from the adjusted temperatures for any day *d*. In the simulation studies (see later) we approximated the distribution of remaining thermal energy of day *d* by a normal distribution with parameters (m_d) and variance (σ_d^2) (Bradford & Roff, 1997).

6.6.2 *The species*

a) Development time

Data on physiological development times of individuals reared under quasi natural conditions were taken from the laboratory study from 2004 (Chapter 3 and 4 of this thesis; Pfenning & Poethke, 2006; Pfenning *et al.*, subm.). In this study the physiological time for teneral development of short-winged adults was calculated to be ≈ 48 °d. This number of degree-days was added to the egg-to-adult development time of each short-winged adult to account for the teneral development. Physiological time of teneral development of long-winged adults was supposed to be twice as long (≈ 96 °d), according to literature data (see Chapter 4 for details). The mean *m* and variance σ^2 of the inverse of the physiological development times (= development rate) from oviposition up to reproductive maturity, were calculated. Then, according to Bradford & Roff (1997), the probability distribution of the development times was modelled with an inverse normal distribution (Sharpe *et al.*, 1977):

$$\Phi(T, m, \sigma) = \frac{1}{\sqrt{2\pi}\sigma T^2} e^{-\frac{(1/T - m)^2}{2\sigma^2}}$$

The distribution of physiological development time from oviposition up to the fourth larval instar (i.e. last instar sensitive to photoperiod), was calculated the same way. Therefore, the egg-development times measured in the study in 2004 were used, while physiological time of the larval instars was taken from a study carried out in 2005 (Pfenning *et al.*, subm). As we could not detect any correlation between the physiological time required for any of the single instars we combined egg-development and larval-development times randomly. Confidence intervals of mean and variance of the resulting distribution have been calculated by repeating the randomization procedure.

b) Mortality

Data on larval mortality μ_l were recorded in a field study in summer 2005. On 19 July a triangular enclosure (0.5 x 0.5 x 0.5m) was installed on the southern littoral zone of each of 8 field-ponds located in the study site. The three corners of each triangular enclosure were formed by wooden sticks which were stuck into the ground of the pond. The sticks were surrounded by a 25cm high stripe of gaze ranging 5cm below and 20 cm above the water surface. Thus, the triangle of gaze was open on the top as well as on the bottom but it prevents the escape of water striders and the intrusion of new striders. For each enclosure fifteen larvae of *G. lacustris* of all larval stages were collected in the corresponding pond and transferred into the corresponding enclosure. The following four days the numbers of larvae that survived (or moulted) were counted daily for each enclosure. During the investigation the mean daily water surface temperature was ~7.5 °C above the lower developmental threshold (data from thermo loggers). Mean larval mortality rate per degree-day was calculated with a negexponential model to be 0.0146 ± 0.0021 $°d^{-1}$.

Intrinsic mortality rate μ_a per °d (Table 6.1) of adults was estimated from eight directly reproducing females reared in the experiment described above, that were kept in the laboratory until death. Furthermore, the age specific fecundity of short-winged individuals was determined from these 8 females. The life-history and the incubation temperature of these females were known from the day of oviposition up to death. After final moult each of the eight females immediately was transferred into a water filled plastic-container (20x10cm) and paired with a male. Temperature of the water surface was measured hourly by thermo-loggers. Pieces of styrofoam (1x3cm) were added as oviposition sites. Every second day the number of newly laid eggs was counted, the eggs were removed and the styrofoam replaced. For each female the number of eggs oviposited per 50 °d (effective temperature) since final moult was calculated. A (symmetric) quadratic function as used by Bradford and Roff (1997) is not suitable to describe the skewed average egg production rate r of waterstriders, a $r \sim axe^{-bx} + c$ relationship was used instead and parameter values were estimated by a nonlinear regression. The additive parameter c has been used to account for the "fat tailed" reproduction rate of females. Nevertheless, this does not mean, that reproduction lasts infinitely as reproduction rate is multiplied by mortality rate.

The reduced overwinter fitness φ of the short- compared to the long-winged individuals and the external short-winged mortality μ_d due to pond drying up could not be determined from field or literature data.

Table 6.1: Mean and standard error/variance of parameters determined from field data and range of values of unknown parameters.

Parameter	Mean	SE/VAR
μ_l (larval mortality per °d)	0.015	0.002082 (SE)
μ_a (adult mortality per °d)	0.0027	0.00034 (SE)
m_{lw} (development rate of long-winged individuals)	0.0019	1.4 E-07 (VAR)
m_{sw} (development rate of short-winged individuals)	0.0022	6.0 E-08 (VAR)
a age specific fecundity, Fec(x) ~ $a\,x\,e^{-bx} + c$	0.029	0.0043 (SE)
b	0.023	0.0022 (SE)
c	0.15	0.026 (SE)
φ (fitness reduction of short-winged individuals)	0.5	[0.1 … 0.9]
μ_d (adult mortality of short winged adults due to pond drying per °d)	0.5	[0 … 0.1]

Summary

Summary

Insects living in temperate latitudes need to adjust their life-history to a seasonally variable environment. Reproduction, growth, and development have to be completed within the limited period where environmental conditions are favourable while climatically adverse conditions have to be spent in a state of diapause. Consequently, questions how individuals adapt their life-history to seasonality and which mechanisms underlie the responses to seasonal cues, like photoperiod, are important issues in the study of life-history strategies (e.g. Roff, 1980; Abrams *et al.*, 1996). Seasonal adaptations and the corresponding trade-offs are, however, complex and encompass very different life-history traits. Thus, Danks (2006) has argued that to fully understand the relevance of a certain life-history attribute as seasonal adaptation we need to consider that pattern in the context of the habitat characteristics (including their variation in space and time) under which it evolved. In this thesis I investigated life-history adaptation to seasonality in the wing-dimorphic common pond skater *Gerris lacustris* L. (Heteroptera: Gerridae). Using a combination of field and laboratory studies as well as mathematical modelling, I adressed how variation in the availability of thermal energy impacts on various aspects of larval development such as accumulated thermal energy (i.e. physiological development time), developmental pathway (direct reproduction vs. diapause) and wing dimorphism.

Life-history strategy of *G. lacustris* populations living in different thermal environments was empirically determined in a field study including two types of habitat: sun-exposed field and shaded forest-ponds. These two types of habitat differed significantly in surface- and water temperature and thus, in (the cumulative) thermal energy available per season. The 63 ponds included in the study were distributed over a spatial scale too small to allow for local genetic differentiation between populations of *G. lacustris*. Nonetheless, I observed significant phenotypic differences in life history patterns between populations from these two habitat types. While *G. lacustris* inhabiting forest-ponds generally showed a univoltine life-cycle, populations on field-ponds usually produced a directly reproducing "midsummer"-generation in addition to the diapausing "winter"-generation. Differences in voltinism were accompanied by a seasonal wing dimorphism. The long-winged morph dominated in the diapausing "winter"-generation in both habitat types. In contrast, the directly reproducing "midsummer"-generation appearing on field-ponds was dominated by individuals with reduced wings.

Laboratory experiments with offspring from "forest-parents" indicate that the switch in life-cycle strategy observed between the two types of habitat can be induced by different raising temperatures in combination with natural

photoperiod. The experiments confirm that the observed life-cycle variation is independent of the genetic origin of individuals and is readily explained as phenotypic plasticity. Eggs and larvae of *G. lacustris* raised under different temperature regimes showed significant differences in their development time. Obviously, significant temperature differences between the two habitat types lead to differences in development time of juvenile *G. lacustris*. In fact, first instar larvae *of G. lacustris* appeared several weeks later on forest than on field ponds. Consequently, larvae in the two habitat types experienced different photoperiod conditions during their development. The latter is the main environmental cue triggering developmental pathway and wing status in *G. lacustris*.

To further determine the influence of thermal energy available during the season for the observed life-history strategies, I estimated the physiological times necessary to complete the different possible combinations of wing morph pattern and voltinism and compared them with the thermal energy actually available in the two natural habitats during an average season. I measured the thermal energy necessary for the completion of different physiological processes in controlled laboratory experiments for each of the two wing morphs. Accordingly, short-winged individuals need to accumulate less thermal energy to complete juvenile development than their long-winged counterparts. The comparison reveals that thermal energy available in the two habitat types strongly limits the life-cycle of *G. lacustris* populations. In good agreement with the field observations, environmental temperatures allow completion of a bivoltine life-cycle on field ponds only. However, the results also show that even in the field a reduction of wings in at least one generation is necessary to allow the safe completion of a bivoltine life cycle in less favourable years. This indicates that wing-dimorphism of *G. lacustris* is affected by the limitation of available thermal energy. Whereas environmental temperature already allows a switch from uni- to bivoltinism, there obviously exists a trade-off between increasing generation number and maintaining flight capability throughout the season.

Beside the environmental temperature, the timing of oviposition within the season should also constrain the thermal energy available for development. Following the development of six cohorts of larvae of *G. lacustris* hatched at different times during the season I could show that late cohorts significantly reduced their physiological time of development and (implicitly) the thermal energy accumulated during development. Such acceleration is clearly adaptive when the season’s end is approaching but presumably requires a higher food uptake. To determine the effect of food limitation on physiological time of development, members of the six cohorts were reared under two different feeding regimes. Across cohorts, physiological time of development was always lower in the high- compared to the low-food group, but both, high- as well as low-food individuals reduced physiological time of larval development

towards the end of the season. However, 20% of the low-food individuals developed into the short-winged morph while all of the high-food individuals became long-winged. A limitation of food may thus lead to a reduced allocation of energy into the development of the flight apparatus and may be responsible for the strong increase in the frequency of short-winged individuals observed at the end of the season in many natural populations.

The option to "decide" between two alternative developmental pathways (diapausing vs. direct reproducing) bears the problem of finding the optimal switching date between developing into either form. In *G. lacustris* I observed a gradual change in the fraction of larvae that developed into directly reproducing and those which became diapausing individuals over a time span of several weeks. The observed inter-individual differences in physiological time of development could not sufficiently explain the length of the empirically observed gradual transition. However, based on a mathematical model of the long-term fitness of different life-history strategies under observed long-term variability of environmental temperature, i.e. thermal energy available for development per season, we could show that the observed strategy can be interpreted as a bet-hedging strategy: A gradual changing production of diapausing and non-diapausing individuals would maximize the long-term fitness in environments with unpredictable season length.

The results of my thesis demonstrate that the common pond skater *Gerris lacustris* has the phenotypic plasticity in physiological development time, developmental pathway and wing dimorphism, to respond to variations in season length. It shows that the thermal energy available for physiological processes is the main environmental factor determining the length of the season and thus strongly influences life-history strategy of *G. lacustris*. This study furthermore emphasizes, that measurement of an organism’s response to a certain seasonal cue is not always sufficient to recognize the link between life-history variation and seasonal adaptation. For a detailed understanding of the relevance of variation in life-history pattern as seasonal adaptation, it is necessary to see the observed life-history strategy in close context with specific habitat characteristics and their variation in space and time.

Zusammenfassung

Zusammenfassung

Insekten in temperierten Breiten müssen ihre Lebenslaufstrategie an eine saisonale Umwelt anpassen. Reproduktion, Wachstum und Entwicklung können nur innerhalb der begrenzten Phase geeigneter Umweltbedingungen stattfinden, während klimatisch ungünstige Bedingungen in einem Stadium der Diapause überdauert werden müssen. Die Fragen, wie Individuen ihre Lebenslaufstrategie an Saisonalität anpassen und welche Mechanismen der Reaktion auf saisonale Umweltreize (insbesondere der Photoperiode) zugrunde liegen, sind daher zentrale Aspekte in der Erforschung von Lebenslaufstrategien (e.g. Roff, 1980; Abrams *et al.*, 1996). Saisonale Anpassungen und die begleitenden Trade-offs sind jedoch sehr komplex und betreffen verschiedenste Lebensbereiche. Um die mögliche Bedeutung eines bestimmten Lebenslaufmusters als saisonale Anpassung zu verstehen, wird daher gefordert, das jeweilige Muster im Zusammenhang mit den Habitatcharakteristika (inklusive deren Variation in Raum und Zeit) zu betrachten, unter denen es evolvierte (Danks, 2006). Diese Arbeit beschäftigt sich mit Anpassungen der Lebenslaufstrategie des flügeldimorphen Gemeinen Wasserläufers *Gerris lacustris* L. (Heteroptera: Gerridae) an Saisonaliät. Mit einer Kombination aus Feld- und Laborstudien sowie mathematischer Modellierung untersuchte ich, wie Variationen in der Verfügbarkeit thermaler Energie auf verschiedene Aspekte der Larvalentwicklung - wie die akkumulierte thermale Energie (physiologische Entwicklungszeit), den Entwicklungsweg (direkte Reproduktion vs. Diapause) und den Flügeldimorphimus – Einfluss nehmen.

Die Lebenslaufstrategie von *G. lacustris* Populationen, die in unterschiedlichen thermalen Umgebungen leben, wurde an zwei Habitattypen – sonnenexponierten Feld- und beschatteten Waldteichen – empirisch aufgenommen. Diese beiden Habitattypen unterschieden sich signifikant in ihrer Oberflächen- und Wassertemperatur und damit in der pro Saison zur Verfügung stehenden (kumulativen) thermalen Energie. Zugleich befanden sich die insgesamt 63 in die Studie einbezogenen Teiche in so großer räumlicher Nähe, dass eine lokale genetische Differenzierung zwischen den einzelnen *G. lacustris*-Populationen ausgeschlossen werden konnte. Dennoch zeigten sich zwischen den beiden Habitattypen signifikante phänotypische Unterschiede im Lebenslaufmuster der dort lebenden Populationen. Während *G. lacustris* an den Waldteichen generell einen univoltinen Lebenszyklus zeigte, brachten die Populationen an den meisten Feldteichen zusätzlich zur diapausierenden "Winter"-Generation eine direkt reproduzierende "Mitsommer"-Generation hervor. Die Unterschiede im Lebenszyklus wurden von einem saisonalen Flügeldimorphismus begleitet. In beiden Habitattypen war die diapausierende "Winter"-Generation überwiegend langflügelig. Im

Gegensatz dazu war in der direkt reproduzierenden "Mitsommer"-Generation, die nur an den Feldteichen vorkam, der Anteil an Individuen mit verkürzten Flügeln stark erhöht.

Laborexperimente mit Nachkommen von Elterntieren aus einer Waldteich-Population zeigten, dass die zwischen den beiden Habitattypen beobachtete Variation in der Lebenslaufstrategie durch Unterschiede in der Aufzucht-Temperatur in Kombination mit der natürlichen Photoperiode induziert werden kann. Dies bestätigt, dass die beobachtete Flexibilität in der Lebenslaufstrategie unabhängig von der genetischen Herkunft der Individuen ist und im Wesentlichen auf phänotypischer Plastizität beruht. Eier und Larven von *G. lacustris*, die unter verschiedenen Temperatur-Bedingungen aufgezogen wurden, zeigten signifikante Unterschiede in ihrer Entwicklungsdauer. Diese Unterschiede wurden offensichtlich auch die deutlichen Temperaturunterschiede an den beiden Habitattypen verursacht. Tatsächlich erschienen Larven des ersten Larval-Stadiums an Waldteichen einige Wochen später als an Feldteichen. Dadurch bedingt erfuhren gleiche Larvenstadien während ihrer Entwicklung in den beiden Habitattypen unterschiedliche Photoperioden. Letztere ist das entscheidende Umweltsignal, das den reproduktiven Status so wie die Flügelausbildung in *G. lacustris* determiniert.

Um die Bedeutung der pro Saison zur Verfügung stehenden thermalen Energie für die beobachteten Lebenslaufstrategien genauer zu analysieren, wurden die physiologischen Zeiten, die zur Durchführung der verschiedenen möglichen Kombinationen von Lebenszyklen und Flügelausbildung notwendig sind, mit der thermalen Energie, die tatsächlich an den beiden Habitattypen in einer durchschnittlichen Saison vorhanden ist, verglichen. Dazu wurden die für die verschiedenen physiologischen Prozesse notwendigen thermalen Anforderungen getrennt für beide Flügelmorphen in kontrollierten Laborversuchen bestimmt. Hier zeigte sich bereits, dass kurzflügelige Individuen weniger thermale Energie zur Durchführung ihrer Juvenilentwicklung akkumulieren müssen als Individuen, die vollständige Flügel ausbilden. Der Vergleich zeigte, dass die in den natürlichen Habitaten zur Verfügung stehende thermale Energie den Lebenszyklus der *G. lacustris* Populationen streng limitiert. Entsprechend der empirisch beobachteten Strategien, erlauben die Temperaturbedingungen nur an den Feldteichen die Durchführung eines bivoltinen Lebenszyklus. Die Ergebnisse zeigten jedoch weiterhin, dass auch an Feldteichen die sichere Komplettierung eines bivoltinen Lebenszyklus während einer Saison die Reduktion der Flügel in wenigstens einer der beiden Generationen erforderte. Dies impliziert, dass auch der von *G. lacustris* gezeigte Flügeldimorphismus von der Limitierung durch die verfügbare thermale Energie beeinflusst wird. Während die zur Verfügung stehende thermale Energie zwar einen Wechsel von Uni- zu Bivoltinismus erlaubt, existiert offenbar zugleich ein Trade-off zwischen der

Erhöhung der Generationszahl und der Erhaltung der Flugfähigkeit im Laufe der Saison.

Neben der Umgebungstemperatur limitiert auch der Zeitpunkt, an dem ein Ei innerhalb einer Saison abgelegt wird, die für Wachstum und Entwicklung zur Verfügung stehende thermale Energie. Durch die Beobachtung der Entwicklung von sechs Kohorten von *G. lacustris*-Larven, die zu unterschiedlichen Zeitpunkten innerhalb der Saison geschlüpft waren, konnte ich zeigen, dass spät geschlüpfte Kohorten ihre physiologische Entwicklungszeit, und damit die während der Entwicklung akkumulierte thermale Energie, signifikant reduzierten. Solch eine Erhöhung der Entwicklungsgeschwindigkeit stellt eine Anpassung an das nahende Ende der Saison dar, setzt aber vermutlich eine erhöhte Energieaufnahme voraus. Um die Auswirkungen einer Futterlimitierung, wie sie Wasserläufer in natürlichen Systemen offenbar erfahren, auf die physiologische Entwicklungszeit zu überprüfen, wurden die Larven der sechs Kohorten unter zwei unterschiedlichen Futterbedingungen aufgezogen. In allen Kohorten war die physiologische Entwicklungszeit in den "high-food"-Gruppen stets niedriger als in den "low-food"-Gruppen, aber beide, "high"- so wie "low-food"-Individuen reduzierten ihre physiologische Entwicklungszeit zum Ende der Saison hin. Es zeigte sich jedoch, dass sich 20% der "low-food"-Individuen zu kurzflügeligen Imagos entwickelten während alle "high-food"-Individuen vollständige Flügel ausbildeten. Die Futterlimitierung könnte daher eine reduzierte Allokation von Energie in die Entwicklung des Flugapparates bewirkt haben, und ist damit möglicherweise verantwortlich für die starke Zunahme des Anteils kurzflügeliger Individuen am Ende der Saison, wie sie in vielen natürlichen Populationen beobachtet wird.

Die Möglichkeit, zwischen zwei alternativen Entwicklungswegen (diapausieren oder direkt reproduzieren) zu "wählen", wirft das Problem auf, den optimalen Zeitpunkt, um zwischen den beiden Entwicklungswegen zu wechseln, zu finden. Bei *G. lacustris* beobachtete ich einen sich über mehrere Wochen erstreckenden graduellen Übergang im Anteil an Larven, die sich in direkt reproduzierende Individuen entwickelten und denen, die nach Abschluss ihrer Entwicklung in Diapause gehen. Individuelle Unterschiede in der physiologischen Entwicklungszeit der einzelnen Tiere konnten die empirisch beobachtete Weite der Übergangszone zwischen den beiden Entwicklungstypen nicht ausreichend erklären. Basierend auf einem mathematischen Model zur Langzeit-Fitness verschiedener Lebenslauf-Strategien unter empirisch erhobenen Langzeit-Fluktuationen der Umgebungstemperatur, d.h. der pro Saison für Entwicklung zur Verfügung stehenden thermalen Energie, konnte jedoch gezeigt werden, dass die beobachtete Strategie als bet-hedging Strategie erklärt werden kann: Der graduelle Übergang von der Produktion direkt reproduzierender zu der

Produktion diapausierender Individuen maximiert offenbar die Langzeit-Fitness von *G. lacustris* in einer Umwelt mit unvorhersehbarer Saisonlänge.

Die Ergebnisse meiner Arbeit zeigen, dass der Gemeine Wasserläufer *Gerris lacustris* hinsichtlich seiner physiologischen Entwicklungszeit, seines Entwicklungsweges sowie seines Flügeldimorphismus die phänotypische Plastizität besitzt, auf Veränderungen der Saisonlänge zu reagieren. Dabei ist die für physiologische Prozesse zur Verfügung stehende thermale Energie der entscheidende Umweltfaktor, der die Saisonlänge bestimmt und damit die Lebenslaufstrategie von *G. lacustris* wesentlich beeinflusst. Die Studie betont zugleich, dass die alleinige Messung der von einem Organismus auf saisonale Umweltsignale gezeigten Reaktionen nicht immer ausreicht, um den Zusammenhang zwischen beobachteter Variation der Lebenslaufstrategie und saisonaler Anpassung zu erkennen. Für ein genaues Verständnis der Bedeutung beobachteter Veränderungen im Lebenslaufmuster als saisonale Anpassungen, muss die gezeigte Lebenslaufstrategie in engem Zusammenhang mit spezifischen Habitateigenschaften und deren räumlicher und zeitlicher Variabilität betrachtet werden.

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(Chapter 3 of this work)

Pfenning, B., Poethke, H.J. & Hovestadt, T. (2007) Dealing with temporal constraints on development: the effect of food availability. *Ecological Entomology*, 32: 273-278.
(Chapter 5 of this work)

Poethke, H.J., Pfenning, B. & Hovestadt, T. (2007) The relative contribution of individual and kin selection to the evolution of density-dependent dispersal rates. *Evolutionary Ecology Research*, 9 (1): 41-50.

Submitted

Pfenning, B., Gerstner, S. & Poethke, H.J. (submitted to Entomologia Experimentalis et Applicata) Alternative life histories in *Gerris lacustris*: temporal constraint on wing morph and voltinism.
(Chapter 4 of this work)

In prep.

Pfenning, B., Mitesser, O. & Poethke, H.J. (In prep) The annual reproductive pattern of the water strider *G. lacustris* in variable environments.
(Chapter 6 of this work)

Conferences & Workshops

Visited Conferences

Conference of the *Gesellschaft für Ökologie* (*GFÖ*) 2001, Basel, Switzerland – *poster presentation*

Annual meeting of the *Deutschen Gesellschaft für Orthopterologie*, 2002, Münster, Germany

'D*ispersal in fragmented landscapes*', 2003, Louvain-la-Neuve, Belgium– *poster presentation*

Second European Conference on Behavioural Biology (ECBB), 2004, Groningen, The Netherlands

Conference of the *Deutsche Gesellschaft für angewandte und allgemeine Entomology (DGaaE),* 2005, Dresden, Germany – *poster presentation*

Visited Workshops

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'*Survival of bush crickets in fragmented landscapes*', 2001, Field Station Fabrikschleichach, University of Würzburg, Germany

'*Small scale movement of bush crickets*', 2002, Westerhever, University of Kiel, Germany

'*Large scale dispersal of bush crickets*', 2003, Field Station Fabrikschleichach, University of Würzburg, Germany

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Erklärung

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der Promotionsordnung der Fakultät für Biologie der
Bayerischen Julius-Maximilians-Universität Würzburg

Hiermit erkläre ich ehrenwörtlich, die vorliegende Arbeit in allen Teilen selbständig und nur mit den angegebenen Quellen und Hilfsmitteln angefertigt zu haben.

Diese Dissertation hat weder in gleicher noch in ähnlicher Form in einem anderen Prüfungsverfahren vorgelegen.

Des weiteren erkläre ich, dass ich früher weder akademische Grade erworben habe, noch zu erwerben versucht habe.

Würzburg, den 11. Februar 2008

(Brenda Pfenning)