Chap. 6: Space - Influence of temperature and humidity on larval development; Measures of larval development as adult female fitness correlates?

6.1. Introduction

Temperature is one of the most important environmental factors for the functioning and effectiveness of physiological and biochemical mechanisms in insects (Willmer 1981). It affects profoundly activity, growth and reproduction (King et al. 1985, Blanckenhorn 1997, Hui & Bakke 1997). If temperature exceeds certain limits, mortality increases. Species differ considerably in their lethal limits (King et al. 1985, Jackson & Elliott 1988, Stiefel et al. 1997). Adult survival of *Diabrotica virgifera virgifera* (Coleoptera: Chrysomelidae) decreased, for example, significantly below 15 and above 31,5°C (Jackson & Elliott 1988).

In the field, unsuitable air-temperatures can, partly, be compensated by actively choosing a suitable microhabitat. As compensation for low air temperatures basking in the sun is a wide spread behaviour (Unwin & Corbet 1991). For example thermoregulation of *Diabrotica undecimpunctata howardi* at low air temperatures was accomplished by microhabitat selection (Meinke & Gould 1987). To cope with hot temperatures, larvae of the Colorado potato beetle, *Leptinotarsa*, moved under leaflets in the field. The proportion of larvae moving under the leaflet increased with both rising air temperature and insolation (Lactin & Holliday 1994).

If such compensation is not sufficient thermal conditions can limit the distribution of species to suitable habitats. In syntopic populations of two cicada species maximum daily egg production occurred at two different temperatures which corresponded with the thermal regime experienced by each species in its respective typical habitat (Toolson 1998). Bryant et al. (1997) showed temperature to be the responsible factor that determined and separated the geographic ranges of four butterfly species feeding on the same host plant.

For developing larvae unsuitable microclimate might either directly affect individual fitness by increasing mortality or indirectly via prolongation of the larval period or a reduction in final body size. Reductions in temperature are generally known to cause ectotherms to mature later at a larger size by lowering the growth rate and prolonging developmental time (Schroeder & Lawson 1992, Zwaan et al. 1992, Berrigan & Charnov 1994, Stiefel 1997).

Life history theory makes several assumptions about the effect of body size and duration of larval development on female reproductive success. (1) Longer development

results in larger adult size (Stearns 1992, Klingenberg & Spence 1997), (2) longer development results in higher larval mortality (Slansky & Scriber 1985, Loader & Damman 1991) and (3) female fitness and fecundity generally increase with body size (Larsson 1990, Honek 1993, Tammaru et al. 1996). A longer developmental period and larger pupal size should, under the same environmental conditions, lead to larger adult size and higher female fecundity. These predictions imply, however, also, trade-offs between reproductive benefits of large body size and costs of prolonged growth periods (e.g. through elevated mortality)(Klingenberg & Spence 1997).

Prolongation of the larval period might be caused by external factors, like food scarcity, low food quality (Slansky and Scriber 1985) or low temperature (Berrigan & Charnov 1994). Low food quality is known to be compensated for by prolonged feeding periods by chrysomelid larvae. Larvae feed until they reach a certain minimum size for pupation (Obermaier & Zwölfer 1999). There might be plasticity either in the duration of development with the result of a fixed final size (Obermaier & Zwölfer 1999) or in size with a fixed duration of development (Strohm, pers. comm.).

In field experiments I found that microclimate was probably responsible for the spatial separation of the beetle community in different microhabitats (chap. 5, chap. 7). In the first part of this chapter I tested this hypothesis in the laboratory. The influence of two different temperatures and humidities on duration of larval development, pupal weight and mortality was examined. Questions specifically investigated, were: (1) Does the “sun”-species *A. roseomarginata* differ in its temperature/humidity tolerance from the two “shade”-species, *A. quinquefasciata* and *A. confinis*, during larval development? (2) Which factor, temperature or humidity, has a stronger influence on development? Do the factors interact? (3) How do developmental time, pupal weight and mortality of every species change at a higher temperature/humidity?

Temperature, as well as other parameters of habitat and food quality (chap. 2 and 5), might influence body size. The second part of the study examined whether pupal weight or duration of larval development have an effect on adult female fecundity in this beetle community. The following questions were tested: (4) Are measures of larval development, like duration of development and pupal weight, correlated with adult female fecundity? (5) Are different measures of adult female fecundity (total lifetime egg number, mean egg number per week, egg laying period, total lifetime) correlated with each other and with adult body weight?

6.2. Material and methods

6.2.1. Larval development at two different temperatures (30°C and 40°C) and humidities (30% and 70%)

Laboratory experiments were performed at the University of Würzburg. As background for choosing certain temperatures for the laboratory experiments, I used two 6-day temperature intervals measured with a squirrel data logger in the field in April and May in 1995 (methods see chap. 5) and analysed them for day- and night time temperatures as well as means and maxima under sun and shade leaves. As a result I chose 25°C as the night time temperature for all treatments. Mean daytime temperature was 31°C (sun) and 29,5°C (shade) under a fresh leaf in the field which resulted in one treatment group with 30°C daytime temperature. Mean maximum daytime temperatures ranged between 37 and 45°C in the field which resulted in a second treatment group of 40°C daytime temperature. Humidity ranged from 30%RH in the dry season to 100%RH in the rainy season in the field. Technical possibilities allowed two humidity groups of 30%RH and of 70%RH. In total I tested four treatment groups: 30°C/30%RH, 30°C/70%RH, 40°C/30%RH and 40°C/70%RH. Three parameters of larval development were examined: developmental time, pupal weight and mortality of the larvae; in *A. confinis* only mortality could be compared because all the larvae of the 40°C treatment group died.

Larvae were kept singly in polyvinyl vials (8 x ∅3 cm) and were provided with single *M. hederacea* leaves, sticking in an eppendorf cup filled with water. The leaves were controlled daily and the ones wilted, heavily fed upon or discolored were substituted by newly harvested leaves. In climatic chambers (Tritec, Hannover) newly hatched larvae (not older than 24h) were exposed in four treatments to two different day temperatures (30°C or 40°C) and humidities (30% or 70% RH) till pupation. The climatic chambers had a 14h light and 10h dark cycle. During the 14h light the ”daytime temperature” (30 or 40°C) was provided, during the 10h dark phase the same ”night temperature” of 25°C was provided for all treatment groups. To avoid methodical errors, larvae, which had died on a wilted leaf or larvae which had died on the day after they had been transferred to a fresh leaf in the vial (probably due to difficulties of keeping attached), were excluded from the experiment. Thus the estimation of mortality is very conservative and much more larvae were tested than shown in the sample sizes of the tables. For *A. roseomarginata* and *A. quinquefasciata* all four treatment groups were tested with 20-46 larvae per group. Due to high mortalities, the treatment group 40°C/30%rh was run two times independently for both species. Only three treatment groups could be tested at the same

time because of a high handling time for the single larva. For *A. confinis* only two groups, 30°C/30% rh and 40°C/30%rh were tested due to a lack of newly hatched larvae in that species. I recorded, as larval parameters, mortality, duration of development of larvae (days from hatching till pupation) and dry weight of pupae.

The host plants for the experiments were cultivated of cuttings of *M. hederacea*-plants from the Comoé Park in the green house of the institute (temperature (day/night): 26°C/20°C, humidity (day/night): 65%/80%RH). A severe and continuous pest problem with Pseudococciodae (Homoptera: Coccina) was controlled by a regular application of *Chrysopa*-larvae (Sautter and Steppner GmbH, biological control company, Ammerbuch). Beetle populations from the field were bred in large plastic containers (27,5x42x30 cm) in a climatic chamber at 13h light (27°C) and 11h dark (24°C) and a constant humidity of 70%rh.

6.2.2. Duration of development and weight of pupae as fitness correlates

Two parameters of larval development, duration of larval development and pupal weight, were correlated with measurements of adult fitness like longevity and number of eggs laid per female. The experiment lasted from November 1996 till August 1997. Larvae of four species from the experiment ”larval development on different host plant species”(chap. 2) were kept until pupation, so that parameters of larval development of each individual were known. For the new experiment, eclosed females were weighed, individually colour marked, mated and kept singly with males in boxes. All were provided with the same food (*Ipomoea batatas*) and kept till oviposition stopped. Adult weight was registered two times, one time directly after eclosure between december 7-19 in 1996(adult weight 1) and a second time after a feeding period when oviposition had already started at May 5 in 1997 (adult weight 2). The number of eggs per week, the total lifetime egg number and the total adult lifetime of every female was recorded. Due to high mortality, sex rate (only females could be used) and loss of color marking, low numbers of individuals of the species remained (*A. quinquefasciata* (4), *A. confinis* (5), *A. indistincta* (9) and *A. nigromaculata* (5)).

6.2.3. Statistics

The influence of temperature and humidity on larval development, investigated in laboratory experiments, was analyzed by two-way anova (GLM; SPSS-package)(developmental time, pupal weight) and by multiway contingency tables (Zar, 1984)(mortality).

Because of low sample sizes, the correlation between measures of larval development and adult fitness was tested with Spearman rank correlation tests. If several correlations were conducted for one data set, probabilities were corrected with the Bonferroni correction (Bortz et al. 1990). To reveal interactions between total egg number per lifetime, total lifetime and mean egg number per week I performed two partial correlation analyses. All statistical procedures were computed with the SPSS-program package (vs. 7.0).

6.3. Results

6.3.1. Larval development in the laboratory at two different temperatures (30°C and 40°C) and humidities (30% and 70%)

Both, temperature and humidity, had a highly significant impact on developmental time of *Acrocassis roseomarginata*-larvae (F=11,29 and 26,13; p<0,001) (Fig. 6.1). The influence of the interaction of temperature and humidity also was significant (F=5,14; p<0,03). Development was faster at 30° than at 40°C and faster at 70% than at 30% rh. But neither pupal weight (F=0,514)(Fig. 6.2) nor mortality (X^2=2,0882)(Fig. 6.3) of the larvae differed significantly between the four treatment groups.

In *Aspidimorpha quinquefasciata* the treatment groups differed highly significantly in developmental time as well as in mortality and, as a trend, in pupal weight (Fig. 6.1, 6.2 and 6.3). I have no data for the 40°C/70%rh-group. Therefore I have no information about an interaction between temperature and humidity from the two way ANOVA. However, both, temperature and humidity alone, had a highly significant impact on developmental time of *A. quinquefasciata* larvae (F=23,52 and 21,16; p=0,001). Development was fastest at 30°C, 70%RH and slowest at 40°C, 30%RH. At 40°C, 70%RH all larvae had died before pupation (Fig. 6.1). In the three-dimensional contingency table, there was a significant interaction for temperature, humidity and mortality (X^2=35,11, p<0,001), temperature having a highly significant partial impact (X^2=31,789, p<0,001) and humidity having a significant partial impact (X^2=10,7802, p<0,05) on the mortality of *A. quinquefasciata*-larvae (Fig. 6.3). Mortality was considerably higher at 40° than at 30°C (76% and 100% vs. 40% and 5,9%). Mortality was lowest at 30°C, 70%RH. There was a trend that pupal weight differed between treatment groups (Fig. 6.2: F=3,196, p=0,055) with a significant impact of the humidity. Larvae grew larger at 30°, 70% than at 30%RH.

A. confinis was only tested at 30%RH for both temperatures. Larval mortality differed highly significantly between 30°C and 40°C (X^2=14,166, p<0,001), with 100% mortality at 40°C (Fig. 6.3).

Among the four treatment groups, the larvae of all beetle species developed best at 30°C and 70%rh (*A. roseomarginata* and *A. quinquefasciata*) or 30°C/30%rh (*A. confinis*) Species differed, however, in their tolerance towards hotter and/or drier conditions. *A. roseomarginata* was by far the most tolerant species with regard to hot temperatures (40°C) and larvae developed at 40°C/70%RH as well as at 30°C/70%RH until pupation. The mortality of *A. roseomarginata* did not differ between the four treatment groups. The mortality of *A.quinquefasciata* and *A.confinis*, in contrast, was very high at 40°C (70-100%).

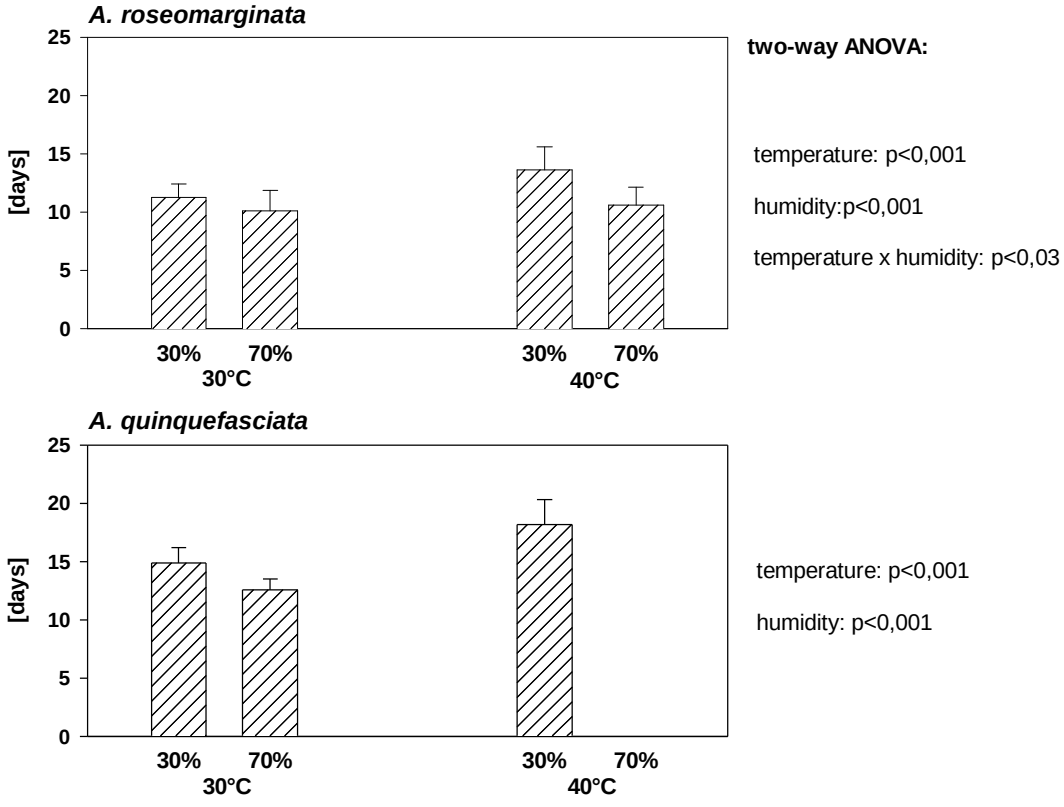

Fig. 6.1: Duration of larval development of two beetle species at two different temperatures and two humidities in the climatic chamber.

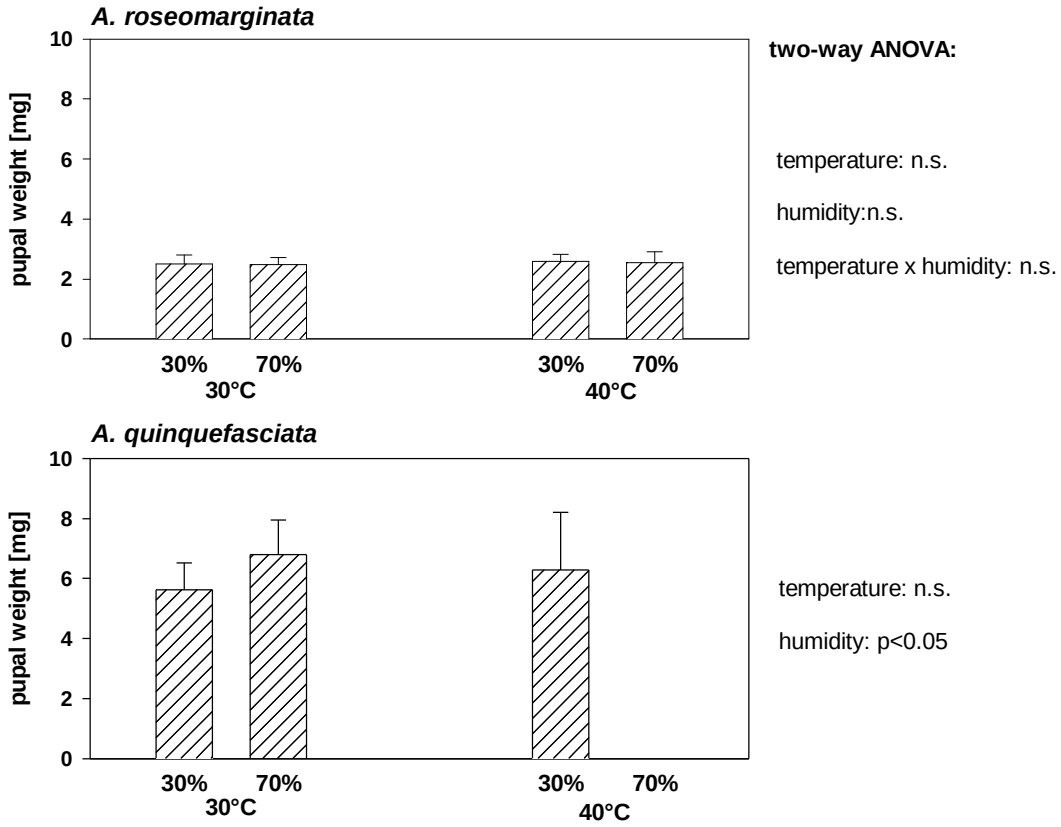

Fig. 6.2: Pupal weight of two beetle species which developed at two different temperatures and two humidities in the climatic chamber.

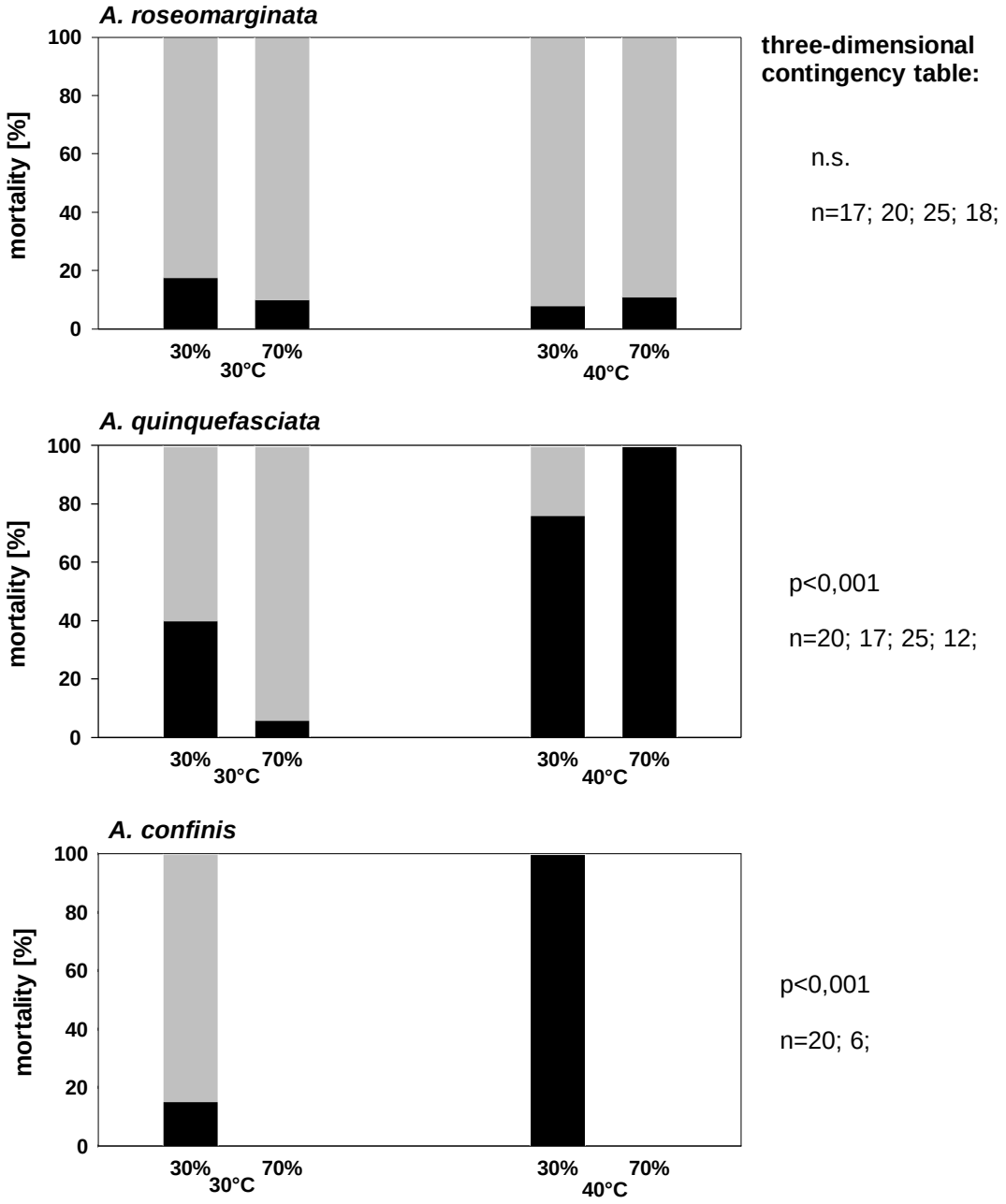

Fig. 6.3: Effects of daytime temperature (30°C and 40°C) and humidity (30% and 70%rh) on the mortality of larvae of *A. roseomarginata*, *A. quniquefasciata* and *A. confinis.*

6.3.2. Measures of larval development, rate of reproduction and fitness of adult females

This experiment was set up to test the hypothesis that high pupal weight and fast development indicate high female reproductive success (high fitness) and thus high habitat/food quality.

6.3.2.1. Life table parameters of four beetle species, referring to larval and adult period

Tab. 6.3 compares the life table parameters of the four beetle species which were tested later on for a correlation between larval development and adult female fitness. The four beetle species differed profoundly in their adult body weight (adult weight 2), their lifetime egg number and their mean egg number per week. The two smaller species, *A. confinis* (36 mg) and *A. nigromaculata* (18 mg) had slightly higher life expectancies and thus longer egg-laying periods than the two larger species, *A. quinquefasciata* (63 mg) and *A. indistincta* (57 mg). The species with the least adult weight, *A. nigromaculata*, had the highest lifetime egg-number (497 eggs) per female, the highest mean egg number per week (22 eggs) and the highest longevity (236 days)(vs. 121 eggs during lifetime, 9 eggs/week and 166 days of lifetime of *A. indistincta)*. All numbers represent means. Egg numbers of *A. quinquefasciata* were only estimated in this comparison because this species laid its eggs in egg clutches which contained different numbers of eggs (3-12; lower numbers occurred more often). Egg number was calculated conservatively as number of egg clutches times 3 (mean egg number)(Tab. 6.3). Egg size of the four species seemed to be approximately the same. Eggs were, however, difficult to weight because of their cover with secretion.

Regarding the larval period, *A. quinquefasciata* was the species with the fastest development (16,8 days). The relation and the size of pupal weight in the four species was similar to adult weight 1 (directly after eclosion without feeding) but changed when adults underwent a feeding period (adult weight 2). Adult females gained 8-35 mg in body weight, and therefore in some cases doubled their weight until oviposition started. *A. indistincta* and *A. quinquefasciata* "switched positions", *A. indisticta* having the heaviest pupae (40,57 mg) and *A. quinquefasciata* the heaviest adults (63,11 mg) of the four species.

Tab. 6.3: Life table parameters of four beetle species, *A. quinquefasciata, A. confinis, A. indistincta* and *A. nigromaculata*. Numbers in brackets mean egg clutches (otherwise single eggs are counted). Mean and standard error.

	A.q.	***A.c.***	***A.i.***	***A.n.***
	x ± SE	**x ± SE**	**x ± SE**	**x ± SE**
Larvae:				
Developmental time [days]	16,8 ± 0,8	19,4 ± 0,5	21,1 ± 0,5	20,2 ± 0,9
Pupal weight [mg]	35,53 ± 3,62	26,24 ± 0,66	40,57 ± 0,92	12,32 ± 0,32
Adult females:				
Adult weight 1 (after eclosure) [mg]	28,23 ± 3,30	20,92 ± 0,46	32,85 ± 0,98	9,56 ± 0,41
Adult weight 2 [mg]	63,11 ± 3,46	36,14 ± 1,25	56,53 ± 1,38	17,90 ± 0,24
Lifetime egg-number	302,4 (100,8 ± 17,5)	367,4 ± 164,8	121,1 ± 41,6	497,4 ± 132,1
Max. egg-number per week	-	47,8 ± 14,5	17,7 ± 2,2	49,0 ± 7,9
Mean egg-number per week	16,8 (5,6 ± 1,1)	20,9 ± 6,8	8,9 ± 1,8	22,1 ± 3,7
Egg-laying period [weeks]	18,8 ± 2,4	35,4 ± 20,3	12,7 ± 3,1	21,6 ± 4,1
Total lifetime [days]	200,8 ± 16,9	230,3 ± 35,5	166,1 ± 22,0	235,8 ± 35,1
N	4	5	9	5

6.3.2.2. Duration of development and pupal weight as fitness correlates

Two measures of larval fitness, duration of development and pupal weight were analysed with each other and with several correlates of adult female fitness, like lifetime egg number, mean egg number per week and total longevity of the beetle individuals. Only the parameter ”adult weight 1” (weight directly after eclosure from pupa) showed a trend for a positive correlation (*A. nigromaculata* and *A. confinis*) or correlated significantly (*A. indistincta*, r=0,833, p=0,005) with pupal weight (Tab. 6.4.a, 6.5.a, 6.6.a). Only in *A. indistincta* adult weight 1

showed also a trend of a negative correlation with developmental time (r=-0,812, p=0,008 (with Bonferroni correction), Tab. 6.4a). In *A. nigromaculata* (Tab. 6.5.a) trends of correlation further could be seen between pupal weight and adult weight 2 and between pupal weight and maximum egg number per week (negative!).

In summary, in the three species tested, there was no significant correlation between measurements of larval development (duration of development, pupal weight) and lifetime (=total) egg number. The measurements of larval development, under laboratory conditions given, did not impart an indication for the further reproductive success and fitness of the adult beetle individuals.

I also correlated different measures of adult female fitness with each other. In *A. indistincta*, the species with the highest sample size examined (n=9), I found several trends and one significant interaction between lifetime egg number and other measures of adult female fitness (Tab. 6.4.b). Total egg number correlated significantly with maximal egg number per week (r=0,795, p=0,01) and showed a trend of a positive correlation with mean egg number per week (r=0,753, p=0,019), egg laying period (r=0,757, p=0,018) and total lifetime (r=0,700, p=0,036). The "most fecund females", with highest egg numbers during lifetime, could have either laid eggs for a longer time and lived longer or laid more eggs per week. To discriminate between these two components I controlled via a partial correlation analyses for (1) total lifetime. The partial correlation coefficient for total egg number vs. mean egg number per week was raised to r=0,8919 (p=0,003, significant). Second, I controlled (2) for mean egg number per week which resulted in even a highly significant partial correlation coefficient of r=0,9733 (p=0,000) for total egg number and total lifetime. This means that both factors had an impact on total egg number and both strategies were persecuted, but the influence of total life time was larger than that of mean egg number per week.

The other two beetle species showed only few results with a significant correlation. In *A. nigromaculata* there was a trend of correlation of total egg number with mean number of eggs per week (r=0,900, p=0,037)(Tab. 6.5.b) and in *A. confinis* total egg number was highly significantly correlated with maximal egg number per week (r=1,000, p=0,000)(Tab. 6.6.b).

Tab. 6.4.a: Measures of larval development of *A. indistincta* correlated with adult female fitness correlates. Bonferoni correction a = 0,05/8 = 0,006. Spearman rank correlation. Light grey columns: trend of correlation, dark grey columns: significant correlation with p<0,006.

		Dev. time	Pupalweight	Adult weight 1	Adult weight 2	Total egg-nr.	Max. egg-nr. per week	Mean egg-nr. per week	Egg laying period (week)	Total lifetime
Developmental time	r_s	-	-0.607	-0.812	-0.395	0.222	0.270	0.331	0.268	0.504
	p	-	0.083	0.008	0.332	0.565	0.482	0.385	0.486	0.166
	n	-	9	9	8	9	9	9	9	9
Pupal weight	r_s	-0.607	-	0.833	0.476	-0.417	-0.636	-0.636	-0.279	-0.217
	p	0.083	-	0.005 *	0.233	0.265	0.066	0.066	0.468	0.576
	n	9	-	9	8	9	9	9	9	9

Tab. 6.4.b: Total egg number during lifetime correlated with different measures of female fitness in *A. indistincta*. Bonferoni correction a = 0,05/5 = 0,01. Spearman rank correlation. Light grey columns: trend of correlation, dark grey columns: significant correlation with p<0,01.

		Adult weight 2	Max. egg-nr. per week	Mean egg-nr. per week	Egg laying period (week)	Total lifetime
Total egg number	r_s	-0.667	0.795	0.753	0.757	0.700
	p	0.071	0.010 *	0.019	0.018	0.036
	n	8	9	9	9	9

Tab. 6.5.a: Measures of larval development of *A. nigromaculata* correlated with adult female fitness correlates. Bonferoni correction a = 0,05/8 = 0,006. Spearman rank correlation. Light grey columns: trend of correlation.

		Dev. time	Pupalw eight	Adult weight 1	Adult weight 2	Total egg-nr.	Max. egg-nr. per week	Mean egg-nr. per week	Egg laying period (week)	Total lifetime
Developmental time	r_s	-	0.700	0.400	0.400	-0.300	-0.600	-0.500	-0.600	0.100
	p	-	0.188	0.505	0.505	0.624	0.285	0.391	0.285	0.873
	n	-	5	5	5	5	5	5	5	5
Pupal weight	r_s	0.700	-	0.900	0.900	0.200	-0.900	-0.100	-0.500	0.100
	p	0.188	-	0.037	0.037	0.747	0.037	0.873	0.391	0.873
	n	5	-	5	5	5	5	5	5	5

Tab. 6.5.b: Total egg number during lifetime correlated with different measures of female fitness in *A. nigromaculata*. Bonferoni correction a = 0,05/5 = 0,01. Spearman rank correlation. Light grey columns: trend of correlation.

		Adult weight 2	Max. egg-nr. per week	Mean egg-nr. per week	Egg laying period (week)	Total lifetime
Total egg number	r_s	0.600	0.100	0.900	0.400	0.500
	p	0.285	0.873	0.037	0.505	0.391
	n	5	5	5	5	5

Tab. 6.6.a: Measures of larval development of *A. confinis* correlated with adult female fitness correlates. Bonferoni correction a = 0,05/8 = 0,006. Spearman rank correlation.

		Dev. time	Pupal weight	Adult weight 1	Adult weight 2	Total egg-nr.	Max. egg-nr. per week	Mean egg-nr. per week	Egg laying period (week)	Total lifetime
Developmental time	r_s	-	0.872	0.616	0.051	0.205	0.205	0.564	0.359	-0.949
	p	-	0.054	0.269	0.935	0.741	0.741	0.322	0.553	0.051
	n	-	5	5	5	5	5	5	5	4
Pupal weight	r_s	0.872	-	0.900	0.100	0.500	0.500	0.600	0.600	-0.800
	p	0.054	-	0.037	0.873	0.391	0.391	0.285	0.285	0.200
	n	5	-	5	5	5	5	5	5	4

Tab. 6.6.b: Total egg number during lifetime correlated with different measures of female fitness in *A. confinis*. Bonferoni correction a = 0,05/5 = 0,01. Spearman rank correlation. Light grey columns: trend of correlation, dark grey columns: significant correlation with p<0,01.

		Adult weight 2	Max. egg-nr. per week	Mean egg-nr. per week	Egg laying period (week)	Total lifetime
Total egg number	r_s	0.700	1.000	0.700	0.700	0.400
	p	0.188	0.000 ***	0.188	0.188	0.600
	n	5	5	5	5	4

6.4. Discussion

6.4.1. Larval development at different temperatures and humidities

Field experiments revealed that microhabitats differed in plant quality as well as in microclimate (chap. 5). Whereas plant quality was more suitable in the shade for all beetle species tested, larvae of different species differed in their response to microclimatic conditions. To test if and which microclimatic factors are responsible for the different performance, larval development at different temperatures and humidities was tested in the laboratory. *A. roseomarginata*, a species preferring sunny microhabitats in the field, was expected to develop better at higher temperatures, whereas *A. quinquefasciata* and *A. confinis* which could be found mainly in the shade were expected to perform better at lower temperatures and high humidities.

As treatments I used the mean daytime temperature (30°C) and the mean maximum daytime temperature (40°C) measured in April and May under leaves of the host plant in the field. Temperature, humidity and the interaction of both had a significant impact on the duration of the developmental period of the larvae of *A. roseomarginata*. Treatments had no impact on pupal weight or mortality. That means, although larvae developed fastest at 30°C/70%RH, individuals of this species could tolerate temperatures as high as 40°C without suffering a higher rate of mortality. Larvae of the two other species investigated, also developed significantly faster at 30°C than at 40°C. Mortality, however, in those species differed significantly between treatment groups. Mortality was significantly higher at 40°C than at 30°C. In two of the experimental groups at 40°C (*A. quinquefasciata* (40°C/70%RH) and *A. confinis* (40°C/30%RH)) there was a 100% mortality. These experiments thus document that *A. roseomarginata* larvae have a stronger tolerance of high temperatures (40°C) than the two other species. Humidity, too, had a significant impact on larval development. Its effect, however, varied. At lower temperatures high humidity could accelerate development and increase pupal weight, at high temperatures , on the contrary, it could increase mortality.

It has been shown before, that the thermal requirements of a species can lead to a different habitat use. Two cicada species, living in New Mexico desert grasslands, achieved maximum daily egg production when shade ambient temperatures reach either 41°C (*Cacama valvata*) or 33°C (*Tibicen bifidus*)(Toolson 1998). These differences correlated with the thermal regime experienced by each species in its respective typical habitat. Of two psyllid species in the UK and Norway using the same host plant, the smaller and darker species could develop more rapidly and thus deal with a lower thermal budget, which explained its larger

distribution area (latitudinal and altitudinal) in comparison to its congener (Bird & Hodkinson 1999). In the case of four species of nettle-feeding nymphalid butterflies temperature requirements broadly explained the relative distributions and differences in voltinism of theses species and were therefore responsible for a geographical separation (Bryant et al. 1997).

Most studies on the effect of temperature on larval development describe a decrease in duration of development and in body size with increasing temperatures (Zwaan et al. 1992, Berrigan & Charnov 1994, Hui & Bakke 1997). Neither one of the two effects could be observed in this experiment. An explanation might be, that the second temperature (40°C) was already beyond the range of suitable temperatures. In the literature, species differed in their range of optimum temperatures and the upper and lower limit at which mortality began to increase. Larvae of *Diabrotica virgifera virgifera* (Chrysomelidae) experienced an optimum development at 21-30°C, adult survival decreased at 15 and 31,5°C (Jackson & Elliott 1988). Optimum temperatures for development of the pea weevil (Chrysomelidae) were 32,7-41,8°C, but temperatures were stage specific (Smith and Ward 1995). Development to adults of *Anomoea flavookansiensis* (Chrysomelidae) was best at 25-29°C, survival decreased dramatically below 21 and above 33°C (Stiefel et al. 1997). In all instars, feeding rates of Colorado potato beetle larvae (Chrysomelidae) were greatest at 29°C and decreased both at higher and lower temperatures. From the second instar on larvae could develop up to a temperature of 42°C (Lactin 1993). Larvae of the elm leaf beetle exhibited high mortality at 36,1°C (optimum temperatures 22,2 and 28,8°C)(King et al. 1985).

The laboratory experiments in this study confirmed the results of the field experiments (chap.5). *A. roseomarginata,* the species with the highest abundance in sunny microhabitats in the field, showed a higher tolerance of high temperatures in larval development. The other two species, both preferring microhabitats in the shade, experienced a very high mortality at 40°C, a temperature which corresponds to mean maximum daytime temperature on the lower side of leaves in the field. A further discrimination of *A. quinquefasciata* and *A. confinis,* which the abundance data in different microhabitats in the field suggested (chap. 5), could not be made with the present data because of too small sample sizes of *A. confinis*. The hypothesis of a spatial niche separation due to competition had to be rejected in the case of *A. roseomarginata*, in favour of a separation of this beetle species by its different thermal biology.

6.4.2. Larval development and adult female reproductive success

Fitness is defined by the reproductive output of an individual and the further success of its offspring. In the first part of the chapter I investigated the influence of temperature and humidity on larval mortality, pupal weight and duration of development. In the second part I tested the hypothesis, that pupal weight and duration of larval development are correlated with adult female fecundity and thus can predict fitness in the beetle species investigated. Duration and weight parameters of larval development were used in several experiments of this study to test food or habitat quality (chap. 2, 5, 6), because of the fast growth rate in that phase, the distinct time span of that period and the relatively easy handling of larvae.

Duration of larval development or pupal weight correlated with none of five measures of adult female fitness (total lifetime egg number, maximal egg number per week, mean egg number per week, egg laying period, total lifetime), in all three species tested. This means that neither larval development nor pupal weight could predict further reproductive success of the beetle individuals in this study. My experimental results might be interpreted with care, due to low sample sizes per species (n=5-9), the long experimental period (Nov.´96-Aug.´97), the pooling of individuals, which were fed as larvae with different plant species (food after pupation was uniform) and the rearing under laboratory conditions. Pupal weight in *A. indistincta* is significantly positively correlated with adult weight 1, at emergence, but no longer with adult weight 2, later in life. No significant correlation between pupal weight and duration of development could be detected. Life history theory predicts, in general, an increase in body size with increasing duration of development (Stearns 1992) and an increase in fecundity with an increase in body size (Ohgushi 1987, Larsson 1990, Honek 1993, Tammaru et al. 1996, Sopow & Quiring 1998). Recent optimisation models, however, contradict such fixed relations and show flexible responses of growth rates, body sizes and development times, depending on other factors such as predation pressure (Abrams et al. 1996).

Although, in this study, larval development did not correlate with adult female fitness measures, duration of larval development can have an implication for the fitness of an individual on its own. Several studies confirmed, that a longer exposure towards predators or parasitoids (prolonged duration of development, prolonged duration of feeding per day), due to low food quality or unsuitable microclimatic conditions, increased mortality during the larval period (Slansky & Scriber 1985, Loader & Damman 1991).

When single life history traits were compared, two *Aspidimorpha* species from a tropical savanna in Indonesia showed some similar patterns as the species in Ivory coast. The

adults in Indonesia showed an extreme longevity with an oviposition period of up to six months in the field as well as in the laboratory (Nakamura & Abbas 1989)(West African species: oviposition period up to 8 months). The prolonged survival was interpreted by the authors as adaptation for living in tropical environments where rainfall is ample but unpredictable.

Three hypotheses, derived from predictions of life history theory, on the effect of unsuitable high temperatures on fitness, were investigated or discussed in this chapter: (1) Very high temperatures increase larval mortality (Willmer 1981). (2) Higher temperatures lead to smaller pupal weight (Berrigan & Charnov 1994). Smaller pupal weight (body size) results in lower female reproductive success (Honek 1993, Tammaru et al. 1996). (3) Higher temperatures reduce duration of development (Berrigan & Charnov 1994) and reduce therefore predator-mortality (Slansky & Scriber 1985, Loader & Damman 1991).

(1) *A. confinis* and *A. quinquefasciata*, but not *A. roseomarginata*, showed a significantly higher larval mortality at 40°C than at 30°C. The latter species obviously had a better tolerance for high temperatures. (2) Pupal weight in this study was not (*A. roseomarginata*), or almost not (*A. quinquefasciata*), significantly affected by temperature (or humidity). The same was true for all other experiments in this thesis which tested pupal weight under diverse treatments (host plant species (chap. 2), habitat and food quality (chap. 5)). This is in accordance with the results in the second part of this chapter, where pupal weight did not correlate significantly with adult female reproductive success in none of three species investigated. There might be a fixed final size which has to be reached before pupation. The larvae might compensate for unsuitable microclimatic conditions or low food quality by longer feeding periods and therefore longer developmental times. This is in agreement with results from a palaearctic species of Chrysomelidae, *Oreina luctuosa*, where duration of development was much more variable than pupal weight (Obermaier & Zwölfer 1999). (3) In spite of predictions from life history theory, a temperature of 40°C (high temperature) significantly prolonged duration of development of *A. roseomarginata*- and *A. quinquefasciata*-larvae. A longer duration of development can have an indirect influence on fitness via an increase in predator-mortality (see above).