Chap. 7: Effect of habitat and predator exclusion on larval parasitism and predation

7.1. Introduction

Possible proximate causes for spatio-temporal abundance patterns of coexisting species of herbivores, living on the same host plant species, are various. They include local microclimate, plant quality, competition, predation/parasitism (Brown et al. 1997) and species specific physiological optima (Bryant et al. 1997). Different predation pressure in different locations can influence the habitat choice and determine the niches (enemy-free space) of species feeding on the same host plant (Berdegue et al. 1996), and contribute finally to the coexistence of those species.

Effects of predators and parasitoids on the spatial distribution of herbivores have been shown in several instances. For example the aphid, *Monaphis antennata*, uses the ”enemy-free space” on the upper leaf side to avoid predators (Hopkins & Dixon 1997). Likewise, caterpillars feed in shaded parts of the plant, even though larval growth is reduced, and thus avoid predatory wasps (Stamp and Bowers 1988). Egg and larval mortality, of three related butterfly species, due to predators and abiotic factors was higher in sunny habitats than in the shade. This had, however, no influence on choice of the oviposition site (Rausher 1979).

Success of parasitoids and predators in different habitats may depend on abiotic factors. Organisms as small as parasitoids are strongly affected by temperature, humidity, wind and/or rain. Only a few field studies on the impact of these abiotic factors, however, exist (Fink and Völkl 1995, Weisser et al. 1997). The results from laboratory studies, examining the effect of temperature or humidity on various life history parameters of parasitoids, differ greatly between species (Tuda and Shimada 1995, Dyer and Landis 1996, Takagi and Murakami 1997, Spring and Kok 1997). Insect parasitoids and predators may differ in their physiological capacities from the ecological preferences of their hosts. These parasitoid-host interactions might lead to spatial patterns in host abundance.

Abiotic factors may also directly influence the survival of ecto-phytophagous larvae. Wash-off by rain or dislodging by wind is likely to contribute to the mortality of larvae (Spring & Kok 1997). Temperature-extremes are known to limit the distribution of herbivorous species even if feeding on the same host plant species (Bird & Hodkinson 1999).

Arthropod predators known to feed on Chrysomelids include hemipteran bugs, spiders, syrphid flies, eumenid wasps and ants (Olmstead & Denno 1993, Chattopadhyay and Sukul 1994, Rank et al. 1996). Parasitoids of Chrysomelid-eggs and larvae are very diverse (Ward

and Pienkowski 1978, Morrison and Strong 1981, Ang and Kok 1995). Exclusion experiments make it possible to assess the quantitative impact of different mortality factors. Quantitative studies using predator exclusion techniques have been conducted only in temperate climates until Memmott et al. (1993), and for tropical regions, very little is known about such interactions over three trophic levels.

Of several factors which may be responsible for spatial niche differentiation within a herbivore community, we examined larval parasitism, predation and other mortality factors. We tested whether the impact of these mortality factors on coexisting leaf beetle species differed among habitats in a way that could explain the distribution and abundance of these species. For the experiments we used two closely related West African species of leaf beetles, *Acrocassis roseomarginata* and *Aspidimorpha quinquefasciata* (Chrysomelidae: Cassidinae), which occur syntopicly on the same host plant system (Fam. Convolvulaceae). Further we tried to assess the importance of the different mortality factors by exclusion experiments. We distinguished three categories: (1) abiotic factors and pathogens, (2) walking and flying predators and (3) parasitoids.

Specifically we asked the following questions: 1. Do the predation/parasitism rates of the larvae of the two investigated chrysomelid species differ among different habitats? 2. Do larvae of the two related species on the same host plant experience different rates of predation/parasitism? 3. Which larval stage suffers the highest mortality? 4. How do different factors contribute quantitatively to total mortality?

7.2. Materials and methods

7.2.1. Study sites, host plants and beetle species

The experiments were conducted in the rainy season in May/June 1995 and repeated in June/July 1997 in the Comoé-National Park in the North East of Côte d´Ivoire.

The beetle species, *Acrocassis roseomarginata* and *Aspidimorpha quinquefasciata* (Chrysomelidae: Cassidinae) occur syntopicly on the same host plants and eggs, larvae, pupae and adults can all be found on the leaves. They were the most abundant species of seven coexisting species of Cassidinae investigated (Obermaier, pers. observ.). All host plant species are members of the family Convolvulaceae. At river side habitats the only host plant is *Merremia hederacea*; in the savanna the most abundant species are *Ipomoea heterotricha* and

Ipomoea eriocarpa. Depending on the time of the year and the site investigated the density of the host plants in either habitat is highly variable,.

Three main habitats were compared experimentally in this study: sunny river side, shady river side and savanna (short: river sun, river shade, savanna). In the savanna the vines grew horizontally and were interspersed among the grass. The grass grew until October and reached heights up to 2 m. Two distinct habitats at the river side were investigated. In full sun vines grew horizontally on large rocks while in deep shade vines grew vertically up to 10m on trees and shrubs. Microclimate showed larger extremes at river bank sites where both beetle species were more abundant than in the savanna. The density of *A. roseomarginata* in the savanna was about half as high compared to the river, while that of *A. quinquefasciata* was about a quarter compared to the river in 1995. *A. roseomarginata* was by far the most abundant species at the river bank as well as in the savanna at the time of its occurrence. At the river side, *A. roseomarginata* was most abundant in very hot, sunny microsites on rocks and in grass in the sun. *A. quinquefasciata* occurred mainly under shrubs and trees in the shade. The two beetle species differed significantly in their distribution over sun and shade microhabitats at the river side in 1995 (X^2=120.29; p<0.001) (Obermaier, pers. observat.).
Minimal and maximal temperatures, as well as the amount of rainfall per day, were recorded in a weather station at the camp site close to the study sites. Temperature in sun and shade habitats was measured with the data logger Squirrel 1200 (Grant Instruments, Cambridge, UK).

7.2.2. Predation and parasitism experiments

Each experimental group consisted of 6-12 individually potted plants (depending on the number of larvae available), that were distributed in the habitats tested; the plant species used for cultivation was *Merremia hederacea*. The plants were cultivated from cuttings, potted after they had started to grow roots and kept under slightly shady conditions until large enough (ca. 30 cm) to provide sufficient food for the larvae (after about 2 weeks). Pots were coated with a ring of glue (tangle foot®) to prevent larvae from leaving the plants. The effect of this glue on crawling predators and therewith on total mortality rates is considered in the context of the exclusion experiments. The pots were placed in the field and six larvae (hatched within the last 24h) per plant were placed, with tweezers, on the leaves of each plant and observed until they started to move independently on the leaf (ca. 2 min.). (In the group ”*A. roseomarginata*, shade, 1997”, 7 larvae per plant were used.)

To compare the two species and three habitats, a total of five (in 1995) and six (in 1997) treatment groups were used. No savanna group existed for *A. quinquefasciata* in 1995. The plants were distributed individually in the three habitats (ca. 5-20m distant from each other), each one close to a naturally occurring host plant. For the habitat type river sun, plants were put on rocks in the open sun or between small grass plants in the sun. In the river shade habitat plants were placed under shrubs in the shade. In the savanna habitat plants were placed between the high grass. In both of these habitats care was taken to prevent any contact between the experimental plants´ leaves with the surrounding vegetation. The plants were watered and the larvae were counted daily till the day of pupation. The pupae were kept in petridishes till either the adult beetles or the parasitoids emerged. The mortality rate per day, the percentage of pupae parasitized and the overall mortality was calculated for each group.

7.2.3. Larval mortality of A. roseomarginata under differing predator exclusion

This experiment was conducted only in 1995. River sun was used as habitat for this experiment since this is where *A. roseomarginata* naturally showed the highest abundance. Different mortality factors were excluded: (1) by cage (no predators), (2) by a stripe of glue around the pots (no walking predators) and (3) no treatment (walking and flying predators admitted). Each treatment group consisted of ten plants. Parasitoids had access to all treatment groups. Because parasitoids emerged from collected pupae, mortality due to parasitism could be separated from the other factors. John Noyes (British Museum, London) determined all parasitoid specimens. Parasitoids could enter the cage, but mortality caused by parasitoids could be separated and was not considered for calculation of ”non-predator mortality”.

The cage measured 1x1x1m^3 and was covered with a metal mesh (about 1mm width). The cage had a closed bottom and was put on wooden legs that were covered with glue as to exclude all predators from the ground. The treatment group ”cage” consisted of ten plants (60 larvae) which were placed in one cage. Larvae within the cage were only subject to abiotic factors and pathogens and therefore assumed to be independent samples. Parasitoids had access to the cage, but could be separated from the other mortality factors. However, to avoid pseudoreplication in any case, no statistical test was applied to this treatment

7.2.4. Egg parasitism of Acrocassis roseomarginata

At the end of May 1000 leaves of *M. hederacea,* on each of 6 river bank sites, were investigated for *A. roseomarginata* eggs. The eggs were classified as ”not yet hatched”,

”parasitoid hatched” and ”beetle larvae hatched”. Whether a beetle larva or an egg parasitoid had hatched could be determined by the shape of the hole: A small, round hole in the centre of the egg was caused by a parasitoid, while a widely torn egg shell meant the hatching of a beetle larvae. For the calculation of parasitism rates only the numbers of hatched eggs were used because we could not know what would emerge from eggs not yet hatched. The result might have been further biased if egg parasitoids needed much longer for hatching or egg shells where beetle larvae hatched were more easily removed by wind or rain. We found, however, no indication that either of these possibilities occurred.

7.2.5. Statistics

Single larvae and pupae but not larvae per plant were treated as replicates of the treatment groups. Larvae of one plant were treated independently because daily mortality records revealed that number of larvae decreased one by one over a long period of time. This clearly indicates that mortality of larvae occurred independently from each other even though they were feeding on the same plant. Percent parasitism or mortality per group was calculated. The three habitats were compared by Chi^2-tests. Pair-wise comparisons of habitats were conducted with Bonferroni-correction. T-Tests were calculated using the program package SPSS.

7.3. Results

7.3.1. Predation and parasitism in different habitats

Three habitats, river sun, river shade and savanna were compared in 1995 and 1997. In March till June mean maximum temperatures on the lower leaf side were 40-49°C in the sun and 38-41°C in the shade. Parasitoids should be, because of their small body size, especially vulnerable towards temperature extremes. Due to more favourable microclimatic conditions, we expected higher rates of parasitism in the shade than in the sun habitat at the river side.

In river side habitats and in savanna habitats respectively, mean maximal densities of *A. roseomarginata* were 11.20 and 4.97 indiv./100 leaves and of *A. quinquefasciata* 2.10 and 0.67 indiv./100 leaves. Densities of both beetle species were higher at river side habitats than in the savanna. Because of possible density dependent, density independent as well as inverse density dependent responses of the parasitoids it was, however, difficult to predict parasitism and mortality in different habitats in advance. Investigating density dependence was beyond the scope of this study, where we treated mortality factors as black box systems.

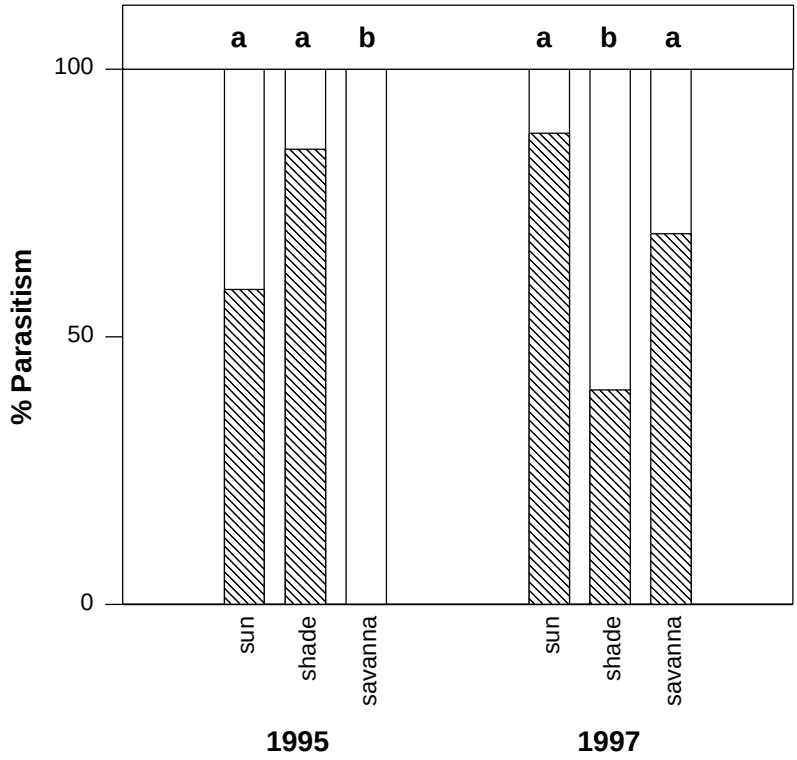

Fig. 7.1: Rates of parasitism of larvae of *Acrocassis roseomarginata* in different habitats in 1995 and 1997. Sample size was the number of larvae pupating in each group (n=17; 20; 16 (1995) and n=18; 10; 13 (1997)). X^2-test. Different letters indicate significant differences between groups ($p<0.05$).

Parasitism of *A. roseomarginata* larvae differed significantly among the three sites in 1995 ($X^2=39.49$, $p<0.001$)(Fig. 7.1). There was no parasitism at all in the savanna habitat. The species showed a trend of higher parasitism in the shade (85% vs. 58.8% in the sun, $X^2=3.11$) which was, however, not statistically significant. In 1997, in contrast, rate of parasitism was lowest at the river side in the shade ($X^2=7.59$, $p<0.05$). Only larvae that had developed till pupation were considered for the calculation. Larvae were parasitized only by one species, *Brachymeria ? straeleni* (Schulz)(Hymenoptera: Chalcididae)(genus name is sure, determination of the species name is with a questionmark (J. Noyes, pers. communication)).

Although parasitism of *A. roseomarginata* made up only for a small proportion of total mortality, habitat-specific trends were similar. In 1995 survival was highest in the savanna ($X^2=33.53$, $p<0..001$)(Fig. 7.2). In 1997 there were no significant differences between the three habitats. In single group comparisons, survival was significantly higher in the river shade than in the sun habitat ($X^2=4.96$, $p<0.05$).

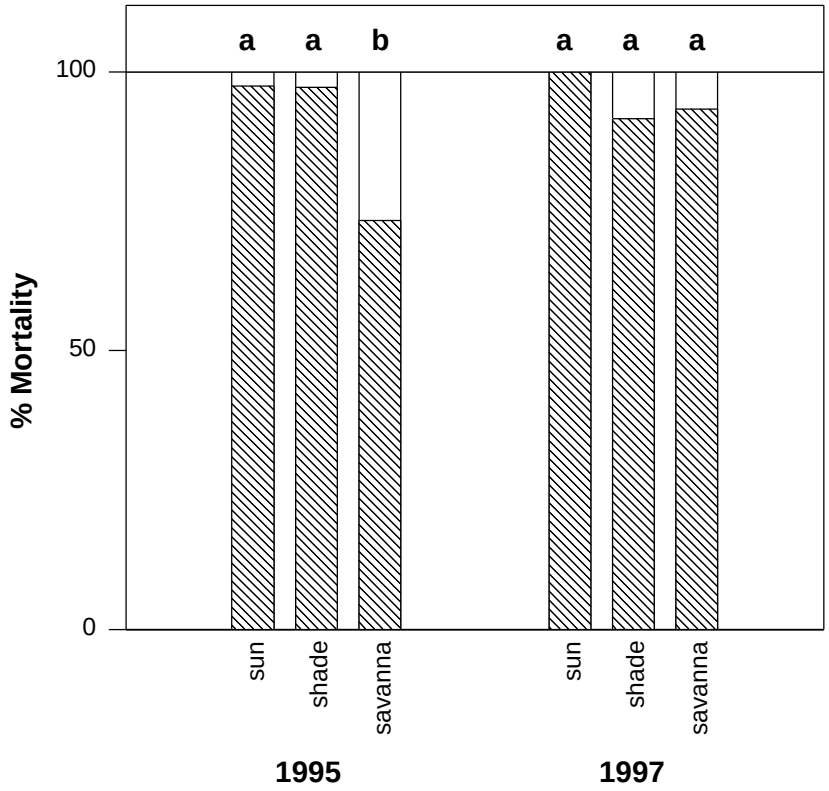

Fig. 7.2: Rates of mortality of larvae of *Acrocassis roseomarginata* in different habitats in 1995 and 1997. Sample size was the number of L1-larvae exposed in each group (n=114; 72; 60 (1995) and n=57; 60; 60 (1997)). X^2-test. Different letters indicate significant differences between groups ($p<0.05$).

In *A. quinquefasciata*, habitat had no influence on larval mortality in 1995 (Fig. 7.3). However, only sun and shade habitats were examined in that year. In 1997, survival in the shade and in the savanna was significantly higher than in river sun habitats ($X^2=8.96$, $p<0.05$). Habitat effects differed between species and years. If a significant difference in mortality or parasitism between habitats occurred, either the savanna or the river shade habitat provided better survival chances for larvae than river side habitats in the sun.

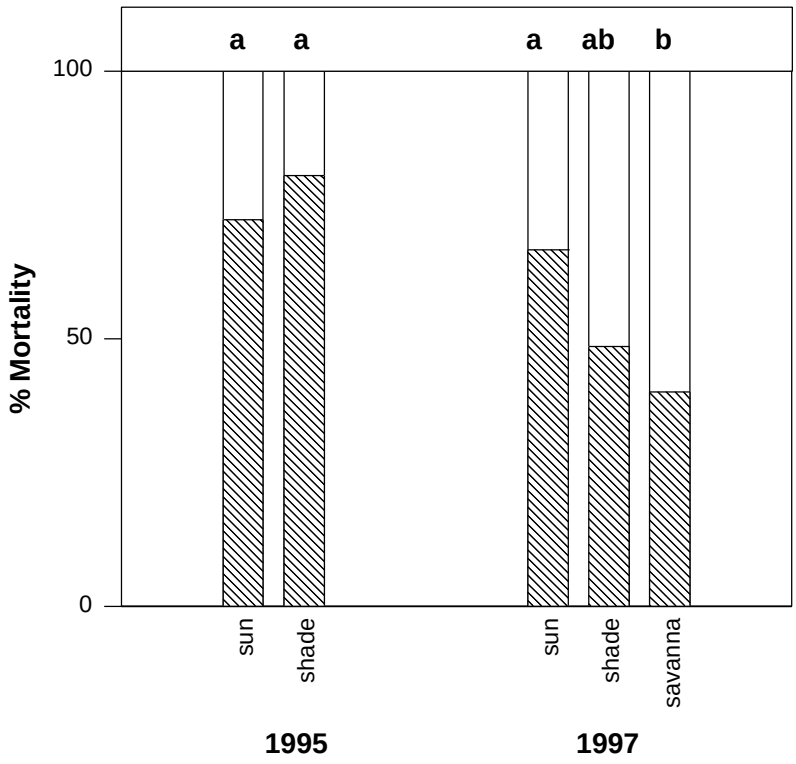

Fig. 7.3: Rates of mortality of larvae of *Aspidimorpha quinquefasciata* in different habitats in 1995 and 1997. Sample size was the number of L1-larvae exposed in each group (n=36; 36 (1995) and n=60; 68; 60 (1997)). X^2-test. Different letters indicate significant differences between groups ($p<0.05$).

The total rate of larval parasitism in *A. quinquefasciata* was very low. Only one individual of 260 L1-larvae of *A. quinquefasciata* exposed, had been found parasitized in the two years of the study. It was the same parasitoid species found in *A. roseomarginata*. In contrast, a high percentage of the larvae of *A. roseomarginata* that developed through to pupation were parasitized (50.9% in 1995 and 70.7% in 1997). In both years *Brachymeria straeleni* was the only larval parasitoid found. Adult parasitoids laid eggs in beetle larvae but these completed their development and reached the pupal state. (Pupae were collected immediately after pupation.)

The total mortality of *A. roseomarginata* from egg eclosion until pupation in both years was very high (91.5% and 94. 9%) and was significantly different from that of *A. quinquefasciata* (76.4% and 51.6%)($X^2(1995) = 29.02$; $X^2(\text{sun}, 1997) = 22.92$; $X^2(\text{shade}, 1997) = 27.61$; $p<0.001$).

7.3.2. Larval mortality during development

The number of *A. quinquefasciata*-larvae per plant decreased almost linearly over time in 1995 (Fig.7.4.a); in 1997 there was a period right at the beginning (between day 4-8) with a steeper decrease, while during the rest of the time the decrease was smoother and more uniform (Fig.7.4.b). In contrast, *A. roseomarginata* larvae showed a much higher rate of mortality during the first period of development (1.-10.day) which became smaller close to pupation in 1995 (Fig.7.4.a). In 1997 a strong decrease started on the 3rd day and lasted longer, (till the 12th day), but showed a similar pattern (Fig.7.4.b). Tab. 7.1 presents the mean daily mortality for the first (1st-10th day) and for the second half of development. *A. roseomarginata* had more than twice as high a mortality rate in the first ten days of development in both years. *A. quinquefasciata* showed similar rates over the course of development and even a higher mortality in the second half. As clearly demonstrated by the Figs. 7.4.a and 7.4.b mortality curves are very distinct in the two investigated species.

Tab. 7.1: Comparison of mortality rates per day averaged for the first and for the second period of larval development of *Acrocassis* and *Aspidimorpha*.

	A. roseomarginata [%mortality/pot/day] x ± SE		*A. quinquefasciata* [%mortality/pot/day] x ± SE	
	1995	1997	1995	1997
1st – 10th day	12.0 ± 1.45	10.8 ± 2.33	4.5 ± 2.14	5.4 ± 1.85
11th day – pupation	5.1 ± 2.13	3.5 ± 1.29	6.5 ± 1.68	3.2 ± 1.15

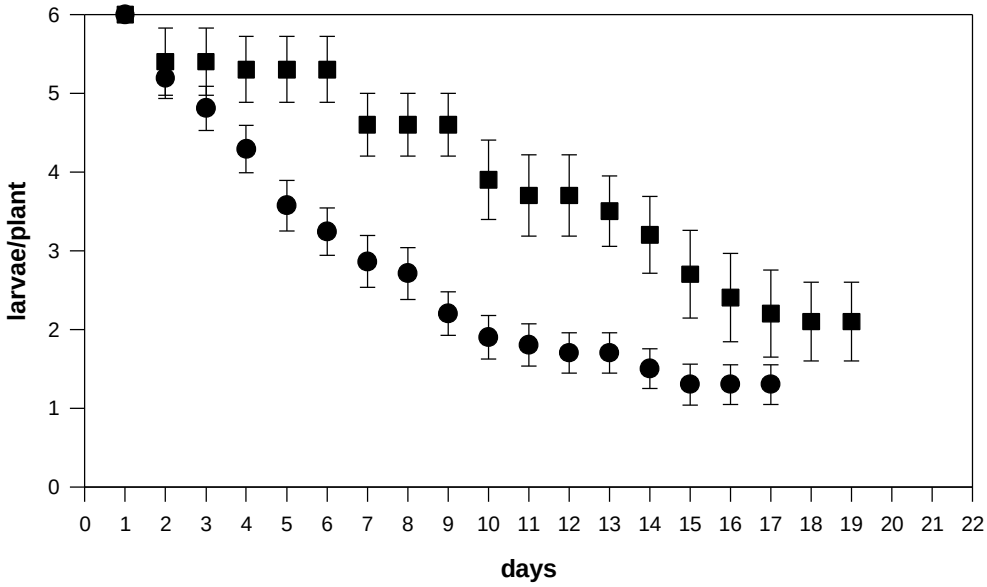

Fig. 7.4.a: Mortality of larvae during larval development in 1995. Mean number of larvae per plant and per day until all larvae pupated. Circles: *Acrocassis roseomarginata*; squares: *Aspidimorpha quinquefasciata*; given are the means and standard errors.

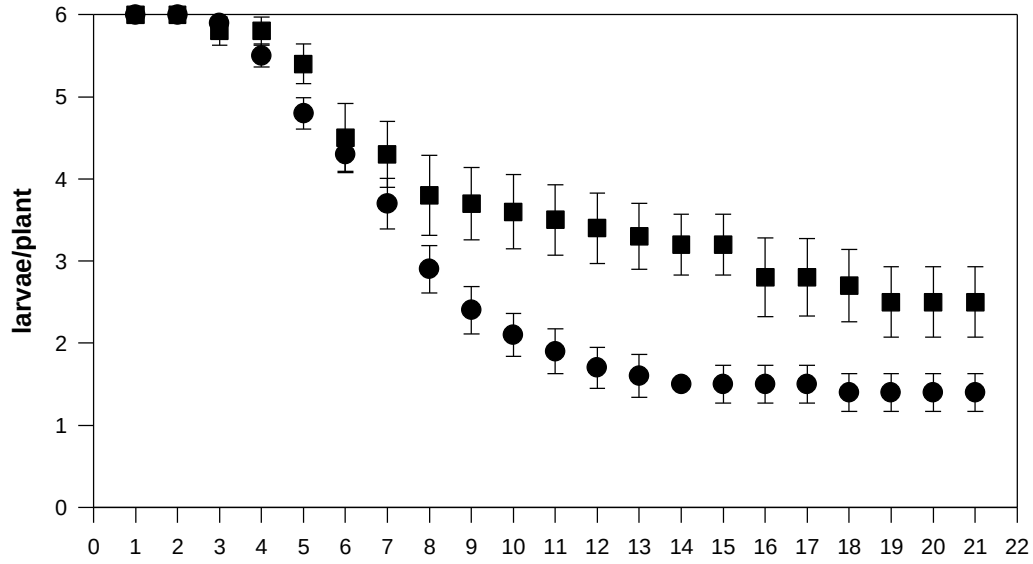

Fig. 7.4.b: Mortality of larvae during larval development in 1997. Mean number of larvae per plant and per day until all larvae pupated. Circles: *Acrocassis roseomarginata*; squares: *Aspidimorpha quinquefasciata*; given are the means and standard errors.

7.3.3. Mortality of A. roseomarginata-larvae under different regimes of predator exclusion

The predator exclusion experiments aimed at quantitatively assessing the contributions of different mortality factors to the overall mortality of *A. roseomarginata*. To avoid any habitat specific differences all three treatment groups were investigated under identical environmental conditions (same habitat: river sun, same span of time). In the cage biotic mortality factors like predators were excluded. The mortality within the cage was called ”non-predator mortality” and included mortality by pathogens (fungi, bacteria, nematodes) and by abiotic factors (wash-off by rain). Parasitism inside the cage took place, but could be separated. Mortality inside the cage amounted to 63.0%, without cage it amounted to 88.3/88.9%. No statistical tests were applied here because all plants were put in one cage.

The mortality without cage was assessed in two additional treatments. One treatment (”glue”), excluded walking predators by a ring of glue around the pots. Larval mortality was 88.9%. In the treatment in which no predators were excluded (”without glue”) larvae suffered 88.3% mortality (both groups also include the ”non-predator mortality”). The mortality of the groups with and without glue was practically identical (no significant difference). This means that predators from the ground were not very important for *A. roseomarginata* larvae. A quarter of the total mortality could therefore be contributed to mortality caused by predators which can jump, fly or are large enough to reach the plant from the ground.

If parasitism is added we arrive at a ”total mortality” of 96.7% (group ”without glue”) or 98.1% (group ”glue”), which is not significantly different between groups. Parasitism therefore added, on average, another 8.8% to total mortality.

7.3.4. Mortality of A. roseomarginata-eggs by egg parasitoids

The previous assessment did not include mortality in the egg stage. We did not observe eggs over time and therefore do not know total egg mortality (including predators and other mortality factors). In other species (e.g. *A. quinquefasciata*) egg clutches consumed by predators could be observed quite often. *A. roseomarginata* eggs might have been better protected because they are deposited singly, which makes them less apparent and less profitable for predators.

Here we investigated only egg parasitism. The mean rate of egg parasitism of *A. roseomarginata* on 6 river bank sites was 56.0 (±6.2)% (Tab. 7.2). Egg parasitoids were not caught, since this was outside the scope of our present study.

Tab. 7.2: Percentage of *Acrocassis*-eggs parasitized on 6 sites. N=number of eggs found on 1000 leaves.

Site	**% eggs parasitized**	**N**
Altes Lager	41.5%	53
Kongomdg.	80%	10
Neues Lager	57.1%	42
Kongobrücke	61.5%	13
Lola	37.8%	45
Vogelfangplatz	58.3%	12
x ± SE	**56.0% ± 6.2**	

7.4. Discussion

7.4.1. Mortality and parasitism in different habitats

We were interested in testing whether spatial patterns of mortality can explain local abundance patterns of the two beetle species. Enemy-free space was found in several studies to be an important factor which could determine the local distribution of herbivorous insects (Strong et al. 1984, Berdegue 1996, Hopkins & Dixon 1997, Gratton & Welter 1999). In most trials we find a significant effect of the habitat on parasitism or mortality. There was a trend for larvae in the river sun habitat to suffer the significantly highest parasitism and mortality while losses in the savanna habitat were lowest. The results, however, stand in no obvious relation to the abundance patterns of the species in the three habitats.

The habitat effects differed between years and species and are therefore difficult to explain without further experimentation. In the following we outline briefly four working hypotheses which may alone or combined contribute to an understanding of the observed patterns: (1) A preference of the parasitoid genus *Brachymeria* for dry, open habitats, (2) a higher wash-off by rain and physiological limits of larvae in the sun habitat, (3) climatic differences between years and (4) density-dependent mortality.

(1) In 1995 we found the lowest rates of parasitism and mortality of *A. roseomarginata* larvae in the savanna habitat. There was no significant difference between river sun and shade habitats. In 1997, however, parasitism of *A. roseomarginata* larvae was significantly lower in the river shade than in the sun habitat. The 1997 results correspond quite well to what is known about the parasitoid genus *Brachymeria*. *Brachymeria nosatoi* preferred lower humidities than two other parasitoid species that were examined experimentally in a study in India (Mohandas and Abdurahiman 1995). Humidity preference agreed with earlier field

studies that showed *B. intermedia* (temperate climate) to prefer open, sunny areas where temperatures were high and humidities low (Minot & Leonard 1976, Weseloh 1979). The parasitism patterns in 1995 can not be explained satisfactorily with the microclimate hypothesis; other effects, like host abundance, might have interacted; population fluctuations of the parasitoid might have been responsible for differing results.

(2) In two of three habitat comparisons, including all three habitats, we found a significantly higher mortality in the sun than in the savanna habitat. In the third comparison we observed a similar although not significant trend. Total mortality in sun and shade habitats did not differ statistically in both years. There was, however, a consistent trend for both species of a lower mortality in the shade in 1997. In 1995, in contrast, the sun habitat showed a trend towards lower mortality in *A. quinquefasciata*.

Abiotic factors like wash off by rain are likely to contribute to the mortality of larvae (DeLittle et al. 1990, Spring and Kok 1997). We found higher numbers of larvae missing after heavy rains than on normal days (Pfeiffer, pers. observ.). Wash off by rain should have been most detrimental in unsheltered, sunny habitats. Further, temperature might have been more suitable for the beetle larvae in shaded habitats than in the sun. In the climate chamber we found a shorter developmental time at 30°C than at 40°C daytime temperature for larvae of both species and a lower mortality for *A. quinquefasciata* when exposed over the whole larval period (Obermaier, pers. observ.). (Mean maximum temperatures of sun leaves were 40-49°C and of shade leaves 38-41°C (March till June)).

(3) To discuss differences between years, we analysed climatic data collected at the weather station of the Comoé-Camp. If only the experimental periods were considered, means of temperature maxima (31.9°C/30.0°C) and minima (22.9/21.7) were quite similar whereas amount of total rainfall was almost twice as high in 1997 (333mm) than in 1995 (175mm). Higher rainfall might have been responsible for the higher mortality in the sun compared to the shade habitats in 1997. Perhaps this difference in rainfall also influenced parasitoid activity, as known from other studies (Fink and Völkl 1995, Weisser et al. 1997), and may partially explain the big difference between years.

(4) Larvae of both species suffered a significantly lower mortality in the savanna than at the river sun habitat in 3 of 5 direct comparisons. In 1995 we further found no incidence of parasitism in the savanna at all, in comparison to 58.8 and 85 % at the river side for *A. roseomarginata*. An important factor besides microclimatic conditions, which differed between habitats, were host densities. Beetle densities of both species in the savanna were much lower

than at the river side habitats. Lower host densities could reduce the host finding efficiency of parasitoids and predators and therefore reduce parasitism and predation rates of beetle larvae in the savanna (density dependence). Can effects of predators/parasitoids on host populations due to habitat characteristics be distinguished from density dependent effects between predators/parasitoids and their hosts? In the case of a habitat-influenced system we would expect a lower predation/parasitism rate in the habitat with the high beetle density, where beetles have managed to escape to (enemy-free space). In the case of a density-dependent reaction (Kato 1994) we would, however, expect the highest predation/parasitism rate in the habitat with the highest host density. Density dependent rather than habitat effects might therefore have been responsible for the differences in predation/parasitism between savanna and river side (sun) habitats. Investigating density dependence was outside the scope of this study.

7.4.2. Interspecific comparison of mortality and parasitism

The two beetle species investigated live on the same host plant species, *Merremia hederacea*, are relatively closely related (both members of the subfamily Cassidinae) and were examined at the same time of the year at the same location. Of *A. quinquefasciata* only 1 individual of 260 larvae was parasitized by *Brachymeria straeleni*, which was probably mistaken for a larva of *A. roseomarginata*. *A. roseomarginata*, however, had a high rate of larval parasitism.

According to the literature, *Brachymeria* (Fam. Chalcididae) has rarely been recorded as parasitoid of chrysomelids but is better known to parasitize lepidopteran larvae. *Brachymeria excarinata* is described to use hosts within lepidopteran families as well as Chrysomelidae and therefore, if there was no identification-problem, seems to be extremely polyphagous (Mohandas 1986). Carroll (1978) describes *Brachymeria* sp. as a parasitoid of pupae of another cassidid beetle, *Stolas* sp.. Nothing was known yet about the biology and host spectrum of *Brachymeria straeleni* (Noyes, pers. com.).

Total larval mortality of *A. roseomarginata* was significantly higher than of *A. quinquefasciata* in both years. If mortality without parasitism of *A. roseomarginata* was compared to total mortality of *A. quinquefasciata* it became more similar but still survival was much higher in *A. quinquefasciata*. Causes for this are yet unknown. Possible explanations for different susceptibility may be the use of different secondary substances in fecal shields or different means of defence with fecal shields by the larvae of the two species (Olmstead and

Denno 1993, Gomez 1997). Also, there might be a different susceptibility for abiotic factors or pathogens (”non-predator” mortality).

There are only few field studies on the mortality of Cassidinae in tropical regions. Nakamura & Abbas (1987) reported for example for *Aspidomorpha miliaris* (Fabricius), feeding on *Ipomoea,* the extremely high larval mortality of 99,91% in Padang, Sumatra (mortality of larvae and pupae). In temperate climate the best studied species is *Cassida rubiginosa*, a thistle feeding shield beetle, examined in Virginia and Maryland, USA. Ward and Pienkowski (1978) found a combined total mortality of larvae and pupae of 56.6% in 1973 and of 31.1% in 1974 (parasitism included). Total mortality of larvae and pupae in the study of Ang and Kok (1995) ranged between 12-47% in 1989 and between 8.6-80% in 1991. Finally Spring and Kok (1997) describe a total mortality from egg to adult stage of 81,7 and 73,3% in 1993 and 1994. Total larval (and pupal) mortalities of our two West African species exceeded in most cases the values in temperate regions. Mortality of *Acrocassis* (91.5% and 94.9%) in both years was distinctly higher than all values for *C. rubiginosa*. Combined mortality of *A. quinquefasciata* (76.4% and 51.6%) were on the upper limit of mortality data of the temperate species. A higher mortality rate of the immature stages of tropical Cassidinae in general in comparison with temperate species might be possible. Our data reflect what is expected for tropical areas. In general higher predation (Sih et al. 1985) and parasitism rates (Moller 1998) are expected in tropical than in temperate regions. Much higher abundances of ants in tropical rainforests are suggested to be responsible for the absence of whole arthropod groups in the canopy (Floren & Linsenmair 1997, 1998). But still the higher predation rate has to be seen with many question marks. Far more species need to be investigated before general conclusions can be drawn.

7.4.3. Mortality during development

Daily mortality of *A. roseomarginata* was more than twice as high in the first ten days than in the second phase of its development in both years. *A. quinquefasciata*, however, had a higher (1995) or a only slightly lower rate of mortality (1997) in the second half of larval development than in the first half. Mortality factors could have been stage-specific and could have differed in early and late larval development and between species. Species-specific mortality factors could have caused the pronounced differences between the two beetle species. Parasitism was not included here.

7.4.4. Quantitative analyses of mortality factors of Acrocassis roseomarginata

Mortality factors contributing to mortality of *A. roseomarginata* during development are summarised in Fig. 7.5. Egg parasitism, calculated from the counting on 6 sites was 56% (see also Tab. 7.2). Total egg mortality including predation and other mortality factors certainly was higher. Survival rates from egg parasitism and larval mortality were multiplied and resulted in a total survival rate of 1.1 adult beetles per 100 eggs laid. Total survival rate is probably still lower because pupae were removed directly after pupation and developed without the natural mortality factors. Morrison and Strong (1981) described egg parasitism as the most common source of egg mortality in a neotropical chrysomelid species (*Cephaloleia consanguinea*) and found rates of parasitism of 35% to 50% during four consecutive years; one neotropical cassidid beetle species, *Stolas sp.*, had 86% of its egg clutches completely parasitized (Carroll 1978). In two Cassidinae from Sumatra total egg mortality reached 71,7% in *Aspidomorpha miliaris* and 58,2% in *Aspidomorpha sanctaecrucis* (Nakamura & Abbas 1989). Other studies on stage-specific mortality of herbivores (immatures) also found the highest mortality in the egg-stage (Knutson & Gilstrap 1990, DeLittle et al. 1990)

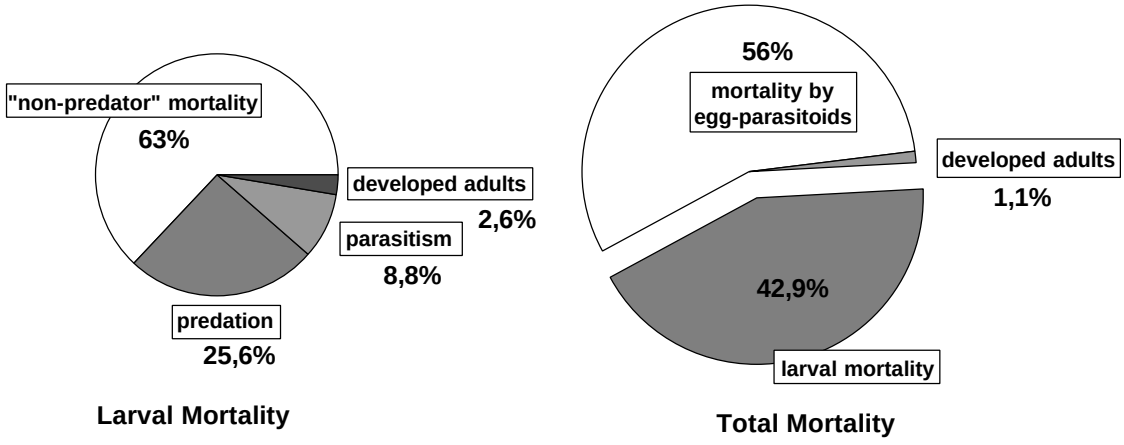

Fig. 7.5: Estimation of the contribution of different mortality factors to larval mortality and to total mortality of *Acrocassis roseomarginata* during development.

Larval mortality was split up into several factors by different means of exclusion (Fig. 7.5). Treatments with glue and without glue did not differ significantly neither in mortality nor in parasitism. Memmott et al. (1993) excluded crawling predators from bamboos attacked by chrysomelid leaf miners which resulted in a reduction of predated larvae from 61% to 29%. In our experiments there was no significant impact of crawling predators (e.g. among the many

ant species living in the same localities), which we had expected. Treatment groups with and without glue were therefore pooled for the diagram. We estimated a total "mortality by predation" of 26% and a mortality due to parasitism of 9% (Fig. 7.5). Parasitism therefore added on average another 9% to total mortality. This might, as a reduction late in the development of *A. roseomarginata*, be an important factor in population regulation if parasitism is density dependent. Additionally, a part of the larvae which had already been eliminated by predator and "non-predator" mortality earlier probably was also parasitized, so that the actual percentage of parasitism is suspected to be much higher (Zwölfer, pers. comm.).

The largest part of larval mortality, 63%, was categorised as "non-predator" mortality and was probably caused by a variety of different factors (only rates of loss had been recorded). It was assessed by excluding predators by a cage covered with a mesh. Contributing mortality factors could have included pathogens like fungi, abiotic factors like desiccation during spells of extremely hot and dry weather and/or drop-off by rain or incomplete development. Knutson and Gilstrap (1990) describe infection by *Beauveria bassiana* (Balsoma) Vuillemin as the most important mortality factor besides intraspecific competition in a study of the southwestern corn borer (Lepidoptera: Pyralidae). In predator exclusion studies herbivore densities became lower with time on open-caged or uncaged plants than in caged plants too (Boavida et al. 1995, Hopper et al. 1995), as was the case in our experiment. In none of the publications was there, however, a discussion about mortality factors contributing to mortality within the cages.

In conclusion, we find significant effects of the habitat on larval mortality and parasitism. The trends were not consistent between habitats and between years and were probably caused by multiple factors. Some of those could be the preference of the parasitoid genus *Brachymeria* for hot and dry conditions, a higher wash off by rain and physiological limits in river sun habitats, a different amount of rain in the two years investigated and different beetle densities in savanna and river side habitats. The two species differed profoundly in their larval mortality experienced and in their susceptibility towards parasitism, although they belong to the same subfamily and feed on the same host plant species. The survival rate of *A. roseomarginata* until pupation (1.1 individuals surviving of 100 eggs laid) was very low in both years and supports the hypotheses of a generally higher rate of parasitism/predation in tropical regions.