

Spatiotemporal density patterns of the pest predator *Rhynchium haemorrhoidale* (F.) along a land-use gradient in cacao agroforestry systems

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Abstract Tropical insect species show year-round breeding activity due to favourable climatic conditions. However, most species also display seasonal reproductive peaks, but little is known about underlying causes of temporal density changes. We investigated population dynamics of the pest predator *Rhynchium haemorrhoidale* (F.) (Hymenoptera: Eumenidae) and its natural enemies in relation to season, climate and varying shade tree composition in cacao agroforestry systems in Central Sulawesi (Indonesia). Nesting of *R. haemorrhoidale* showed clear seasonality with highest densities in the wet season and lowest in the dry season, which was not related to changes in temperature. Wasp densities increased with land-use intensity, presumably because less-shaded areas offer more favourable climatic conditions and higher densities of the major prey, the cacao pest *Agathodes*

caliginosalis (Lepidoptera: Pyralidae). Pupal body size was higher in June than in November indicating increasing intraspecific competition due to high wasp densities and food shortage at the beginning of the wet season. Body size between habitat types was similar, thus season appeared to be more important than habitat in terms of food supply. High wasp densities in the wet season were associated with high diversity of the altogether seven parasitoid species. In conclusion, we found a pronounced seasonality of the wasp *R. haemorrhoidale* and a preference for little shaded agroforestry, which may be due to enhanced temperature and density of its prey. Our data indicate a high potential for biological control of a major cacao pest by management of nesting sites of *R. haemorrhoidale*.

Keywords Biological pest control · Ecosystem functioning · Host–parasitoid interactions · Intraspecific competition · Population dynamics · Resource availability

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Introduction

Density and reproduction of tropical species show mostly distinct temporal peaks even though breeding seems to be possible all year round (Brown and Shine 2006). Hypothesized proximate causes for seasonality in tropical zones include abiotic factors (mainly rainfall), food limitation and top-down regulation by

natural enemies (Harris and MacDonald 2007; Richards and Coley 2007; Richards and Windsor 2007). For some taxa, such as shrews or butterflies, it has been shown that they synchronize breeding with optimal climatic conditions (Kemp 2001; Nicolas et al. 2005).

Land use intensification in tropical agroecosystems reduces diversity of predators, thus reducing the potential ecosystem service of pest control (Perfecto et al. 2004; Philpott et al. 2007). Habitat quality has been discussed to be a crucial factor influencing species density due to microclimatic conditions or food resource availability in tropical and temperate regions (Schmidt et al. 2005; Lambert et al. 2006; Clough et al. 2007; Richards and Windsor 2007).

In this study we try to identify whether season or habitat more strongly influence the density of an important insect pest predator in agroforestry systems of different land-use intensity throughout a year. We asked whether food supply, climate, parasitism rate and entomopathogenic infection may be responsible for seasonal fluctuations in the density of a predator such as the eumenid wasp studied here. A major factor important to animal population dynamics is larval food supply. Due to changes in food resources between season and habitat, adult sex ratio, body size or mortality, as some crucial aspects of a predator's population dynamic, might also vary (King 1996; Strohm and Linsenmair 1997; Cleary and van Ginkel 2004; Boggs and Freeman 2005). Predators are strongly affected by fluctuations in prey density (Forsman and Lindell 1997; Salamolard et al. 2000; Norrdahl and Korpimäki 2002). Even though generalist predators exploit a broader array of resources than specialists, which may enhance stability of population densities, they may also face the problem of food limitation in space and time (Östman 2005). Decreased population density of an insect predator due to food limitation can be caused by intraspecific competition (Bommarco 1999). Besides larval food supply, climatic conditions are often an important factor, influencing the density of predacious wasp species. For some Hymenoptera, such as Vespidae, nesting activity is correlated with daily or seasonal changes in climate (Elisei et al. 2005; Ribeiro et al. 2006). Temperature dependent activity of the nest-building adults influences generation times and population density due to different provisioning times (Strohm and Linsenmair 1998). In temperate zones ontogenesis of insects is strongly related to seasonality, including specific hibernation stages as egg, larva, pupa or imago. Minor climatic fluctuations

occur in tropical areas but might nevertheless influence reproduction and fitness (e.g. temperature and photoperiod). Parasitism rate is also well known to affect host population dynamics and may increase with increasing host density (e.g. Tscharrnke 1992; Bischoff 2003; Teder and Tammaru 2003; Steffan-Dewenter and Schiele 2008). As parasitoids vary in space and time, they might be a crucial factor for host densities in different seasons and habitats (Zhou et al. 2001; Liu et al. 2007). Further mortality factors influencing density, may be often unknown, such as nematode or fungal infections due to increased humidity (Furlong and Pell 2001; Morton and Del Pino 2007). We investigated factors that may influence seasonality and spatial distribution of the solitary, predatory wasp *Rhynchium haemorrhoidale* (F.) (Eumenidae, Hymenoptera) along a land-use gradient of agroforestry systems in Sulawesi, Indonesia. The only prey species of *R. haemorrhoidale* was a cacao leaf-feeding larvae of *Agathodes caliginosalis* (Snellen) (Pylalidae, Lepidoptera).

In the investigated agroforestry systems cacao plants are grown under different levels of shade tree diversity and densities as determinants of land-use intensity. Agroforestry systems become increasingly interesting for the conservation of global species richness and ecosystem services (Millennium Ecosystem Assessment 2005; Dietsch et al. 2007, Steffan-Dewenter et al. 2007). We were therefore interested in the question, whether agricultural habitats of different management intensities can maintain high densities of the predatory wasp species *R. haemorrhoidale* providing an important ecological function. We also examined, whether climatic conditions and food resource availability are more relevant for spatiotemporal patterns in the density, body size and sex ratios of *R. haemorrhoidale*. Furthermore, we evaluated the influence of parasitism rate and mortality due to unknown reasons (henceforth: non-parasitism mortality) on seasonality and habitat preferences of *R. haemorrhoidale*.

Method

Experimental site and design

Sampling was conducted on the western margin of the Lore Lindu National Park in Central Sulawesi, Indonesia, in the agroforestry systems surrounding the

village of Toro (E 120°2', S 1°30', 800–1,100 m above sea level). Agricultural landscapes at the margin of the tropical rainforests are dominated by cacao agroforestry and paddy fields. The landscape is heterogeneous resulting in alternating habitat types on a small scale.

We selected plots belonging to four habitat types ranging from natural forests to a gradient in land-use intensity of agroforestry systems. Each plot had a minimum core area of 30 × 50 m, where we placed the trap nests. The cacao agroforestry systems formed a gradient according to the composition of shade tree species and thereby canopy cover, with low management intensity agroforestry having natural forest trees as shade trees (high canopy cover), medium intensity systems having a diverse shade tree community planted by farmers (medium canopy cover) and high intensity plots with only a few planted shade tree species such as *Gliricidia sepium* (Jacq.) and *Erythrina subumbrans* (Hassk.) (low canopy cover). The different habitat types were situated close together but randomly mixed (see UTM data in Table 1). Four replicates were chosen for each habitat type.

Canopy cover was measured with a spherical densiometer (Model-C, Robert E. Lemmon, Forest Densiometers, 5733 SE Cornell Dr., Bartlesville, OK

74006) by two people independently at 12 random positions within each plot above cacao tree canopy.

We used trap nests to assess relative densities of the above ground-nesting wasp *R. haemorrhoidale*. Trap nests consisted of PVC tubes (length 28 cm, diameter 14 cm) with internodes of the grass *Saccharum spontaneum* (Poaceae) of varying diameter (3–25 mm) and a length of 20 cm inserted (Tscharntke et al. 1998). Sixteen trap nests per site were installed from October 2004 until September 2005 in different heights from understorey to canopy. The trap nests were checked every month and sticky glue was applied to the edge of the PVC tube to deter ants from colonizing the trap nests. We collected all internodes, which were occupied by Hymenopterans readily identifiable by the type of caps closing the internode opening, and incubated all larvae and pupae including parasitoids in glass tubes until they hatched, for later species identification. Due to simplification of terminology, we equated the term density with number of brood cells, as done in former studies (Gathmann et al. 1994; Steffan-Dewenter 2003). The eumenid predatory wasp *R. haemorrhoidale* was identified by Dr. J. Gusenleitner from Linz, Austria. Voucher specimens are kept at the Bogor Agricultural University (IPB) in Indonesia.

Pupal body size is a widely used fitness-related trait for insects and can be used as a surrogate for food supply (e.g. Harvey et al. 2000; Östman 2005). We could not estimate the density of the prey (see: 'Study organisms') of the predator *R. haemorrhoidale* in the field, because the prey larvae fed in higher strata of the cacao tree canopies. We measured body length (henceforth: body size) of *R. haemorrhoidale* pupae with a vernier calliper in November 04 and June 05 for a seasonal comparison. Larvae of this species completely ate prey larvae in the brood cells, therefore we used pupae size as a surrogate for food resource availability. Assessment of sex ratio and sex determination was also done in November 04 and June 05. We compared months throughout the year and effects of season when we compared November (wet season) with June (dry season). We recorded individuals of *R. haemorrhoidale* that were not parasitized, but died as egg, larva or pupa for unknown reasons, such as infections by entomopathogenic organisms (viral, bacterial, nematode or fungal infection), for every month. In order to lessen the mortality associated with breeding in glass tubes, we attempted to create close to optimal conditions for *R. haemorrhoidale*. The climatic conditions air temperature, humidity, solar

Table 1 Canopy cover and location according to the Universal Transverse Mercator (UTM) system of each replicate per habitat type

Habitat/Replicate	Canopy cover in %	UTM easting	UTM northing
Primary forest 1	96.8	171,125	9,832,974
Primary forest 2	97.0	168,961	9,835,116
Primary forest 3	93.7	171,204	9,832,688
Primary forest 4	95.0	171,759	9,834,927
Dense shade agrof 1	69.6	169,333	9,833,896
Dense shade agrof 2	61.6	169,489	9,834,158
Dense shade agrof 3	82.3	170,737	9,833,172
Dense shade agrof 4	76.5	169,828	9,834,447
Medium shade agrof 1	76.0	170,450	9,832,604
Medium shade agrof 2	66.2	170,637	9,833,602
Medium shade agrof 3	57.0	169,937	9,833,662
Medium shade agrof 4	46.3	169,911	9,834,876
Low shade agrof 1	81.6	170,125	9,832,058
Low shade agrof 2	51.3	170,485	9,834,798
Low shade agrof 3	57.1	169,577	9,834,508
Low shade agrof 4	42.5	168,735	9,832,676

radiation and precipitation were measured at a climate station in the centre of the research area to assess seasonal fluctuations.

Study organisms

We used the tropical cavity nesting eumenid wasp species *R. haemorrhoidale* (F.) (Eumenidae, Hymenoptera) for this study. *R. haemorrhoidale* is a solitary, predatory wasp, building nests with several brood cells. It was the most abundant species out of 23 predacious wasps. *R. haemorrhoidale* can be considered as an effective pest predator, as we found that each brood cell was provided with approximately seven larvae of the pest organism *A. caliginosalis*. The generation time from egg to adult never went below one month, which was the sampling frequency for the trap nests and therefore we can exclude that wasps developed, hatched and flew out unrecognized from trap nests. Parasitoids of *R. haemorrhoidale* comprise a spectrum from cletoparasitoids (Chrysididae and Rhippiphoridae), ectoparasitoids (Leucospidae) and endoparasitoids (Ichneumonidae) to hyperparasitoids (Trigonalyidae).

Statistical analysis

We used main effects ANOVA to test for differences in density and sex ratio per plot between months (density) and seasons (sex ratio), respectively, and habitat. Density was defined as number of brood cells occupied. Density and sex ratio were used as dependent variables and habitat type and month/season as categorical predictors. Sex ratio was calculated as number of male individuals per plot divided by number of female individuals. We show density values in primary forest plots only in Fig. 4 and did not include the individuals from this habitat for further statistics, because *R. haemorrhoidale* proved to be a species depending on less dense forested habitats, such as agroforestry systems. Only 24 individuals of *R. haemorrhoidale* occurred in all four primary forest plots throughout the year.

We used Spearman rank correlation to test whether wasp density per plot and month and canopy cover per plot were correlated.

We used a correlation matrix to test whether the climatic factors temperature, humidity, solar radiation and precipitation were correlated. In another correlation matrix we tested whether monthly density values of *R.*

haemorrhoidale were correlated with climatic factors. We correlated density with climatic values not just from the same month, but also from the previous three months as density response of *R. haemorrhoidale* to climatic changes might be temporally delayed when climate influences prey density and thereby density of *R. haemorrhoidale*. Due to four replications of the model with climate values from different months, we used a Bonferroni corrected α of 0.0125.

To test whether habitat or season influenced food resource availability, we used main effects ANOVA with body size of the pupae as dependent variable and habitat and season as categorical predictors. We did the analysis for both sexes separately, as females were significantly larger than males.

We conducted a general linear model (GLM) to identify the factors that influence parasitism of *R. haemorrhoidale* and non-parasitism mortality rate. The two models included parasitism and non-parasitism mortality rate respectively as response variables, habitat and month as categorical predictors and *R. haemorrhoidale* (host) density as continuous variables. Parasitism rate was calculated as number of infested host individuals divided by number of parasitized individuals per plot. Non-parasitism mortality rate was calculated as total number of individuals per plot divided by number of individuals that died for reasons others than parasitism. To test the effect of habitat and month on species richness of parasitoids of *R. haemorrhoidale* we conducted a main effects ANOVA with number of species as response variable and month and habitat as categorical predictors.

Square root transformation was done to assure for homogeneity of variance if necessary. We used type-I (sequential) sum of squares for each model. We give arithmetic mean \pm standard error in the text.

Results

In total we reared 11,090 individuals from 50 species in the trap nests. Twenty three of these species were specialized predatory wasps with *R. haemorrhoidale* (7,403 individuals), a larvae hunting eumenid wasp, the most abundant species, comprising 67% of all individuals and therefore used as the organism of interest. Canopy cover varied between plots, with primary forest plots having the densest canopy (95.6 \pm 0.8%), followed by low intensity plots (72.5 \pm

4.5%), medium intensity plots ($61.4 \pm 6.3\%$) and high intensity plots ($58.1 \pm 8.4\%$) (Table 1). We therefore refer to the different agroforestry plots as high, medium and low shade plots.

Season and habitat quality

Density of *R. haemorrhoidale* was strongly influenced by season with rising number of brood cells from October until January ($r^2 = 0.484$, $F_{11,107} = 11.8$, $P < 0.001$) (Fig. 1) and increased number of brood cells with increased land-use intensity ($r^2 = 0.066$, $F_{2,107} = 8.8$, $P < 0.001$) (Fig. 2). High shade agroforestry plots had significantly fewer individuals

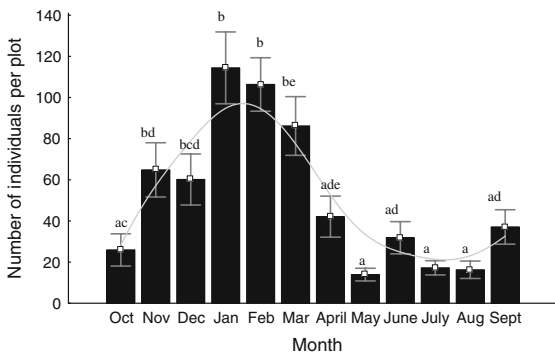


Fig. 1 Numbers of individuals of *R. haemorrhoidale* per month and plot from October 2004 until September 2005. Mean \pm standard error are shown. Significant differences ($P < 0.05$) are indicated by different letters. The grey fitting line represents distance weighted least squares

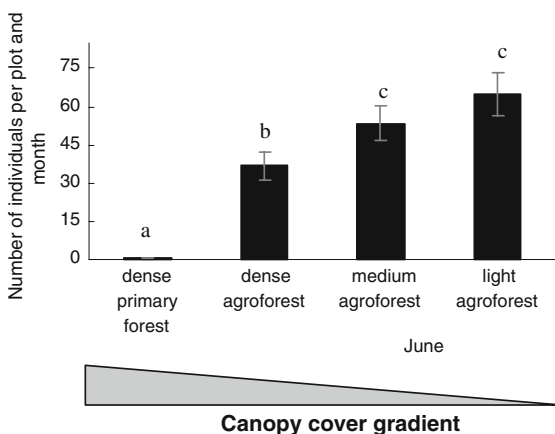


Fig. 2 Numbers of individuals of *R. haemorrhoidale* per month and replicate for 1 year and for four habitat. Mean \pm standard error are shown. Different letters indicate significant differences between habitat types

per month and plot (36.7 ± 5.67 , $n = 48$) compared to medium (53.3 ± 6.78) and low shade agroforestry plots (64.8 ± 8.5). There was no interaction between season and land-use intensity ($r^2 = 0.051$, $F_{22,107} = 0.63$, $P = 0.897$). Canopy cover and wasp density per plot and month were negatively correlated ($n = 16$, $R = -0.54$, $P = 0.033$). Neither habitat ($r^2 = 0.09$, $F_{2,19} = 1$, $P = 0.384$) nor season ($r^2 = 0.06$, $F_{1,19} = 1.31$, $P = 0.267$) influenced sex ratio of the wasp.

Climatic variables

Climatic variables were not intercorrelated and no climatic variable was correlated with density of *R. haemorrhoidale* from the same month or the previous month. In a correlation matrix with climatic factors from the previous month, density was also not correlated with climate. Solar radiation did not influence *R. haemorrhoidale* ($n = 12$, $R = 0.6$, $P = 0.039$, $\alpha = 0.0125$).

Food resources

Seasonal differences in pupal size were similar in either sex. Females and males were larger in the dry season (June) compared to wet season (November) (females June: 1.83 ± 0.014 cm; November: 1.69 ± 0.0123 cm; $r^2 = 0.13$, $F_{1,387} = 58.06$, $P < 0.0001$; males June: 1.48 ± 0.012 cm; November: 1.34 ± 0.013 cm; $r^2 = 0.15$; $F_{1,374} = 64.54$; $P < 0.001$) (Fig. 3). Habitat did not influence pupal size in either sex (females: $r^2 < 0.01$; $F_{2,387} = 1.54$; $P = 0.215$; males: $r^2 < 0.01$; $F_{2,374} = 1.64$; $P = 0.195$).

Parasitism and non-parasitism mortality

We found 579 individuals of parasitoids from *R. haemorrhoidale* belonging to seven species (see Methods, Study organism). These were 3 ± 0.38 parasitoids and 39 ± 3.5 individuals of the host *R. haemorrhoidale* on average from each plot per month. For statistical analyses we pooled all parasitoid species, as all species caused mortality of *R. haemorrhoidale*. Parasitism rate of *R. haemorrhoidale* differed between months ($r^2 = 0.24$, $F_{11,109} = 3.146$, $P = 0.001$), with November having a higher parasitism rate compared to October, August and September (Fig. 4), but did not show a difference between habitats ($r^2 = 0.01$, $F_{2,109} = 0.8$, $P = 0.449$) or host

density throughout the year ($r^2 < 0.01$, $F_{1,109} = 0.57$, $P = 0.45$). Parasitoids of *R. haemorrhoidale* showed higher species richness in the rainy season ($r^2 = 0.62$, $F_{11,22} = 3.3$, $P = 0.008$) with significantly more species in February (3.66 ± 0.33) compared to October (1 ± 0), whereas habitat had no influence on species richness ($r^2 < 0.01$, $F_{2,22} = 0.04$, $P = 0.96$).

The rate of non-parasitism mortality was not influenced by any predictor variable (habitat: $r^2 = 0.05$, $F_{2,109} = 3.06$, $P = 0.051$; month: $r^2 = 0.13$,

$F_{11,109} = 1.56$, $P = 0.122$; density: $r^2 = 0.05$, $F_{1,109} = 0.06$, $P = 0.8$).

Discussion

Density of *R. haemorrhoidale* was strongly influenced by month and land-use intensity, but not directly related to seasonal temperature variation. We found a strong seasonality of *R. haemorrhoidale* with higher monthly densities in the wet season. We could not find a significant direct synchronization between wasp density and climate, even though increased flight and foraging activity, has been shown to depend on temperature (Strohm and Linsenmair 1998; Ribeiro et al. 2006). Furthermore, wasp density was influenced by land-use intensity, with densely shaded agroforest plots having fewer individuals compared to medium and light shaded agroforests and almost none in highly shaded primary forests. This might be explained by more favourable abiotic conditions or by higher food availability. In less shaded plots solar radiation penetrates through the canopy and reaches the ground, thus increasing temperature and reducing humidity (Grimmond et al. 2000). Vespidae are known to profit from solar radiation and temperature (Ishay and Lior 1990; Elisei et al. 2005), in particular in terms of nest building and foraging activity. Thus the effect of habitat type on wasp densities might be due to the influence of canopy cover on climatic conditions in the plots as wasp density and canopy cover were negatively correlated. Further, the choice of nesting

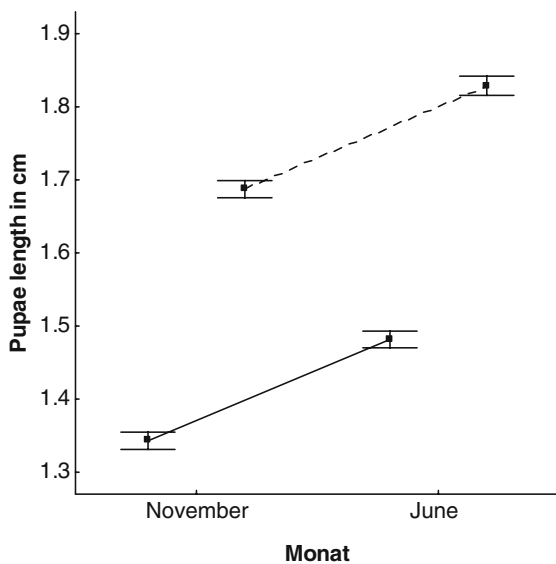
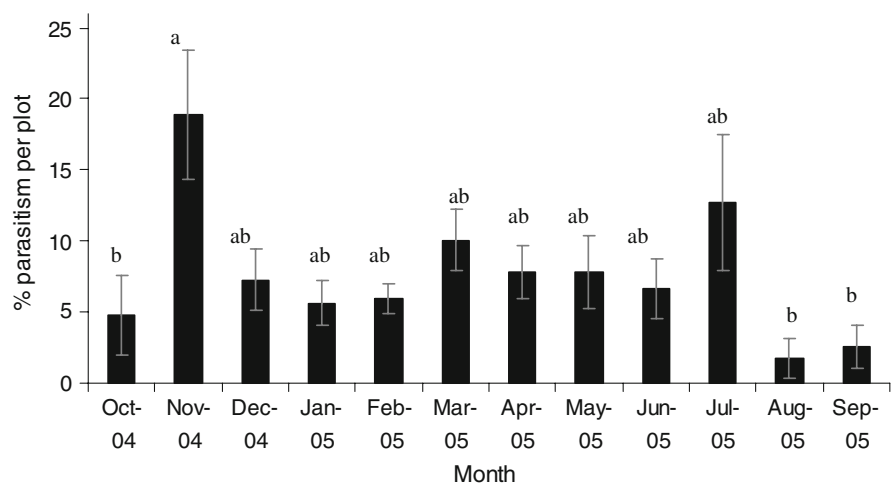


Fig. 3 Wasp pupae lengths of *R. haemorrhoidale* for 2 months, with dashed line representing female individuals and solid line representing male individuals. Mean \pm standard error are shown

Fig. 4 Parasitism rate of *R. haemorrhoidale* by seven species of parasitoids per month and plot from October 2004 until September 2005. Mean \pm standard error are shown. Significant differences ($P < 0.05$) are indicated by different letters



sites might have been also influenced by other habitat characteristics, such as natural nesting site availability and prey availability.

Body size of females and males of *R. haemorrhoidale* was higher in June, indicating better larval food supply in the beginning of the dry season, rather than at the end of the dry season. Reduced food supply in November could be due to intraspecific competition for food resources, as wasp density increased in November. In seasons with high wasp density, intraspecific competition could reduce individual food supply and result in smaller individuals, as abundant wasp species with a narrow prey spectrum, such as *R. haemorrhoidale*, can effectively reduce prey densities in the field (Harris 1996; Schenk and Bacher 2002). Temporal variation in body size was synchronized among sites, showing the superposing effect of seasonal change on food supply independent of habitat type (Östman 2005). Klein et al. (2004) showed that *R. haemorrhoidale* adjusted foraging trip duration to habitat quality and its density was not correlated with foraging time, indicating that food resource availability may not directly affect *R. haemorrhoidale* density.

Sex ratio was similar between seasons, thus independent of prey availability. Sex ratio has been discussed to depend on environmental factors, whereby unfavourable conditions lead to more males (Frank and Swingland 1988), as found for the European beewolf (*Philanthus triangulum* F., Sphecidae) (Strohm and Linsenmair 1997). Male individuals represent the ‘cheaper sex’ with higher relative fitness under poor conditions, such as food shortage. Also non-parasitism mortality was not influenced by food supply, since it was not higher in the season with smaller individuals. However, some authors discuss a positive relation between fitness (e.g. development time, mating success, survivorship) and body size of insects, such as braconids, odonates and carabids (Harvey et al. 2000; Sokolovska et al. 2000; Östman 2005).

Parasitism rate in November was considerably higher compared to August, September and October. This peak appeared to be a response to increasing host densities at the beginning of the wet season, but parasitism rate throughout the year is not correlated with host density. Species richness of parasitoids of *R. haemorrhoidale* was also higher in the middle of the rainy season compared to the end of the dry season. For example, the *Chrysis* sp. *smaragdula* group occurred only in the rainy season.

In conclusion, food resource availability and climate may contribute to seasonal changes in life history traits in temperate zones as well as in the tropics (Kemp 2001; Nicolas et al. 2005; Polidori et al. 2007). However, it is often difficult to determine the proximate reasons for seasonality of tropical species. We showed that habitat choice for nesting was related to canopy cover and season, in that density of *R. haemorrhoidale* was higher in sunny agroforestry and in the wet season, which may be related to prey availability.

We show that agroforestry systems in agricultural landscapes, can maintain high densities of a potentially important cacao pest predator. The moth larvae-hunting *R. haemorrhoidale* was almost absent in the primary forest and its density increased with land-use intensity. Our results suggest that by adding nesting resources for this specific pest predator biological pest control could be significantly improved in intensively managed agroforestry systems where density and diversity of other natural enemies tends to be low (Klein et al. 2002). However, we could not measure effects on cacao defoliation and other potential predators of pest insects might get lost during agroforestry intensification.

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