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**Influence of field and landscape characteristics on condition,
reproductive potential and activity density of two carabid beetles in
winter oilseed rape**

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1. ABSTRACT

1. The common carabid beetles, *Amara similata* and *Poecilus cupreus*, were investigated in oilseed rape (OSR) fields according to the influence of field and landscape characteristics on their condition, reproductive potential and activity density.
2. The soil index, stand density, soil cultivation index, plant cover and pest length (as a proxy for prey density) were considered as field parameters. Landscape parameters comprised the percentage of crop area, woody area, fallows, OSR fields, settlements, the length of roadside strips and of hedgerows and the Shannon-Wiener diversity index, all measured at eight different radii around each study field. Moreover, the distances to the next fallow, dry near-natural grassland, forest and OSR field were included.
3. Pest length influenced the condition factor (CF) and activity density of both species and sexes significantly (positive response for CF, negative for activity density). Furthermore, the CF of female *A. similata* was significantly positively influenced by stand density, the CF of male *A. similata* by soil index. In *P. cupreus* activity density of both sexes was significantly related to soil index. Oocyte numbers of *A. similata* were significantly negatively related to the distance to the next fallow. When analysing exclusively the influence of the OSR pests *Meligethes aeneus*, *Ceutorhynchus napi* and *Dasineura brassicae*, the abundances of *M. aeneus* and *C. napi* were most important in explaining the CF and activity density of both carabid species and sexes, except the CF of female *A. similata*.
4. In eight of ten cases analysing simultaneously the influence of field and landscape parameters by General Linear Models, pest length proved to be the most important parameter explaining the CF, reproductive potential and activity density of *A. similata* and *P. cupreus*. Landscape characteristics at various spatial scales were far less important.

Keywords: activity density, *Amara similata*, *Brassica napus*, condition factor, field parameters, landscape parameters, *Poecilus cupreus*, reproductive potential

2. INTRODUCTION

The significance of oilseed rape (OSR, *Brassica napus*, Brassicaceae) as a source for the production of nutritional and industrial oil and for the extraction of fuel has been increasing worldwide during the last few decades. For example, in Austria area grown with oilseed rape increased more than ten fold from 3940 ha in 1980 to 48509 ha in 2007 (Griesmayr *et al.*, 2006, Statistik Austria, <http://duz.lebensministerium.at/duz/duz/category/1035>). In the USA OSR area increased from 53000 ha in 1992 to 283080 ha in 1997 (FAOSTAT, <http://faostat.fao.org/site/567/default.aspx>) accompanied with a 60-fold increase in pesticide use (Gianessi & Marcelli, 2000). Due to the increasing economic importance of OSR it is necessary to know under which conditions natural enemies of OSR pests are well fed and reproduce successfully thus establishing large populations.

Many carabid beetles are polyphagous predators commonly found in arable crops and considered important natural control agents of agricultural pests (Bohan *et al.*, 2000; Warner *et al.* 2000; Thomas *et al.*, 2001; Symondson *et al.* 2002; Holland *et al.*, 2005; Bommarco *et al.*, 2007). Carabids, together with other predatory arthropods commonly found in arable land, were observed to reduce populations of OSR pests emerging within rape fields (Zaller *et al.*, 2008a). In Central Europe, the carabid beetles *Anchomenus dorsalis*, *Amara similata*, *Harpalus affinis*, *Poecilus cupreus* and *Pseudophonus rufipes* frequently consume major insect pests of OSR (Schlein & Büchs, 2006; Schlein *et al.*, 2006). The present work focuses on the response of nutritional condition, reproductive potential and activity density of two of these pest consuming carabids, *A. similata* and *P. cupreus*, to a suite of field and landscape characteristics. These two carabids were investigated because they were the largest species among the five most abundant carabids occurring in all 29 study fields. High abundance and large body size render them potentially interesting natural control agents in arable crops like OSR. *A. similata* and *P. cupreus* are polyphagous predatory spring breeders common in agricultural land (Thiele, 1977; Pfiffner & Luka, 1996; Luka *et al.*, 1998; Langmaack *et al.*,

2001). *A. similata* has traditionally been considered mainly to be a granivore feeding on seeds available in the field (Jorgensen & Toft, 1997). However, now it must be considered both phytophagous and predacious as it recently was shown to feed upon insects, too (see above). Predatory carabids are often food limited (Pearson & Knisley, 1985; Bommarco, 1998a). Feeding by adult predatory carabids provides major parts of the resources used for reproduction (Sota, 1985; Juliano, 1986), and food quantity and quality will affect the fitness of individuals and the dynamics in carabid assemblages of agricultural landscapes (Wallin *et al.*, 1992; Bommarco, 1999; Östmann, 2005). The activity density of the beetles is also influenced by food availability with high prey densities leading to satiated, less active beetles (Lenski, 1984). In the laboratory, egg production of *P. cupreus* was positively correlated with food intake of adults (Bommarco, 1998b) and the eggload of females is considered a good indicator for habitat quality (van Dijk, 1983). Consequently, carabid beetles in habitats with larger food supply should be of better constitution and higher fecundity, which in turn leads to more offspring. *P. cupreus* was better nourished and females contained more ripe eggs in more diversely structured wildflower areas than rather monotonous cereal fields (Zangger *et al.*, 1994), and the nutritional condition and the number of ripe eggs of *P. cupreus* were larger in more diversely structured older wildflower areas compared to newly established rather monotonous ones (Barone & Frank, 2003). This, together with the fact that arthropod numbers often increase with the amount of non-crop habitats in agricultural landscapes (e.g. Drapela *et al.*, 2008) leads to the hypotheses that nutritional condition and reproductive potential of *A. similata* and *P. cupreus* will be enhanced, activity density on the other hand will be lowered by i) increased food supply on the local field scale (hypothesis 1) and ii) increasing amount of non-crop habitats at the scale of surrounding landscape (hypothesis 2). The aim of our study was to establish which field and landscape characteristics influence *A. similata* and *P. cupreus* in winter OSR fields. Whereas many studies focused separately on the influence of either field or landscape parameters on carabid beetles (Honěk & Jarošík,

2000; Pfiffner & Luka, 2003; Menalled *et al.*, 2007), this is to our knowledge the first study that examines simultaneously both the influence of field and landscape parameters on nutritional condition, reproductive potential and activity density of common carabid beetles in OSR.

3. MATERIALS AND METHODS

3.1 Study area

Our study was conducted in 29 winter oil seed rape fields in eastern Austria, about 40 km south-east of Vienna (coordinates of the central area: 16°57' E, 48°04' N). The study area, covering about 240 km², was situated in an agricultural landscape with wheat, maize, barley, OSR, sunflower, sugar beet and poppy seed as the main crops. Fallows, hedges and forest remnants were the non-crop habitats characterizing the study area. The selected OSR fields were embedded in differently structured landscapes ranging from structurally simple to structurally complex (Drapela *et al.*, 2008; Zaller *et al.*, 2008a, 2008b).

Oilseed rape was sown by the farmers from August to September 2004 with seeding rates of 3.1 to 5.2 kg ha⁻¹ (common seeding rates of OSR are between 2.5 and 10.0 kg ha⁻¹; Cramer, 1990). The OSR fields were fertilised and treated with herbicides, fungicides and insecticides following common agricultural practice until December 2004. From January 2005, within each OSR field an area of 1 ha was excluded from pesticide applications and used for sampling epigeic carabids. The position of this ha depended on field size but was always placed at one field edge. In cases where the field size was not larger than one ha, the whole field was excluded from pesticide applications. Influences of insecticide use from the surrounding landscape were not recorded.

3.2 Carabid sampling

Pitfall traps, consisting of plastic cups with an upper diameter of 6.5 cm and a height of 10 cm, were used for carabid sampling. The traps were filled with 100 ml 4% formaldehyde solution and emptied fortnightly from the end of March until the end of June, the time OSR was harvested. We used 3 traps per field, all set in a line at 8 m distance to the field edge. Traps in a line were 20 m apart. Beetles were preserved at -17°C in the freezer until morphometric measurements were taken and dissections were performed.

3.3 Carabid characteristics

To detect the peak of the reproduction period, ten females per species from each sampling week were dissected and the number of ripe eggs was counted. For *P. cupreus* this peak was between 16 May and 12 June 2005 comprising two sampling periods (there was a difference in oocyte numbers of 11% to earlier caught beetles and 21% to later caught beetles). The reproduction peak for *A. similata* lasted two weeks longer, from 16 May to 26 June 2005, comprising three sampling periods (almost no oocytes were found in beetles earlier in the season). Only beetles collected in these periods were used for subsequent analyses.

Ten females and ten males per sampling period, field and species were randomly chosen from the available collections, resulting in 20 specimens per sex and field for *P. cupreus* and maximum 30 for *A. similata*. Activity density of *A. similata* in some fields was not high enough to reach these numbers, so all available specimens were used. Fields that yielded less than five beetles per species and sex were excluded from analyses.

The condition factor (CF, Le Cren, 1951; Juliano, 1986) is based on the relationship between the length (L) and weight (W) of an individual expressed by the formula $W = aL^b$, where a and b are constants (Jarošík, 1989). CF is a good measure for the nutritional state of carabid beetles (Barone and Frank, 2003). For obtaining this data, the length of the left elytra of each beetle was measured under a stereo-microscope with a measuring eyepiece at ten fold

magnification (measurement accuracy: $\pm 0.03\text{mm}$); elytra length is a good indicator of overall body length in carabids (Juliano, 1986; Nelemans, 1987). In order to find the point of constant dry weight in air-dried beetles, a drying curve was calculated, plotting weight against time. According to this data, dry weight was achieved after 7 days air drying for the larger *P. cupreus* and after 5 days for *A. similata*. After the respective period, each beetle was weighed to the nearest 0.1 mg on a Mettler AK 160 balance. Length and weight of every single beetle were then plotted against each other and the constants a and b were calculated using a regression curve (ordinary least square regression, Excel for Microsoft® Windows^{XP}). Thereafter, the CF was ascertained by using the formula $CF_i = W_i/(L_i)^b$. A high CF indicates that the beetle is heavy relative to its length, thus the individual is well fed (Frank *et al.*, 2007). After measurement and weighing, females of *P. cupreus* and *A. similata* were dissected and the mature oocytes in the ovaries were counted. Mature oocytes were defined as being at least two thirds of the size of a laid egg (Ernsting *et al.*, 1992). For dissection it was necessary to soften the cuticle and inner structures. This was done by soaking the females in a mixture of 4% acetic acid and 0.3‰ washing up liquid (Frosch ®, 5-15 % anionic surfactants, <5 % amphoteric surfactants) for at least four hours. Furthermore, activity density of both species, measured as number of individuals caught during their peak of reproduction, was recorded.

3.4 Field parameters

For each of the study fields five parameters were recorded by questioning the concerning farmers. As a measure for soil quality, the soil index was determined (Drapela *et al.*, 2008; Zaller *et al.*, 2008a, 2008b). This index is defined through the yield capacity of a field in relation to the maximum yield capacity in this area, with values ranging from 0 to 100. A value of 0 indicates soils with lowest yield capacity and 100 indicates soils with highest yield

capacity. This integrative relative index is influenced by soil type, humus content, soil depth, texture, density, structure, lime content, gleying and soil congregation (ÖBG, 2001).

As a measure of disturbance within the field, a soil cultivation index was based on the farmer's statements about ploughing, harrowing, milling and grubbing. These specific actions have impact on soil biota by mechanically disturbing their horizontal and vertical distribution differentially. We rated these soil cultivation methods according to the impact these methods exert on soil biota, with low disturbances leading to low values and high disturbances leading to high values (impact-values: ploughing: 8, grubbing: 3, harrowing: 1, milling: 1). If the method was executed several times a year on one field, the appropriate impact-value was multiplied with the number of executions. The soil cultivation index is the result of summing up the products of the impact-value and the number of executions for all cultivation methods of one field. The soil cultivation index reached values between 6 and 15. Percentage cover of oilseed rape on the surface was estimated in November 2004 on 3 randomly positioned 1 m² plots on every field. It was measured because sites with increasing cover on the ground in late autumn were shown to favour density of overwintering carabids and staphylinids (Frank & Reichhart, 2004). Stand density of rape plants was measured shortly before OSR was harvested by counting the number of stems within two 1 m² plots per field. Rape stand density can affect humidity and temperature in the field, which are two abiotic factors being important for the distribution of carabid beetles (Thiele, 1977; Wallin, 1986). Moreover, increasing stand density can enhance the amount of available OSR seeds as food source for the partially granivorous *A. similata*. Additionally, mean larval pest density m⁻² was calculated for each study field by Zaller *et al.* (2008b, 2009). Pest density refers to abundances of pollen beetle (*Meligethes aeneus*), ceutorhynchid stem weevil (*Ceutorhynchus napi*) and brassica pod midge (*Dasineura brassicae*) on OSR plants. Pest abundance was assessed in April and May 2005 on randomly chosen OSR plants or pods along a 50 m transect located in the central area of each study field. Pollen beetle abundance was calculated by putting a plastic bag on the top

raceme of 25 OSR plants, cutting the raceme off and counting the larvae in the laboratory (Zaller *et al.*, 2009). Ceutorhynchid stem weevil abundance was calculated by dissecting 25 randomly chosen OSR plants and counting the larvae within the stems. Brassicae pod midge abundance was assessed by counting the larvae within 100 randomly chosen pods from the top raceme of OSR plants (Zaller *et al.*, 2008 b). All pest abundance data were expressed on a 1m² basis by using OSR stand density data (average number of stems assessed in two 1m² frames). These OSR pests were shown to be eaten by common arable carabids (e.g. *A. similata* and *P. cupreus*; Schlein *et al.*, 2006; Schlein & Büchs, 2006). Larvae of the pest species are of different size and therefore of different nutritional value for carabids. To include this information in our analyses, larval counts were multiplied with values for mean larval length (*M. aeneus* 3.75 mm, *C. napi* 7 mm, *D. brassicae* 1.5 mm; see Berger *et al.*, 1989; Hoffmann & Schmutterer, 1999; Paul, 2003), to obtain a proxy for prey biomass available for carabids at each field.

3.5 Landscape parameters

Landscape analysis was performed using the software packages ArcGIS 9.1 and ArcView GIS 3.3 (ESRI Redlands, CA, USA). The study was based on a detailed land use map, elaborated from real colour orthophotos (minimum resolution 0.25 m) in 2005.

Around each study field, 8 circular radii were established ranging from 250 m to 2000 m. Within these circles, the percentage of crop areas, areas dominated by woody plants, fallows, OSR fields, and settlements, as well as the length of roadside strips and of hedgerows was calculated. For estimating landscape diversity the Shannon-Wiener diversity index was calculated. We differentiated between 14 habitat types (arable fields, fallows dominated by grass, fallows with shrubberies, copses, dry near-natural grasslands (harbouring more plant diversity than fallows), dry shrublands, dry forests, alluvial forests, forests along rivers, hedges along roads or field margins, settlements, water bodies, roads and vineyards).

Additionally, the distances to the next OSR field, forest, fallow and dry near-natural grassland were calculated and included in the statistical models.

3.6 Statistical analyses

For all analyses the captures of carabid beetles per field were pooled across the sampling periods considered.

Landscape parameters were transformed by using the arcsin $\sqrt{}$ transformation for all parameters measured as percentages and the log transformation for distances to meet the requirements of general linear regression models. Correlation analyses between carabid characteristics were performed using Pearson's correlation coefficient and multiplicity correction of P-values was done by controlling the false discovery rate (FDR, Waite & Campbell, 2006)

Factor analyses (Suchard-Ficher *et al.*, 1982) were used to reduce the multidimensional predictor set (consisting of field parameters, landscape parameters measured at eight different radii and the distance parameters) to lower dimensions for regression calculations. Referring to Kaiser's criterion, only principle components with an eigenvalue of at least 1.00 were considered for subsequent analyses.

The first factor analysis, including only field parameters, resulted in habitat quality (soil index and pest length) and plant cover during winter as new predictor parameters. These parameters accounted for 60.9 % of the variance. Stand density and soil cultivation index were not significantly associated with these two factors. Distance parameters were reduced using a second factor analysis, resulting in the minimum distance to the next grassy site (minimum distance to the next fallow or dry near-natural grassland) and the minimum distance to the next non-grassy site (minimum distance to the next OSR field or woody area) as new parameters; these two parameters accounted for 69.2 % of the variance.

Factor analyses were also used to reduce the large number of landscape parameters measured at eight different radii. The eight radii of these parameters (the percentage of crop area, area dominated by woody plants, fallows, settlements, the length of roadside strips and of hedgerows and the Shannon-Wiener diversity index) were reduced to two new parameters, resulting in a near (250 - 750 or 1000 m) and far (1000 or 1250 - 2000 m) component (parameters accounted for 82.3-94.3 % of the variance). Only the percentage of OSR area resulted in just one new parameter (250 – 2000 m, 82.9% of explained variance). The resulting near and far components and the percentage of OSR area were used in another factor analysis, whereas only two new parameters were allowed (no further referring to Kaiser's criterion). These two parameters are called diversity near (percentage of crop area from 250-1000 m, of fallows from 250-750 m and the Shannon Diversity index from 250-1000 m radii) and diversity far (percentage of crop area from 1250-2000 m and the Shannon diversity index from 1250-2000 m; parameters accounted for 42.6 % of the variance).

The new predictor parameters (habitat quality, cover, distance to the next grassy site, distance to the next non-grassy site, diversity near and diversity far) resulting from all four factor analyses, are called 'grouped predictor parameters' in the further context.

The mean CF of carabid beetles, separately for both sexes, and the mean number of mature oocytes of a female were calculated for each field and species. These means, as well as the activity density of males and females of both species, were used as response variables (10 altogether) relative to the afore mentioned grouped predictor parameters through multiple linear regression analysis.

For each response variable, Akaike's Information Criterion (AIC; Ward, 2008) was used to find the best, and most simple regression model, respectively. The best model was defined by the lowest AIC value, whereas the simplest model was a compromise between the lowest number of predictor variables and a rather low AIC value. Afterwards, multiple or simple linear regressions with the results from AIC were performed to get the percentage of

explained variance of these models. As the simplest model according to AIC consisted of one factor calculated by factor analysis, this factor was divided into its original components in the following step, and again single linear regressions were calculated.

Factor analysis is accompanied by the loss of information by the reduction of parameters. As in all cases but one field parameters proved to be important, AIC was calculated to face this problem of information loss, including all collected field parameters but no further landscape parameters in the analyses. Only the simplest model found through AIC was used for regression calculations. These calculations were not repeated for landscape parameters at the different radii as they had no influence on carabids.

If pest length was the best parameter, additional regression analyses were made where all three pest species were tested separately to detect possible food preferences of carabids for a specific pest. For these analyses focusing on each single pest species we used the original mean pest abundance data (instead of their length) per field.

4. RESULTS

4.1 Numbers and characteristics of carabid beetles

1418 individuals of *A. similata* (558 males and 860 females, sex ratio 1:1.5) and 28001 individuals of *P. cupreus* (12700 males and 15301 females, sex ratio 1:1.2) were caught in the pitfall traps. These two species comprised 63% of all carabids caught in the 29 study fields during our study period.

There was a significantly positive relation between CF and oocyte numbers for *A. similata* and *P. cupreus* females. Oocyte numbers and activity density of *P. cupreus* females, and CF and activity density of female and male *P. cupreus*, were significantly negatively correlated (Table 1).

Table 1: Pearson correlation coefficients between CF and activity density (ActDens), CF and oocyte numbers (oocytes), and between oocyte numbers and activity density of *A. similata* and *P. cupreus*.

** $P < 0.01$; *** $P < 0.001$

	<i>A. similata</i> female	<i>A. similata</i> male	<i>P. cupreus</i> female	<i>P. cupreus</i> male
CF / ActDens	-0.17	-0.31	-0.54**	-0.49**
CF / Oocytes	0.56**		0.81***	
Oocytes / ActDens	0.29		-0.51**	

4.2 Influence of field and landscape parameters

4.2.1 Multiple regression analyses including grouped predictor parameters

In five out of ten cases, the simplest model was also the best one according to AIC (Table 2).

This was true for the CF of *A. similata* males, the females' CF of both species and the oocyte numbers of both species. All but one regression model (oocyte numbers in *A. similata*)

contained just the one single parameter habitat quality (Table 2). Habitat quality, plant cover and distance to the next grassy site explained the CF of male *P. cupreus* best, whereas the

simplest model was made up by habitat quality alone. Activity density of male *A. similata* was best explained by a model consisting of the parameters habitat quality, plant cover, distance to the next grassy site, distance to the next non-grassy site and diversity far. Again, the simplest

model was made up by habitat quality as single parameter. The best model for activity density of female *A. similata* consisted of habitat quality and plant cover, the simplest model of

habitat quality alone. Activity density of *P. cupreus* females and males responded to habitat quality and the distance to the next non-grassy site, the simplest model contained only habitat

quality. Additionally, multiple linear regression models, including all variables from factor analysis, were calculated to allow comparisons between the full models and the parameter-

reduced models (best and simplest models). The full models explained most of the activity

density of female and male *A. similata* and *P. cupreus* significantly, and the CF of *P. cupreus* males (Table 2).

Table 2: AIC and regression results for carabid characteristics. The table shows the full, best and simplest model according to the AIC and gives the results from multiple and single linear regression calculations. Furthermore, the results from factor splitting single linear regression analyses (Parameter 1, Parameter 2) are shown.

CF = condition factor, HQ = habitat quality, C = plant cover, DG = minimum distance to the next grassy site, DNG = minimum distance to the next non-grassy site, DIVN = diversity near, DNF = diversity far, dist. fallow = distance to the next fallow, dist. dry grassland = distance to the next dry near-natural grassland.

Significant models are printed in bold.

Species & Sex	Carabid Characteristics	Grouped predictor parameters			Factor splitting ^(a)	
		Full Model	Best Model	Simplest Model	Parameter 1	Parameter 2
<i>Amara similata</i> female	CF	HQ, C, DG, DNG, DIVN, DIVE	HQ	HQ	pest length	soil index
		$R^2 = 0.344$ $P = 0.122$	$R^2 = 0.244$ $P = 0.006$	$R^2 = 0.244$ $P = 0.006$	$R^2 = 0.220$ $P = 0.009$	$R^2 = 0.032$ $P = 0.354$
<i>Amara similata</i> female	Oocytes	HQ, C, DG, DNG, DIVN, DIVE	DG	DG	dist. Fallow	dist. dry grassland
		$R^2 = 0.163$ $P = 0.643$	$R^2 = 0.047$ $P = 0.257$	$R^2 = 0.047$ $P = 0.257$	$R^2 = 0.156$ $P = 0.034$	$R^2 = 0.014$ $P = 0.537$
<i>Amara similata</i> female	Activity Density	HQ, C, DG, DNG, DIVN, DIVE	HQ, C	HQ	soil index	pest length
		$R^2 = 0.434$ $P = 0.035$	$R^2 = 0.379$ $P = 0.002$	$R^2 = 0.225$ $P = 0.009$	$R^2 = 0.215$ $P = 0.011$	$R^2 = 0.077$ $P = 0.145$
<i>Amara similata</i> male	CF	HQ, C, DG, DNG, DIVN, DIVE	HQ	HQ	pest length	soil index
		$R^2 = 0.228$ $P = 0.461$	$R^2 = 0.192$ $P = 0.022$	$R^2 = 0.192$ $P = 0.022$	$R^2 = 0.184$ $P = 0.026$	$R^2 = 0.143$ $P = 0.044$
<i>Amara similata</i> male	Activity Density	HQ, C, DG, DNG, DIVN, DIVE	HQ, C, DG, DNG, DIVE	HQ	pest length	soil index
		$R^2 = 0.575$ $P = 0.005$	$R^2 = 0.570$ $P = 0.002$	$R^2 = 0.220$ $P = 0.013$	$R^2 = 0.192$ $P = 0.022$	$R^2 = 0.060$ $P = 0.220$

Table 2 continued

Species & Sex	Carabid Characteristics	Grouped predictor parameters			Factor splitting ^(a)	
		Full Model	Best Model	Simplest Model	Parameter 1	Parameter 2
<i>Poecilus cupreus</i> female	CF	HQ, C, DG, DNG, DIVN, DIVE	HQ	HQ	pest length	soil index
		$R^2 = 0.366$ $P = 0.092$	$R^2 = \mathbf{0.218}$ $P = \mathbf{0.011}$	$R^2 = \mathbf{0.218}$ $P = \mathbf{0.011}$	$R^2 = \mathbf{0.197}$ $P = \mathbf{0.016}$	$R^2 = 0.044$ $P = 0.275$
<i>Poecilus cupreus</i> female	Oocytes	HQ, C, DG, DNG, DIVN, DIVE	HQ	HQ	pest length	soil index
		$R^2 = 0.260$ $P = 0.303$	$R^2 = \mathbf{0.176}$ $P = \mathbf{0.024}$	$R^2 = \mathbf{0.176}$ $P = \mathbf{0.024}$	$R^2 = 0.128$ $P = 0.056$	$R^2 = 0.091$ $P = 0.111$
<i>Poecilus cupreus</i> female	Activity Density	HQ, C, DG, DNG, DIVN, DIVE	HQ, DNG	HQ	pest length	soil index
		$R^2 = \mathbf{0.506}$ $P = \mathbf{0.009}$	$R^2 = \mathbf{0.479}$ $P < \mathbf{0.001}$	$R^2 = \mathbf{0.324}$ $P = \mathbf{0.001}$	$R^2 = \mathbf{0.288}$ $P = \mathbf{0.003}$	$R^2 = \mathbf{0.189}$ $P = \mathbf{0.018}$
<i>Poecilus cupreus</i> male	CF	HQ, C, DG, DNG, DIVN, DIVE	HQ, C, DG	HQ	pest length	soil index
		$R^2 = \mathbf{0.462}$ $P = \mathbf{0.022}$	$R^2 = \mathbf{0.444}$ $P = \mathbf{0.002}$	$R^2 = \mathbf{0.326}$ $P = \mathbf{0.001}$	$R^2 = \mathbf{0.290}$ $P = \mathbf{0.003}$	$R^2 = 0.081$ $P = 0.135$
<i>Poecilus cupreus</i> male	Activity Density	HQ, C, DG, DNG, DIVN, DIVE	HQ, DNG	HQ	pest length	soil index
		$R^2 = \mathbf{0.447}$ $P = \mathbf{0.028}$	$R^2 = \mathbf{0.411}$ $P = \mathbf{0.001}$	$R^2 = \mathbf{0.304}$ $P = \mathbf{0.002}$	$R^2 = \mathbf{0.278}$ $P = \mathbf{0.003}$	$R^2 = \mathbf{0.167}$ $P = \mathbf{0.028}$

^(a) based on single predictor parameters

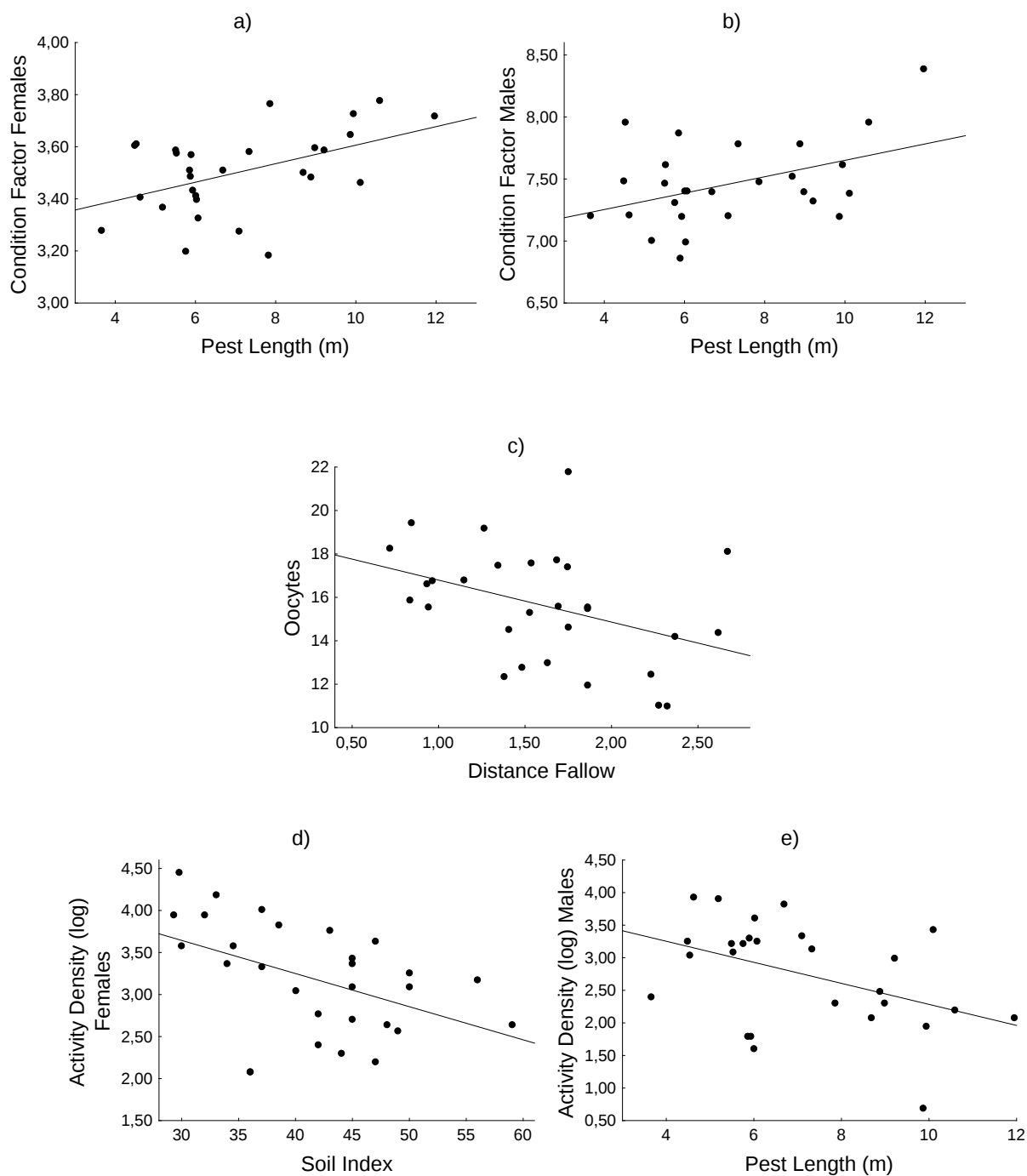


Figure 1: Regression analyses for *A. similata* after factor splitting

a) $y = 3.2506 + 0.0356 x$; $n = 29$ b) $y = 6.9893 + 0.0661 x$; $n = 27$

c) $y = 18.7267 - 1.9322 x$; $n = 29$

d) $y = 4.8262 - 0.0394 x$; $n = 29$ e) $y = 3.8988 - 0.1615 x$; $n = 27$

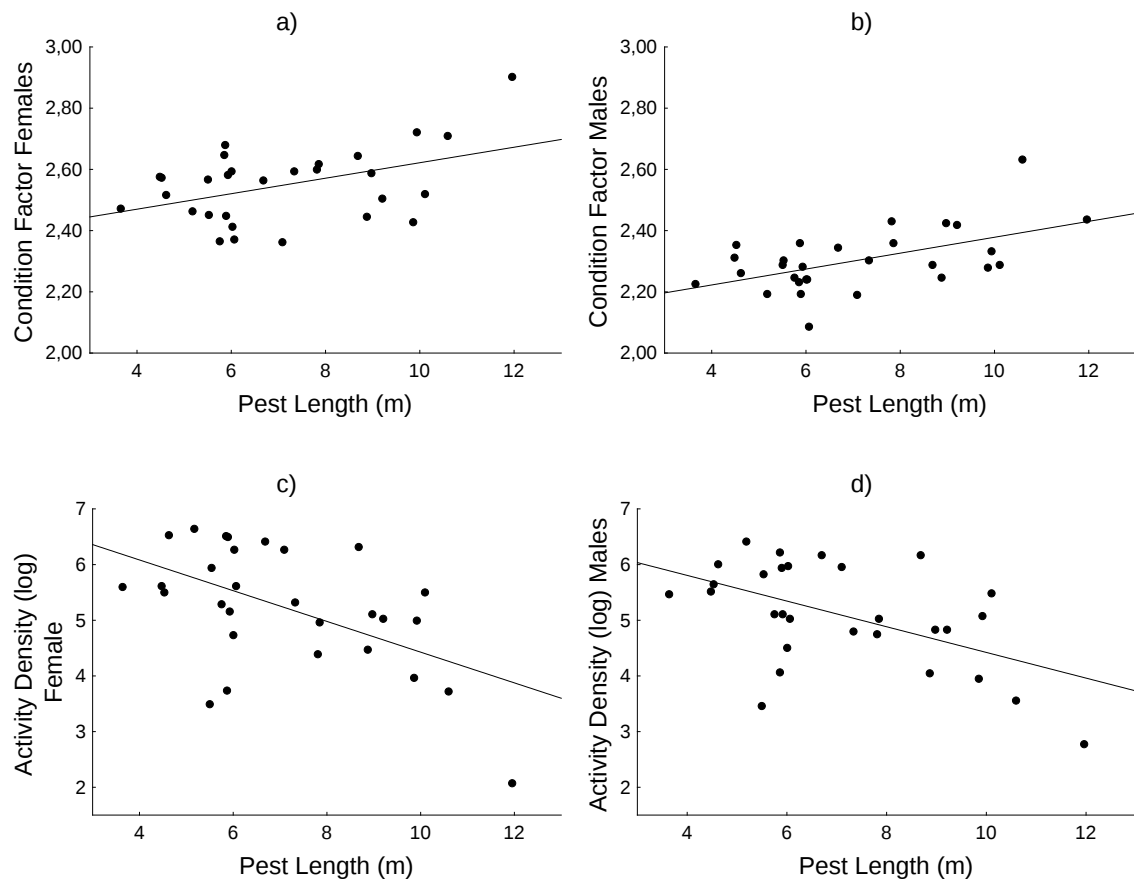


Figure 2: Regression analyses for *P. cupreus* after factor splitting (n = 29 each)

a) $y = 2.3689 + 0.0253 x$ b) $y = 2.1186 + 0.0026 x$

c) $y = 7.1872 - 0.276 x$ d) $y = 6.728 - 0.2306 x$

4.2.2 Factor splitting

To find the most important individual parameters explaining the carabid characteristics, additional regression models were calculated by splitting up the predictor contained in the simplest model (as revealed by AIC) into its underlying components. Habitat quality was therefore divided into soil index and pest length, and distance to the next grassy site was partitioned into the distance to the next dry near-natural grassland and the distance to the next fallow. CF of female *A. similata* was best explained by pest length (Table 2). For male *A. similata*, pest length and soil index were almost equally important, with pest length explaining 18% and soil index 14% of the variance, respectively. Similarly, pest length was

the most important predictor parameter for the CF of both sexes of *P. cupreus*. All these relations were positive (Figure 1 and 2). Oocyte production of *A. similata* females decreased significantly with increasing distance of study fields to the next fallow (Figure 1). Oocyte numbers of *P. cupreus* tended to respond to pest length (Table 2). Pest length explained activity density of male *A. similata* and both sexes of *P. cupreus* significantly (Table 2), with all relationships being negative (Figure 1 and 2). Activity density of female *A. similata* was best explained by a significantly negative response to soil index (Figure 1).

4.2.3 Field parameter regressions

In all but one cases, the simplest model was identical to the best explaining model calculated in the factor splitting regression analyses (for results see Table 2, Parameter 1). Only the CF of female *A. similata* was an exception as being significantly positively influenced by stand density (single linear regression, multiple $R^2 = 0.25$, $P = 0.006$).

4.3 Significance of individual pest species for carabid characteristics

Pollen beetle was the most abundant pest species with a mean abundance of 1797.13 ± 535.71 individuals m^{-2} , followed by brassica pod midge with an average of 113.27 ± 58.09 individuals m^{-2} , and ceutorhynchid stem weevil larvae with 26.90 ± 17.62 individuals m^{-2} . In seven out of eight cases carabid characteristics were significantly influenced by pollen beetle abundance (Table 3). Significant regression models for carabid characteristics were also found in six out of eight cases for ceutorhynchid stem weevil abundance, whereas only the CF of male *P. cupreus* was significantly influenced by brassicae pod midge abundance. These relationships for CF were positive, those for activity density were negative (Table 3).

Table 3: Significance of individual pest species for carabid characteristics. The table shows the results of single linear regression analyses of carabid characteristics and pest species abundance.

CF = condition factor, R^2 = multiple R^2 , + = positive response, - = negative response
Significant models are printed in bold.

Species & Sex	Carabid characteristics	Pest Species		
		<i>Meligethes aeneus</i>	<i>Ceutorhynchus napi</i>	<i>Dasineura brassicae</i>
<i>Amara similata</i> female	CF	$R^2 = 0.214$ P = 0.011 +	$R^2 = 0.233$ P = 0.008 +	$R^2 = 0.083$ P = 0.129
<i>Amara similata</i> male	CF	$R^2 = 0.180$ P = 0.027 +	$R^2 = 0.126$ P = 0.069	$R^2 = 0.035$ P = 0.351
<i>Amara similata</i> male	Activity Density	$R^2 = 0.181$ P = 0.027 -	$R^2 = 0.271$ P = 0.005 -	$R^2 = 0.031$ P = 0.380
<i>Poecilus cupreus</i> female	CF	$R^2 = 0.194$ P = 0.017 +	$R^2 = 0.168$ P = 0.027 +	$R^2 = 0.006$ P = 0.683
<i>Poecilus cupreus</i> female	Oocytes	$R^2 = 0.131$ P = 0.054	$R^2 = 0.095$ P = 0.103	$R^2 = 0.001$ P = 0.857
<i>Poecilus cupreus</i> female	Activity Density	$R^2 = 0.277$ P = 0.003 -	$R^2 = 0.267$ P = 0.004 -	$R^2 = 0.063$ P = 0.190
<i>Poecilus cupreus</i> male	CF	$R^2 = 0.278$ P = 0.003 +	$R^2 = 0.154$ P = 0.035 +	$R^2 = 0.201$ P = 0.015 +
<i>Poecilus cupreus</i> male	Activity Density	$R^2 = 0.267$ P = 0.004 -	$R^2 = 0.255$ P = 0.005 -	$R^2 = 0.057$ P = 0.213

5. DISCUSSION

In carabid beetles as holometabolous insects adult length fully depends on larval food intake (Knisley & Juliano, 1988; Ernsting *et al.*, 1992), whereas weight is also strongly modulated by food availability during the adult stage (Bommarco, 1998b). Larval and adult stages of *P. cupreus* are considered to be carnivorous (Chiverton, 1988; Ekbom *et al.*, 1992), even though some studies revealed a more omnivorous diet which even includes plant material to some extent (e.g. Koprdoва *et al.*, 2008). Our regression models corroborate a carnivorous feeding habit of *P. cupreus* with the CF being best explained by pest length as a proxy of prey availability. To a lesser extent, CF in *P. cupreus* was also related to soil fertility, which again indicates that food availability at the scale of the field is most important. However, pest length and soil index were significantly positively correlated to each other, as were pest length and stand density, or stand density and soil index. Hence, all these field parameters are just collinear measures of local productivity and thus food availability.

No single landscape parameter recorded at different scales had any detectable direct influence on the condition. However, some indirect effects of surrounding landscape may occur. Pest length was significantly ($P < 0.05$) positively related to landscape diversity at larger scales (1250-2000 m), percentage of areas dominated by woody plants at largest scales (1750-2000 m), length of hedgerows (1000-1250 m) and of roadside strips at 250 m. Yet, these correlations were usually weak (R^2 : 0.38-0.51), and they did not consistently show up at all spatial scales. Pest length was also negatively correlated with the distance to the next dry near-natural grassland.

These results indicate that there is at most an indirect dependence of the CF of *P. cupreus* on landscape characteristics, since the available prey may be enhanced by non-crop habitats surrounding OSR fields. Good soil quality, in contrast, will lead to higher stand density of OSR plants, which in turn could positively influence pest length. These assumptions are confirmed by Zaller *et al.* (2008b) who investigated pest abundance on the same 29 study

fields. They observed pollen beetle and brassica pod midge abundance to be positively related to soil index and landscape diversity. Furthermore, the percentage of woody area influenced pod midge abundance significantly advantageously.

Carabid larvae are generally thought to be carnivorous. *A. similata* larvae, however, are granivorous; they are not able to survive on a strict insect diet and even suffer from a mixed diet (Jørgensen & Tøft, 1997). Adult *A. similata* is recorded to be mainly granivorous (Honěk *et al.*, 2003), although in laboratory feeding experiments this species was found to be entomophagous to a large extent, comparable to *P. cupreus* (Schlein & Büchs, 2004). In line with these studies, the CF of *A. similata* males depended on pest length in our study, which indicates a carnivorous feeding habit for male *A. similata*.

As pest length was correlated with soil index and stand density the influence of pest length on the CF of male *A. similata* may have been overestimated. However, single linear regressions between the CF of male *A. similata* and pest length ($R^2 = 0.18$, $P = 0.026$), soil index ($R^2 = 0.15$, $P = 0.044$) and stand density ($R^2 = 0.03$, $P = 0.420$) proved pest length to be the most important parameter. The CF of female *A. similata*, on the other hand, responded similarly to stand density ($R^2 = 0.25$, $P = 0.006$) and pest length ($R^2 = 0.23$, $P = 0.009$), but not to soil index ($R^2 = 0.03$, $P = 0.354$). Maybe there are differences in the feeding habits of male and female *A. similata*, with females being more polyphagous than males. *Amara* species in general are recorded to feed on seeds of Brassicaceae (Lindroth, 1945) and therefore eat oilseed rape seeds, too (Luka *et al.*, 1998). Thus, the CFs of female *A. similata* may be higher in fields with more OSR plants per area as there are more OSR seeds available. Moreover, higher stand density may increase pest length, which in turn may lead to higher prey availability and thus may positively influence the CF of female *A. similata*.

Food intake not only affects the CF of a beetle but also its fecundity (Wallin *et al.*, 1992). For egg production not only the quantity but also the composition of food consumed is essential. Edwards *et al.* (2004) found *Coccinella septempunctata* (Coleoptera: Coccinellidae) to

produce more eggs when fed on aphids than on weevils, and Evans & Gunther (2005) reported that *Harmonia axyridis* (Coleoptera: Coccinellidae) only laid eggs when fed on aphids while a weevil-diet caused the beetle to stop egg production. For Coccinellidae, Hodek (1962) and Hodek & Honěk (1996) distinguished between essential prey, which is needed for larval growth and development as well as for reproduction, and alternative prey, which only serves as energy source but does not enhance development or reproduction. Our study revealed the oocyte numbers in the ovaries of *A. similata* to respond to the distance to the next fallow, although the parameter was just barley significant. However, assuming that essential prey is also necessary for carabids, it might be that for egg production *A. similata* needs food that was not available in our study fields. Weed abundance in the OSR fields of our study was low (Zaller, J. G., personal communication), but Saska (2008) and Jørgensen & Toft (1997) found in laboratory feeding experiments certain arable weed species (e.g. *Capsella bursa-pastoris*, *Tripleurospermum inodorum*, *Taraxacum* sp.) to be attractive food for *A. similata*. This may cause the females to search for weeds as an essential food in fallows close to the studied OSR fields.

For *P. cupreus* no significant model was found for the explanation of oocyte numbers, but we detected a positive trend between fecundity and pest length. Overall, food shortage in animals is one main factor limiting population growth (White, 1978). The carabid beetle *Calathus melanocephalus* was proved to be food limited in the field (van Dijk, 1986). For *Nebria brevicollis* a minimum of 0.4 mg fresh weight of food was discovered to be the threshold below which egg production is stopped (de Ruiter & Ernsting, 1987). Barone & Frank (2003) observed an increase in nutritional condition and eggload of *P. cupreus* in 2 to 4-year-old wildflower areas compared to 1-year-old ones. They concluded that a higher food supply in 2 to 4-year-old wildflower areas may have influenced the reproductive potential of *P. cupreus*, as was previously shown for the closely related *Poecilus versicolor* (van Dijk, 1994). All these studies indicate the importance of food intake for reproduction. Thus, even though our

results were not significant, the amount of available high-quality food for *P. cupreus* may also determine its fecundity.

In an earlier study, fecundity of *P. cupreus* was negatively influenced by the proportion of annual crops in the landscape, and positively influenced by a high perimeter-to-area ratio of arable fields (Bommarco, 1998a). These findings are in contrast to our study. However, we found pest length to be correlated with roadside strips at 250 m. The amount of roadside strips may be comparable to the perimeter-to-area ratio because roadside strips usually surround arable fields, thus the increase of both parameters represents a more heterogeneous landscape with smaller fields. Small-sized fields appear to have a positive influence on the availability of food for *P. cupreus* and therefore on the fecundity of this beetle, as edge effects become more prevalent.

Activity density of *A. similata* males and of both sexes of *P. cupreus* increased with decreasing pest length which may be explained by prey availability. When there are few pests available, beetles are more active in search for food, which in turn may lower their CF. High pest densities lead to less active and satiated beetles (Lenski, 1984). This explanation is supported by a negative correlation between the CF of female and male *P. cupreus* and their activity densities, and between oocyte numbers of female *P. cupreus* and their activity density, indicating that activity of *P. cupreus* is low when they are well fed. In *A. similata* female activity density was negatively correlated with the soil index of a field. As the activity of a beetle is mainly influenced by its nutritional state (Lenski, 1984) this indicates that *A. similata* females were probably hungrier when soil index was low. Fields with high soil index and therefore high soil quality may produce more oilseed rape seeds, thus perhaps increasing the availability of possible food for *A. similata*. These results confirm the assumption that a good trophic quality at local scale negatively influences the activity densities of carabid beetles. Larvae of all three major OSR pest species may be encountered by the carabids when dropping to the ground for pupation from May to June. At that time they are vulnerable for

being consumed by *A. similata* and *P. cupreus* that are searching for food on the ground. Pest species analyses revealed pollen beetle and ceutorhynchid stem weevil abundance to explain most of the carabid characteristics in our study. In accordance with our findings, Schlein *et al.* (2006) observed *P. cupreus* to feed on pollen beetle. Schlein & Büchs (2006) detected *A. similata* to prey on brassica pod midge in the laboratory. In the field, Warner *et al.* (2000) found no spatial relation between brassica pod midge and *A. similata*, indicating brassica pod midge to be no essential prey for *A. similata*; this agrees with our findings. Due to the particularly small size and the low energetical value of brassica pod midge larvae they were possibly not eaten by *A. similata*.

Performance and abundance of the mostly carnivorous *P. cupreus* was always best explained by pest length, which supports our hypothesis 1 that nutritional status and reproductive potential will be enhanced but activity density will be lowered by increased local food supply. The same was true for male *A. similata* and the CF of female *A. similata*. Overall, support for this hypothesis came from eight out of 10 response variables, whereas we obtained but weak support for hypothesis 2 (fitness of carabid beetles on OSR fields is positively modulated by features of the surrounding landscape) in just one case, viz. the relation between the oocytes of *A. similata* and the distance to the next fallow.

Our observation that pest length was the single most important parameter explaining carabid characteristics indicates that *P. cupreus* and *A. similata* may exert natural control of insect pests in OSR fields. This is in line with recent findings for *Anchomenus dorsalis* and *P. cupreus* as predators of ceutorhynchid stem weevils in OSR fields (Zaller *et al.*, 2008a). The effectiveness of carabid beetles in reducing pest species abundance may depend on the time of their presence in the field and the period when pest species are most vulnerable to predation. Thus, to establish the extent to which carabid beetles are effective in reducing pest populations in OSR fields, further studies should be conducted comprising laboratory feeding experiments and gut analyses including molecular methods from beetles caught in the field.

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8. APPENDIX

8.1 Zusammenfassung

1. Es wurde der Einfluss von Feld- und Landschaftsparametern auf den Ernährungszustand, die potentielle Reproduktionsleistung und Aktivitätsdichte von *Amara similata* und *Poecilus cupreus* in Rapsfeldern untersucht.
2. Die Feldparameter, die in die Studie Eingang fanden, waren die Bodenzahl, der Bodenbearbeitungsindex, die Pflanzenbedeckung im November, die Bestandesdichte der Rapspflanzen sowie die Schädlingslänge (als Maß für die verfügbare Beute im Feld). Die Landschaftsparameter wurden auf acht verschiedenen Radien um jedes Untersuchungsfeld gemessen. Sie umfassten den Anteil an Ackerflächen, an Flächen mit überwiegend holzigen Pflanzen, an Flächen mit Brachen, an Flächen mit Rapsfeldern, an Siedlungsflächen, sowie die Länge an Straßenrändern, die Länge an Hecken und den Shannon-Wiener Diversitätsindex. Außerdem wurde die Distanz zum nächsten Wald, zur nächsten Brache, zum nächsten Trockenrasen und zum nächsten Rapsfeld ermittelt und in die Studie miteinbezogen.
3. Die Schädlingslänge beeinflusste den Ernährungszustand und die Aktivitätsdichte beider Arten und Geschlechter signifikant (positive Beziehung für den Ernährungszustand, negative für die Aktivitätsdichte). Zusätzlich wurde der Ernährungszustand der weiblichen *A. similata* signifikant positiv von der Bestandesdichte, der Ernährungszustand der männlichen *A. similata* signifikant positiv von der Bodenzahl und die Aktivitätsdichte beider Geschlechter von *P. cupreus* signifikant negativ von der Bodenzahl beeinflusst. Die Oocytenzahl von *A. similata* zeigte einen signifikant negativen Zusammenhang mit der Distanz zur nächsten Brache. Weiterführende Regressionen mit den Abundanzen der Rapsschädlinge *Meligethes aeneus*, *Ceutorhynchus napi* und *Dasineura brassicae* zeigten, dass für die Erklärung des Ernährungszustandes und der Aktivitätsdichte der männlichen *A. similata* und beider Geschlechter von *P. cupreus* sowohl *M. aeneus* als auch *C. napi* von Bedeutung sind.

4. Bei der gleichzeitigen Analyse von sowohl Feld- als auch Landschaftsparametern durch allgemeine lineare Modelle, zeigte sich in acht von zehn Fällen, dass die Schädlingslänge der meist erklärende Faktor in Hinblick auf Ernährungszustand, potentielle Reproduktionsleistung und Aktivitätsdichte von *A. similata* und *P. cupreus* ist. Die Landschaftsparameter, aufgenommen auf verschiedenen räumlichen Skalen, waren für deren Erklärung deutlich weniger wichtig.

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