



Is the age of forest habitats affecting the reproductive rate of generalist predatory ground beetle species?

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Abstract: This study aimed at the effects of habitat age on the reproductive rate of three ground beetle species that are common and widely distributed in forest ecosystems of Europe (*Abax parallelepipedus* (Pill. & Mitt.), *Pterostichus oblongopunctatus* (F.), *Pterostichus burmeisteri* (Heer.)). The study sites comprised comparable age classes, i.e., young stands, mature stands, and mature forests with upcoming and established natural regeneration of four different forest types, namely pure stands of spruce and Douglas fir, and mixed stands of spruce-beech and oak-beech. As an indicator for the reproductive rate of female beetles, the number of ripe eggs in the ovaries and the duration of the reproduction period were investigated from captures of pitfall trapping ($n = 8$ per site). The dissection of a total of 1236 females uncovered 1704 eggs. A broad spectrum of environmental factors including microclimate (temperature, humidity, precipitation), soil parameters (moisture, pH, thickness and coverage of litter layer) and vegetation characteristics (coverage of moss, herb, grass, shrub and natural regeneration, degree of canopy closure) was assessed to reveal the relevant factors influencing the reproductive success.

Within the forest types, the egg-load of the ground beetle species showed statistically significant relations to the age of the stand type. For *A. parallelepipedus*, a quite uniform reaction pattern was evident with significantly higher egg-loads in the mature forests compared to the young stands. This was accompanied by a longer duration of the reproduction period. A stronger influence of the forest type was obvious for the egg-load of *Pt. oblongopunctatus* and *Pt. burmeisteri*. The reproductive rate was generally increasing with temperature aspects in forest sites and was significantly influenced by moisture parameters. The mean maximum temperature of the habitat cared for most of the variation in *A. parallelepipedus* (61.4%), while the mean minimum temperature explained 60.7% of the reproductive potential in *Pt. oblongopunctatus*. The variation of *Pt. burmeisteri* was best explained by the humidity of the air (49.4%). Thus, the results of our study emphasize the role of abiotic parameters on the reproductive rate of ground beetles.

Nomenclature for carabids: Trautner et al. (1997).

Introduction

The age of forest habitats with all its successional alterations is likely to influence the fitness of individual arthropods and the composition of communities including the soil-dwelling predacious taxa (Brown and Southwood 1987, Hurd and Fagan 1992, Heyborne et al. 2003). As forests in Europe are mostly human-induced environments that change continuously with the successional dynamics (Fagan 1992, Paquin and Coderre 1997, Dajoz 2000), the age of forest habitats and the resulting changes in environmental conditions are often reflected in significant effects on the relative abundance of ground beetles (Southwood et al. 1979, Niemelä et al. 1996, Butterfield

1997, Ziesche et al. 2004, Magura et al. 2003, 2006). Thus, soil dwelling carabid beetles have proved to be a useful arthropod group for monitoring and detecting changes in the environment (Eyre and Luff 1990, Rainio and Niemelä 2003) and many species are non-randomly distributed with respect to distinct environmental requirements. While the carabid species distribution pattern in forests of different tree composition is a well-investigated field (Loreau 1986, Butterfield et al. 1995, Ings and Hartley 1999), the reproductive potential as a measure of habitat aptitude along the successional development of forests is still a matter of research. As a study of Van Dijk (1983) showed, the egg-load of females is considered to be a good indicator of habitat quality in this context.

As habitat age is the result of the specification of a broad variety of environmental factors, the question raises if there are specific habitat parameters that affect the reproductive potential of carabid species in forest habitats. Barone and Frank (2003) documented that increasing habitat age promoted the reproductive potential of *Poecilus cupreus* in early successional stages of wildflower meadows. This was also an effect of better nutritional condition of individuals with increasing vegetation cover (Bommarco 1998, Denys and Tschamtkke 2002).

Van Dijk (1982, 1986b) found direct and sharp reactions in carabid fecundity upon experimental changes in quantities and the kind of food under constant temperature. Quantity as well as quality and composition of available food is known to affect fitness and the egg production rate of carabid beetles in experimental studies (Mols 1979, Van Dijk 1979, Heessen 1980, Lenski 1982, Van Dijk 1983, Grün 1984, Sota 1985, Juliano 1986, Wallin et al. 1992). Szyszko et al. (1996) suggested that changes in food availability for the larvae and adults of *Pt. oblongopunctatus* arose in the course of successional changes in forests. But, on the other hand, the respiration rate of adult beetles as an indicator of consumption rate decreased in this study with increasing age of forests. Food limitation during the developmental cycle of polyphagous carabids is likely to appear frequently in the course of the season (Van Dijk 1986b, Bilde and Toft 1998, Bommarco 1999) and the food availability is an intrinsic feature of the habitat (Schneider 1997), but is still less well studied (Pearson and Knisley 1985, Van Dijk 1986a).

Besides the nutritional influence on the number of eggs laid, there is strong indication that microclimatic conditions during the reproductive period directly influence the reproduction rate (Van Dijk 1994). Until now, few studies considered the impact of detailed environmental conditions on carabid reproduction in the course of forest succession. For example, the egg production was found to be highly temperature dependent under constant feeding conditions in laboratory studies (Van Dijk 1979, 1982, 1983, Ernsting and Huyer 1984). Usually it is a complex of factors, like food availability, temperature and humidity, that determines the egg production in the field (Thiele 1975, 1977, Van Dijk 1986a, Begon et al. 1996).

The aim of this study was to test the hypothesis that the reproductive rate of various ground beetle species is affected by the age of forest habitats. Moreover, it is assumed that the relation between habitat age and reproductive rate is due to the performance of environmental parameters varying with the characteristic features of the successional stages. Thus, the reproductive rate of three

common silvicolous ground beetle species (*A. parallelepipedus*, *Pt. oblongopunctatus*, *Pt. burmeisteri*) was examined in four forest types of different age classes.

Materials and methods

Study sites

The investigation was carried out in the cultural landscape around Augsburg (48°19′/11°06′, Central Bavaria, South Germany), with a high share of forested area. The study area belongs to the Tertiary hill country of the government district Swabia. It is predominantly characterized by a subatlantic climate with annual mean temperatures of 7.5 to 8.0°C. The average of annual precipitation ranges between 700–900 mm. The soils developed on these sites are fertile brown and parabrown earths. They originate from sediments of the Upper Miocene, overlaid by a fine, more or less mighty loam layer which is derived from loess loam.

The study sites (n = 12) comprised forest ecosystems of four different tree species compositions (stand type), which are representative for the cultural landscapes of South Germany: pure stands of spruce (*Picea abies*) and Douglas fir (*Pseudotsuga menziesii*), mixed stands of spruce and beech (*Picea abies*, *Fagus sylvatica*), as well as mixed stands of oak and beech (*Quercus robur*, *Fagus sylvatica*). The following age classes (successional stages) were included in the study design, as far as they were part of the silvicultural practice of the stand type and present in the study area: young stand (YS), mature stand (MS), mature stand with upcoming (MR) and established regeneration (eMR; Table 1). The age classes referred to silvicultural thinning measures representative for regional forestry practice (YS: age class of young stands which passed through the first thinning measure after planting of trees; MS: age class of mature stands before thinning measures to promote natural regeneration; MR: age class of mature stands after thinning measures to promote natural regeneration).

The study sites corresponded to one another in terms of altitude, soil and macroclimatic conditions, namely mean annual rainfall and mesoclimatic temperature.

In the center of each study site (1 ha), a core investigation area of 50 m × 50 m was established for the sampling of ground beetles and the assessment of environmental parameters. The core area of each study site was surrounded by a belt of at least 25 m of forest of the same tree composition representing a buffer zone (Molnár et al. 2001) and beyond that by further forest ecosystems up to a distance of several kilometres, to exclude side effects from adjacent forests.

Table 1. Characteristics of the study sites (1 ha). Age class: YS (young stand), MS (mature stand), MR (mature stand with upcoming natural regeneration), eMR (mature stand with established regeneration). The degree of canopy closure refers to the summer aspect under complete foliation, the same applies to relative air humidity and soil moisture.

| Stand structure | Pure stand | | | | | | Mixed stand | | | | | |
|--------------------------------|--------------------|-------------|-------------|------------------------------|------------------|---|-------------------|-------------------|--------------------|---|----------------|-----------------|
| Stand composition | spruce (YS) | spruce (MS) | spruce (MR) | Douglas fir (YS) | Douglas fir (MR) | spruce-beech (YS) | spruce-beech (MS) | spruce-beech (MR) | spruce-beech (eMR) | oak-beech (YS) | oak-beech (MS) | oak-beech (eMR) |
| | <i>Picea abies</i> | | | <i>Pseudotsuga menziesii</i> | | <i>Picea abies</i> / <i>Fagus sylvatica</i> | | | | <i>Quercus robur</i> / <i>Fagus sylvatica</i> | | |
| Stand age [years] | 30 | 62 | 89 | 15 | 80 | 38 | 73 | 89 | 105 | 28 | 75 | 112 |
| Vegetation cover average [%] | 4.4 | 10.6 | 34.4 | 20.5 | 86.9 | 0.64 | 10 | 31.3 | 16.3 | 34.4 | 23.8 | 11.9 |
| Canopy closure in summer [%] | 69-79 | 50-53 | 38-50 | 42-46 | 38-43 | 67-82 | 45-72 | 49-69 | 18-46 | 45-68 | 54-83 | 48-70 |
| T d - season [C°] | 10.57 | 11.25 | 11.50 | 10.79 | 11.62 | 10.48 | 11.25 | 11.58 | 11.32 | 10.97 | 11.23 | 11.54 |
| T min [C°] in summer | 12.34 | 13.07 | 13.32 | 12.73 | 13.73 | 12.35 | 13.31 | 13.35 | 12.93 | 12.97 | 13.32 | 13.75 |
| Humidity air [%] in summer | 79.63 | 92.74 | 89.19 | 69.49 | 91.29 | 75.0 | 52.5 | 88.1 | 89.53 | 49.69 | 74.27 | 56.04 |
| Soil moisture [%] in summer | 50.19 | 46.32 | 43.79 | 40.13 | 32.58 | 44.32 | 34.25 | 47.49 | 48.54 | 32.33 | 33.40 | 32.31 |
| Upper soil pH H ₂ O | 3.5-4.1 | 3.4-3.8 | 3.3-3.8 | 4.48-4.96 | 3.98-4.26 | 3.58-4.16 | 3.73-4.06 | 3.55-4.05 | 3.49-4.03 | 4.54-4.86 | 3.98-4.91 | 4.06-4.18 |

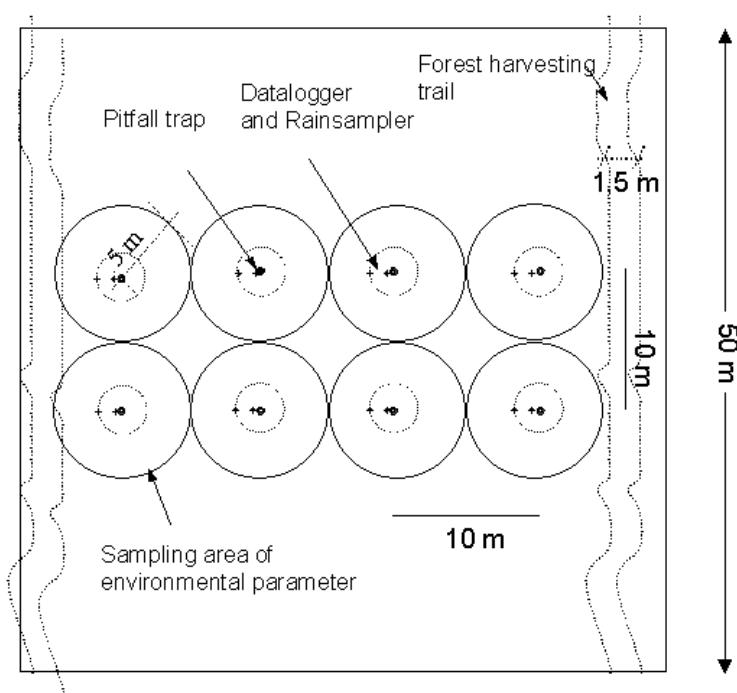


Figure 1. Sampling design in the core investigation area (50 m × 50 m) within each study site (1 ha).

Sampling of carabid beetles and assessment of the reproductive rate

Carabid beetles were sampled by pitfall trapping (8 replicates per study site, volume: 370 ml, Ø 7.5 cm, fixing agent: solution of saturated benzoic acid and detergent). The traps were arranged in the center of a core area (50 m × 50 m) of the study site in two linear transects with 4 traps each. The distance of the traps between and within the transects covered 10 m (Fig. 1). The study period started on March 12 and lasted until October 22, 2002. The pitfall traps were emptied every 4 weeks.

To assess the reproductive rate of the ground beetle species, the number of ripe eggs in the ovaries and oviducts of the females was analysed (Van Dijk 1983). The females, preserved in pure alcohol, were dissected according to Renner (1999). To complete the picture about the reproduction pattern, the duration of the reproduction period was calculated from sampling intervals with females carrying developed eggs. The proportion of females carrying eggs was calculated likewise from the total catch-results of females in pitfall traps of each study site.

Assessment of environmental variables

During the study period, twenty five environmental parameters were recorded for statistical analyses regarding the influence of habitat factors of forest successional stages on the number of eggs in the ovaries. Soil temperature was measured continuously during the investigation period every 45 minutes at each trap ($n = 8$ per study site ($\Sigma = 96$) in a depth of 1 cm in the litter layer) by data loggers (Tinytalk II, TK – 0023, Spectra Computersysteme, Leinfelden-Echterdingen), air temperature and humidity every 90 minutes twice in a trap line ($n = 2$ per study site ($\Sigma = 24$) 80 cm above the ground) by Tinytags Ultra (TG 1500, Spectra Computersysteme Leinfelden-Echterdingen). From the recordings were calculated daily, monthly and seasonal (spring: March 8 to June 5, summer: June 6 to August 28, fall: August 29 to October 23) values of mean temperature and air humidity, mean minimum and maximum temperature, the temperature variation between t_{\min} and t_{\max} , the number of days with a mean temperature above 8°C. The temperature aspects were also applied to the time span of reproduction for each species (i.e., *A. parallelepipedus*: 08.03.-27.08., *Pt. oblongopunctatus*: 12.03.-30.07., *Pt. burmeisteri*: 10.04.-27.08.). Precipitation was measured at each pitfall trap by rain samplers (funnel diameter: 7.6 cm) gathering the precipitation of four week intervals, which corresponded with the sampling periods of ground beetles. Also, every 4 weeks the composition and thickness of the litter layer were recorded in a radius of 1 m around each trap, the cover value of litter in a radius of 5 m around each trap. At the same time intervals, structural parameters of the vegetation were assessed within a radius of 5 m around each pitfall trap including an estimation of the degree (%) of canopy closure and – according to Braun-Blanquet (Mühlenberg 1989) – the coverage (%) and standing height (cm) of moss, herbs, grass and natural regeneration. Species composition of the vegetation (moss, herb, grass, shrub layer) as well as soil and litter samples for the determination of moisture (% water content; Scheffer and Schachtschnabel 1989) and $\text{pH}_{(\text{H}_2\text{O})}$ were taken in spring (April 9), summer (July 30) and fall (September 24), 2002.

Statistical analyses

Statistical analyses were based on the software SPSS 11.5. To test the impact of the successional stage of each forest type on the number of eggs in the ovaries of species one-way ANOVA was applied on trap level followed by Tukey's honestly significant difference test (HSD).

To acquire the correlation between mean egg-loads and mean environmental parameters of the study sites (n

$= 12$, on site level), a stepwise multiple linear regression analysis was performed for each species. The data of each pitfall trap of sites ($n = 8$) were averaged over time for the analyses. Subsequently, a regression model with the significant habitat factors explaining the gradient in the egg-load of ground beetle species was run. To analyse the influence of habitat age on egg-load, the regression analysis was performed for all stand types classified in age classes ($n = 4$, YS, MS, MR, eMR).

A stepwise multiple linear regression analysis was performed to elucidate the effects of specific environmental habitat parameters on the number of eggs produced per female in each species based on the results of single pitfall traps ($n = 96$, on microhabitat level). Spearman rank correlations of mean egg numbers per female were applied to reveal correlations between the egg-load and the environmental conditions for each trap and species (significance level: $P^{**} < 0.01$, $P^* < 0.05$).

Results

The species *Abax parallelepipedus*, *Pterostichus oblongopunctatus* and *Pterostichus burmeisteri* counted for 3218 specimen and made up 74.7% of the total catch of ground beetles. *A. parallelepipedus* and *Pt. oblongopunctatus* are known as eurytopic generalists and were caught at each study site in almost every pitfall trap. *Pt. burmeisteri* was nearly missing at two study sites (spruce-beech: eMR; Douglas fir: MR) and additionally missing in single pitfall traps of other study sites (Table 2). Consequently, on these sites the sample size of *Pt. burmeisteri* was too low to judge potential effects of habitat age on the reproductive rate.

In total, 1174 eggs were detected in *Pt. oblongopunctatus*, 217 eggs in *A. parallelepipedus* and 313 eggs in *Pt. burmeisteri*. Egg size ranged from 0.8 – 0.85 mm in *Pt. oblongopunctatus*, 2.4 – 2.52 mm in *Pt. burmeisteri* and 3.12 – 3.24 mm in *A. parallelepipedus*. The number of eggs in the ovaries of individual females varied within each species between 1-15 in *A. parallelepipedus*, 1-14 in *Pt. oblongopunctatus* and 1-23 in *Pt. burmeisteri*.

Egg-load of ground beetle species at forest stands differing in tree species composition and age class

In all forest types – except the pure stands of Douglas fir – the egg-load of the ground beetle species showed statistically significant relations to the age of the stand type (Table 3). However, the effects of habitat age on the egg-load varied between the ground beetle species and the forest types.

Table 2. Number of adult beetles (males, females) of *A. parallelepipedus*, *Pt. oblongopunctatus* and *Pt. burmeisteri* in forests of different tree species composition and age class - according to pitfall catches during the vegetation period of 2002.

| Stand structure | Pure stand | | | | | | Mixed stand | | | | | |
|-----------------------------|--------------------|-------------|-------------|------------------------------|------------------|-------------------|---|-------------------|--------------------|---|----------------|-----------------|
| Stand composition | spruce (YS) | spruce (MS) | spruce (MR) | Douglas fir (YS) | Douglas fir (MR) | spruce-beech (YS) | spruce-beech (MS) | spruce-beech (MR) | spruce-beech (eMR) | oak-beech (YS) | oak-beech (MS) | oak-beech (eMR) |
| | <i>Picea abies</i> | | | <i>Pseudotsuga menziesii</i> | | | <i>Picea abies</i> / <i>Fagus sylvatica</i> | | | <i>Quercus robur</i> / <i>Fagus sylvatica</i> | | |
| Stand age (years) | 30 | 62 | 89 | 15 | 80 | 38 | 73 | 89 | 105 | 28 | 75 | 112 |
| <i>A. parallelepipedus</i> | 33 | 47 | 31 | 103 | 182 | 32 | 137 | 89 | 93 | 36 | 96 | 98 |
| male: | 17 | 23 | 15 | 74 | 99 | 25 | 89 | 55 | 55 | 20 | 57 | 71 |
| female: | 16 | 24 | 16 | 29 | 83 | 7 | 48 | 34 | 38 | 16 | 39 | 27 |
| (fem. with eggs): | (26%) | (43%) | (71%) | (15%) | (12%) | (40%) | (28%) | (38%) | (27%) | (8%) | (11%) | (27%) |
| <i>Pt. oblongopunctatus</i> | 21 | 129 | 220 | 82 | 58 | 53 | 179 | 313 | 55 | 86 | 28 | 202 |
| male: | 11 | 68 | 132 | 52 | 36 | 34 | 112 | 186 | 32 | 43 | 15 | 113 |
| female: | 10 | 61 | 88 | 30 | 22 | 19 | 67 | 127 | 23 | 43 | 13 | 89 |
| (fem. with eggs): | (30%) | (53%) | (57%) | (63%) | (65%) | (50%) | (83%) | (69%) | (58%) | (73%) | (50%) | (66%) |
| <i>Pt. burmeisteri</i> | 11 | 31 | 80 | 17 | 2 | 53 | 101 | 201 | 2 | 130 | 142 | 45 |
| male: | 8 | 21 | 58 | 14 | 2 | 41 | 83 | 148 | 1 | 66 | 79 | 27 |
| female: | 3 | 10 | 22 | 3 | 0 | 12 | 18 | 53 | 1 | 64 | 63 | 18 |
| (fem. with eggs): | (33%) | (30%) | (14%) | (0%) | (0%) | (8.3%) | (23.5%) | (11.5%) | (100%) | (23%) | (6.4%) | (22%) |

Table 3. Number of ripe eggs (mean±SD) per female in *A. parallelepipedus*, *Pt. oblongopunctatus*, *Pt. burmeisteri*, in forests of different tree species composition and age class, according to the catch results of pitfall traps during the vegetation period 2002. Egg-loads marked with the letter "a" differed significantly from egg-loads marked with the letter "b" according to one-way ANOVA, Tukey-HSD-test ($P < 0.05$).*A. parallelepipedus*

| | YS | MS | MR | eMR | df | F | P |
|--------------|---------------|---------------|---------------|---------------|------|--------|--------|
| Spruce | 0.63 ± 1.41 a | 2.02 ± 2.03 b | 1.69 ± 2.15 b | | 2.21 | 14.621 | <0.001 |
| Spruce-beech | 0.63 ± 1.77 a | 1.53 ± 1.64 b | 1.56 ± 1.59 b | 1.13 ± 1.46 b | 3.28 | 3.209 | =0.038 |
| Oak-beech | 0.01 ± 0.04 a | 1.13 ± 1.89 b | | 1.25 ± 2.44 b | 2.21 | 15.974 | <0.001 |
| Douglas fir | 1.00 ± 1.41 a | | 1.21 ± 1.19 a | | 2.21 | 10.369 | =0.365 |

Pt. oblongopunctatus

| | YS | MS | MR | eMR | df | F | P |
|--------------|---------------|---------------|---------------|---------------|------|--------|--------|
| Spruce | 0.81 ± 1.51 a | 3.87 ± 1.02 b | 2.90 ± 1.21 b | | 2.21 | 12.19 | <0.001 |
| Spruce-beech | 3.19 ± 2.59 a | 3.89 ± 1.82 a | 4.15 ± 1.00 a | 1.46 ± 2.02 b | 3.28 | 13.771 | <0.001 |
| Oak-beech | 2.82 ± 1.66 a | 1.63 ± 2.26 a | | 4.19 ± 0.95 b | 2.21 | 18.708 | <0.001 |
| Douglas fir | 3.46 ± 2.04 a | | 2.36 ± 2.73 a | | 2.21 | 2.286 | =0.201 |

Pt. burmeisteri

| | YS | MS | MR | eMR | df | F | P |
|--------------|---------------|---------------|---------------|---------------|------|---------|--------|
| Spruce | 0.01 ± 0.03 a | 1.92 ± 4.05 b | 0.13 ± 0.35 a | | 2.21 | 29.729 | <0.001 |
| Spruce-beech | 0.01 ± 0.02 a | 4.13 ± 5.05 b | 1.46 ± 2.74 b | 0.01 ± 0.02 a | 3.28 | 182.997 | <0.001 |
| Oak-beech | 4.94 ± 4.39 a | 2.00 ± 5.66 b | | 1.75 ± 4.95 b | 2.21 | 44.634 | <0.001 |
| Douglas fir | 0 ± 0 | | 0 ± 0 | | 2.21 | 0.0 | <0.001 |

A clear and uniform relation between habitat age and egg-load of the ovaries was obvious for *A. parallelepipedus*. The females of *A. parallelepipedus* carried significantly more ripe eggs at the older (MS, MR, eMR) than at the young stands of spruce, spruce-beech and oak-beech (Table 3). Between the age classes of mature forests (MS, MR, eMR), the egg-load did not differ significantly.

Nevertheless, at spruce and spruce-beech there was a tendency of decreasing egg-load of the females at stands with upcoming (MR) or established regeneration (eMR), respectively.

A stronger impact of the specific stand type on the number of ripe eggs was evident for *Pt. oblongopunctatus* and *Pt. burmeisteri*. In the pure spruce stand series the

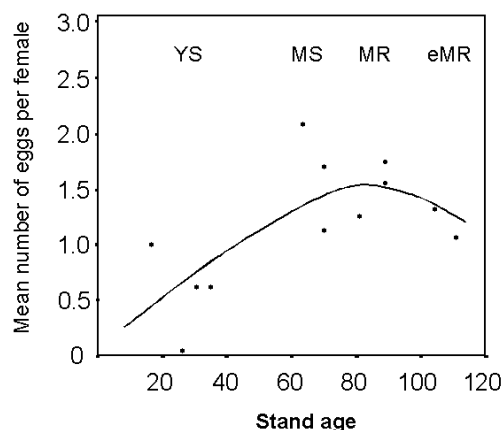


Figure 2. Egg-load (mean \pm SD) per female of *A. parallelepipedus* in the different age classes of all forest types ($F_{1,10} = 5.024$, $R^2 = 0.333$, $P = 0.049$, $n = 12$).

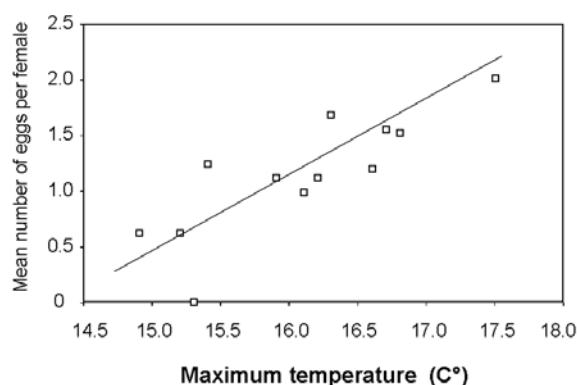


Figure 3. Relationship between the number of eggs in the ovaries of *A. parallelepipedus* and the mean maximum soil surface temperature of the different age classes of the forests during the reproduction period (8th of March till 27th of August), according to the results of the regression analysis ($F_{1,10} = 15.91$, $R^2 = 0.614$, $P = 0.003$, $n = 12$).

egg-load pattern of *Pt. oblongopunctatus* and *Pt. burmeisteri* corresponded with that of *A. parallelepipedus*, showing the significantly lowest reproductive rate in the young stand (YS), the highest in the mature stand (MS). The differences between YS and MR were significant for all species, the differences between MR and MS only for *Pt. burmeisteri* (Table 3). At the spruce-beech stands, females of *Pt. oblongopunctatus* carried a high load of ripe eggs in all age classes, except the mature stand with established regeneration (eMR). Considering spruce-beech, *Pt. burmeisteri* carried the lowest number of ripe eggs in the young stand and the mature stand with established regeneration. In the oak-beech series, the egg-load of females decreased with increasing age of the forest habitat (Table 3).

In the oak-beech stands, the egg-load of *Pt. oblongopunctatus* was high in the young stand, decreased to the lowest level in the mature stand and reached its (statisti-

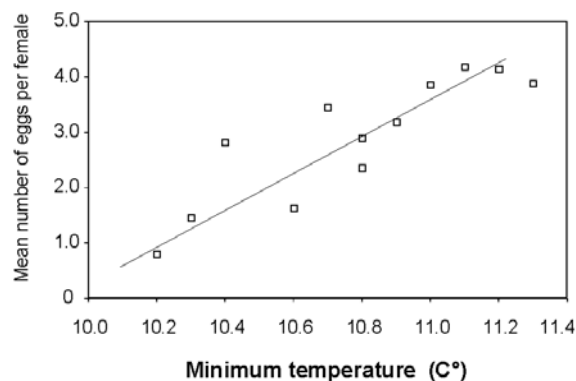


Figure 4. Relationship between the average egg-load in the ovaries of *Pt. oblongopunctatus* and the minimum soil surface temperature of study sites within the reproduction period of March to August according to the results of the regression analysis ($F_{1,11} = 15.447$, $R^2 = 0.607$, $P = 0.003$, $n = 12$).

cally significant) maximum in the mature stand with established regeneration.

Effect of environmental parameters on the egg-load of carabid species

On site level. The stepwise multiple linear regression analysis for each species revealed different habitat factors explaining the gradient in site specific egg-load. As the linear regression analysis uncovered, the habitat age was no significant criterion for *Pt. burmeisteri* and *Pt. oblongopunctatus*. For *Abax parallelepipedus*, it accounted for 33.3% of the variation of egg-load ($F_{1,10} = 5.024$, $R^2 = 0.333$, $P = 0.049$, $n = 12$). The low degree of explanation of variance is shown to be attributed to the low eggload in mature forests with established regeneration (Fig. 2).

The result of a regression analysis of the relation of mean maximum soil surface temperature and the egg-load of *A. parallelepipedus* is displayed in Figure 3. This abiotic parameter explained 61.4% of the variation in a regression model (multiple stepwise forward) (Fig. 3). Adding the thickness of the litter layer explained 79.8% of the variation, adding additionally the litter moisture 83.9% ($F_{1,9} = 17.818$, $R^2 = 0.839$, $P = 0.001$, $n = 12$). The variation in egg-load at site level for *Pt. burmeisteri* was best explained by the humidity of air (49.4%, negative), the mean maximum soil surface temperature and the degree of canopy closure accounting for 91.5% ($F_{1,8} = 28.865$, $R^2 = 0.915$, $P = 0.0001$, $n = 12$), while the egg production in *Pt. oblongopunctatus* was found to increase with the mean minimum soil surface temperature explaining 60.7% of variation (Fig. 4). The vegetation parameters had no significant effect on the species egg-load.

On microhabitat level. The Spearman rank correlations and the multiple linear regression analyses revealed the

Table 4. Results of the Spearman rank correlations and regressions of environmental parameters and the egg-load of ground beetle species. Highly significant negative or positive correlations are underlined. The significant parameters according to the stepwise forward regression analyses are marked by (R). Spearman's rho given for significant correlations (* $p < 0.05$, ** $p < 0.01$).

| | <i>A. parallelepipedus</i> | <i>Pt. burmeisteri</i> | <i>Pt. oblongopunctatus</i> |
|----------------------|----------------------------|------------------------|-----------------------------|
| habitat age (y) | .218(*) | | |
| litter depth (cm) | .212(*) | | |
| T max (C°) | <u>.236(**)</u> | | |
| T min (C°) | | | .217(*) |
| canopy closure (%) | | <u>.246(**)</u> | |
| moss cover (%) | .211(*) (R) | <u>-.243(**)</u> | |
| litter pH | <u>-.246(**)</u> (R) | | |
| soil pH | -.170(*) | | .187(*) |
| litter moisture (%) | .221(*) | | (R) |
| soil moisture (%) | | -.219(*) | |
| regeneration cover % | | .202(*) | |
| grass cover (%) | | .175(*) | |
| dead wood (%) | | | -.236(*) (R) |
| litter cover (%) | | | -.237(*) (R) |
| humidity air (%) | <u>.238(**)</u> | <u>-.388(**)</u> (R) | -.200(*) (R) |

Spearman rank correlation ** $P < 0.01$
Spearman rank correlation * $P < 0.05$

| | <i>A. parallelepipedus</i> | <i>Pt. burmeisteri</i> | <i>Pt. oblongopunctatus</i> |
|-------------|----------------------------|------------------------|-----------------------------|
| temperature | eurythermic | cold preferent | eurythermic |
| humidity | xerophilic | xerophilic | hygro- & mesophilic |
| light | dark preferent | dark preferent | euryphotic |

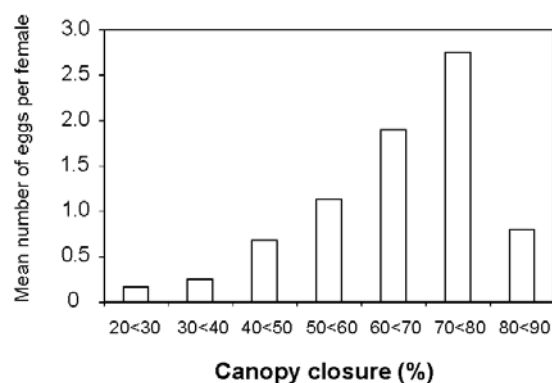


Figure 5. Relationship between the mean number of eggs found in the ovaries of *Pt. burmeisteri* and the degree of canopy closure based on the results of the stepwise regression analyses on microhabitat level ($n = 96$).

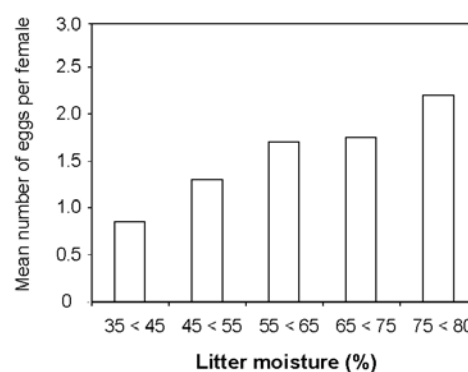


Figure 6. Relationship between the mean egg-load per female of *Pt. oblongopunctatus* and the water content of the litter layer in spring time based on the results of the stepwise regression analyses on microhabitat level ($n = 96$).

environmental parameters relevant for the egg-load per female at each pitfall trap (Table 4). *A. parallelepipedus* showed highly significant enhanced egg-loads at microsites with lower pH of the litter layer, increased air humidity and soil temperature (Spearman ρ $p < 0.01$).

In addition, significant ($P < 0.05$) effects were obvious for litter moisture, habitat age, litter thickness, the share of soil surface covered with moss, and the soil pH (Table 4). For *Pt. burmeisteri*, the Spearman rank correlation analysis identified significantly increased egg-loads per female at microsites with dry air conditions (this

was confirmed by multiple linear regression analysis), with a high degree of canopy closure (Fig. 5), and low moss cover (Table 4). Additionally, a higher level of egg-load was found in patches of decreased soil moisture, as well as in patches covered with natural regeneration or grass (Table 4). Higher egg-loads of *Pt. oblongopunctatus* were positively correlated with minimum soil surface temperatures and the pH of the soil (Table 4). Extended litter cover and air humidity were leading to a significantly lower number of eggs in the ovaries of this ground beetle species. In addition, linear regression analysis revealed the litter moisture as a strong impact factor for the

Table 5. Time span of females carrying eggs during the investigation period of 2002. The numbers representing the percentage of assessed females with eggs in the ovaries.

| Stand structure | Pure stands | | | | | Mixed stands | | | | | | |
|-----------------------------|-------------|------|------|-------------|------|--------------|------|------|-------|-----------|------|-------|
| Stand composition | spruce | | | Douglas fir | | beech-spruce | | | | oak-beech | | |
| | (YS) | (MS) | (MR) | (YS) | (MR) | (YS) | (MS) | (MR) | (eMR) | (YS) | (MS) | (eMR) |
| <i>A. parallelepipedus</i> | | | | | | | | | | | | |
| 12.03.-10.04. | | | | | | | | | | | | |
| 11.04.-07.05. | | | | | | | | | | | | |
| 08.05.-04.06. | 50 | 10 | | 29 | 27 | | 55 | 17 | 19 | | 30 | 27 |
| 06.06.-02.07. | | 70 | 50 | 57 | 33 | | 9 | 8 | | 100 | 50 | |
| 03.07.-30.07. | 50 | 10 | 43 | 14 | 40 | 100 | 27 | 42 | 75 | | 20 | 64 |
| 08.07.-27.08. | | 10 | 7 | | | | 9 | 33 | 6 | | | |
| 28.08.-24.09. | | | | | | | | | | | | |
| 25.09.-22.10. | | | | | | | | | | | | 9 |
| <i>Pt. oblongopunctatus</i> | (YS) | (MS) | (MR) | (YS) | (MR) | (YS) | (MS) | (MR) | (eMR) | (YS) | (MS) | (eMR) |
| 12.03.-10.04. | | 2 | 6 | | 5 | | 1 | 7 | | 2 | | |
| 11.04.-07.05. | | 14 | 32 | 29 | 42 | 22 | 33 | 29 | | 20 | 60 | 7 |
| 08.05.-04.06. | 75 | 82 | 36 | 47 | 53 | 44 | 34 | 44 | 97 | 65 | 20 | 70 |
| 06.06.-02.07. | 25 | 2 | 26 | 18 | | 33 | 28 | 18 | | 11 | 20 | 19 |
| 03.07.-30.07. | | | | 6 | | | | | | | | 4 |
| 08.07.-27.08. | | | | | | | | | | | | |
| 28.08.-24.09. | | | | | | | | | | | | |
| 25.09.-22.10. | | | | | | | 5 | 1 | 3 | 2 | | |
| <i>Pt. burmeisteri</i> | (YS) | (MS) | (MR) | (YS) | (MR) | (YS) | (MS) | (MR) | (eMR) | (YS) | (MS) | (eMR) |
| 12.03.-10.04. | | | | | | | | | | | | |
| 11.04.-07.05. | | | | | | | | | | | | |
| 08.05.-04.06. | | | | | | | 25 | 18 | | 13 | 20 | 25 |
| 06.06.-02.07. | | 20 | | | | | 75 | 27 | 100 | 10 | | |
| 03.07.-30.07. | 100 | | 67 | | | 100 | | 9 | | 55 | 80 | 50 |
| 08.07.-27.08. | | 20 | | | | | | 45 | | 16 | | |
| 28.08.-24.09. | | | | | | | | | | | | |
| 25.09.-22.10. | | 60 | 33 | | | | | | | 6 | | 25 |

egg-load (Fig. 6). The age of the study sites had no significant effect on the species egg-load on the basis of single trap data in the latter two species.

Time span of females carrying eggs

Referring to *A. parallelepipedus*, the time span of pit-fall trapped females carrying eggs lasted longer in the mature forests (MS, MR) compared to the young stands and the oldest sites (eMR) (Table 5). Only with the Douglas fir forests the reproduction period did not depend on the age class of the stands.

The deviating pattern of *Pt. burmeisteri* and *Pt. oblongopunctatus* in the oak-beech age class series was evident. The egg carrying period of these ground beetle species in the young stand (YS) reached or exceeded that of the oldest site (eMR). The females in the mature site (MS) generated eggs for a decreased period of time, which corresponds with the egg-load pattern per female. The majority of females in *Pt. oblongopunctatus* carrying eggs were assessed in spring and early summer (10.04.-02.07.), while the female capture in *A. parallelepipedus* (07.05.-27.08.) and *Pt. burmeisteri* (07.05.-27.08./22.10.) prevailed between late spring and fall.

Discussion

With the capture and dissection of female ground beetles a moment survey of fecundity was assessed, since carabids lay eggs over a period of time during the repro-

ductive season (Den Boer 1968, Thiele 1977). The amount of reproduction is a highly variable feature of individual females (Van Dijk 1979) and even age-dependent in ground beetles (Van Heerdt et al. 1976) (in *Calathus melanocephalus*, *Pterostichus coerulescens*). However, each female has a characteristic level of reproductive rate which varies only slightly with time under constant and optimal conditions (Van Dijk 1979). Van Dijk (1981, 1986a) showed for several species that there is a general relationship between the weekly number of eggs in the ovaries and the weekly number of eggs laid. Thus, the egg-load of the ovaries seems to be a good indicator for the reproductive rate of ground beetle species in the field.

Confirming our hypothesis we could clearly show in this investigation, that – except for Douglas fir stands – the age of forests is affecting the reproductive rate of ground beetle species. But the reaction pattern was species specific. A quite uniform reaction pattern was evident for *A. parallelepipedus*. For that species, the reproductive rate increased with the age of forest stand. In *Pt. oblongopunctatus* and *Pt. burmeisteri*, the reaction depended on the cover tree species.

As the egg-load is considered to be an indicator of the habitat quality (Van Dijk 1983), the results document strong alterations in the suitability of different age classes of forests for ground beetle species. This impression was confirmed by analysing the time span of females carrying

eggs. Hence, longer periods of egg-production were documented at sites of increased egg-load per female. Those habitats also favour the duration of the reproduction period and likely the number of generations involved in egg production (Van Heerdt et al. 1976) and thus the fecundity. The increased egg production as well as the increased time period of reproduction might as a matter of fact promote the stability and growth of a population.

Moreover, the species specific relation between habitat age and reproductive rate indicates the influence of distinct environmental parameters on the reproduction level of a species. Van Dijk (1979, 1994) found that the reproduction level depends besides the availability of food on weather conditions.

The statistical analyses revealed the maximum temperature for *A. parallelepipedus* (61.4%) and the minimum temperature for *Pt. oblongopunctatus* (60.7%) to be an important impact factor influencing the egg-load of females in the forest habitats. The egg-laying period as well as the number of eggs laid per female were affected by temperature aspects in a beneficial way for all three species. Thiele (1977) stated that even forest species, living generally under lower temperature conditions than open land species, benefit from increased temperature. Apart from individual differences between females (Van Dijk 1979), the temperature will contribute considerably to the variation in numbers of eggs laid per female (Van Dijk 1983, Lenski 1984, Mols 1988, Van Dijk and Den Boer 1992). Also, the number of eggs laid and temperature have been shown to be highly correlated under constant feeding conditions (Ernsting and Huyer 1984). Thus, also *Pt. burmeisteri*, a cold and dark preferring species, carried increased egg-loads in the ovaries at sites of high maximum temperatures.

To reveal the effects of environmental parameters on the egg-load of ground beetle species on a microhabitat level we conducted analyses on single pitfall trap level, because a considerable variation of species distribution and environmental conditions on a small scale level has been measured. Similar small scale distribution patterns, which are maintained over periods of time (Baars 1979, Brunsting 1981, 1983), have been described in earlier investigations on forest carabids (Niemelä et al. 1996, Antvogel and Bonn 2001). There are also strong indications that females show distinct preferences for certain microhabitats within a forest to lay their eggs. Reise and Weidemann (1975) described the patchy distribution of adult and larval stages in *Pt. oblongopunctatus*. Thiele (1977) observed a difference in habitat affinity of male and female ground beetle species in forests, which he referred to certain egg-laying behaviour. Huk and Kühne (1999)

described behavioural differences in *Carabus clathratus* females after copulation, which indicates that oviposition site selection is an important factor in the life cycle of some carabid beetles.

Our investigation revealed significantly more eggs in the ovaries of females in places of ecologically preferred habitat conditions (Thiele 1975, 1977, Koch 1989) in the studied ground beetle species. Thus, the egg number per female analysed on single trap level increased significantly under moist litter conditions and was positively influenced by the temperature parameters in *A. parallelepipedus* and *Pt. oblongopunctatus*. Thiele (1977) observed in temperature gradient experiments that the females of *Pt. oblongopunctatus* seek for higher temperatures than the males and in doing so they choose a temperature that corresponds to the improved natural conditions of the larvae, laying their eggs in a site that is thermally suited to the needs of the hatching larvae. Van Dijk and Den Boer (1992) found, when taking the results of rearing carabid beetles into account, that abiotic factors, especially temperature and soil moisture, largely determine the survival of all three larval stages. Litter moisture may play an important role in protecting carabids from desiccation and may improve the density of prey. Huk and Kühne (1999) showed for the hygrophilous *Carabus clathratus* a significant substrate- and soil moisture selection in egg-laying behaviour regarding the habitat preference of the adult beetles and it becomes reasonable that the favourable conditions for the development of the less mobile offspring stages are leaned towards the preferences of adult beetles and that reproductive success is strongly dependent on breeding site characteristics (Bernado 1996, Rudolf and Rödel 2005). Also, soil and litter moisture and humidity of the air of the study sites showed a strong impact on the reproduction of the species on the site level, as has been shown to promote carabid assemblages in a study of Magura et al. (2006).

In addition, females of *Pt. oblongopunctatus* are known to prefer for the egg deposition the well-structured litter (Heessen 1980), perhaps making it more difficult for predators to prey on eggs and thus reduce egg mortality, compared to low structured litter layers. However, extended litter cover was not leading to increased egg-loads as has been observed for the activity density of adults that increased in plots of added leaf-litter in a study of Koivula et al. (1999) and Magura et al. (2004).

Thiele (1977) described *Pt. burmeisteri* as a cold preferent, xerophilic and dark preferent forest species, which was reflected in the reproduction value of female beetles. In our study, the reproduction of *Pt. burmeisteri* was increased in dry microhabitats under closed canopy. Be-

sides, we found that microhabitats with natural regeneration and dense grass cover resulted in an increased egg-load. Also highly significant for *Pt. burmeisteri* was the decrease in egg-load at microsites covered only with moss. The regeneration and grass vegetation may as well serve as a shelter against predation and desiccation for this species (Sanderson et al. 1995). Barone and Frank (2003) found that fecundity and nutritional state of *P. cupreus* were promoted by increased vegetation cover in wildflower meadows.

Conclusions

Despite the study of only one age-class set of stand types due to logistic difficulties and the time intensity of the investigations, we found distinct habitat parameters influencing the egg-load in three forest carabid species of coniferous and deciduous woods. Especially temperature conditions significantly influenced the reproduction in a positive way in all species at study site level, as well as the litter moisture in *A. parallelepipedus* and *Pt. oblongopunctatus* in a positive and humidity and soil moisture in *Pt. burmeisteri* in a negative way. While female choice of favourable microhabitat conditions for egg deposition enhances the chance for development of subadult and survival of adult stages (Paarmann 1966, Rudolf and Rödel 2005) we assume that presence and frequency of patches with species specific favourable environmental conditions in a forest ecosystem play an important role in carabid fecundity.

The results document, when discussing the factors limiting and improving the reproductive rate and the survival of subadult and adult beetles in nature, that reproduction not only depends on the availability of food (White 1978, Van Dijk 1981, Dempster and Pollard 1981), but also on abiotic habitat parameters. Moreover, the accessibility of food in the field is significantly influenced by the fact that the amounts and nutritional qualities of food together with the activities of the beetles will also be influenced by weather conditions (Van Dijk 1982), since prey species also react to abiotic factors (Van Dijk and Den Boer 1992). The impact of temperature on the reproduction of ectotherms (Huey and Berrigan 2001) has been described in laboratory studies, which not only affects the egg production (Ernsting and Isaak 2000), but also the egg size and thus the size of the first larval stage (Ernsting and Isaak 1997), the feeding rate of larvae and adults (Ernsting et al. 1992), the duration of development (Heessen et al. 1982) and mortality rate of subadult stages (Heessen and Brunsting 1981). Those factors also contribute to the size of single females and reproduction processes in a population (Wallin et al. 1992, Bommarco

1999). Consequently, the measured habitat parameters explain to a high degree the variance of reproductive rate of ground beetles. Because these intrinsic habitat parameters often change with successional stages (Dajoz 2000), effects of forest age on the reproductive rate of carabid beetles are demonstrated.

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References

- Antvogel, H. and A. Bonn. 2001. Environmental parameters and microspatial distribution of insect: a case study of carabids in an alluvial forest. *Ecography* 24:470-482.
- Baars, M.A. 1979. Patterns of movement of radioactive carabid beetles. *Oecologia* 44:125-140.
- Barone, M. and T. Frank. 2003. Habitat age increases reproduction and nutritional condition in a generalist arthropod predator. *Oecologia* 135:78-83.
- Begon, M.E., J.L. Harper and C.R. Townsend. 1996. *Ecology*, 3rd ed. Blackwell Science, Oxford.
- Bernado, J. 1996. Maternal effects in animal ecology. *Am. Zool.* 36:83-105.
- Bilde, T. and S. Toft. 1998. Quantifying food limitation of arthropod predators in the field. *Oecologia* 115:54-58.
- Bommarco, R. 1998. Stage sensitivity to food limitation for a generalist arthropod predator. *Environ. Entomol.* 27:863-869.
- Bommarco, R. 1999. Feeding, reproduction and community impact of a predatory carabid in two agricultural habitats. *Oikos* 87:89-96.
- Brown, V.K. and T.R.E. Southwood. 1987. Secondary succession patterns and strategies. In: A. J. Gray, M. J. Crawley and P. J. Edwards (eds), *Colonization, Succession and Stability*. Blackwell, Oxford. pp. 315-339.
- Brunsting, A.M.H. 1981. Distribution patterns, life cycle and phenology of *Pterostichus oblongopunctatus* F. (Col., Carabidae) and *Philonthus decorus* Grav. (Col., Staphylinidae). *Neth. J. Zool.* 31:418-452.
- Brunsting, A.M.H. 1983. The locomotor activity of *Pterostichus oblongopunctatus* F. (Col., Carabidae). *Neth. J. Zool.* 33:189-210.
- Butterfield, J. 1997. Carabid community succession during the forestry cycle in conifer plantations. *Ecography* 20:614-625.
- Butterfield, J., M.L. Luff, M. Baines and M.D. Eyre. 1995. Carabid beetle communities as indicators of conservation potential in upland forests. *For. Ecol. Manage.* 79:63-77.
- Dajoz, R. 2000. *Insects and Forests – The Role and Diversity of Insects in the Forest Environment*. Editions Tec & Doc, London.
- Den Boer, P.J. 1968. Spreading of risk and stabilization of animal numbers. *Acta Biotheoretica* 18:165-194.

- Denys, C. and T. Tschamtkke. 2002. Plant-insect communities and predator-prey ratios in field margin strips, adjacent crop fields, and fallows. *Oecologia* 130:315-324.
- Dempster, J.P. and E. Pollard. 1981. Fluctuations in resource availability and insect populations. *Oecologia* 50:412-416.
- Ernsting, G. and F.A. Huyer. 1984. A laboratory study on temperature relations of egg production and development in two related species of carabid beetle. *Oecologia* 62:361-367.
- Ernsting, G. and J.A. Isaak. 1997. Effects of temperature and season on egg size, hatchling size and adult size in *Notiophilus biguttatus*. *Ecol. Entomol.* 22:32-40.
- Ernsting, G. and J.A. Isaak. 2000. Ectotherms, temperature, and trade-offs: size and number of eggs in a carabid beetle. *Am. Nat.* 155:804-813.
- Ernsting, G., J.A. Isaaks and M.P. Berg. 1992. Life cycle and food availability indices in *Notiophilus biguttatus* (Coleoptera, Carabidae). *Ecol. Entomol.* 17:33-42.
- Eyre, M.D. and M.L. Luff. 1990. The ground beetle (Coleoptera: Carabidae) assemblages of British grasslands. *Entomologist's Gazette* 41:197-208.
- Fagan, W.F. 1992. Cursorial spiders and succession: age or habitat structure? *Oecologia* 92:215-221.
- Grüm, L. 1984. Carabid fecundity as affected by extrinsic and intrinsic factors. *Oecologia* 65:114-121.
- Heessen, H.J.L. 1980. Egg production of *Pterostichus oblongopunctatus* (Fabricius) (Col., Carabidae) and *Philonthus decorus* (Gravenhorst) (Col., Staphylinidae). *Neth. J. Zool.* 30:35-53.
- Heessen, H.J.L. and A.M.H. Brunsting. 1981. Mortality of Larvae of *Pterostichus oblongopunctatus* (Fabricius) (Col., Carabidae) and *Philonthus decorus* (Gravenhorst) (Col., Staphylinidae). *Neth. J. Zool.* 31:729-745.
- Heessen, H.J.L., M.A. Wildschut and A.M.H. Brunsting. 1982. Duration of the developmental stages and timing of the end of the reproductive season of *Pterostichus oblongopunctatus* (Fabricius) (Col., Carabidae) and *Philonthus decorus* (Gravenhorst) (Col., Staphylinidae). *Neth. J. Zool.* 32:49-62.
- Heyborne, W.H., J.C. Miller and G.L. Parsons. 2003. Ground dwelling beetles and forest vegetation change over a 17-year-period, in western Oregon, USA. *For. Ecol. Manage.* 179:123-134.
- Huk, T. and B. Kühne. 1999. Substrate selection by *Carabus clatratus* (Coleoptera, Carabidae) and its consequences for offspring development. *Oecologia* 121:348-354.
- Hurd, L. and W.F. Fagan. 1992. Cursorial spiders and succession: age or habitat structure? *Oecologia* 92:215-221.
- Huey, R.B. and D. Berrigan. 2001. Temperature, demography, and ectotherm fitness. *Am. Nat.* 158:204-210.
- Ings, T.C. and S.E. Hartley. 1999. The effect of habitat structure on carabid communities during the regeneration of a native Scottish forest. *For. Ecol. Manage.* 119:123-136.
- Juliano, S.A. 1986. Food limitation of reproduction and survival for populations of *Brachinus* (Coleoptera: Carabidae). *Ecology* 67:1036-1045.
- Koch, K. 1989. *Die Käfer Mitteleuropas. Vol. 1 Ökologie*. Goecke and Evers, Krefeld.
- Koivula, M., P. Punttila, Y. Haila and J. Niemelä. 1999. Leaf litter and the small-scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forest. *Ecography* 22:424-435.
- Lenski, R. 1982. Effects of forest cutting on two *Carabus* species: Evidence for competition for food. *Ecology* 63:1211-1217.
- Lenski, R. 1984. Food limitation and competition: a field experiment with two carabid species. *J. Anim. Ecol.* 53:203-216.
- Loreau, M. 1986. Niche differentiation and community organization in forest Carabid beetles. In: P.J. den Boer, M.L. Luff, D. Mosakowski and F. Weber (eds.), *Carabid Beetles*. Fischer, Stuttgart. pp. 465-487.
- Magura, T., B. Tóthmérész and Z. Elek. 2003. Diversity and composition of carabids during a forestry cycle. *Biodivers. Conserv.* 12:73-85.
- Magura, T., B. Tóthmérész and Z. Elek. 2004. Effects of leaf-litter addition on carabid beetles in a non-native norway spruce plantation. *Acta Zoologica Academiae Scientiarum Hungaricae* 50:9-23.
- Magura, T., B. Tóthmérész and Z. Elek. 2006. Changes in carabid beetle assemblages as Norway spruce plantations age. *Community Ecol.* 7:1-12.
- Molnár, T., T. Magura, B. Tóthmérész and Z. Elek. 2001. Ground beetles (Carabidae) and edge effect in oak-hornbeam forest and grassland transects. *Eur. J. Soil Biol.* 37:297-300.
- Mols, P.J.M. 1979. Motivation and walking behaviour of the carabid beetle *Pterostichus coerulescens* L. at different densities and distributions of the prey. A preliminary report. *Misc. Papers LH Wageningen* 18:185-198.
- Mols, P.J.M. 1988. Simulation of hunger, feeding and egg production in the carabid beetle *Pterostichus coerulescens* L. (= *Poecilus versicolor* Sturm). *Agric. Univ. Wageningen Pap.* 88:1-99.
- Mühlenberg, M. 1989. *Freilandökologie*. Quelle & Meyer Verlag, Heidelberg, Wiesbaden.
- Niemelä, J., Y. Haila and P. Punttila. 1996. The importance of small-scale heterogeneity in boreal forests: variation in diversity in forest-floor invertebrates across the succession gradient. *Ecography* 19:352-368.
- Paarmann, W. 1966. Vergleichende Untersuchungen über die Bindung zweier Carabidenarten (*P. angustatus* Dft. und *P. oblongopunctatus* F.) an ihre verschiedenen Lebensräume. *Z. Wiss. Zool. Abt. A.* 174:83-176.
- Paquin, P. and D. Coderre. 1997. Changes in soil macroarthropod communities in relation to forest maturation through three successional stages in the Canadian boreal forest. *Oecologia* 112:104-111.
- Pearson, D.L. and C.B. Knisley. 1985. Evidence for food as a limiting resource in the life cycle of tiger beetles (Coleoptera: Cicindelidae). *Oikos* 45:161-168.
- Rainio, J. and J. Niemelä. 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodivers. Conserv.* 12:487-506.
- Reise, K. and G. Widemann. 1975. Dispersion of predatory forest floor arthropods. *Pedobiologia* 15:106-128.
- Renner, M. 1999. *Kükenthal's Leitfaden für das Zoologische Praktikum*, 23rd ed. Fischer, Stuttgart.
- Rudolf, V.H.W. and M.O. Rödel. 2005. Oviposition site selection in a complex and variable environment: the role of habitat quality and conspecific cues. *Oecologia* 142:316-325.
- Sanderson, R.A., S.P. Rushton, A.J. Cherrill and J.P. Byrne. 1995. Soil, vegetation and space: An analysis of their effects on the invertebrate communities of a moorland in north-east England. *J. Appl. Ecol.* 32:506-518.
- Scheffer, F. and P. Schachtschnabel. 1989. *Lehrbuch der Bodenkunde*. F. Enke Verlag, Stuttgart.
- Schneider, D.W. 1997. Predation and food web structure along a habitat duration gradient. *Oecologia* 110:567-575.

- Sota, T. 1985. Limitation of reproduction by feeding condition in a carabid beetle, *Carabus yaconinus*. *Res. Popul. Ecol.* 27:171-184.
- Southwood, T.R.E., V.K. Brown and P.M. Reader. 1979. The relationship of plant and insect diversities in succession. *Biol. J. Linn. Soc.* 12:327-348.
- Szysko, J., H.J.W. Vermeulen and P.J. den Boer. 1996. Survival and reproduction in relation to habitat quality and food availability for *Pterostichus oblongopunctatus* F. (Carabidae, Col.). *Acta Jutlandica* 71:25-40.
- Thiele, H.U. 1975. Interactions between photoperiodism and temperature with respect to the control of dormancy in the adult stage of *Pterostichus oblongopunctatus* F. (Col., Carabidae). *Oecologia* 19:39-47.
- Thiele, H.U. 1977. *Carabid Beetles in their Environments*. Springer, Berlin.
- Trautner, J., G. Müller-Motzfeld and M. Bräunicke. 1997. Rote Liste der Sandlaufkäfer und Laufkäfer Deutschlands (Coleoptera: Cicindelidae et Carabidae). 2. Fassung, Stand Dezember 1996. *Naturschutz und Landschaftsplanung* 29:261-273.
- Van Dijk, T.S. 1979. On the relationship between reproduction, age and survival in two carabid beetles: *Calathus melanocephalus* L. and *Pterostichus coerulescens* L. *Oecologia* 40:63-80.
- Van Dijk, T.S. 1981. The influence of food and temperature on the amount of reproduction in carabid beetles. How to translate the results of laboratory experiments into the reality of the field? In: P. Brandmayer, P. J. Den Boer and F. Weber (eds.), *The Synthesis of Field and Laboratory Experiment*. Pudoc, Wageningen, pp. 105-123.
- Van Dijk, T.S. 1982. On the relationship between availability of food and fecundity in carabid beetles: How far is the number of eggs in the ovaries a measure of the quantities of food in the field? In: P. J. den Boer, L. Grüm and J. Szysko (eds.), *Fifth Meeting of European Carabidologists at Stara Brda Pilska*. Warsaw Agr. U. Press. pp. 105-121.
- Van Dijk, T.S. 1983. The influence of food and temperature on the amount of reproduction in carabid beetles. How to translate the results of laboratory experiments into the reality of the field? In: P. Brandmayer, P. J. Den Boer and F. Weber (eds.), *The Synthesis of Field and Laboratory Experiment*. Pudoc, Wageningen, pp. 105-123.
- Van Dijk, T.S. 1986a. How to estimate the level of food availability in field populations of carabid beetles? In: P. J. Den Boer, M. L. Luff, D. Mossakowski and F. Weber (eds.), *Carabid Beetles, their Adaptions and Dynamics*. Fischer, Stuttgart. pp. 371-384.
- Van Dijk, T.S. 1986b. On the relationship between availability of food and fecundity in carabid beetles: How far is the number of eggs in the ovaries a measure of the quantities of food in the field? In: P. den Boer, L. Grüm and J. Szysko (eds.) *Feeding Behaviour and Accessibility of Food for Carabid Beetles*. Warsaw Agricultural University Press, Warsaw. pp. 105-121.
- Van Dijk, T.S. 1994. On the relationship between food, reproduction and survival of two carabid beetles: *Calathus melanocephalus* and *Pterostichus versicolor*. *Ecol. Entomol.* 19:263-270.
- Van Dijk, T.S. and P.J. den Boer. 1992. The life histories and population dynamics of two carabid species in a Dutch heathland. *Oecologia* 90:340-352.
- Van Heerdt, P.F., B. Blokhuis and C. van Haaften. 1976. The reproductive cycle and age composition of a population of *Pterostichus oblongopunctatus* (Fabricius) in the Netherlands (Coleoptera: Carabidae). *Tijdschrift voor Entomologie*:1-13.
- Wallin, H., P.A. Chiverton, B.S. Ekbom and A. Borg. 1992. Diet, fecundity and egg size in some polyphagous predatory carabid beetles. *Entomol. Exp. Appl.* 65:129-140.
- White, T.C.R. 1978. The importance of a relative shortage of food in animal ecology. *Oecologia* 33:71-86.
- Ziesche, T., G. Förster and M. Roth. 2004. Die Lebensraumfunktion von Wäldern für Gliederfüßer (Arthropoda): Einfluss der Baumarten und des Bestandesalters. In: Mosandl, R. and B. Felbermeier (eds.), *Ökosystem Management*. Vol. 1. Verlag B. Felbermeier, Weilheim. pp. 27-37.

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