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Influence of temperature and humidity on the activity of three *Carabus* species

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Summary

Carabid beetles were trapped in summer 1987 and spring 1988 in the Plateau des Tailles (Province Luxembourg, Belgium). The traps were checked every morning during 10 trapping sessions (79 days). Temperature and humidity were recorded continuously on the site during the whole period. The influence of these two meteorological variables was studied using a Stepwise Linear Regression Model in order to study the information added by the different variables.

In spring, the higher the mean daily temperature, and the lower the day-night temperature contrast and the mean daily humidity, the more *Carabus problematicus* and *C. auronitens* were active.

The activity of *Carabus problematicus* and *C. auronitens* in summer, and of *C. violaceus* in spring was positively correlated with the mean daily temperature.

C. violaceus is active in spring mainly in nights during which the humidity at midnight is between 85 and 97%.

Introduction

Most studies on the influence of temperature and humidity on carabids' activity have been conducted in the laboratory, and have shown that both factors may show distinctive influences; e.g. *Carabus problematicus* displayed different activity patterns at 90% and at 95% humidity levels (Thiele 1977), but Weber (1983) already mentioned the difficulty of applying laboratory results of *C. problematicus* locomotion records to natural situations.

The influence of temperature, as the most important meteorological variable, on the activity of carabid beetles has been studied in the field by several authors (e.g. Althoff *et al.* 1994), but humidity, as an important second variable, has generally been discarded, as in the case of the negative interrelationship observed between temperature and humidity in open habitats (e.g. Desender 1983). The use of a Stepwise Linear Regression Model, however, allows the additive significant information given by different variables to be studied (Berenson *et al.* 1983).

Materials and methods

During a recent study of the movements of *C. auronitens* and *C. problematicus* (Nève & Baquette 1990), temperature and humidity were recorded on the site of capture in order to study their effects on the catchability, taken as an index of the activity of the studied species. A total of 147 pitfall traps were put in a beech forest (Luzulo-Fagetum) in the Plateau des Tailles (50° 15'N, 5° 44'E, Province Luxembourg, Belgium). The pitfall traps consisted of half plastic bottles 17 cm height, 8.5 cm diameter, buried so that their rim was at the same level as the surrounding soil surface, as described by Dufrêne (1988). Temperature and humidity were recorded continuously with a mechanical thermo-hydrometer placed on the ground, and the traps were checked every morning one out of two weeks from 22 July to 19 September 1987, and from 20 April to 8 July 1988. At the beginning of the latter period 24 extra traps were set, raising the total to 171. Totals of 87 and 295 catches of *C. auronitens*, 568 and 96 catches of *C. problematicus* and 43 and 25

Table 1. Variables most correlated with the daily catches, as chosen by a Stepwise Linear Regression Model; the variables are selected as long as they meet a 0.05% level for entry in the model. TP1 and TP2 denotes the first two axes of the Principal Component Analysis of the temperature variables, and HP1 the first one of the PCA on humidity

Carabus problematicus

Summer 1987 (9 August–19 September) n = 20

Variables	Parameter estimate	Partial R ²	F
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TP1	4.65	33%	8.26*
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Spring 1988 (20 April–8 July) n = 51

Variables	Parameter estimate	Partial R ²	F
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TP1	0.26	12%	6.32**
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TP2	-0.96	9%	6.10**
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HP1	-0.53	7%	6.51*
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Σ		28%	
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Carabus auronitens

Summer 1987 (22 July–4 September) n = 26

Variables	Parameter estimate	Partial R ²	F
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TP3	-1.18	27%	7.72*
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TP1	0.21	30%	12.94***
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Σ		57%	
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Spring 1988 (20 April–23 June) n = 41

Variables	Parameter estimate	Partial R ²	F
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TP1	1.39	35%	20.22***
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HP1	-1.55	14%	17.24***
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TP2	-2.72	7%	14.92***
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Σ		56%	
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Carabus violaceus

Spring 1988 (11 June–8 July) n = 41

Variables	Parameter estimate	Partial R ²	F
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TP1	0.11	24%	11.89**
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*p < 0.05, **p < 0.01, ***p < 0.001.

C. violaceus were recorded in summer 1987 and spring 1988, respectively. During the whole period there were 29 and 50 capture days, grouped in 10 trapping sessions.

Statistical analysis and results

For the statistical analysis, the values of temperature and humidity were input at 2 hourly in-

Fig. 1. Equilibrium circle of the temperature descriptors, as given by axes 2 and 3 of the Principal Component Analysis of the temperatures of the 24 hours preceding the trap check (8.00 a.m.). TN and TX are the minimum and maximum observed temperatures and the figures the different times of observation.

tervals, as well as the maximum and minimum of each 24 hour period preceding the trap check (8.00 a.m., West European Summer Time). As the studied species show marked seasonal differences in their activity, *C. problematicus* being an autumn breeder (Houston 1981) and *C. auronitens* a spring breeder (Hemmer *et al.* 1986), the data sets from summer 1987 and spring 1988 were analysed separately. As the 14 daily values of each temperature and humidity were correlated with each other, the multiple linear regression method could not be used on the raw data, because of the colinearity of the independent variables (Legendre & Legendre 1984). The influences of temperature and humidity were analysed separately because there were only occasional correlation values (mostly $P > 0.10$) between these two sets of variables, in contrast to the high correlation of both temperature and humidity values within each 24 hour period ($P < 0.001$); and a Principal Component Analysis (PCA), after z-transformation, on both variables taken together gave a first axis determined mainly by temperature values (percentage of values accounted for 43.6%) and a second axis by humidity values

Fig. 2. (a) Spring catches of *C. auronitens* and (b) *C. problematicus*, and (c) summer catches of *C. problematicus* and their values as predicted by the Stepwise Multiple Linear Regression Model.

(percentage of values accounted for 38.1%). The first three axes of the PCAs on these two variables retained 85, 8 and 4% of the variance of the 14 original temperature values; and 72, 10 and 6% of the variance of the original 14 humidity values. During each season, only the periods during which significant numbers of the considered species were continuously caught were kept, in order

Fig. 3. Spring 1988 catches of *C. violaceus*, as a function of observed humidity at 0.00 the night previous to the trap check.

to account for the seasonality of activity of the different species. The coordinates of the days, given by the first three axes of the PCA on both humidity and temperature were then used in a Stepwise Linear Regression Model (procedure REG, SAS 1990) in order to detect the greatest influences on the daily catches of the studied species (Table 1).

The first two axes of the PCA of temperature values and the first one of humidity values are highly significant in explaining the variation of *C. problematicus* and *C. auronitens* numbers caught in spring. The first axes of both the temperature and the humidity PCAs give indices of the magnitude of the considered temperatures and humidities respectively, the second temperature axis is a measure of the contrast between day and night temperatures and the third axis of the temperature PCA is an index of the difference between late morning and early night temperatures (Fig. 1).

Discussion

C. problematicus and *C. auronitens* morning spring catches respond positively to the temperatures of the previous 24 hours and negatively to temperature variation and mean humidity values (Table 1). In summer however, as it responds negatively to the contrast between late morning

and early night temperatures (3rd PCA axis), *C. auronitens* seems to be active preferably in relatively warm early nights, which is in accordance with the observations of Hemmer *et al.* (1986) who showed that *C. auronitens* is mostly active in early night and that its spring activity is correlated with the temperature at this time (20.00–22.00), which is also true in our case (20.00: $R^2 = 0.21$, $P < 0.01$, 22.00: $R^2 = 0.18$, $P < 0.01$). In both spring and summer, as the first axis of the temperature PCA was chosen as the most correlated variable, *C. auronitens* and *C. problematicus* activity depends on the temperatures of the circadian rhythm taken as a whole, even within their preferred season of activity. Using the meteorological variables chosen by the Stepwise Linear Regression Model, it is possible to model the number of captures of the species studied (Fig. 2).

For *C. violaceus*, only the first axis of the PCA temperature analysis showed a good correlation with the numbers caught in spring, discarding any effect of humidity values; this is possibly due to the very low numbers of *C. violaceus* captured. It seems nevertheless that the species responds strongly to humidity levels, as 88% of the individuals were captured at humidities from 85 to 97% at midnight in spring 1988 (Fig 3).

This clearly shows that a linear regression is not applicable in all cases. Vogt *et al.* (1983) showed that several meteorological variables (temperature, wind speed, ...) induce positive responses in the catchability of *Lucilia cuprina* (Calliphoridae), up to a certain level where the catchability levels off. Hemmer *et al.* (1986) showed the minimum early night temperature at which *C. auronitens* begins to be active in early spring is around 6–7°C; a lack of cold (<7°C) period on the study site in April 1988 did not allow the fluctuations of numbers caught above and below this critical temperature to be studied.

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