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ORIGINAL ARTICLE

Seasonal shift in carabid phenology over a period of 18 years

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Abstract. The present study is based on a 20-year study of fields that were previously farmed conventionally and then changed to being farmed organically and a 10-year study of a conventionally farmed field in south-eastern and central Schleswig-Holstein, North Germany, respectively. The carabid beetles were sampled throughout each year using pitfall traps. The analysis aimed to study the changes in the phenology in terms of activity-density associated with changing climate. Climate data revealed an increase in temperature during the period of this study, which was not significant during the single study periods, but significant if a longer period of 70 years is considered. In particular, spring temperatures (March/April) increased. Approximately 36% of the species became active earlier. For 25% of the species their earlier start was not significant but nevertheless associated with temperature increase in spring or the number of cold days (< 0°C) and warm days (> 5°C) in March/April. In total, the earlier start of 69% of the species can in some way be associated with a change in climate in spring. Species with a flexible response to temperature were mostly indifferent to the temperature increase. Comparisons of the data over the 30-year period indicate that the process lasted for at least one to three decades. It is likely that the changes in biological processes caused by global climate change will affect the composition of species and competition between them in the future.

INTRODUCTION

Global warming affects biological systems in various ways. On the one hand, ecosystem changes can be expected due to its effect on ecosystems processes and functions such as biomass production or litter decomposition (Chapin, 2003; Dielemann et al., 2015). Rising sea levels will dramatically decrease the area of habitat of the salt-preferring soil fauna (Irmler et al., 2002) and global warming will markedly change the distribution and community composition due to the northward shift in the distribution of southern species (Crozier, 2003; Avtaeva et al., 2021; Brygadyrenko et al., 2021). On the other hand, changes in phenology may decouple former seasonal relations between species (Abarca, 2019; Neumüller et al., 2021), especially plant herbivore interactions (Bezerner & Jones, 1998). In particular, northern regions will suffer most under the predicted climate change (Ernakovich et al., 2014).

The present study is based on 20 years of monitoring an organically managed farm and its adjacent near-natural habitats in terms of changes in the activity of carabid beetles. It is complemented by a nearly 10-year-long study of a conventionally farmed field some 100 km away. Two questions were addressed: (1) Which species became active earlier and which climate factors triggered this change in their phenology? (2) Why did the phenology of some species remain the same?

SITES AND METHODS

Arable fields and their adjacent near-natural habitats consisting of grassland, hedges and wet pond margins were monitored. The study area "Hof Ritzerau" is located in south-eastern Schleswig-Holstein, North-Germany, near the city of Mölln. The 290-ha farm is part of a diverse landscape with forests, creeks and ponds of which 180 ha consists of arable fields and approximately 18 ha of near-natural habitats. For many years the farm was the property of the city of Lübeck and then inherited by Günther Fielmann in 1998, who changed the management from intensive conventional farming to organic farming based on "Bioland" rules in 2001. Since 2004, the entire field was organically farmed. Another field located near Bornhöved in central Schleswig-Holstein was compared with the Ritzerau fields. The Bornhöved field was conventionally farmed over the entire period of the study. Soils are similar with that in the fields at "Hof Ritzerau". In addition, the landscape was similar with adjacent forests, grasslands and hedges. More details of the Bornhöved area are in Blume et al. (2008).

The investigations at Ritzerau started in May 2001. Crop rotation when conventionally farmed from 2001 to 2003 consisted of corn, winter wheat and winter rape; crop rotation when organically farmed since 2004 included winter wheat, summer wheat, winter rye, summer barley, peas and a grass-clover mixture. From time-to-time, parts were used as sheep pasture. The period of study of the Bornhöved field lasted from 1988 to 1996. Crop rotation included maize, oat, rape and grass.

Since 2001, ground beetles were recorded in arable fields at "Ritzerau Hof" and the adjacent field margins including hedges, shrubs and grassland. Over the course of the study 96 pitfall traps were set in the arable fields and 27 in near-natural habitats. The pitfall traps in the fields were arranged in a grid pattern. The location of the pitfall traps was defined by GPS to verify the identical locations in each of the years. From 2001 to 2004, there was a yearly investigation and during the monitoring after 2004, pitfall traps were only set every second year. Pitfall traps were commercially available glass jars with a 5.7 cm diameter opening and height of 11 cm. They were filled with monoethylen glycol. Transparent plastic shelters provided protection against rainfall. Pitfall traps were changed at monthly intervals throughout most of each year, but removed in August and parts of September, when crops were harvested and seed planted. In cold, snow-rich winters, monthly changes of the pitfall traps were sometimes not possible. For the present study, the data recorded from 2002 to 2018 was used. The year 2001 was omitted because data was not available for the whole year. In addition, the years 2004 and 2005 were not included because in the monitoring phase pitfall traps were installed in accordance with the agricultural year from September to July the following year. Thus, in 2004 and 2005 pitfall traps were also not set during the entire year. In the Bornhöved field, only 3 pitfall traps were installed in the centre of the field from 1988 to 1996. Otherwise, the installation and change of traps were similar as in the fields at "Hof Ritzerau". More details are in Irmler (2003).

The climate in the Ritzerau area is of the transitional Atlantic type with a mean yearly temperature (30 years mean) of 9.39°C and an annual rainfall between 487 to 970 mm. During this study there was not a significant increase in temperature. In the Bornhöved area with a more Atlantic climate the 30-year mean was 8.5°C and annual rainfall amounted to 697 mm. Annual temperature means varied between 8.0 and 9.1 from 1988 to 1996 and the rainfall ranged between 490 and 980 mm.

The climate data used in the analysis was obtained from the meteorological station at Grambeck, which is nearest to the study area at Ritzerau. The Grambeck data was also used for the comparison between the two areas. The Grambeck data was complemented by data from Hamburg airport for the period before 1980.

Statistical calculations were made using the program PAST3 (Hammer et al., 2012). Seasonality of carabids was characterised using the weighted mean of yearly occurrence. Weighted mean months were calculated as: $wM = \Sigma\ (n * month\ (1–12)\ /N)$; n = abundance in month (1–12), N = sum of total abundance.

The GLM multifactorial ANOVA was used for testing the association between climate data and wM and the comparison between the 1988/96 using the Ritzerau data. To have enough data for the comparison (only 3 pitfall traps at Bornhöved), the values for three years were combined. Thus, only 3 values were available for each of the three decades.

RESULTS

Change in climate during this study

There was a significant long-term trend of approximately +1°C from 1950 to 2018. In the same period annual rainfall increased from 576 mm y^{-1} to 737 mm y^{-1}, but not significantly so. The annual temperature increased by t(°C) = 0.027 – 44.85 ($p < 0.001$) and spring temperature by t(°C) = 0.035 – 64.4 ($p < 0.001$). According to the trend over 70 years, both annual and spring temperatures increased by 0.27°C and 0.35°C, respectively, in the 10 years of this study. Thus, the increase in spring temperature was slightly higher during this period than that of the annual temperature.

Climate data from the Grambeck meteorological station were analysed for trends occurring over the period of this study (Fig. 1). Annual rainfall varied greatly between years, fluctuating between 487 mm y^{-1} and 958 mm y^{-1}. The mean for the period of this study was 713 mm y^{-1}. Thus, annual rainfall varies approximately by up to 20% of the mean, but there was no trend. There were, however, non-significant trends in different components of temperature over the period of this study. Mean temperatures (°C) increased by: aT = 0.045y – 80.5 ($p = 0.096$); T(M/A) = 0.045y – 83.1 ($p = 0.502$); T(J/F) = 0.016y + 33.1 ($p = 0.853$); y: years; aT: annual mean temperature; T(M/A): mean temperature in March and April; T(J/F): mean temperature in January and February. Thus, the mean annual temperature and the temperatures in March/April increased by nearly 0.5°C in ten years, whereas the temperature in January/February remained at the same level over nearly 20 years of this study. For some species, inhibiting or enhancing temperatures may be of importance for their development. Therefore, the number of days with temperatures lower than 0°C and higher than 5°C were also checked and found to be very variable. The number of frost days ranged between 0 and 21 in these two months and warmer days (> 5°C) between 21 and 54 days. The trends were: Days (< 0°C) = –0.19y + 378.5 ($p = 0.53$) and days (> 5°C) = 0.21y – 391.4 ($p = 0.58$). Thus, frost days decreased approximately by 2 days in ten years. In contrast, warmer days increased by nearly the same value of approximately 2 days in ten years.

The sum of the temperatures for the months March/April was also checked because it is relevant for the development of many carabid species. The values were also very variable but approximately 200 and 540. The relationship between time and sum of temperatures (sT) was: sT = 2.70y – 5035 ($p = 0.51$). Thus, the sum of temperatures increased by 27 in 10 years, which is more than one fourth of the lowest temperature sum within the period of the nearly 20 years of this study.

The comparison of the period from 1988 to 1996 with the period of this study revealed that the annual mean temperature was slightly cooler with 8.8°C (vs. 9.4°C) and the spring temperature was 6.1°C (vs. 6.5°C). There were no trends in the annual and spring temperatures during the period from 1988 to 1996.

Response of species to the changes in temperature between 2001 and 2018

In total, 97 species of carabids were recorded between 2001 and 2018. Among them, 75 species were recorded in the arable field and 88 in field margins. Most of them were only rarely found. A more detailed overview on the succession, distribution and migration processes are given in Irmler (2020). Fifty-five of the most frequently caught species were selected for analysing any seasonal shift over the period of the study (Table 1). Among the 55 species, 20 species showed significant shifts to becoming active earlier in the year. This is 36% of the species analysed. On average, the shift amounts to 0.84 months per 10 years with a range of between 0.3 to 1.9 months per 10 years. In addition, in 18 of the 55 species it was significantly associated

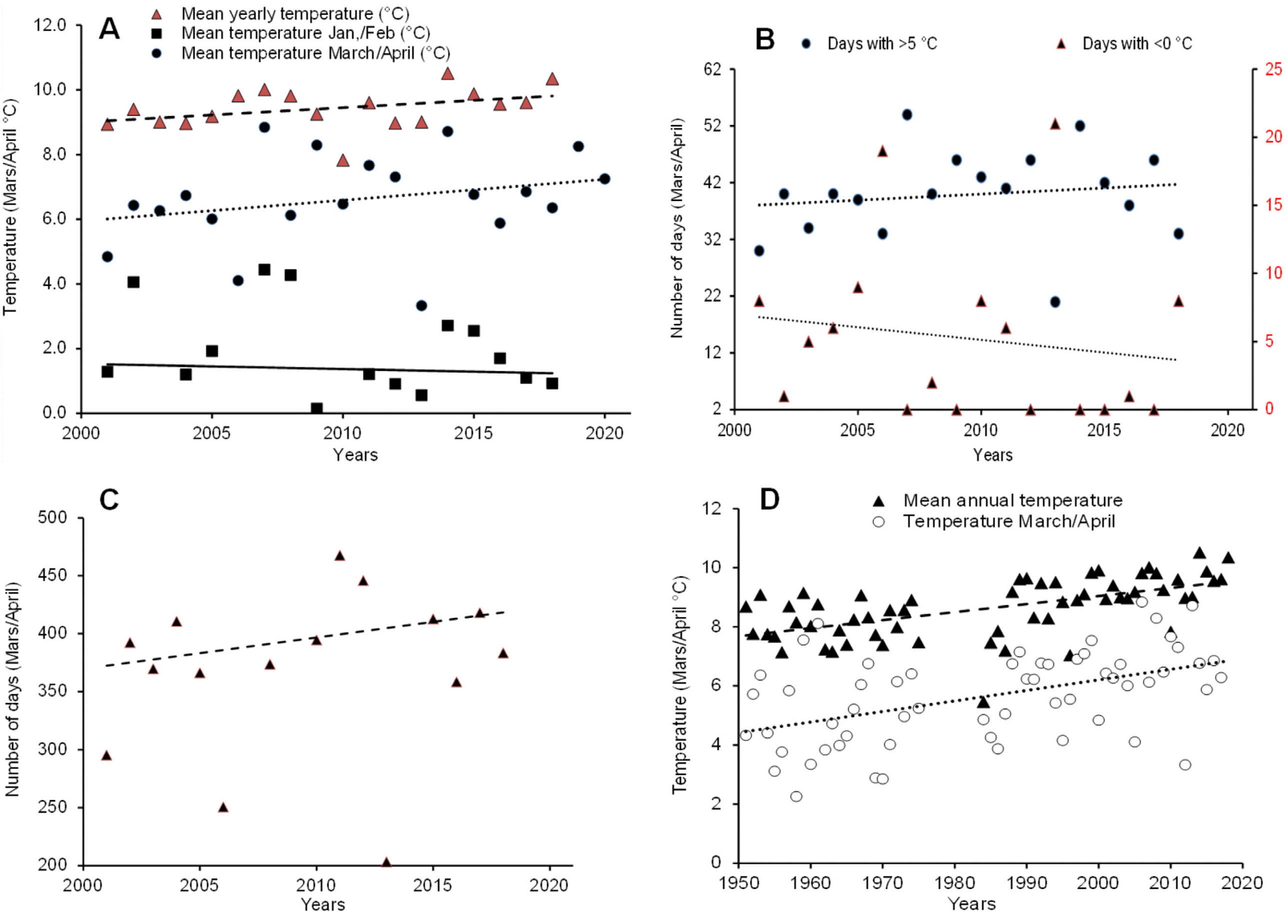

Fig. 1. Climatic conditions recorded during the period of the study. A – Annual mean temperatures (°C), mean temperatures (°C) in spring (March, April) and winter (January, February); B – number of days with < 0°C and > 5°C; C – sum of temperatures in March and April at Ritzerau (Grambeck); D – long-term change in annual temperatures and spring temperatures (March, April) based on data from Hamburg airport and Grambeck.

with the increase in spring temperature, temperature sums, or number of cold or warm days in March/April. Thus, the earlier onset of activity in nearly 69% of the species can in some respect be associated with a change in climate in spring.

That of seven species was significantly associated with mean temperature and the temperature sum in March/April, and in a few cases also with frost and warm days in the two spring months.

A group of 13 species showed a significant monthly shift, but with no association with March/April temperatures. The weighted mean monthly shift revealed no difference between these two groups with 6.1 for the 1st group and 5.9 for the 2nd group. Furthermore, the shift was very similar in the two groups with 0.86 months in 10 years and a range of between 0.4 and 1.7 months. Thus, the species in the second group certainly did not only respond to spring temperature in the respective years.

A further group of 9 species showed no significant seasonal shift in activity, although there was a slight shift to earlier activity of only an average of 0.4 months for the period of 10 years with a range between 0.04 and 0.7 months. The average weighted mean (in months) of the shift in this group is 6.2 and, thus, nearly equal to the two preceding groups. In this species group, there were associations with spring temperatures and number of frost or warm days. Therefore, it is likely that the warmer spring temperatures only slightly affected the seasonal shift in these species.

Five species showed shifts to earlier activity, but not significantly so, and the association with warmer spring temperatures is restricted to different factors. For some species, the temperature sum reflects a significant effect, whereas others respond to the number of frost or warm days during spring. Nevertheless, on average the monthly shift is similar to that in the first and third group with a similar range of between 0.2 and 1.4 months in 10 years. Various factors may be responsible for this response.

For the following ten species, neither a significant shift in activity nor an association with any of the temperature factors was recorded. Four species in this group have clear spring and autumn bimodal seasonality, which may prevent a shift in spring, or they are summer-active because the weighted monthly mean of the species is 6.5, on average, which is higher than in the preceding groups. Spring temperatures, thus, may have no effect on their summer or autumn activity.

In a last group of 11 species, a shift to later activity in the year was recorded, although it was only significant for four species. In this group, too, there were remarkably higher numbers of autumn or winter breeders. In addition, most

Table 1. Slope and statistical significance of the changes in weighted mean months from 2002 to 2018.

Species	Month Weight. Mean	Annual increment		March/April (p)			
		Slope	p	Mean temp.	Temp. sum	Days < 0°C	Days > 5°C
Amara aenea	5.8	–0.048	*0.07*	*0.026*	*0.029*	0.166	0.325
Amara familiaris	5.8	–0.082	*0.04*	*< 0.001*	*< 0.001*	*0.031*	*0.044*
Amara similata	6.4	–0.067	*0.01*	*0.041*	*0.047*	*0.045*	0.434
Anchomenus dorsalis	5.9	–0.032	*0.08*	*0.045*	*0.041*	0.498	0.555
Calosoma maderae	6.3	–0.190	*< 0.001*	*0.029*	*0.028*	0.328	0.160
Harpalus signaticornis	6.7	–0.064	*0.01*	*0.049*	*0.049*	0.473	0.325
Pterostichus anthracinus	5.6	–0.091	*0.03*	*0.013*	*0.012*	0.113	0.123
Abax parallelpipedus	6.0	–0.077	*0.01*	0.481	0.476	0.510	0.442
Agonum mülleri	6.1	–0.047	*0.08*	0.250	0.301	0.551	0.910
Agonum sexpunctatum	5.5	–0.067	*< 0.001*	0.609	0.600	0.728	0.850
Agonum viduum	6.4	–0.117	*0.03*	0.784	0.813	0.555	0.959
Carabus auratus	5.5	–0.072	*0.03*	0.234	0.271	0.805	0.744
Carabus granulatus	5.7	–0.057	*0.04*	0.103	0.109	0.690	0.306
Demetrias atricapillus	5.2	–0.036	*0.05*	0.894	0.829	0.333	0.565
Limodromus assimilis	5.7	–0.077	*0.01*	0.603	0.626	0.679	0.887
Microlestes minutulus	6.4	–0.135	*0.05*	0.895	0.920	0.224	0.604
Pterostichus diligens	5.4	–0.102	*0.03*	0.452	0.477	0.197	0.575
Pterostichus melanarius	6.8	–0.058	*< 0.001*	0.090	0.090	0.209	0.291
Pterostichus oblongopunctatus	5.4	–0.173	*< 0.001*	0.588	0.546	0.479	0.631
Synuchus vivalis	7.1	–0.097	*< 0.001*	0.130	0.126	0.513	0.335
Carabus nemoralis	5.4	–0.043	0.15	*< 0.001*	*< 0.001*	*0.049*	0.131
Calathus fuscipes	7.6	–0.044	0.34	*0.035*	*0.029*	0.533	*0.048*
Harpalus affinis	6.1	–0.069	0.15	*0.008*	*0.009*	0.161	0.183
Harpalus rubripes	6.2	–0.066	0.41	*< 0.001*	*< 0.001*	*0.002*	*0.045*
Notiophilus biguttatus	6.1	–0.021	0.64	*0.017*	*0.023*	*0.043*	0.375
Poecilus cupreus	5.5	–0.032	0.19	*0.003*	*0.003*	0.216	*0.049*
Poecilus versicolor	5.4	–0.027	0.38	*0.013*	*0.013*	0.213	0.138
Pterostichus niger	7.3	–0.056	0.12	*0.007*	*0.009*	0.273	0.087
Stomis pumicatus	6.0	–0.004	0.94	*0.003*	*0.002*	*< 0.001*	*< 0.001*
Amara communis	6.6	–0.026	0.60	0.773	0.695	0.933	*0.045*
Amara plepebja	7.3	–0.024	0.73	0.075	*0.048*	*0.041*	0.155
Bembidion lunulatum	4.7	–0.109	0.33	0.042	*0.044*	*0.050*	0.271
Bembidion obtusum	**2.8**/11.6	–0.142	0.61	0.495	0.498	*0.018*	0.724
Pterostichus nigrita	6.8	–0.069	0.12	0.031	*0.028*	0.132	0.065
Blemus discus	7.5	–0.021	0.38	0.884	0.815	0.542	0.337
Clivina fossor	5.9	–0.002	0.96	0.331	0.346	0.902	0.579
Dyschirius globosus	6.6	–0.136	0.21	0.259	0.280	0.205	0.945
Harpalus rufipes	6.7	–0.064	0.15	0.108	0.110	0.319	0.392
Loricera pilicornis	6.0	–0.005	0.89	0.503	0.547	0.964	0.896
Poecilus lepidus	6.3	–0.112	0.48	0.640	0.681	0.859	0.842
Agonum fuliginosum	**5.3**/10.7	–0.108	0.14	0.782	0.820	0.543	0.883
Bembidion tetracolum	**4.4**/11.0	–0.010	0.80	0.411	0.419	0.441	0.766
Nebria brevicollis	**4.9**/10.0	–0.049	0.47	0.385	0.438	0.963	0.785
Pterostichus strenuus	**4.7**/10.8	–0.004	0.93	0.270	0.284	0.910	0.409
Acupalpus exiguous	**5.3**/11.6	0.014	0.87	0.151	0.141	0.438	*0.037*
Amara lunicollis	6.3	0.034	0.45	0.940	0.863	0.850	0.184
Bembidion guttula	5.6	0.011	0.76	0.182	0.171	0.597	0.069
Bembidion lampros	6.1	0.024	0.65	0.359	0.374	0.523	0.650
Pterostichus vernalis	7.3	0.068	*0.02*	0.994	0.978	0.458	0.860
Trechoblemus micros	6.3	0.060	0.69	0.118	0.128	0.128	0.337
Acupalpus meridianus	**5.0**/11.6	0.043	0.55	0.252	0.246	0.605	0.158
Bembidion properans	**5.4**/10.7	0.020	0.74	0.305	0.335	0.662	0.766
Calathus cinctus	3.6/**10.5**	0.004	0.96	0.575	0.661	0.430	0.483
Nebria salina	4.9/**10.7**	0.377	*0.01*	0.620	0.634	0.473	0.922
Trechus quadristriatus	3.4/**10.8**	0.158	*0.02*	0.837	0.833	0.283	0.839

species are summer-active as can be shown by the high value of 6.3 for the average weighted mean month. It is assumed that several species in this group avoid high summer temperatures by being active in the cooler periods in late summer or autumn.

Comparison of the seasonality in 2001 and 2018, and with that in the 1990s

On the field near Bornhöved, species richness was lower than at Ritzerau with 50 species recorded in the 10-year period. This may be due to the lower number of 3 pitfall traps, the shorter period of study or conventional farming

Table 2. Comparison of the weighted mean seasonality recorded in the three decades with the results of the GLM multifactorial ANOVA. Calc. – calculated weighted mean from the corresponding 2002/2018 regression; df1: 1; df2: 7. Bold numbers indicate significance.

Years (decade)	1988/96				2001/09		2010/18		F	P
Species	n	Calc.	Mean	S.d.	Mean	S.d.	Mean	S.d.		
Poecilus versicolor	101	6.0	[a] 6.3	0.9	[ab] 6.0	0.3	[b] **5.3**	**0.2**	6.4	0.040
Carabus granulatus	30	6.8	[a] 6.3	1.7	[b] **6.2**	**0.3**	[b] **5.4**	**0.2**	13.5	0.026
Amara aenea	15	6.6	[a] 6.8	0.5	[a] 6.6	0.7	[b] **5.5**	**0.1**	9.3	0.034
Limodromus assimilis	25	6.7	[a] 6.4	0.7	[ab] 5.6	0.4	[b] **4.9**	**0.3**	18.8	0.003
Carabus nemoralis	13	6.3	[a] 6.7	1.2	[ab] 5.7	0.1	[b] **5.1**	**0.2**	8.5	0.022
Clivina fossor	73	5.9	6.7	0.3	6.5	0.9	5.9	1.0	1.7	n.s.
Harpalus affinis	26	7.3	6.7	0.8	7.0	0.7	5.8	0.5	2.4	n.s.
Bembidion lampros	93	6.7	[a] 7.1	0.6	[ab] 6.2	0.3	[b] **5.6**	**0.3**	21.7	0.020
Bembidion tetracolum	199	6.1	[a] 7.1	0.7	[ab] 6.3	1.2	[b] **5.6**	**0.8**	4.7	0.057
Loricera pilicornis	24	6.1	7.1	0.5	6.3	0.6	6.7	0.3	4.9	n.s.
Agonum muelleri	56	6.8	[a] 7.2	0.7	[ab] 6.5	0.5	[b] **5.9**	**0.7**	7.4	0.029
Amara similata	23	7.5	[a] 7.3	1.1	[b] **6.7**	**0.3**	[b] **6.0**	**0.1**	11.4	0.048
Pterostichus melanarius	233	7.4	[a] 7.4	0.2	[ab] 6.9	0.2	[b] **6.5**	**0.4**	9.5	0.049
Harpalus rufipes	272	7.6	[a] 7.8	0.1	[ab] 7.1	0.5	[b] **6.4**	**0.3**	38.0	< 0.001
Bembidion properans	18	6.0	[a] 8.0	0.1	[ab] 7.1	1.2	[b] **6.0**	**0.9**	9.5	0.020
Pterostichu niger	64	8.0	[a] 8.1	0.2	[ab] 7.6	0.4	[b] **6.6**	**0.1**	46.1	< 0.001
Trechus quadristriatus	56	4.9	8.8	0.3	7.4	1.8	6.8	2.6	2.0	n.s.
Calathus fuscipes	60	8.2	[a] 8.9	0.1	[ab] 8.3	0.7	[b] **7.1**	**1.3**	7.4	0.029
Nebria brevicollis	47	8.6	[a] 9.2	0.3	[ab] 7.8	1.3	**7.0**	**1.6**	5.4	0.050

practices. Nevertheless, several species occurred in both fields and allowed a comparison with the 2002 to 2018 period. Fig. 2 shows for some frequently caught species the seasonal changes in their activity in the two periods, which comprised approximately 30 years. The 10-year steps revealed that the seasonal activity of several species, e.g. *Pterostichus melanarius*, *Agonum muelleri*, *Bembidion lampros* and *Carabus granulatus*, was later in the 1990s than 20 years later with an intermediate pattern at the beginning of the 2000s. Moreover, the species showed only one peak in the 1990s, but a second but much smaller peak in the 2000s.

For the comparison the weighted means recorded in the three decades from 1988/96 to 2018, for 19 species, were used. The results support the trend recorded in two decades in the 2000s. In total, 15 species showed significant differences. The four species for which the results were insignificant were also insignificant in the 2000s. In most cases only in the last decade, were they significantly more active earlier than in the first decade in the 1990s, whereas in the intermediate decade of 2001 to 2009 they were neither significantly different to that recorded in the first nor the last decade. *Carabus granulatus* and *Amara similata* were the only species that were already active earlier in the intermediate decade. Nevertheless, 74% of the species showed the same trend as recorded in 2001/2018.

DISCUSSION

Long-term investigations on arthropods are rare. A study using also pitfall traps indicates a vertical shift in the Dolomites over the last thirty years (Brandmayr & Pizzolotto, 2016). Another long-term study in The Netherlands concentrates on habitat changes and dispersal (Turin & den Boer, 1988). Recent monitoring for a similarly long period of over 20 years in Great Britain (Pozsgai et al., 2018) reports a decrease in the abundance of species of ground beetles (Pozsgai & Littlewood, 2014). The results of Pozsgai et al. (2018) support the results found in the present study. According to their results, 11 out of 28 species showed a significant earlier start in their activity during the period from 1993 to 2013, which is 39% of the species they studied. They noted that the temperatures from April to June were major factors controlling the earlier activity with the most pronounced effect in spring. The analysis of the data presented indicates that the March/April temperatures were mainly associated with the earlier activity recorded in the area studied. In the Ritzerau study, 20 out of 56 species became active earlier, which is 36% of the species studied. This was partly associated with higher temperatures in spring, including a higher sum of temperatures during the spring period. However, the activity of several species that did become significantly active earlier, nevertheless, was associated with spring temperatures and/or the number of frost (< 0°C) or warm days (> 5°C) in this period. In total, the activity of 69% of the species can in some way be associated with the change in the climate in spring.

The comparison of the species with a significant earlier start in activity in the UK and in Ritzerau revealed similar results in terms of the trend. However, it was only significant for *Abax parallelepipedus* in both studies. This may be due to geographic differences with a more Atlantic climate in the UK, the different years studied and the individual reaction of carabid species to these two factors. The seasonal activity density pattern reflects life cycles and the reproduction dynamics of Carabidae (Thiele, 1977). According to Thiele (1977), five reproductive types exist that differ in the type of dormancy and the influence of temperature with differing combinations for females and males. Paarmann (1979) reports three types of annual reproduction rhythms for temperate zones and two additional types for the subtropical zone (summer and winter breeders). Among them, only the first type (spring breeders) is not influenced by

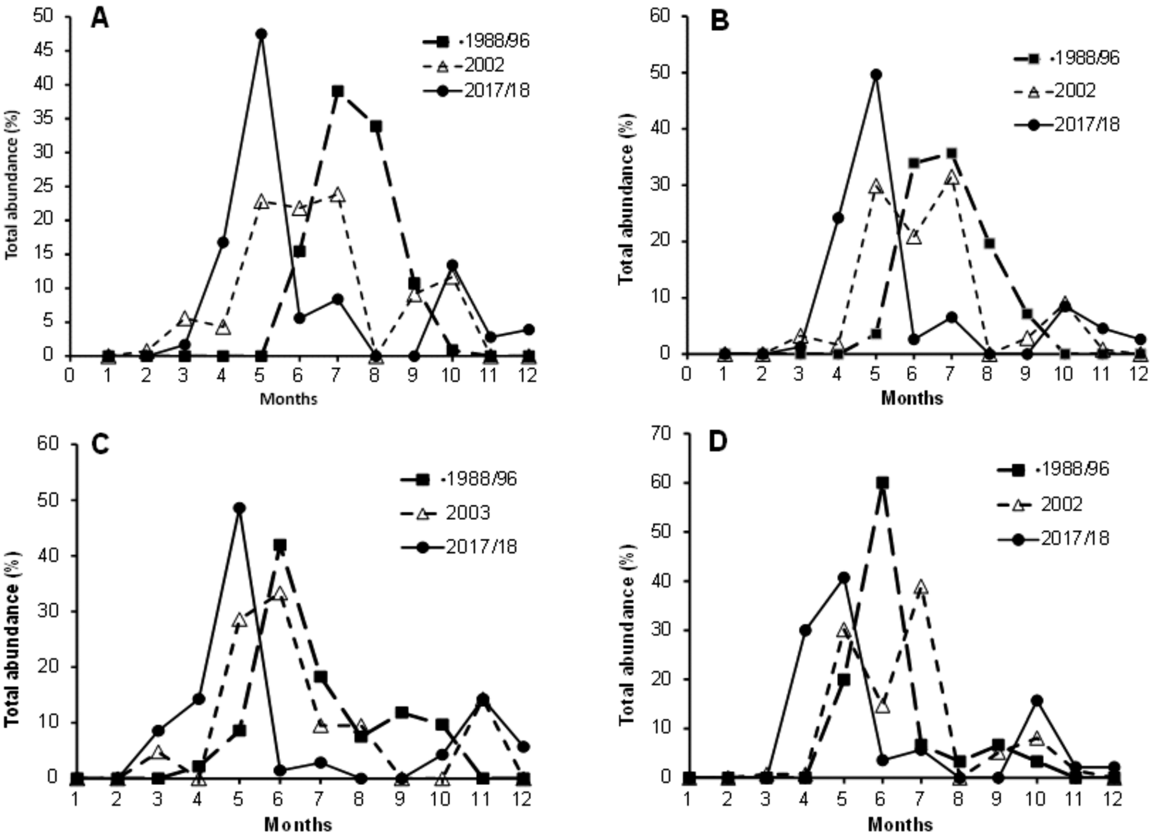

Fig. 2. Percentage abundance recorded each month of four species in the three decades investigated. A – *Pterostichus melanarius*, B – *Agonum muelleri*, C – *Bembidion lampros*, D – *Carabus granulatus*.

temperature. In contrast, species with unstable hibernation conditions or species in the subtropical zone are strongly affected by temperature. However, the reactions of a lot of species, particular those recorded in arable fields, are flexible to annual changes in climate (Fadl & Purvis, 1990; Irmler, 2007). It is likely that the activity of species with an insignificant earlier activity, but significant association with temperature is controlled more by photoperiod than spring temperatures. Species-specific type of reproduction is known for many species and is included in a list of traits provided by Homburg et al. (2014). The list contains trait information for 317 Central European species. Unfortunately, species-specific information on types of reproduction is poor. In the case of the present study, only 40% of the species could be assigned to a particular type of reproduction, which is too small for a statistical analysis. Therefore, only examples are discussed here.

It is unlikely that the phenology of type 1 species (spring breeders), which is only affected by photoperiod, is influenced by warmer temperatures in spring. *Nebria brevicollis* (Thiele, 1977) and *Nebria salina* (Telfer & Butterfield, 2004) belong to this group and, thus, showed no significant response to increasing spring temperatures. However, *Nebria salina* seem to have a longer activity period in autumn. Another spring breeder, *Pterostichus oblongopunctatus*, is also affected by photoperiod (Thiele & Könen, 1975), but short-day effects can be suppressed by high temperatures. The significant earlier start in activity recorded for *P. oblongopunctatus* may be explained by the combined effect of photoperiod and temperature, although spring temperatures had no significant effect on its phenology.

The great effect of temperature on *Amara* species is already known (Saska & Honek, 2003). The three *Amara* species in the first group support these results. It seems that the spring temperature is the major factor determining the onset of activity in species of this genus, because it was significantly associated with spring temperatures, the sum of temperatures and partly cold and/or warm days. The preference of *Amara* species for high temperatures is supported by their day time activity. Temperature is also known to affect the development and phenology of *Notiophilus biguttatus* (Ernsting & Isaak, 1997). Nevertheless, no significant trend in the phenology was recorded for this species, although their activity was strongly associated with spring temperatures. This reaction may also indicate a combined effect of photoperiod and temperature for this species as recorded for *Pterostichus oblongopunctatus*.

No change in the pattern of activity was recorded for several small species, such as *Trechus quadristriatus* and *Bembidion lampros*. According to Fadl & Purvis (1990), they belong to a group of species with a flexible reaction to changes in climate from year to year. They potentially reproduce throughout the year. This is also true for *B. obtusum,* which is mainly active in winter (Kennedy, 1994) and lays eggs in March/April. In the Ritzerau area, this species is also most active in late autumn/winter (Irmler, 2019).

The significant association with cold days in spring indicates a preference for cold spring temperatures and earlier activity in order to avoid warm spring temperatures. The earlier activity recorded for this species is certainly not due to earlier development, but rather the avoidance of high temperatures. Both *Trechus quadristriatus* and *Bembidion obtusum*, are typical winter-active species (Irmler, 2019) in the Ritzerau region. According to Weber (1965), both species tolerate cold temperatures, but *B. obtusum* is adapted to lower temperatures than *T. quadristriatus*. An optimum temperature range for *B. obtsum* is 5°C to 10°C. In the field, minimum temperatures at which they were recorded active was –2°C and 0°C, respectively, for *B. obtusum* and *T. quadristriatus*. This may be the reason why *T. quadristriatus* was active for longer in autumn and *B. obtusum* was not active in warm periods in spring. Overall, warmer winters will also result in an increase in the activity of these species.

Life cycles longer than one year may account for some species including the climate in preceding years in their response to global warming. Nearly all species with a lifespan longer than one year, e.g. *Abax parallelepibedus*, all *Carabus* and *Calosoma* species, and *Pterostichus niger*, started activity significantly earlier. As at least a part of the population exists of fully developed adults, species can be active whenever temperatures are suitable.

Thus, a variety of factors may determine changes in phenology, which are species dependent. The beginning of a recorded trend in an earlier start of activity may, therefore, also vary. The monitoring project in the UK (Pozsgai et al., 2018) was carried out nearly 10 years earlier than the Ritzerau study. The data included in the other long-term study at Bornhöved enabled us to estimate the time of the start of activity over a period of 30 years. For most species, only in the decade 2010–2018 were the values significantly different from that recorded two decades previously. Only the activity of *Carabus granulatus* and *Amara similata* was recorded as starting significantly earlier in 2001 to 2009 than 1988–1996.

The present results indicate that species react differently to the ongoing change in climate and that spring temperatures played a major role in this process in the region studied over at least the last one to three decades. These responses are likely to have resulted in changes in the composition of species and competition between species. To evaluate the results of the effects of management is, therefore, difficult. Such processes are overlain by long-term climate changes, varying climate conditions between years and succession following changes in management. Thus, long-term monitoring programs are urgently needed if we are to understand the underlying biological processes and avoid wrong conclusions.

CONCLUSIONS

Temperature in the region studied increased over the last 70 years by approximately 1°C. In particular, spring temperatures in March/April increased. 36% of the species of carabids responded to the change in spring climate by becoming active earlier. Approximately 69% of the species showed a significant response to the increase in temperature. Responses of the individual species differed depending on their sensibility to temperature and photoperiod. Few species with winter and autumn peaks of activity revealed a longer autumn active phase or avoided warmer spring temperatures. Overall, it is concluded that the former compositions of seasonal species and competition between species will change due to the different reactions of individual species.

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