

Behaviour-driven micro-scale niche differentiation in carabid beetles

S. Kamenova^{1,2}, K. Tougeron², M. Cateine², A. Marie² & M. Plantegenest^{2*}

¹UMR 7372 Centre d'Etudes Biologiques de Chizé, Villiers-en-Bois, France, and ²UMR 1349 Institut de Génétique, Environnement et Protection des Plantes, Rennes, France

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Abstract

Carabid beetles form rich and abundant communities in arable landscapes. Their generalist feeding behaviour and similar environmental requirements raise questions about the mechanisms allowing the coexistence of such species-rich assemblages. We hypothesized that subtle niche partitioning comes into play on spatial, temporal, or trophic basis. To test this, we performed experiments and made observations on the behaviour of two sympatric carabid species of similar size and life cycle, *Bembidion quadrimaculatum* L. and *Phylla obtusa* Audinet-Serville (both Coleoptera: Carabidae: Bembidiini). We compared plant climbing behaviour, daily activity patterns, and trophic preferences between the two carabid species under laboratory conditions. Whereas no clear difference in trophic preference was observed, our results suggest temporal niche differentiation at the nycthemeron scale (a period of 24 consecutive hours), with one of the species being more diurnal and the other more nocturnal, and spatial differentiation in their habitat use at the plant stratum scale. Intra-specific variation suggests that micro-scale spatio-temporal niche differentiation could be mediated by behavioural plasticity in these two carabid species. We speculate that such behavioural plasticity may provide carabid beetles with a high adaptive potential in intensively managed agricultural areas.

Introduction

Intensive farming is widely questioned for its impacts on biodiversity and human health (Krebs et al., 1999; Tilman, 1999; Hole et al., 2005). The consequent loss of ecosystem services in intensively managed monocultures could undermine long-term food security (Godfray et al., 2010). Several studies have shown the role of biodiversity for ecosystem functioning (Naeem & Li, 1997; Cardinale et al., 2012). It has been stated that species-rich communities generate temporal and spatial complementarity for a given function thus ensuring constant delivery of ecological services (Cottingham et al., 2001; Loreau et al., 2003). These findings bring particular attention to arthropod communities in arable landscapes and recent studies have evidenced that diversified communities of natural enemies provide the best service of natural biological control

(Tscharnatke, 1992; Cardinale et al., 2003; Trichard et al., 2013).

Despite collective awareness of the importance of maintaining biodiversity of natural enemies, mechanisms generating diversity patterns and their possible consequences on ecosystem functioning in farmland insect communities have rarely been investigated. Understanding forces driving the coexistence of natural enemies is ecologically relevant. Identifying the mechanisms that structure species interactions could provide valuable tools for the conservation and management of biodiversity (Waage, 1991; Borer et al., 2004; Snyder et al., 2008). Moreover, the level of species redundancy or complementarity determines the efficiency and the resilience of ecosystem services provided by biodiversity (Peralta et al., 2014). Carabid beetles are the most important and diversified community of large arthropods in agricultural landscapes, and many species are believed to be biological control agents (Kromp, 1999). Carabids are generalist predators and they offer a real advantage compared to other natural enemies, because they can be present in the field from an early stage of pest colonization (Ekbom et al., 1992).

*Correspondence: S. Kamenova, UMR 1349 Institut de Génétique, Environnement et Protection des Plantes, Agrocampus-Ouest – Ecologie et Santé des Plantes, 65 Rue de Saint-Brieuc, 35042 Rennes, France. E-mail: stefaniya.kamenova@gmail.com

The carabid guild provides an interesting model for investigating mechanisms of co-existence at the community scale: carabids form highly abundant and easy-to-catch populations with up to 200 species occurring in the same agricultural area during the activity season (Roger et al., 2012). Such diversity remains puzzling in relatively homogeneous and disturbed agricultural areas (Matson et al., 1997). One might expect that present diversity patterns of carabids in agricultural landscapes are the resultant of past competitive interactions, which led to niche differentiation. Such adaptive diversification in an agricultural context has already been evidenced for herbivorous pest species as the pea aphid complex with trophic specialization to a particular plant host (Peccoud et al., 2009). Thus, co-occurring carabid species are expected to differ in at least one dimension of their niche (MacArthur & Levins, 1967; Schoener, 1974). Body size is usually a common proxy of niche because it usually reflects trophic habits and competitiveness (Hutchinson, 1959).

Although size range varies considerably in carabid communities (2–40 mm, according to species), many species remain similar in size, sharing the same habitat and the same feeding habits. Moreover, carabid beetles are generally considered as opportunistic feeders regardless of their body size (Luff, 1978; Lövei & Sunderland, 1996; Meyhöfer, 2001) and literature fails to provide strong evidence for trophic specialization in carabid populations (Laroche, 1990; Kotze et al., 2011). However, it has been demonstrated that sympatric species, sharing resources, could adjust their spatial or temporal activity via behavioural plasticity (Chao et al., 2013; Navaro et al., 2013) resulting in niche partitioning.

In our study, we aimed to assess whether apparent ‘twin’ species of carabid beetles observed in crop fields actually exhibited subtle niche differentiation. We hypothesized that two species similar in size and food regime, caught in the same field at the same period should exhibit a differentiation for at least one niche dimension, such as microhabitat preference, food preference, and/or circadian rhythm of activity. To test this hypothesis, we combined experimental settings and video recordings under laboratory conditions to observe carabid spatio-temporal activity and feeding behaviour.

Materials and methods

Model species and sampling

For this study, we focused on two small carabid species, *Bembidion quadrimaculatum* L. and *Phylla obtusa* Audinet-Serville (both Coleoptera: Carabidae: Bembidiini), both very abundant in intensively managed European agricultural areas (Kromp, 1999). Adults of both species are

considered diurnal spring breeders (Holland, 2002; Matalin, 2007) and are similar in body size (3–4 mm for *B. quadrimaculatum* and 2–3 mm for *P. obtusa*) suggesting the exploitation of the same range of resources. Both species are generalists, known to consume a large spectrum of plant and animal tissues (Hance & Rossignol, 1983; Grafius & Warner, 1989; Baines et al., 1990; Hagley & Allen, 1990; Laroche, 1990; Kennedy, 1994). These two species are thus seemingly sharing the same habitat at medium temporal (season) and spatial (field) scale, and sharing the same trophic regime.

The two carabid species were sampled by hand, actively searching the soil surface. Regular trapping sessions occurred in April 2013 in one experimental field of INRA Le Rheu (Ille-et-Vilaine, France; 48°6′N, 1°48′S). The cover crop consisted of a mixture of ryegrass and red clover. All live beetles were brought to the laboratory where they were identified to species level and individually placed in small plastic Petri dishes (5 cm diameter). Beetles were continuously provided with water and shelter during 2 weeks and starved during 24 h prior experiments.

Microhabitat preferences

To investigate potential differentiation in carabid spatial patterns of microhabitat use, we focused on foraging behaviour. In these two species, foraging behaviour consists in prospecting the ground and the upper vegetation especially when prey is detected (Chiverton, 1987). Thus, we tested patterns of climbing behaviour for both carabid species in an experimental setting with aphid-infested plants. We used two separate rectangular plastic boxes (35 × 25 × 15 cm), one for each carabid species. Boxes were filled with loam and we put inside four broad bean plants [*Vicia faba* L. (Fabaceae)], each with 20 adult pea aphids, *Acyrtosiphon pisum* Harris (Hemiptera: Aphididae). Each plant was ca. 10 cm high. Immediately after adding the plants, we released four individuals of *B. quadrimaculatum* or *P. obtusa* and we monitored their climbing behaviour for 2 h by focal group sampling (Altmann, 1974). The climbing behaviour was recorded as the frequency of climbs for each individual. A climb was considered either as positive if an individual was up on the plant, no matter how high, or as negative, if it remained on the ground. At the end of the 2 h, the carabids were replaced with four new individuals. Plants and aphids were replaced with every replacement of carabid individuals. This experimental setting was repeated 10×, for a total of 40 observations per species.

Circadian rhythms of activity

To investigate temporal differentiation in carabid activity, we continuously monitored their circadian rhythms of

activity during 24 h using two high-definition and high-sensitivity video cameras (Opto Vision AP-B9511-SRTL; Opto Vision, Toulouse, France). For this, each individual of each carabid species was placed alone in a new plastic Petri dish, filled with Fontainebleau sand (Sibelco, Paris, France). Shelter, water, and food were provided. Each camera could monitor up to four individual Petri dishes at the same time. With the two cameras, eight Petri dishes (four of each carabid species) were monitored together. In total 20 individuals per species were observed.

Beetles were exposed to a L12:D12 photoperiod, with 615-lux luminosity during daytime. One hour of twilight was simulated at the beginning and at the end of the day (25 lux). Light conditions reflected natural luminosity experienced by beetles in the fields during the same period. During the night, cameras were connected to an infrared light source (DC-Infra, 620.5–645 nm; Detecvel, Treffendel, France), to record the nocturnal behaviour of the carabids without disturbing them (Allema et al., 2012). Infrared light was automatically turned on with the decrease of daylight. Each camera was connected to a DVR recorder (AverMedia-3104H[®], Opto Vision). All video recordings were displayed with the software USB Playback Console (AverMedia-3104H[®]).

To facilitate data analysis, whole 24-h video recordings were watched 10 min out of every 30 min. For each 10-min period, we noted whether the beetles were active or not. Individuals were considered active if they were observed feeding or moving around the Petri dish. When an activity event occurred, we also recorded the time spent feeding or moving.

Food preferences

To investigate differentiations in the trophic regime, we used the same video recordings as mentioned above. For this, carabids were provided with four food items: oilseed rape seeds [*Brassica napus* L. (Brassicaceae)], wheat grains [*Triticum aestivum* L. (Poaceae)], freshly killed adults of pea aphids (*A. pisum*), and freeze-killed mealworms [larvae of *Tenebrio molitor* L. (Coleoptera: Tenebrionidae)]. These prey types were selected because they are readily available and are potentially attractive for both carabid beetles. Moreover, given their size and shape, these prey items are easily discernable on video record, also during the night period.

Every carabid beetle was placed separately in a plastic Petri dish with one grain each of oilseed rape and wheat and one freeze-killed specimen each of pea aphid and mealworm, and its behaviour was recorded continuously during 24 h. Eight Petri dishes (four of each carabid species) were monitored together. Twenty beetles per species were tested. Of the whole 24-h video recordings 10-min

sequences were watched out of every 30 min. For each 10-min period, we noted the time spent feeding and the identity of consumed prey items. Food items were considered consumed if they had been handled for several seconds by the beetle. Prey consumption was confirmed by looking for bite marks, at the end of each 24-h video recording, by careful examination of prey items under a stereoscopic microscope.

Statistical analysis

We performed General Linear Models (family = binomial) to test for differences in climbing behaviour between the two species. Distribution of circadian activity within each species was compared using non-parametric Wilcoxon Rank-Sum tests. Differences in total time spent in activity and total time spent in feeding between individuals within species were assessed using non-parametric Wilcoxon Rank-Sum tests. Differences between the two species in circadian activity, total time spent in activity, and time spent in feeding were compared using Mann-Whitney tests.

The number of prey items consumed by each species was compared using non-parametric Wilcoxon Rank-Sum tests. The number of prey items consumed was compared between the two species using Mann-Whitney tests. Mann-Whitney tests for each prey type were carried out for testing for differences in food choices between species. All tests were run in R (R Core Team, 2013).

Results

Microhabitat preferences

Both carabid species were able to climb plants and feed on the aphids, but *P. obtusa* climbed on plants significantly more frequently than *B. quadrimaculatum* (Figure 1).

Circadian rhythms of activity

Video monitoring of circadian activity indicated differences in temporal patterns between the two carabid species. Interspecific differences in percentage active beetles were significant on all occasions [Wilcoxon rank-sum test, daily activity: $W = 254$, $P < 0.05$ (08:00–13:00 hours) and $W = 270$, $P < 0.05$ (14:00–19:00 hours); nightly activity: $W = 103$, $P < 0.01$ (20:00–01:00 hours) and $W = 93$, $P < 0.01$ (02:00–07:00 hours); Figure 2].

Bembidion quadrimaculatum was mostly day-active (59% of total circadian activity occurred between 08:00 and 20:00 hours) but differences in day/night activity were non-significant (Wilcoxon rank-sum test: $W = 146$, $P = 0.14$; Figure 3A). In contrast, *P. obtusa* was significantly more night-active (74% of total circadian activity

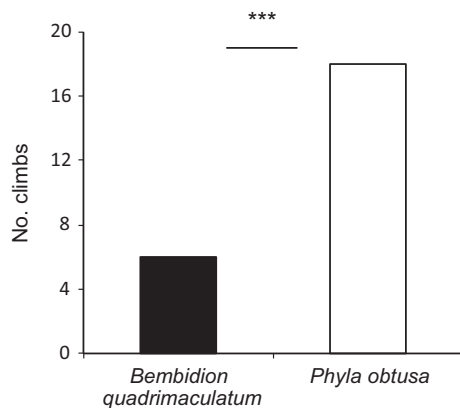


Figure 1 Total number of climbs for *Bembidion quadrimaculatum* and *Phyla obtusa* ($n = 40$ per species). GLM: *** $P < 0.001$.

between 20:00 and 08:00 hours; $W = 338$, $P < 0.001$; Figure 3B).

Average global time spent in activity per 24 h was higher for *P. obtusa* than for *B. quadrimaculatum* (Wilcoxon rank-sum test: $W = 54$, $P < 0.001$; Figure 4). Both species spent equally long on feeding ($W = 158$, $P = 0.92$; Figure 4).

Food preferences

The two carabid species consumed all prey types offered and there were no significant interspecific differences in prey choices, although *P. obtusa* seemed slightly more prone to eat plant food than *B. quadrimaculatum* (Figure 5, Table 1).

Discussion

No clear trophic differentiation was found between the two carabid species: they exhibited quite similar prefer-

ences and fed all four food items. Both seemed to prefer animal food sources, with a preference for *T. molitor* larvae compared to aphids. Although considered carnivorous, *B. quadrimaculatum* accepted both types of seed, suggesting an omnivorous feeding habit. Consequently, given the experimental conditions, the regimes of the two species appeared not divergent. Obviously, this could be different in field conditions where the available resources are more diverse (Symondson et al., 2002). However, our experimental results are an indication that the trophic niches of the two species are overlapping.

The searching behaviour of the two species, on the other hand, appeared clearly divergent. Although both showed their ability to climb plants in search for prey, *B. quadrimaculatum* appeared to be more reluctant and *P. obtusa* more prone to exhibit such behaviour. In the field, this micro-scale habitat differentiation would probably result in contrasting prey accessibility for the two species. It would notably allow *P. obtusa* to more easily access the aphids, an important resource for entomophagous predators in crop fields (Sopp & Chiverton, 1987; Sunderland et al., 1987). Furthermore, although both species are considered diurnal, a significant differentiation in their circadian rhythms of activity was recorded. The two species can be active all day long; however, *P. obtusa* displayed a strong preference for nocturnal activity, whereas *B. quadrimaculatum* exhibited a less marked circadian rhythm of activity with some diurnal tendency. This micro-scale temporal niche differentiation should result in a reduction of direct competitive interactions in the field, but also a likely reduction of indirect competitive interactions (competitive interactions resulting from the exploitation of a common resource), as the range of animal prey available during day and during night could be quite different (den Boer et al., 1986; Bauer & Kredler, 1993).

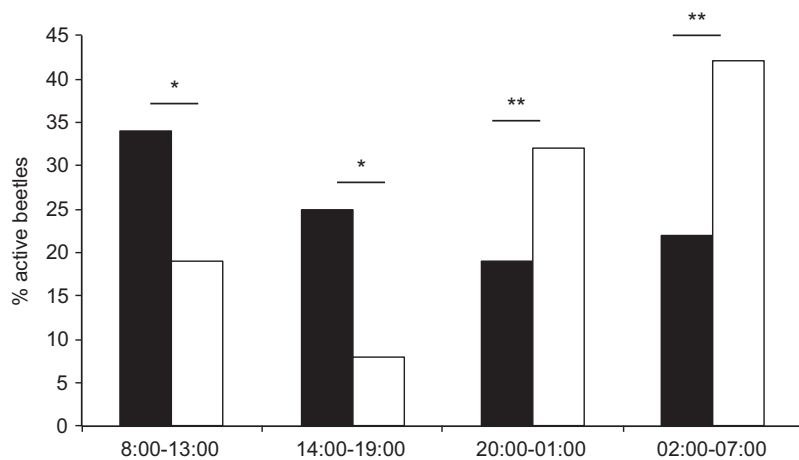


Figure 2 Interspecific differences in circadian activity at sampling periods of 5 h for *Bembidion quadrimaculatum* (black) and *Phyla obtusa* (white). Scotophase from 20:00 to 07:00 hours, photophase from 08:00 to 19:00 hours. At each sampling period, $n = 20$ for each species. Wilcoxon rank-sum test: ** $P < 0.01$, * $P < 0.05$.

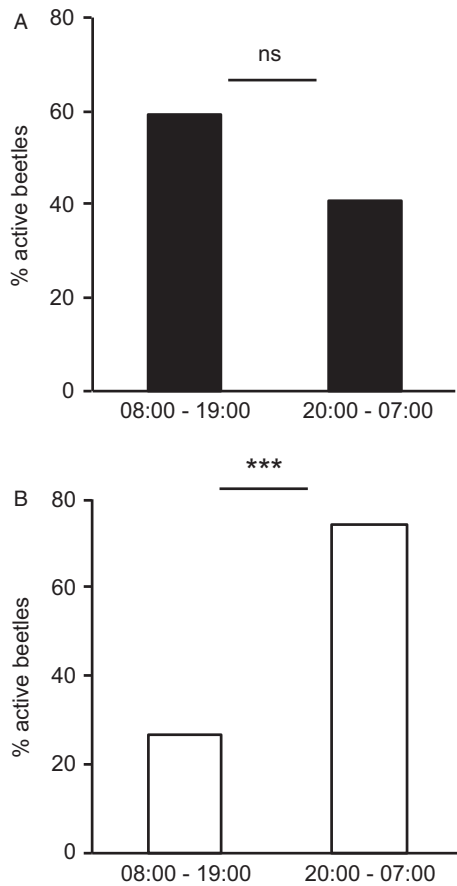


Figure 3 Intraspecific differences in circadian activity between day and night for (A) *Bembidion quadrimaculatum* and (B) *Phylla obtusa*. Scotophase from 20:00 to 07:00 hours, photophase from 08:00 to 19:00 hours. At each sampling period, $n = 20$ for each species. Wilcoxon rank-sum test: *** $P < 0.001$; ns, $P > 0.05$.

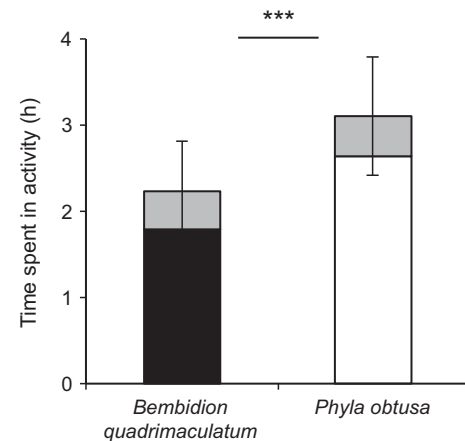


Figure 4 Average ($\pm$ SE) time spent in activity over a 24-h period, recorded during 10 min every 30 min, for *Bembidion quadrimaculatum* ($n = 20$) and *Phylla obtusa* ($n = 20$). In grey, the average time spent in feeding. Mann–Whitney test: *** $P < 0.001$.

Consequently, despite the fundamental (potential) trophic niches of the two species being probably overlapping, their actual trophic niches are likely to be differentiated, thus promoting the coexistence of the two species. Sasakawa et al. (2010) had previously suspected such a small-scale, subtle niche differentiation in two co-occurring species of the carabid genus *Amara*. It is noticeable that in either case, niche differentiation arose not from strict behavioural differentiation, but rather from contrasted preferences. This suggests behavioural plasticity in the three studied niche dimensions (trophic, spatial, and temporal) between the two species. Such plasticity confers

Figure 5 Average ($\pm$ SE) number of bites per prey type over a 24-h period, recorded during 10 min every 30 min, for *Bembidion quadrimaculatum* ($n = 20$) and *Phylla obtusa* ($n = 20$). Means within a beetle species capped with different letters are significantly different (Mann–Whitney tests: $P < 0.05$).

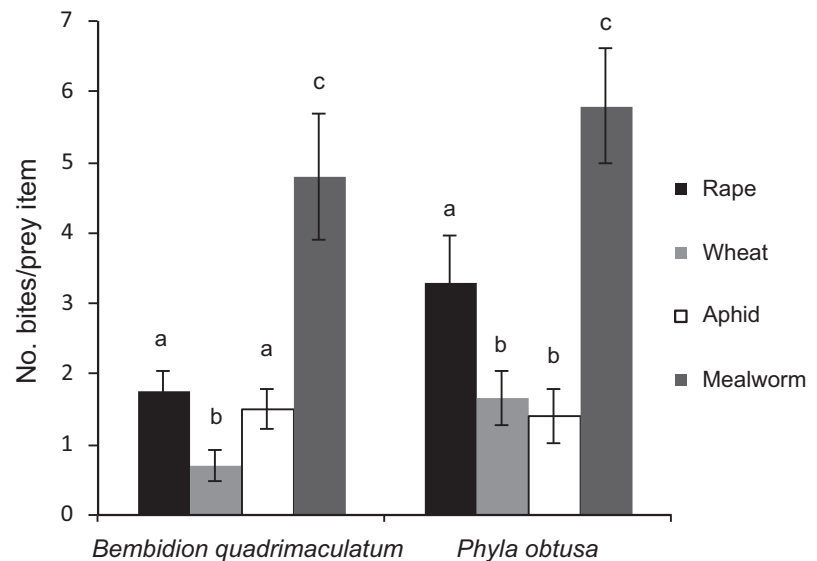


Table 1 P-values for Wilcoxon and Mann–Whitney tests on the intra- and interspecies comparisons for time spent in feeding on each of four prey types. Each comparison is based on 20 *Bembidion quadrimaculatum* and 20 *Phyla obtusa*

	Prey type	Rape	Wheat	Aphid	Mealworm
<i>B. quadrimaculatum</i>	Rape	/			
	Wheat	0.01	/		
	Aphid	0.5	0.04	/	
	Mealworm	0.02	0.00	0.01	/
<i>P. obtusa</i>	Rape	/			
	Wheat	0.05	/		
	Aphid	0.04	0.7	/	
	Mealworm	0.03	0.01	0.00	/
Between species		0.4	0.1	0.2	0.1

adaptive potential to environmental changes (Law, 2000; Ebert et al., 2014; Gardner et al., 2014). It also raises the question of the stability of niche differentiation and to what extent the partial behavioural specialization we observed results from local interactions between species and would vanish in the absence of competitors. This question is of importance because it determines the exchangeability of species and the sensitivity of the ecological function to the loss of a particular species. On one hand, species plasticity suggests that the loss of a given species may be (partly) compensated by niche enlargement in the remaining species. On the other hand, species plasticity allowing niche differentiation may result in a fine complementarity of species that would result in a positive relationship between biodiversity and functional efficiency provided by the entire community. To assess functional plasticity of the community would require the comparison of species niche-widths in communities varying in species richness to estimate more accurately the plasticity of behavioural preferences. Indeed, the inconsistency in the literature concerning carabid traits could be symptomatic of their large plasticity and rapid evolvability (Lövei & Sunderland, 1996; Kotze et al., 2011). Finally, the potential of species to quickly change their behaviour to match environmental conditions and the available resources could account for the large success of carabids to adapt to environmental changes provoked by agriculture (Kromp, 1999; Purtauf et al., 2004, 2005).

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