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Diurnal Activity Rhythms and Niche Differentiation in a Carrion Beetle Assemblage (Coleoptera: Silphidae) in Opava, the Czech Republic

Petr Kočárek

Department of Ecology, Palacky University, Olomouc, Czech Republic

Abstract

Diurnal activity rhythms of carrion beetles (Coleoptera: Silphidae) were investigated in the surroundings of Opava in the Czech Republic. Beetles were collected in automatic pitfall traps at two-hour catch intervals during three one-month periods in spring (May), summer (July) and autumn (October) in forest and meadow habitats. Five Nicrophorinae species: *N. vespillo*, *N. vespilloides*, *N. humator*, *N. fossor* and *N. investigator* and three Silphinae species: *Thanatophilus sinuatus*, *T. rugosus* and *Oiceoptoma thoracica* occurred in the study sites. *T. sinuatus*, *T. rugosus* and *O. thoracica* showed exclusively diurnal activity patterns. *N. fossor* and *N. investigator* were active from the late afternoon to the nightfall. The other carrion beetles did not show a restricted pattern of diurnal activity. Patterns of temporal utilisation among species were compared using Levins' measure of niche breadth and Horn's index of niche overlap. Lower niche overlap was found between species with different habitat preference. During the autumn period niche release was observed, due to lesser competition for carrion with species that only need feeding before hibernation.

Keywords: Diurnal activity, competition, niche segregation, habitat preference, carrion, Silphidae, *Nicrophorus*.

Introduction

Carrion is a limited and ephemeral food source and therefore subject to interspecific competition (Putman, 1983). Intense competition leads to segregation by niches of the dominant carrion occupying species (Kočárek, 1998). Insect groups that play a major role in carrion decomposition processes are the carrion blowflies (Diptera: Calliphoridae) and the silphids (Coleoptera: Silphidae), especially the burying beetles (Silphidae: Nicrophorinae) (Putman, 1983).

Address correspondence to: Petr Kočárek, Koblovská 93, CZ-711 00 Ostrava 2, Czech Republic. E-mail: kocarek@email.cz

Burying beetles conceal small vertebrate carcasses underground and prepare them for the consumption by their young; adult beetles are predators and feed on the larvae of carrion blowflies and other carrion insects, and are able to kill and consume other burying beetles as well (Scott, 1998). Since only a single pair of beetles will use a carcass as food source for their young, in instances when several pairs find the same carcass, fighting takes place to determine possession of the resource (Milne & Milne, 1976). Carrion beetles (Silphidae: Silphinae) are all necrophagous and occupy carrion in the late decomposition stages; their larvae continue to feed on carrion remains after blowfly larvae have pupated.

Burying beetles have a number of adaptations which allow them to compete successfully for small carcasses in a diverse carrion-feeding community that includes congeners, other insects and vertebrate scavengers (Trumbo, 1990). The niche segregation can be observed in three main dimensions — phenology, habitat preference and preference of carcass size (Scott, 1998). Another important niche segregation can be observed in daily periodicity (Kočárek, 1998). The activity of beetles at different times of day allows resource partitioning among the burying beetles to co-occur within the guild and reduce the incidence of interspecific fights.

The daily periods of activity of certain carrion beetles have been studied by several authors (Reed, 1958; Payne, 1965; Shubeck, 1971; Schoenly, 1983; Ohkawara et al., 1998), but quantitative data on the diurnal rhythms is practically absent, since the majority of authors distinguish only between nocturnal, diurnal or crepuscular activity. Špicarová (1972, 1974) studied the patterns of diurnal emergence from soil of two *Nicrophorus* species after the metamorphosis of adults.

Material and Methods

The study of daily periodicities of silphids visiting carrion was conducted in the surroundings of the town of Opava (Suché Lazce village; 49°54″N; 18°00″E), the Czech Republic.

The daily activity patterns were observed by the means of carrion-baited automatic traps with two-hour catch intervals. The trap consists of four basic parts: (1) an external metal case (20 cm diameter) buried in the ground with the lip flush with the soil surface; (2) an internal part with 12 collecting vessels (filled with water solution of ethylene glycol) laid on an electronic clock mechanism which poses one vessel opposite the opening in external part every two hours; (3) a basin with the bait (approximately 100 g of raw beef heart) protected by nylon-netting and lodged in the centre of the internal part; and (4) a metal roof (30 × 30 cm). Traps were placed in two different habitats: grassy meadow and deciduous forest.

Sampling was conducted during three one-month periods which were chosen in spring (May), summer (July) and autumn (October) aspects in the years 1997–1998. The traps were serviced every day, the insects in the solution were preserved in 70% ethyl alcohol and identified in the laboratory. The daily maximum and minimum ground surface temperatures were recorded.

Patterns of temporal utilisation among species were compared using Levins' measure of niche breadth and Horn's index of niche overlap (Krebs, 1989):
Levins' measure:

$$B = \frac{1}{\sum p_j^2}$$

B is Levins' measure of niche breadth and p_j is the importance value (proportion of individuals) of the i^{th} species found on j resource units. The resource units in this study refer to time of carcass visitation by individual species; thus, there were 12 two-hour resource units. Niche breadth values range from 0 to 1. A value 1 indicates carrion utilisation on all 12 resource units, whereas a value approaching 0 indicates very restricted use of carrion.
Horn's index:

$$R_0 = \frac{\sum (p_{ij} + p_{ik}) \log(p_{ij} + p_{ik}) - \sum p_{ij} \log p_{ij} - \sum p_{ik} \log p_{ik}}{2 \log 2}$$

where R_0 is Horn's index of niche overlap for species j and k; p_{ij} proportion resource i is of the total resources utilised by species j and p_{ik} proportion resource i is of the total resources utilised by species k. The measure of niche overlap ranges from 0 (no resource unit used in common) to 1 (complete overlap).

Results and Discussion

The total numbers of carrion beetles captured by the automatic pitfall traps in different seasons of the year are summarised in Table 1. Figures 1–5 show the diurnal activity rhythms for the individual species in May, July and October at both sites studied. Based on these results I conclude that all three Silphinae species (*Thanatophilus sinuatus*, *T. rugosus*, *Oiceoptoma thoracica*) are exclusively diurnal in all seasons (Figs. 1–5). The temporal niche breadths are relatively low (Table 1), except that of *T. sinuatus* in the spring period (0.45). *T. sinuatus* and *T. rugosus* strictly preferred the non-forest habitat, on the contrary the species *O. thoracica* strictly preferred the forest habitat. Among the Nicrophorinae species there were several differences. *Nicrophorus vespillo* specimens were collected from noon to midnight with the greatest abundance of catches in the afternoon (spring period: Figs. 1, 2) or around the nightfall (summer: Fig. 4 and autumn: Fig. 5); the temporal niche breadth value was relatively low during all three seasons (Table 1). Preference of non-forest habitat was observed. *N. vespilloides* was active from daybreak to midnight, but majority of the specimens showed diurnal activity (Figs. 1, 3, 5). The temporal niche breadth was the highest among *Nicrophorus* species (Table 1). *N. vespilloides* was found predominantly in the forest habitat (with the exclusion of data from autumn). The activity of *N. humator* varied from the afternoon to the midnight period with higher activity after nightfall (Figs. 1, 3, 5); the temporal niche breadth was low and well-balanced in all the periods (Table 1). During spring and summer this species was

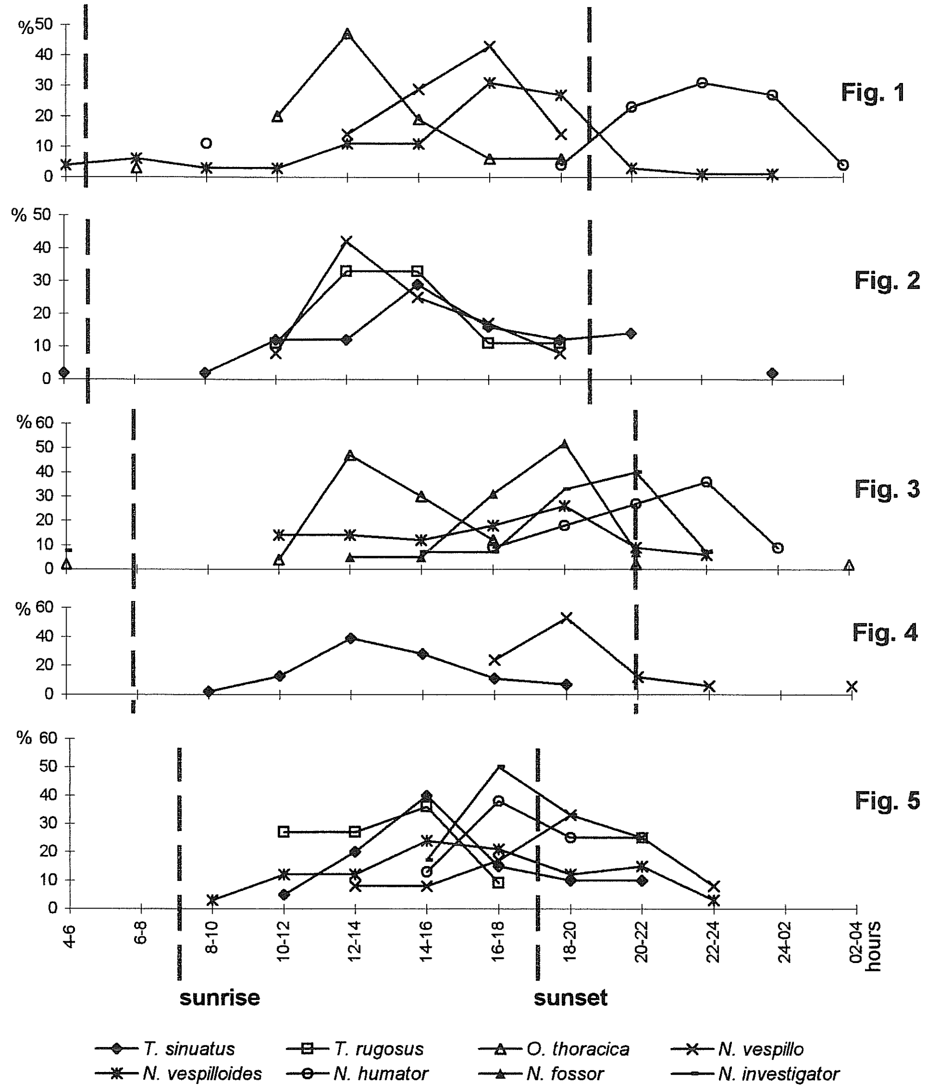
Table 1. Numbers of Silphidae individuals caught in each period. *n* — number of specimens; *B* — Levins' measure of niche breadth value (see Material and methods); diurnal activity patterns: *D* — diurnal species, *N* — nocturnal species, *A* — species active during late afternoon and dusk; habitat preferences: *F* — forest habitats, *N* — non-forest habitats.

Species	spring		summer		autumn		diurnal activity	habitat preference
	n	*B*	*n*	*B*	*n*	*B*		
Thanatophilus sinuatus	58	0.45	46	0.15	20	0.28	*D*	*N*
Thanatophilus rugosus	9	0.26	7	0.21	11	0.22	*D*	*N*
Oiceoptoma thoracica	70	0.20	60	0.19	–	–	*D*	*F*
Nicrophorus vespillo	157	0.21	17	0.16	12	0.32	*D/A/N*	*N*
Nicrophorus vespilloides	145	0.40	47	0.33	40	0.42	*D/A*	*F*
Nicrophorus humator	32	0.26	15	0.23	14	0.25	*A/N*	*F*
Nicrophorus fossor	–	–	42	0.15	–	–	*A*	*F*
Nicrophorus investigator	–	–	15	0.22	11	0.13	*A*	*F*
Total	471		249		108			

found predominantly in the forest habitat. *N. fossor* and *N. investigator* were active from late afternoon to the nightfall (Figs. 3, 5). The temporal niche breadth values were low in both species (Table 1). *N. fossor* was collected exclusively in the forest habitat, *N. investigator* was collected only in the forest habitat except in autumn.

If we want to evaluate the temporal niche differentiation among the species within the carrion beetle assemblage, we must differentiate two modes of carcass utilisation. The first group represent the species of subfamily Nicrophorinae. These species conceal small vertebrate carcass underground and females lay eggs in a specially constructed underground chamber (Pukowski, 1933). The carcass is normally utilised by only one pair of beetles or rarely by a few pairs (Scott, 1998). On that account, the competition among Nicrophorinae is very intense and leads to the niche differentiation in few different dimensions (e.g., Anderson, 1982). The second group are the species of Silphinae subfamily. Their females lay eggs in the soil around the carcass corpse and the larvae hatch during the later stages of decomposition (after blowfly larvae have emigrated). The larvae utilise the carrion en masse and accordingly the competition is not as intensive. The seasonal activity patterns of all three species found during this study are approximately identical (Kočárek & Benko, 1997; Novák, 1966), differences can be observed only in the dimension of habitat preference. Species of genus *Thanatophilus* prefer open non-forest habitats and *Oiceoptoma thoracica* forest habitats (Růžička, 1994; Kočárek & Benko, 1997). During this study, high values of the temporal niche overlap were found between all the species pairs (Table 2).

The niche of *Nicrophorus* species differs from site to site, suggesting that each species has a large fundamental niche in a few dimensions (Ohkawara et al., 1998) and the niche could be restricted by interactions among the members of a commu-



Figures 1–5. Diurnal activity of Silphidae species in Opava, the Czech Republic. Fig. 1. spring period, forest habitat; Fig. 2. spring period, non-forest habitat; Fig. 3. summer period, forest habitat; Fig. 4. summer period, non-forest habitat; Fig. 5. autumn period, non-forest habitat.

nity, particularly by competition. The niche of each *Nicrophorus* species is probably affected by the composition of each carrion assemblage; shifts of seasonal activities or habitat preferences have been observed (Novák, 1964; Ohkawara, 1998). The same shifts can be observed in diurnal activities.

Table 2. Horn's index of niche overlap values for pairs of Silphinae species in each period of year.

pair of species	spring	summer	autumn
Thanatophilus sinuatus × *T. rugosus*	0.86	0.92	0.83
T. sinuatus × *Oiceoptoma thoracica*	0.77	0.91	–
O. thoracica × *T. rugosus*	0.94	0.87	–

Table 3. Horn's index of niche overlap values for pairs of *Nicrophorus* species in each period of year.

pair of species	spring	summer	autumn
N. vespillo × *N. vespilloides*	0.88	0.80	0.83
N. vespillo × *N. humator*	0.17	0.74	0.98
N. vespillo × *N. fossor*	–	0.87	–
N. vespillo × *N. investigator*	–	0.74	0.70
N. vespilloides × *N. humator*	0.23	0.60	0.81
N. vespilloides × *N. fossor*	–	0.90	–
N. vespilloides × *N. investigator*	–	0.73	0.74
N. humator × *N. fossor*	–	0.58	–
N. humator × *N. investigator*	–	0.84	0.77
N. fossor × *N. investigator*	–	0.74	–

The ascertained values of temporal niche overlap between all pairs of species are summarised in Table 3. High values of temporal niche overlap were found particularly in the species with a different habitat preference (*N. vespillo* × *N. vespilloides*; *N. vespilloides* × *N. fossor*). The lowest values of niche overlap were found between species *Nicrophorus vespillo* and *N. humator* (0.17) and between species *N. vespilloides* and *N. humator* (0.23) during the spring period. The values of the same pairs grew with the season and reached the highest values in autumn period. *N. vespillo*, *N. vespilloides* and *N. humator* reproduce three times during the year and the last period of reproduction is in August (Novák, 1962; Kočárek, 1996). Adults present in October period are young individuals of the next year generation that need only to feed before they hibernate. Consequently they do not compete for breeding purposes and the decrease of niche overlap (= increase of niche overlap value) is an example of niche release. The same niche release can be observed in the dimension of habitat preference, when the species found in a forest habitat during the spring and summer were found in the field habitat in October (Fig. 5). No carrion beetles were found in the forest site during this month. The ground temperatures (and the possibility of passive warming-up of the beetles' bodies) in the open non-forest habitat were increased by the insolation during the sunshine. The maximum day temperatures in the non-forest habitat ($r = 16.3$°C) were higher than the same in the forest ($r = 13.6$°C) (paired *t*-test: $t_{(1,20)} = 4.97$, $p < 0.01$) and the minimum day temperatures were significantly lower in non-forest habitat ($r = 5.7$°C) than in the forest one ($r = 6.6$°C) (paired *t*-test: $t_{(1,20)} = -2.66$, $p < 0.01$).

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