Phenology and Habitat use among Nicrophorine Beetles of the Genus *Nicrophorus* and *Ptomascopus* (Coleoptera: Silphidae)

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Abstract Both *Nicrophorus* and *Ptomascopus*, subfamily Nicrophorinae, use small vertebrate carrion for their reproduction. *Nicrophorus* beetles have elaborate parental care whereas *Ptomascopus* beetles do not show explicit parental care. We investigated their habitat association and phenologies as measured by baited traps in Southern Kanto, Japan (four stations at two sites), and their reproductive seasonality by laboratory experiments. At the study site, there occur three *Nicrophorus* species (*N. maculifrons*, *N. quadripunctatus* and *N. concolor*) and *Ptomascopus morio*. All *Nicrophorus* beetles mainly inhabited unmanaged forests, while seasonal abundance and seasonal reproductive activity were different among species. Seasonal abundance and seasonal reproductive activity of *P. morio* were similar to *N. concolor*. *N. quadripunctatus* showed significant correlation between its seasonal fluctuation in the field and reproductive phenology in the laboratory, also *N. maculifrons* showed same tendency. However, almost all *N. concolor* and *P. morio* reproduce throughout the season in the laboratory unrelated with seasonal fluctuation in the field. Many *P. morio* were trapped in forest margins and managed closed forests where the number of *Nicrophorus* beetles were small, so they were at least partly segregated ecologically from *Nicrophorus* species.

Key words: habitat association, interspecific competition, *Nicrophorus*, phenology, *Ptomascopus*

Introduction

Carrion is a rare and ephemeral resource in nature with greatly variable quantity and quality, and its occurrence is highly unpredictable (Kentner & Streit, 1990; Hanski, 1990; Eggert & Müller, 1997). Because carrion is such an extremely nutrient-rich resource, diverse terrestrial animals use carrion as a food and reproductive resource (Bornemissza, 1957; Reed, 1958; Payne, 1965). Hence, we expect that competition for carcasses is intense. Indeed, there are several studies reporting the occurrence of severe competition among consumers of carrion (e.g., Kneidel, 1984).

*Nicrophorus* and *Ptomascopus* are closely related in the subfamily Nicrophorinae—a relationship supported by morphological and molecular analysis (Anderson, 1982a; Dobler & Müller, 2000). Both of them use carrass of small vertebrates, such as mice, for their reproduction (Pukowski, 1933; Peck, 1982), while their reproductive strategies are very different from each other. *Nicrophorus* species have elaborate biparental care (e.g., Pukowski, 1933; Trumbo, 1996; Eggert & Müller, 1997; Scott, 1998). Their males and females independently search for carcasses (Fabre, 1899). Usually a pair buries the carcass into soil, removes fur or feathers, rolls it into a ball, and treats it with anal and oral secretions (Pukowski, 1933; Milne & Milne, 1976; Hallfther et al., 1983; Eggert et al., 1998; Suzuki, 2001a). The female lays eggs in the soil surrounding the carcass, and the parents feed hatched larvae and protect the carcass and larvae from aggressive
intruders and predators until the larvae leave to pupate (e.g., Pukowski, 1933; Scott, 1998). Unlike *Nicrophorus*, the life history of *Ptomascopus* is not well known. Peck (1982) observed *Ptomascopus morio* reproduction in the laboratory. He concluded that adults of *P. morio* do not show explicit parental care and their larvae can develop without parents. Trumbo et al. (2001) reported that *P. morio* acted as a brood parasite of *Nicrophorus*, especially *N. concolor* (*P. morio* larvae in broods of *Nicrophorus* tended by *Nicrophorus* adults) and no evidence of *P. morio* breeding independently in Kyoto, Japan was found. In addition, they investigated the reproductive biology of *P. morio*, and postulated that *P. morio* might be an obligate brood parasite of *Nicrophorus* in the field.

There are many studies about interspecific competition and niche segregation among *Nicrophorus* species, but little is known about species of *Ptomascopus*. In *Nicrophorus*, usually a pair of the largest species monopolizes a carcass (Pukowski, 1933; Wilson & Fudge, 1984; Wilson et al., 1984; Otronen, 1988; Trumbo, 1990a, 1994; Suzuki, 2000a). Carcasses are frequently usurped and all larvae are killed by conspecific or congeneric intruders (Wilson & Fudge, 1984; Trumbo, 1990b; Scott, 1990, 1994, 1997; Robertson, 1993; Eggert & Sakaluk, 2000; Suzuki, 2000b). Therefore, many coexisting *Nicrophorus* species have different spatio-temporal niches (Pukowski, 1933; Anderson, 1982b; Shubeck, 1983. Wilson et al., 1984; Trumbo, 1990c; Beninger & Peck, 1992; Beninger, 1994; Lingafelter, 1995; Lomolino et al., 1995; Lomolino & Creighton, 1996, Scott, 1998; Trumbo & Bloch, 2000). In *Ptomascopus*, Katakura et al. (1986) studied spatio-temporal distributions among microphorines in Hokkaido, northern Japan, and they reported that the habitat preference of *P. morio* was different from that of *Nicrophorus* species (*Nicrophorus* was abundant in forests and *P. morio* abundant in grasslands). However, the microphorine fauna of Hokkaido is different from Honshu. Trumbo et al. (2001) studied the faunas in Kyoto Honshu, and reported the seasonal abundance of *P. morio* to be similar to that of *Nicrophorus concolor*. However they did not document spatial distributions. Accordingly, the spatio-temporal distribution and the comprehensive ecological relationship among microphorine species in Honshu are not well understood. Thus, we investigated the spatio-temporal distribution among microphorine beetles in Honshu, with regard to their reproductive season.

### Materials and Methods

#### Study sites

The study was conducted in the Tama Forest Science Garden (TFSG), Hachioji-city, Tokyo metropolitan, and in the Yokohama Nature Sanctuary (YS), Yokohama-city, Kanagawa prefecture. Both areas are located in the southern Kanto region, central Japan, which belong to a warm-temperate climate zone. We selected four different stations in both sites, and set traps baited with rotten chicken meat (6 days during the last 10 days of each month). The study in TFSG was conducted from October to November in 1998, and from March to September in 1999; in YNS, from April to November in 1998 and March in 1999. The environments of each station were as follows.

#### Tama forest Science Garden (TFSG)

This area is located at the foot of Mount Takao (lat. 35°39'N; long. 139°17'E; alt. about 200 m; average annual temp. 14°C). The majority of this area is covered with an artificial forest, but primary forest remains in some portions (about 13 ha). We placed one station in a primary forest (T1) and three stations in artificial forests (T2–4).

- **T1**: (primary forest). The dominant tree was oak, *Quercus acuta*. The dominant shrub tree was Japanese aucuba, *Aucuba japonica*. Undergrowth was sparse. The litter layer was thicker than 6 cm.

- **T2**: (Unmanaged forest). The dominant tree was oak, *Q. myrsinaefolia* which were planted more than 70 years ago, and have not been managed. The dominant shrub tree was Japanese aucuba. Undergrowth was sparse. The litter layer was thicker than 6 cm.

- **T3**: (Managed closed forest). Planted trees were diverse, there was no dominant tree, most of these trees were shorter than 8 m, and the canopy was almost closed. Due to annual mowing, there was almost no shrub layer, but herbs (mostly lily, *Ophiopogon japonicus* and *Liriopemuscari*) grew abundantly. The litter layer was thinner than 5 cm.

- **T4**: (Managed open forest). Like T3, this station had various trees, and there was no dominant tree. Trees were taller than 12 m, but with low density, and the canopy was partly opened. The shrub layer was almost absent due to annual mowing and the undergrowth was
abundant (mostly lily, *O. japonicus* and *L. muscari* with some lianas). The litter layer was thinner than 3 cm.

**Yokohama Nature Sanctuary (YNS)**

This site is located at the base of the Miura Peninsula and the foot of Mount Enkai (lat. 35°20'N; long. 139°35'E; alt. about 100 m, annual average temp. 15°C). The vegetation is mainly broad-leaved deciduous secondary forest, with a small remnant of primary temperate evergreen broad-leaved forest.

Y1: (Inner secondary forest). This station was situated at least 50 m apart from the forest margin. The dominant tree was oak, *Quercus serrata*. The dominant shrub was Japanese aucuba, *Aucuba japonica*. Most of the undergrowth was lily, *Ophiopogon japonicus* and *Liriope muscari*. The litter layer was thicker than 5 cm.

Y2: (Secondary forest near margin). This station was 2–5 m apart from the forest margin. The dominant tree was also oak, *Q. serrata* and the dominant shrub was Japanese aucuba but the tree density was lower and the shrub density was higher than Y1. There were many saplings such as *Q. acuta*, *Ilex integra* and *Cinnamomum japonicum*. Undergrowth plants were not abundant. The litter layer was thicker than 4 cm.

Y3: (Grassland near forest margin). This station was between the secondary forest and a road, being approximately 10 m apart from either the forest or the road. There were few trees and no shrubs due to mowing every late autumn, but grasses such as Japanese pampas grass, *Miscanthus sinensis* and goldenrod, *Solidago altissima* were abundant in spring though autumn. The litter layer was thinner than 3 cm.

Y4: (Grassland). There were neither trees nor shrubs for the same reason of Y3, but grass coverage was thick. The dominant grasses were the same as Y3. Litter was almost absent.

**Sampling**

Beetles were trapped in aluminum cans (height: 16.5 cm, diameter: 6.5 cm, diameter of opening: 2.0 cm) with two holes (about 0.2 cm) at the bottom to drain rainwater. A piece of fresh chicken meat (about 20 g) was placed in each can as bait. Two types of traps were set. One was buried so that its rim was flush with the soil surface, and covered with square cardboard (length: about 15 cm, about 10 cm above the opening) to protect the trap from rainfall and as a marking. Other traps were hung from trees using fishing line at a height of 1.5–2.0 m above the ground. In each station, 10 ground traps and 10 hung traps were set alternately, at least 20 m apart from each other and in as straight a line as possible. However, in the TFSG stations, from June to September, twelve to fifteen ground traps were set because many ground traps were destroyed by vertebrate scavengers. All traps were opened for six days and carrion beetles were collected on the last day. Collected microphorine beetles were identified and counted. After recording, most beetles were released at their station of capture, but some were brought to the laboratory for the measurements and experiments described below.

**Body size measurement**

Randomly selected beetles from TFSG and Kawajiri, Siroyama, Kanagawa (located near TFSG) were sexed, and their pronotal width was measured to the nearest 0.05 mm using calipers. The pronotal width is known to be a good index of body mass (Smith et al., 2000).

**Laboratory experiments**

We examined the reproductive ability of microphorines caught in field in the laboratory. The beetles were collected at TFSG, YNS and six other sites in the South Kanto area. Experiments began within five days after the beetles were captured. Prior to use, beetles were housed in plastic containers, and fed pieces of chicken liver (less than 2 g). We gave a piece of chicken meat to a pair (a male and a female) or a single female in a soil-filled container (*N. concolor*: 34 × 18 cm width and 12 cm depth, other three beetles: 12 cm diameter and 9.5 cm depth). The size of the meat piece was 50–100 g for *N. concolor*, the largest species, and 15–50 g for other three species. We kept *N. concolor* and *P. morio* at 20 or 25 °C, and *N. maculifrons* and *N. quadripunctatus* at 15 or 20°C in continuous darkness. After three or four days, we checked whether eggs were deposited or not.

**Data analysis**

Degree of niche overlap was estimated by C index (Kimoto, 1967).

\[
C_i = \frac{2\Sigma n_i \times n_j}{(\Sigma n_i^2 + \Sigma n_j^2) N_i}
\]

\[
\Sigma n_i^2 = \Sigma n_j^2 = \frac{\Sigma n_i^2}{N_i^2}, \quad \Sigma n_j^2 = \frac{\Sigma n_j^2}{N_j^2}
\]

where *N* and *N* are the total number of individuals of
species \( i \) and \( i' \), and \( n_i \) and \( n_{i'} \) are the total numbers of species \( i \) and \( i' \) collected at station \( j \) (for habitat niche) or at season \( j \) (for seasonal niche). The values change from 0 to 1 as the degree of niche overlap is greater.

**Results**

In both TFSG and YNS, we collected three *Nicrophorus* species (*N. maculifrons* Kraatz, 1877, *N. quadripunctatus* Kraatz, 1877, and *N. concolor* Kraatz, 1877) and *Ptomascopus morio* Kraatz, 1877.

A total of 768 traps was set in TFSG from March to November, but only 673 traps provided data because some traps were destroyed by vertebrate scavengers. In total, 1664 nicrophorine beetles were collected. The most abundant species was *P. morio* (795 exs.) followed by *N. quadripunctatus* (614 exs.), *N. maculifrons* (130 exs.), and *N. concolor* (125 exs.). In YNS, 720 traps were set, and 660 traps were collected in total. The total number of beetles was 957. The most abundant species was *N. quadripunctatus* (619 exs.), followed by *P. morio* (310 exs.), *N. concolor* (27 exs.) and *N. maculifrons* (1 ex.). Because the collected number of *N. maculifrons* in YNS was small, this beetle was excluded from the following analyses.

**Body size**

*Nicrophorus concolor* was the largest species, the next largest was *N. maculifrons*, then *N. quadripunctatus*, and *P. morio* was the smallest (Table 1, one-way ANOVA, Scheffé’s method, d.f. = 7, \( F = 746, P < 0.05 \)).

**Differences of collected number by ground traps and hung traps**

The proportion of the collected number of beetles by ground traps and hung traps is shown in Fig. 1. The number of *Nicrophorus* beetle collected with hung traps was significantly larger than that with ground traps (\( \chi^2 \) test, \( P < 0.01 \)). However, the number of *P. morio* collected by ground traps was significantly larger than with hung traps (\( \chi^2 \) test, \( P < 0.01 \)).

**Habitat association**

Fig. 2 shows the abundance of four nicrophorine species in each habitat. The number of nicrophorine beetles in the managed open forest (T4) in TFSG and grassland (Y4) in YNS were significantly small when compared with the most abundant station of each site (one-way ANOVA, Scheffé’s method, d.f. = 3, \( P < 0.01 \)), except *N. concolor* in YNS (one-way ANOVA, \( P = 0.21 \)). In TFSG, the number of *N. maculifrons* and *N. quadripunctatus* was significantly larger in the primary forest (T1) and unmanaged forest (T2) than in the managed forests (T3 and T4) (one-way ANOVA, Scheffé’s method, \( P < 0.01 \)). The number of *N. concolor* was significantly larger in primary forest (T1) than in managed forest (T3 and T4) (one-way ANOVA, Scheffé’s method, \( P < 0.001 \)). In contrast, the number of *P. morio* in the managed closed forest (T3) was larger than in the primary forest (T1) and the unmanaged forest (T2), although these were not significantly different (one-way ANOVA, Scheffé’s method, \( P > 0.05 \)). In YNS, the number of *N. quadripunctatus* was significantly larger inside of the forests (Y1 and Y2) than outside (Y3 and Y4) (one-way ANOVA, Scheffé’s method, \( P < 0.0001 \)). The number of *P. morio* was significantly smaller inside the forests (Y1) than on the forest margin (Y2 and Y3) (one-way ANOVA, Scheffé’s method, \( P < 0.05 \)).

**Table 1**. Pronotal width of four nicrophorine beetles (mm).

<table>
<thead>
<tr>
<th>Species</th>
<th>male</th>
<th>female</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>N. maculifrons</em></td>
<td>5.7±0.11&quot; (37)</td>
<td>5.7±0.09&quot; (42)</td>
</tr>
<tr>
<td><em>N. quadripunctatus</em></td>
<td>4.8±0.05&quot; (19)</td>
<td>4.9±0.05&quot; (117)</td>
</tr>
<tr>
<td><em>N. concolor</em></td>
<td>11.3±0.16&quot; (35)</td>
<td>10.6±0.25&quot; (37)</td>
</tr>
<tr>
<td><em>P. morio</em></td>
<td>4.3±0.05&quot; (53)</td>
<td>4.2±0.04&quot; (59)</td>
</tr>
</tbody>
</table>

All values are mean±SE (n). Values with the same letters are not significantly different (one-way ANOVA, Scheffé’s method, d.f. = 7, \( F = 747, P < 0.05 \)).
Phenology and Habitat difference in Nicrophorinae

Seasonal fluctuation
Seasonal fluctuation of the number of collected beetles is shown in Fig. 3. The numbers of *N. quadripunctatus*, *N. concolor* and *P. morio* were significantly correlated between TFSG and YNS (Spearman's correlation coefficient, *N. quadripunctatus* n = 9, r = 0.95, P < 0.01; *N. concolor* n = 9, r = 0.90, P < 0.05; *P. morio* n = 9, r = 0.93, P < 0.01).

*Nicrophorus maculifrons* was collected for the first time in late March, and this period was the most abundant period for this species in TFSG. They declined in June with many individuals captured again in July. Although none were caught in August and September, some were trapped in October. *N. quadripunctatus* was collected from March to November in TFSG, and from April to November in YNS. They had two activity peaks in April.
to May and September. *N. concolor* was collected from April to October with a single peak in August. *Ptomascopus morio* was collected from May to October, with a single pronounced peak in August.

Reproductive seasonality in laboratory conditions

*Nicrophorus quadripunctatus* showed significant correlations between its reproductive phenology in the laboratory (Fig. 4) and its seasonal fluctuation in the field (Fig. 3) (Spearman's correlation coefficient, $n = 7$, $r_s = 0.82$, $P < 0.05$), while the other three species did not show a significant correlation (*N. maculifrons*, $n = 6$, $r_s = 0.70$, $P = 0.12$; *N. concolor*, $n = 6$, $r_s = -0.65$, $P = 0.14$; *P. morio*, $n = 6$, $r_s = 0.82$, $P = 0.10$). Most *N. maculifrons* females caught in March and April deposited eggs in the laboratory, while few females oviposited in other seasons. Most *N. quadripunctatus* caught from April to May, and from September to October, deposited eggs, while females caught in other seasons (particularly July and August) showed no reproductive behavior. Almost all females of *N. concolor* and *P. morio* oviposited throughout the season (from April to September).

Niche overlap

Overlap of habitat niche was large (Table 2a) and temporal niche was small (Table 2b) in each *Nicrophorus* species. In contrast, *P. morio* showed a different pattern of niche overlap in both sites. The overlap of the temporal niche between *P. morio* and *N. concolor* was large. However, degrees of habitat niche overlap among *P. morio* and other *Nicrophorus* species were smaller than that among *Nicrophorus* species.

Discussion

Each *Nicrophorus* species did not segregate by habitat (Fig. 2 and Table 2a). In contrast, their seasonal abundance showed greater differences (Fig. 3 and Table 2b). Almost all *N. maculifrons* and *N. quadripunctatus* that were collected off-peak of their abundance did not oviposit even if carrion was provided in the laboratory. Nishimura et al. (2002) reported that temperature and day length influence *N. quadripunctatus* reproductive activity, and both high temperature (25°C) and long day length suppressed the reproductive behavior. Therefore, it is possible that the reason beetles collected off-peak of their abundance did not oviposit is physiological conditions of each species, and it cause these differences of their seasonal abundances.

In YNS, *N. quadripunctatus* is abundant in Y1 and Y2, but *N. maculifrons* and *N. concolor* are few. Forest management largely affect in carrion beetle community (Suzuki, 2001a).

Trumbo et al. (2001) reported that *P. morio* acts as a brood parasite of *Nicrophorus*, and supposed that because the carrion-feeding community is highly competitive,
Table 2. Niche overlap of four nicrophorine beetles estimated by the Cr index
(Kimoto, 1967).

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<tr>
<th></th>
<th>TFSG</th>
<th>N. q</th>
<th>N. c</th>
<th>P. m</th>
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<td>N. m</td>
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<tr>
<td>N. m</td>
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<tr>
<td>N. q</td>
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<td>0.94</td>
<td>0.73</td>
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<td>N. c</td>
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b. Temporal niche

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<td></td>
</tr>
<tr>
<td>N. m</td>
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<td>0.16</td>
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<td>N. q</td>
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<td>N. c</td>
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<td>0.88</td>
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<tr>
<td>N. m</td>
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</tr>
<tr>
<td>N. q</td>
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<td>0.29</td>
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<tr>
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<td>0.87</td>
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</table>

independent reproduction by *P. morio* in the field might be rare to absent making this species an obligatory brood parasite of *Nicrophorus*. However, our results show many *Nicrophorus* inhabit areas where the number of *Nicrophorus* is relatively small. Katakur et al. (1986) also reported that the habitat preference of *P. morio* was different from that of *Nicrophorus* species. This suggests that the habitat of *P. morio* would be not be same but slightly differing in *Nicrophorus* beetles.

Collected number using pitfall and hung trap differ between *Nicrophorus* and *Pitmacopus*. Okawara (1991) reported flight height differences among *Nicrophorus*, and suggested the difference in food searching strategy. The paper seems to show that flight height of smaller species (*N. quadripunctatus, N. maculifrons*, and *N. vespidoides*) is lower, and larger species (*N. investigator* and *N. tenuipes*) is higher. Size of *P. morio* is very small, thus *P. morio* may be collected mostly in pitfall traps. Okawara (1991) suggested that flying near the ground is advantageous in searching concentrate in small area in higher carrion density, *P. morio* is possible to take such searching strategy.

Especially the seasonal abundance and reproductive season of *P. morio* was similar to *N. concolor*, but *P. morio* was partly segregated from *N. concolor* by habitat. Almost all females of both *N. concolor* and *P. morio* oviposited throughout the season (from April to September) and reproduced in the same conditions. Thus the physiological differences of these two species such as temperature, seems not to the cause of habitat difference between the two. To know the habitat difference between the *P. morio* and *N. concolor*, there need investigation about other physical condition or interspecific interaction.

**Acknowledgement**

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**Summary**

Nicrophorine beetles are feeders that live in carrion. They are cold-blooded animals that do not contain food in their bodies. The reason for their cold-blooded nature is that the amount of energy obtained from carrion is limited. They usually live in groups and have an advantage in searching food. Their habitats are small areas in high carrion density. *P. morio* is a very small species, thus it may be collected mostly in pitfall traps. Okawara (1991) suggested that flying near the ground is advantageous in searching concentrate in small area in higher carrion density, *P. morio* is possible to take such searching strategy.
M. Nagano and S. Suzuki

The Japanese Society of Soil Zoology

Reference


