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Niche differentiation of burying beetles (Coleoptera: Silphidae: Nicrophorinae) in carcass use in relation to body size: Estimation from stable isotope analysis

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Abstract
Adult burying beetles use the carcasses of small vertebrates for food and breeding their young. Some species are known to have optimum carcass sizes related to their body sizes, but their carcass use is difficult to observe *in situ*. We explored their size-related niche differentiation in carcass resource using stable isotope analysis. The largest *Nicrophorus* species in Japan (*N. concolor*) showed the highest δ^{15}N, and the smallest *Nicrophorus* species in Japan (*N. montivagus*) showed the lowest δ^{13}C and δ^{15}N among all *Nicrophorus* species, suggesting that their niches are differentiated from those of other species in carcass resource. We also revealed a positive correlation between δ^{15}N and body size. *Ptomascopus morio* showed significantly higher δ^{15}N than all studied *Nicrophorus* species. This species does not show parental care behavior and the adults may feed on quite different resources from *Nicrophorus* species.

Key words: δ^{13}C; δ^{15}N; *Nicrophorus*; *Ptomascopus*; body length

INTRODUCTION

Vertebrate carcasses are scarce but nutrient-rich food resources and are used by many necrophagous species (Kentner and Streit, 1990; Eggert and Müller, 1997; Scott, 1998; Jenson and Miller, 2001; Tabor et al., 2004). Burying beetles (Coleoptera: Silphidae: Nicrophorinae) are one of the groups feeding on the carcasses of small vertebrates, and they also use carcasses for breeding their young (Scott, 1989; Scott and Gladstein, 1993). Food niche differentiation among necrophagous species such as temporal succession with carcass decay has been well recognized (Kentner and Streit, 1990; Jenson and Miller, 2001; Tabor et al., 2004). Some species of burying beetles are known to have optimum carcass sizes related to their body sizes (Scott, 1998; Xu and Suzuki, 2001): small species have difficulty handling large carcasses while large species need large carcasses for breeding their young. It is therefore expected that the food niche of burying beetles is differentiated in relation to body size, but *in-situ* observation of carcass use is usually difficult.

The carbon- and nitrogen-stable isotope ratios of animals depend on what they eat. It is reported that δ^{13}C and δ^{15}N are generally 1‰ and 3‰ higher in consumers than in their food (DeNiro and Epstein, 1978, 1981; Minagawa and Wada, 1984; Tooker and Hanks, 2004). These stable isotope ratios have been used to estimate the food habits of various invertebrates (e.g. Kurata et al., 2001; McNabb et al., 2001; Tayasu et al., 2002; Uchida et al., 2004). We assumed that stable isotope analysis might suggest the carcasses used by burying beetles. In this study, we explored a broad pattern of size-related niche differentiation in carcass resources among burying beetles using stable isotope analysis. In addition, we examined isotopic differences between *Nicrophorus* and *Ptomascopus* species. Since *Ptomascopus* species do not show explicit parental care and sometimes behave as brood parasites (Trumbo et al., 2001; Nagano and Suzuki, 2003), the main food resources used by *Ptomascopus* adults are different from the carcasses used by *Nicrophorus* species.

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MATERIALS AND METHODS

We hypothesized that δ^{13}C and δ^{15}N of adult burying beetles reflect those of the carcasses used for their parental care. Adult burying beetles feed on insects and carcasses until reproductive competence is attained (Trumbo et al., 1995), and they use the carcasses for food as well as for breeding (Scott, 1989; Scott and Gladstein, 1993). The carcasses may significantly contribute to the biomass of adult burying beetles, even though adults certainly use food resources other than carcasses (Trumbo et al., 1995; Trumbo and Robinson, 2004). We collected burying beetles from 40 localities across Japan (Hokkaido to Kyushu) by using pitfall traps with rotten chicken meat as an attractant. Seven *Nicrophorus* species (*Nicrophorus concolor* Kraatz, *N. japonicus* Harold, *N. tenuipes* Lewis, *N. investigator* Zetterstedt, *N. maculifrons* Kraatz, *N. quadripunctatus* Kraatz, *N. montivagus* Lewis) and *Ptomascopus morio* Kraatz were collected. The numbers of sampled localities and individuals for each species are shown in Table 1. The body length of collected individuals was measured.

Collected individuals were starved for more than 72 h to empty their guts, and were oven dried at 60°C for more than 72 h. The whole body of each sample was ground using a bead cell disrupter. We measured δ^{13}C and δ^{15}N using the combined system of an elemental analyzer (NC2500; Thermo Electron, Bremen, Germany) and an isotope ratio mass spectrometer (MAT252; Thermo Electron); otherwise, they were measured by the National Agriculture and Bio-oriented Research Organization.

Isotope ratios were expressed as parts per thousand (‰) relative to the international standard:

$$\delta^{13}\text{C}, \delta^{15}\text{N} = (\text{Rsample} - \text{Rstandard})/\text{Rstandard} \times 1000$$

where R $= {}^{13}$C/^{12}C or ^{15}N/^{14}N. Peedee belemnite and atmospheric nitrogen were used as the carbon and nitrogen isotope standards, respectively. We combined the data of both sexes for each species since we did not detect any differences in δ^{13}C and δ^{15}N between sexes.

To compare δ^{13}C and δ^{15}N among species or among the localities of each species, we firstly conducted one-way multivariate analysis of variance (MANOVA) on δ^{13}C and δ^{15}N with each species or locality as factors, and if MANOVA detected a significant difference, separate univariate ANOVA was performed (i.e. MANOVA-protected ANOVA: Scheiner and Gurevitch, 2001). Tukey's post-hoc tests were performed when the stable isotope ratios were significantly different among species. Significance level was set at $\alpha = 0.05$ for statistical analyses.

Table 1. Number of localities, sample sizes for stable isotope analysis (SI) and measuring body length (BL)

	Localities	Sample size for SI	Sample size for BL
Nicrophorus concolor	9	17	11
N. japonicus	3	7	8
N. tenuipes	1	3	4
N. investigator	1	6	7
N. maculifrons	8	10	17
N. quadripunctatus	24	59	69
N. montivagus	7	10	10
Ptomascopus morio	4	7	7

RESULTS

Carbon and/or nitrogen stable isotope ratios were significantly different among species (MANOVA: Pillai Trace=0.75, $F_{14,226} = 9.63$, $p < 0.001$). The following separate ANOVAs indicated that both δ^{13}C and δ^{15}N were different among species (δ^{13}C: $p < 0.05$, δ^{15}N: $p < 0.001$) (Figs. 1–3). *P. morio* showed the highest δ^{15}N, which was significantly different from all *Nicrophorus* species. *N. concolor*, which is the largest *Nicrophorus* species in Japan, showed the highest δ^{15}N among *Nicrophorus* species, and its δ^{15}N was significantly different from those of *N. investigator*, *N. quadripunctatus* and *N. montivagus*. *N. montivagus*, the smallest *Nicrophorus* species in Japan, showed the lowest δ^{13}C and δ^{15}N among the studied species. The δ^{13}C was significantly different from *N. maculifrons*, and δ^{15}N from *N. concolor*, *N. japonicus*, *N. maculifrons* and *N. quadripunctatus*. The δ^{15}N and body size (converted to $\log_{10}$) of *Nicrophorus* species were positively correlated ($r = 0.834$, $n = 7$, $p = 0.021$). The δ^{13}C and δ^{15}N of *N. quadripunctatus* differed significantly among localities (MANOVA: Pillai Trace=1.20, $F_{46,70} = 2.30$, $p < 0.01$; ANOVAs: δ^{13}C: $p < 0.05$, δ^{15}N: $p < 0.01$) and the difference was not

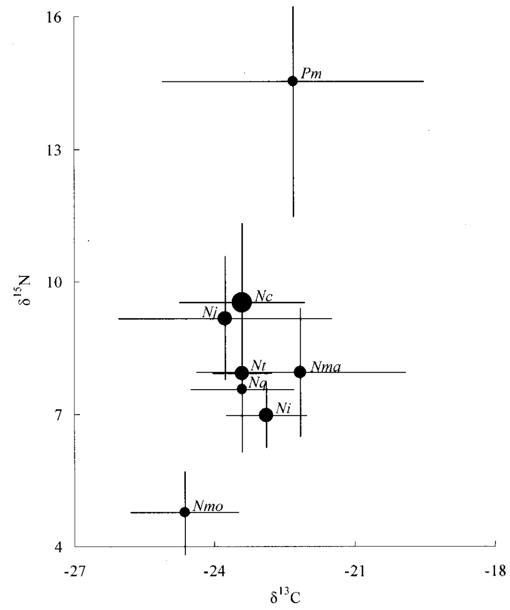

Fig. 1. δ^{13}C and δ^{15}N (means±SD) of each burying beetle. Circle sizes are related to the mean of body lengths. *Nc*: *N. concolor*; *Nj*: *N. japonicus*; *Nt*: *N. tenuipes*; *Ni*: *N. investigator*; *Nma*: *N. maculifrons*; *Nq*: *N. quadripunctatus*; *Nmo*: *N. montivagus*; *Pm*: *P. morio*.

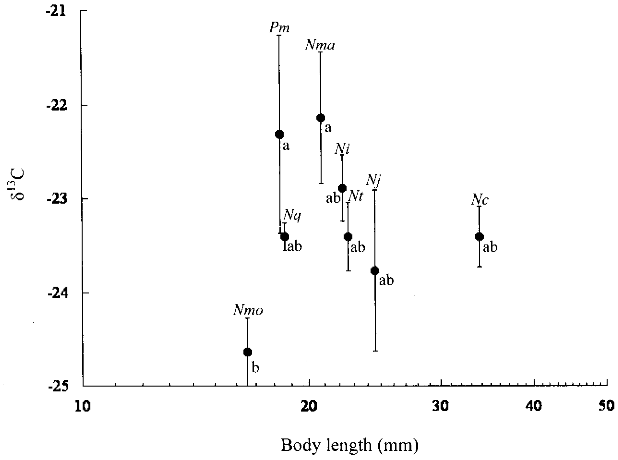

Fig. 2. Body length and δ^{13}C (means±SE) of each burying beetle. Different letters indicate significant differences in δ^{15}C. Italic abbreviations for the species names are those given in Fig. 1.

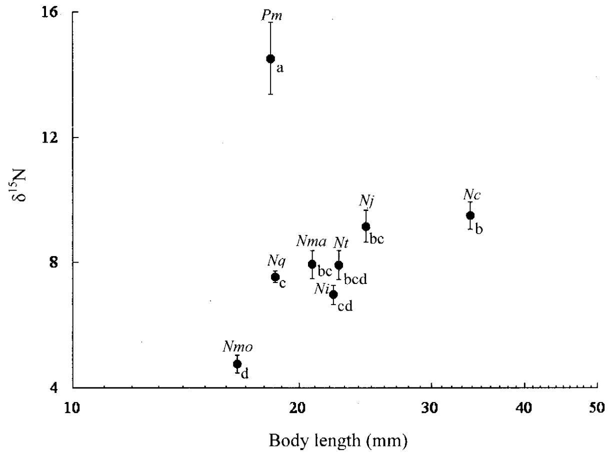

Fig. 3. Body length and δ^{15}N (means±SE) of each burying beetle. Different letters indicate that δ^{15}N significantly differed. Italic abbreviations for the species names are those given in Fig. 1.

related to occurrences in other species.

DISCUSSION

The stable isotope ratios of the largest species (*N. concolor*) and the smallest species (*N. montivagus*) were significantly different from those of other *Nicrophorus* species. In addition, the largest species showed the highest δ^{15}N whereas the smallest species showed both the lowest δ^{13}C and δ^{15}N among all *Nicrophorus* species. These results suggest size-related niche differentiation in carcass use in *Nicrophorus* species. On the other hand, *N. montivagus* showed different stable isotope ratios from *N. maculifrons* and *N. quadripunctatus*, whose body sizes are slightly larger. Considering that these species were always collected together, niche differentiation of their carcass use might result from interspecific competition. The δ^{15}N and body size were positively correlated in *Nicrophorus* species. It is possible that larger *Nicrophorus* species use the carcasses of larger vertebrates in higher trophic level, although it is not known whether the nitrogen isotope ratio in the carcass of vertebrates reflects that in live bodies, or whether δ^{15}N and body size are positively correlated.

P. morio showed extremely higher δ^{15}N than all the other studied *Nicrophorus* species, including the samples of *N. concolor* and *N. quadripunctatus* collected from the same localities. These results suggest that the food resources of *P. morio* adults are different from the carcasses used by *Nicrophorus* species. Although *P. morio* adults oviposit around the carcasses dominated by *Nicrophorus* species (Trumbo et al., 2001; Nagano and Suzuki, 2003), these carcasses may not be the main food resource. Several studies report that *N. pustulatus*, being similar to *P. morio* in body size, is a formidable interspecific brood parasite (Trumbo, 1994; Scott, 1998) as well as a parasitoid of snake eggs (Blouin-Demers and Weatherhead, 2000).

The δ^{13}C and δ^{15}N of *N. quadripunctatus* varied among local populations. This is probably because different populations use different carcass resources. Another probable explanation is that the isotopic ratios of carcasses of the same vertebrate species may vary among localities. In the expected studies, variations among local populations should be considered in stable isotope analysis for burying beetles.

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