

BURYING BEETLES (COLEOPTERA: SILPHIDAE) OF THE APOSTLE ISLANDS, WISCONSIN: SPECIES DIVERSITY, POPULATION DENSITY AND BODY SIZE

Stephen T. Trumbo<sup>1</sup> and Shelly Thomas<sup>2</sup>

ABSTRACT

Over 2400 burying beetles, representing six species (*Nicrophorus defodiens*, *N. sayi*, *N. orbicollis*, *N. tomentosus*, *N. vespilloides*, and *N. pustulatus*), were trapped from 27 June to 4 August, 1996 at nine study sites (3 small islands, 3 large islands, and 3 mainland locations) centered around the Apostle Islands National Lakeshore in northern Wisconsin. Species diversity was greatest on the mainland and least on the smallest islands (< 600 ha). *Nicrophorus defodiens*, the smallest of the six species, was marginally over-represented on the smallest islands. We hypothesize that this occurred because *N. defodiens* can maintain a larger population for a given resource base than its larger congeners. Estimates of population density for *N. defodiens* were made on the two smallest islands (Raspberry and Devils) and ranged from 16–24/ha. On the small and isolated Devils Island, *N. defodiens* had significantly greater pronotal width compared to conspecifics at each of the other eight sites. We hypothesize that the larger body size at this site which is dominated by *N. defodiens* may be selected because of the greater frequency of intraspecific encounters.

Island groups have figured prominently in ecological and evolutionary studies (MacArthur and Wilson 1967). Depauperate communities on islands often differ markedly from the mainland in the number and types of competitors. Reproductive isolation can facilitate adaptation to such local biotic differences. Because water acts as a barrier to migration for terrestrial organisms, islands permit the ecologist to work with a semi-confined population. Thus, for organisms that move extensively in their environment, estimates of population size and community composition are more feasible on islands than on the mainland.

In this study, burying beetles (Silphidae: *Nicrophorus* Fabricius) were trapped at nine study sites centered around the Apostle Islands National Lakeshore (three each of small islands, large islands and mainland locations). The following predictions were tested: (1) Species diversity would be positively related to habitat area, being greatest on the mainland and least on small islands (MacArthur and Wilson 1967). (2) Of the three primary late spring/early summer breeding burying beetles in this geographic region (*N. defodiens* Mannerheim, *N. sayi* Laporte and *N. orbicollis* Say), the smallest,

<sup>1</sup>Department of Ecology & Evolutionary Biology, University of Connecticut, Waterbury, CT 06710.

<sup>2</sup>Department of Biological Sciences, University of Maine at Orono, Orono, ME 04469.

*N. defodiens*, would be proportionately more common on small islands. Smaller species of burying beetle, such as *N. defodiens*, can maintain larger populations for a given level of resource (Trumbo 1992) and might be less prone to extinctions at sites with a limited and variable resource base. (3) Body size (as measured by pronotal width and foretarsus length) of *N. defodiens* would be greatest on islands on which this species is ecologically dominant as compared to other sites, especially at isolated sites. This prediction is based on an expected shift from interspecific to intraspecific competition when the only competitors of *N. defodiens* are conspecifics (Trumbo 1990a, 1992).

In addition, we made population estimates of *N. defodiens* on the two smallest islands. Estimates on mainland sites have proven problematical because of the extensive movement of these insects in search of resources.

**Burying beetle life history.** Burying beetles exploit a wide size range of vertebrate carrion for use as a breeding resource (*N. defodiens*, 3–100 g; *N. orbicollis*, 5–300 g; Trumbo 1992). Exploitable carcasses are a rare and valued resource (Wilson 1971); in northern Michigan nearly every fresh vertebrate carcass under 200 g is found within 48 h during good weather (Trumbo 1990b, 1992). After locating a carcass, a single female or male-female pair will enter the carcass, remove hair or feathers, and deposit secretions over the carcass to control the decomposition (Pukowski 1933). Larger breeding groups sometimes exploit larger carcasses (Trumbo 1992, Eggert 1992, Scott and Williams 1993). Females oviposit eggs in the surrounding soil in as little as 18 h after finding a carcass. After several days, the young hatch and crawl to the carcass to feed where they are cared for by their parent(s).

Burying beetles regulate the size of their brood such that young disperse from a range of carcass sizes at an equivalent mass (Wilson and Fudge 1984, Trumbo 1990c, Trumbo and Fernandez 1996). *Nicrophorus defodiens*, for example, will produce larvae of the same size over carcasses ranging in size from 5–20 g (Trumbo 1992). Females normally lay many more eggs around a carcass than can be supported (Müller 1990). During the first day that larvae are on the carcass, the parent(s) kill a subset of the young so that the surviving brood will have adequate resources (Bartlett 1987). For a given sized resource, a smaller species such as *N. defodiens* will usually raise three- to fourfold the number of larvae as its larger competitor *N. orbicollis* (Trumbo 1990a, 1992).

A parent that limits reproductive output and thereby produces larger offspring can be compensated by the superior competitive ability of the young. Larger individuals almost always win intraspecific contests for resources (Otronen 1988, Bartlett and Ashworth 1988), and larger species commonly displace smaller congeners from carcasses (Milne and Milne 1976, Scott 1994). *Nicrophorus defodiens* loses a high proportion of resources to larger competitors when larger competitors are abundant (there is very little overlap of body size between *N. defodiens* and *N. orbicollis* and, therefore, larger size of *N. defodiens* would confer no advantage in interspecific contests; Scott 1994). Smaller species remain competitive with larger rivals in a number of ways in addition to their advantage in reproductive output. *Nicrophorus defodiens*, for example, is active before sunset at a warmer period of the day than the nocturnal *N. sayi* and *N. orbicollis* (Wilson et al. 1984). *Nicrophorus defodiens* can therefore search for carcasses on days on which congeners will not become active because of cool nocturnal temperatures. This species also will exploit very small carcasses (3–5 g) that the larger *N. orbicollis* rejects, presumably because of the limited number of offspring that could be raised (Trumbo 1990a). In the absence of large competitors, *N. defodiens* would

have greater opportunity to exploit larger carcasses which attract more (intraspecific) rivals (Trumbo 1990a, 1992, Eggert and Müller 1997; Scott 1998). Selection for larger size and superior competitive abilities might then be expected.

### METHODS

The study was conducted in and around the Apostle Islands National Lakeshore in northern Wisconsin. Three of the study sites were small islands (< 600 ha: Raspberry, Devils and Manitou), three large islands (2000—4000 ha: Oak, Outer and Stockton), and three mainland locations (Peninsula, part of the National Lakeshore; Chequamegon National Forest, northern section approximately 24 km SW of the Bayfield Visitor Center; and the Porcupine Mountain State Park on the Upper Peninsula of Michigan, approximately 110 km east of Bayfield, Wisconsin) (see map and land areas, Fig. 1). Habi-

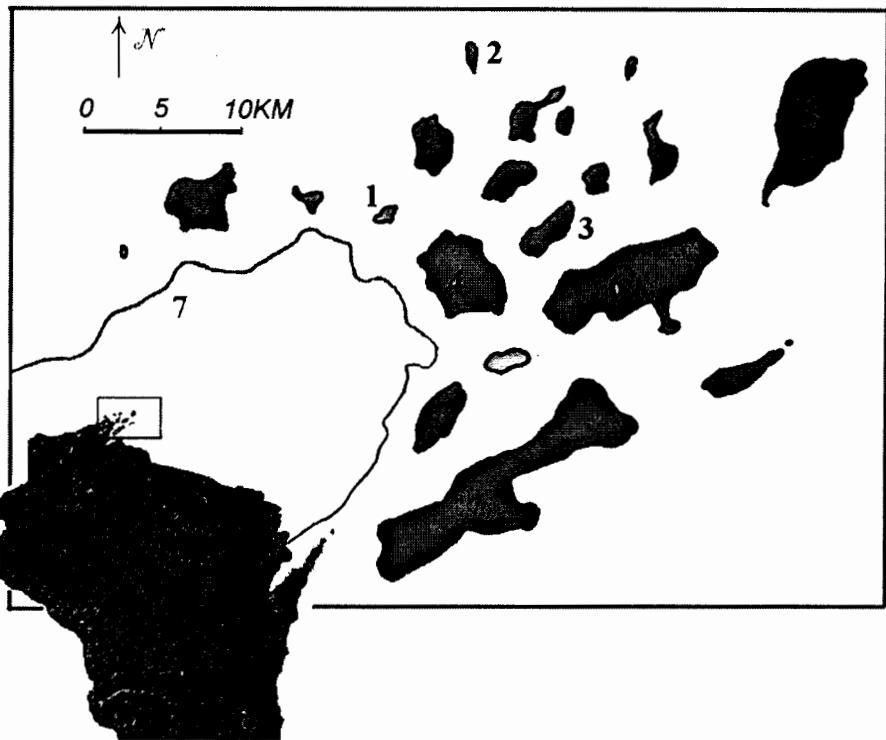


Figure 1. Study sites at the Apostle Islands National Lakeshore (hectares in parentheses): 1—Raspberry (119), 2—Devils (219), 3—Manitou (552), 4—Oak (2056), 5—Outer (3239), 6—Stockton (4070), 7—Peninsula. Chequamegon National Forest and Porcupine Mountain State Park not shown.

tats on these sites, characterized by a mix of northern hardwoods and boreal conifers, are quite varied and are dependent on the frequency and last occurrence of disturbance (primarily logging), distance from shore, and microclimatic differences (Judziewicz and Koch 1993).

We trapped burying beetles from 27 June to 4 August, 1996. The number of successful trapping dates per island varied from 2 to 10 (Manitou, Porcupine—2; Oak, Stockton, Chequamegon—5; Outer—6; Raspberry, Peninsula—7; Devils—10), and the number of traps per date from 3 to 34. We used two primary types of traps. Pitfall traps were dug into the ground, the rim flush with the soil surface, and baited with 2–3 large laboratory rats, and covered by a rain protector. On two islands (Raspberry and Devils) which were intensively studied to estimate population density, single rats were placed on top of the leaf litter to bait beetles. One end of a 0.5 m string was tied to the hind leg of the carcass and the other end to a stake. The string allowed the carcass to be tracked underneath the leaf litter so the beetles could be removed and the carcass could be brought to the surface to be used again for baiting.

We estimated species diversity at each of the nine sites using the Shannon-Wiener index ( $H^1$ ):

$$H^1 = - \sum p_i (\ln p_i)$$

where  $p_i$  is the proportion of the  $i$ th species.

We obtained population estimates of *Nicrophorus defodiens* on the two smallest islands, Raspberry and Devils. From 16–19 July, we trapped 343 individuals on Devils using a combination of 33 pitfall traps and single rats along a trapline extending the length of the island. We marked (a small notch placed on the elytra) and released beetles, and baited a second time during 26–29 July. Recaptures were noted to derive the first population estimate, and then we marked and released all beetles again. We trapped a final time on 3 August to derive a second estimate. Because some beetles died in the traps, we used the following modified formula (Campbell 1996) to derive population estimates:

Estimated population size =

$$\begin{aligned} & (\# \text{ dead at 1st trapping}) + (\# \text{ marked at 1st trapping}) \times \\ & \left[ \frac{(\# \text{ caught at 2nd trapping})}{(\# \text{ of recaptures at 2nd trapping})} \right] \end{aligned}$$

From 12–26 July, we marked and released 110 individuals on Raspberry Island. The second trapping occurred on 1 August. This single estimate of population size on Raspberry was hampered by a large number of individuals that died in the traps and by a limited number of recaptures.

The population estimates assume no significant migration between islands (none of the 785 marked beetles were trapped on other islands), and no significant emergence or mortality (other than mortality accounted for in pitfall traps) during the period in which the estimates were made.

We measured pronotal width and length of the right foretarsus of all trapped beetles to 0.05 mm using precision calipers. Pronotal width and elytral length have been shown to be related to body mass and are preferred measurements of body size because they do not vary with adult nutrition and reproductive condition (Bartlett and Ashworth 1988, Otronen 1988). Foretarsus length was measured as part of a larger study of sex differences in morphology.

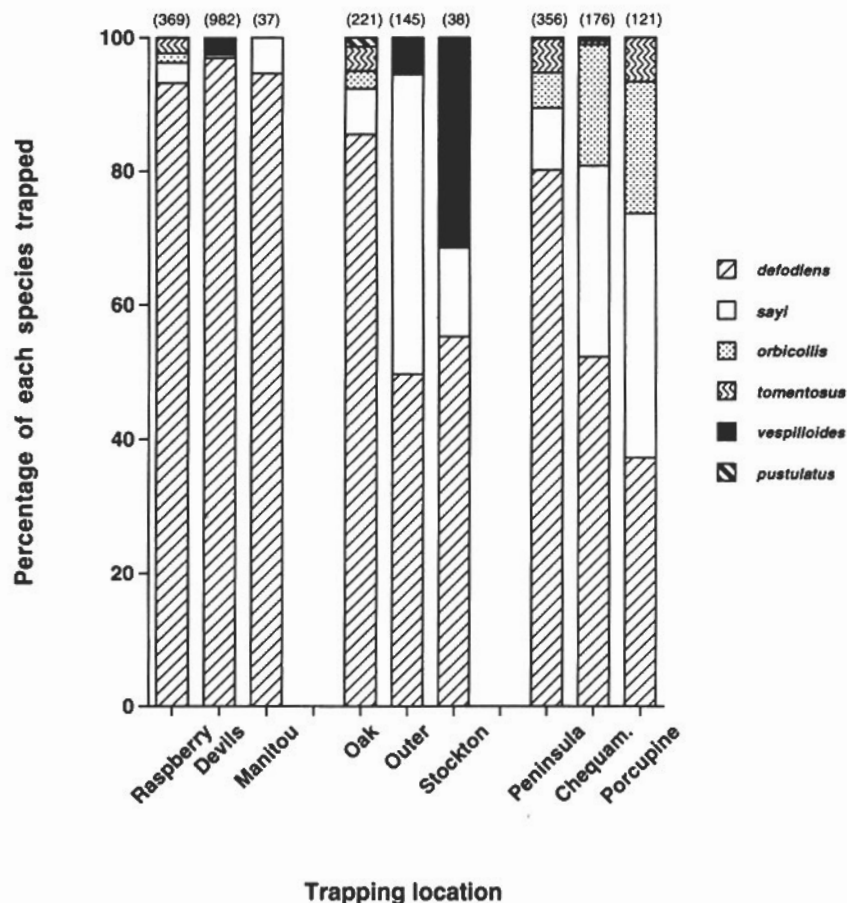


Figure 2. Percentage of *Nicrophorus* species trapped at the nine study sites. Total number of individuals trapped shown in parentheses.

## RESULTS

From 27 June until 4 August, we trapped 2445 individuals belonging to six species (*Nicrophorus defodiens*, *N. sayi*, *N. orbicollis*, *N. tomentosus* Weber, *N. vespilloides* Herbst and *N. pustulatus* Herschel). The total number of individuals trapped per island and the proportions for each species are shown in Fig. 2. Differences in the total number of individuals trapped were primarily due to differences in the number of traps set and the number of nights on which trapping occurred.

**Species diversity.** Species diversity of burying beetles increased with habitat size (one-way ANOVA,  $F_{2,6} = 13.45$ ,  $P < 0.01$ ; area categorized by 3 levels [small island, large island, mainland]). A logarithmic function plotted

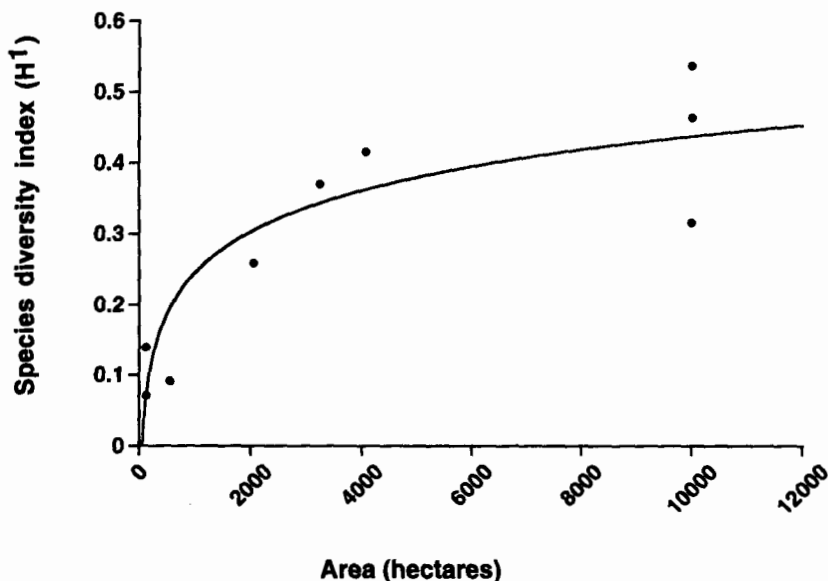


Figure 3. Shannon-Wiener species diversity indices ( $H^1$ ) measured at each study site as a function of habitat area. 10,000 ha was chosen arbitrarily as the area for each of the three mainland sites.

to the data accounts for significant variation ( $r^2 = 0.79$ ,  $P < 0.001$ ; Fig. 3). At no site did we trap all six species although all species are likely to be found on mainland sites that include bog habitat.

As in previous studies, *N. pustulatus* was extremely rare (4 specimens) and *N. vespilloides* was confined to sites with bogs, its critical habitat (Outer, Devils, Stockton Islands, and Chequamegon N. F.) (Shubeck 1977, Anderson 1982, Trumbo 1990b, Robertson 1992, Beninger and Peck 1992, Beninger 1994). *Nicrophorus tomentosus* is a late summer breeder in the Great Lakes region and was just becoming active at the conclusion of the study; undoubtedly its abundance was underestimated.

*Nicrophorus defodiens* was the most commonly trapped species at each of the nine sites. In the Great Lakes region three species of burying beetle (*N. defodiens*, *N. sayi*, *N. orbicollis*) breed in woodlands in late spring/early summer and can be locally abundant (Anderson 1982, Wilson et al. 1984, Beninger 1994). The percentage of *N. defodiens* is shown as a function of habitat area in Fig. 4. On each of the small islands (< 600 hectares), over 90% of all burying beetles trapped were *N. defodiens*. The relative abundance of *N. defodiens* was not related significantly to habitat area (one-way ANOVA,  $F_{2,6} = 3.55$ ,  $P = 0.09$ ; area categorized by 3 levels [small island, large island, mainland]). The relationship is marginally significant if habitat area is used as a continuous dependent variable (simple regression,  $F_{1,7} = 7.06$ ,  $P = 0.03$ ; significance is maintained when chosen values for mainland area range from 4000 to 25,000 hectares). Thus, the relationship between habitat

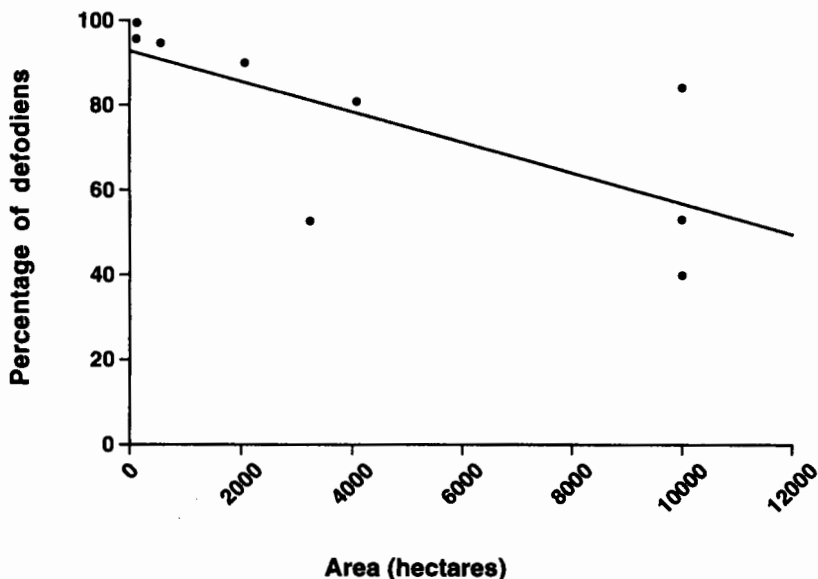


Figure 4. The percentage of late spring/early summer *Nicrophorus* trapped that were *N. defodiens*, as a function of habitat area. 10,000 ha was chosen arbitrarily as the area for each of the three mainland sites.

area and proportion of *Nicrophorus defodiens* must be regarded as quite tentative.

**Population size.** We estimated population size of *N. defodiens* on Devils Island during 16–19 July and during 26–29 July. Of the 343 individuals trapped, marked and released during 16–19 July, we recaptured 45 during 26–29 July, giving an estimate of 2916 for the island (see Methods). We recaptured 101 individuals on 3 August (from a pool of 675 marked individuals), giving a second estimate of 2054. Population density estimates were 22.6 and 16.0 per hectare for the two periods, respectively. Our single population estimate for Raspberry Island during 25–26 July (2895 for the island, 24.2/hectare) must be taken with considerable caution because of the small number of individuals marked (110) and recaptured (4).

**Body size.** We predicted that *N. defodiens* would be larger in size on isolated islands dominated by this species because of an expected shift from interspecific to intraspecific competition. This prediction was difficult to test because only one site (Devils) met both criteria. Raspberry, Manitou and Stockton appeared to be dominated by *N. defodiens* (relative to *N. sayi* and *N. orbicollis*) but were not well isolated from the mainland and other islands (see Fig. 1). Outer Island was isolated but contained a substantial population of the larger *N. sayi*. On Devils Island, *N. defodiens* had a significantly broader pronotum than their counterparts at each of the other 8 sites (t-tests, all  $p < 0.05$ ; Table 1). The mean difference in pronotal width between Devils and other islands was 6%. Foretarsus length of *N. defodiens* was significantly greater on Devils Island than on each of the other islands, with the

Table 1. Mean ( $\pm$  SE) pronotal width (mm) and right foretarsus length (mm) for *Nicrophorus* species for which at least 20 individuals were trapped at a study site. Sample sizes are shown in parentheses beneath the site name for *N. defodiens*, *N. sayi*, and *N. orbicollis*, respectively.

Site	<i>N. defodiens</i>		<i>N. sayi</i>		<i>N. orbicollis</i>	
	pronotal width	foretarsus length	pronotal width	foretarsus length	pronotal width	foretarsus length
Raspberry (344)	4.82 (0.02)	2.41 (0.02)				
Devils (952)	5.05 (0.02)	2.45 (0.01)				
Manitou (35)	4.82 (0.07)	2.29 (0.04)				
Oak (189)	4.84 (0.03)	2.35 (0.02)				
Outer (72, 65)	4.78 (0.05)	2.38 (0.03)	6.17 (0.08)	3.35 (0.05)		
Stockton (21)	4.72 (0.07)	2.26 (0.06)				
Peninsula (285, 33)	4.71 (0.03)	2.31 (0.02)	6.28 (0.09)	3.47 (0.07)		
Chequam. (92, 50, 32)	4.74 (0.05)	2.27 (0.03)	5.92 (0.12)	3.18 (0.09)	6.44 (0.14)	3.47 (0.10)
Porcupine (45, 44, 24)	4.71 (0.07)	2.28 (0.05)	6.23 (0.10)	3.50 (0.06)	6.89 (0.20)	4.00 (0.09)

exception of Raspberry (t-tests,  $P$ 's  $< 0.05$ ; Table 1). As expected, mean foretarsus length of *N. defodiens* was related significantly to mean pronotal width (regression,  $F_{1,7} = 12,21$ ,  $P = 0.01$ )

## DISCUSSION

Burying beetles on the Apostle Islands demonstrate increasing species diversity with increasing habitat area. Small islands commonly have depauperate fauna because of less habitat variation, less immigration and greater rates of extinctions of small populations (MacArthur and Wilson 1967). Species may be more likely to persist, therefore, if they maintain larger populations on a limited resource base. Among burying beetles, smaller species may persist on small islands which are unable to support viable populations of larger species. *Nicrophorus orbicollis*, for example, requires 3–4 times as much carrion resource to raise the same number of brood as its smaller competitor, *N. defodiens* (Trumbo 1992). We found weak support for the prediction that *N. defodiens*, the smallest burying beetle in North America, would



be more abundant in habitats of smaller area. Study at additional sites could provide more definitive tests. In particular, North Twin Island (71 ha) and Eagle Island (10 ha) are both isolated and small; both community composition and body size of *N. defodiens* at these sites would be of interest. The high estimated population densities of *N. defodiens* on Raspberry and Devils Islands, and the existence of *Nicrophorus* on very small islands (< 10 ha) off the coast of Maine (Roux, pers. comm.), suggest that burying beetles may be present on these smaller islands.

The scarcity of *N. orbicollis* on the Apostles is likely due to both its larger body size and its temperature preferences. Of the three late spring/early summer woodland breeders (*N. defodiens*, *N. sayi*, *N. orbicollis*), *N. orbicollis* is the most successful in warmer climates. *Nicrophorus orbicollis* is the most abundant burying beetle of summer from the southeastern U.S. to southern New England and across to southern Michigan (Shubeck 1977, Anderson 1982, Wilson et al. 1984, Trumbo 1990b, Robertson 1992). On the Apostles, unusually cool summers might cause local extinctions of *N. orbicollis* on some islands, and recovery might be slow.

In regions warmer than the Apostles, *N. sayi* breeds primarily in late spring and ceases breeding when *N. orbicollis* becomes more active (Wilson et al. 1984, Beninger 1994). This pattern was less apparent on the Apostles as *N. sayi* was trapped throughout July. At sites such as Outer Island, on which substantial number of *N. sayi*, but not *N. orbicollis*, were trapped, it would be of interest to determine whether reproductive phenology covaries with changes in community composition.

Estimating population density of burying beetles is difficult because of their mobility. Islands provide ideal environments for examining population size because movements between islands are likely to be rare during the short time required for obtaining the estimate. Population estimates of *N. defodiens* (> 90% of all *Nicrophorus*) on Raspberry and Devils were surprisingly high (16–24/ha or an estimated biomass of 1.7–2.5 g/ha based on mass of *N. defodiens* in northern Michigan; Trumbo 1990a). The absence of larger vertebrates on the islands may favor burying beetles in two ways. The lack of non-avian predators on small islands of the Apostles (Julie Van Stappen, pers. comm.) may result in higher population densities of small vertebrate prey species, the only resource burying beetles use for breeding. In addition, the scarcity of non-avian predators and of larger vertebrate scavengers in forested habitats may leave more carrion for insect carrion feeders.

There have been two other attempts to estimate population size for *Nicrophorus* although density estimates are uncertain because of difficulties in determining habitat size. Kozol et al. (1988) estimated that Block Island, Rhode Island supported more than 500 of the endangered *N. americanus* Olivier, the largest burying beetle in North America (approximately 8 times the mass of *N. defodiens*). Sikes (1996) estimated that the Big Creek, California population of *N. nigrita* was 4565. Marking and trapping in nearby canyons demonstrated that the Big Creek site was an effective island of woodland habitat with little migration.

Burying beetles are extremely abundant throughout the Great Lakes region, especially so on islands. Because burying beetles appear to establish sizable populations on even quite small wooded islands, opportunities are present for the study of community ecology and life history adaptation at isolated sites. The ease of trapping burying beetles and their widespread distribution suggest that surveys of *Nicrophorus* on islands in this region may prove profitable.

## ACKNOWLEDGMENTS

We thank Julie Van Stappen and staff of the Apostle Islands National Lakeshore for permission to work and for valuable and kind logistical support. We also thank Linda Parker at Chequamegon National Forest and staff at Porcupine Mountain State Park for collecting privileges. Bill Kinjorski (Outer Island) and Jo and Don Person (Devils) kindly helped with collecting. This research was supported by NSF RUI grant 9420985.

## LITERATURE CITED

- Anderson, R.S. 1982. Resource partitioning in the carrion beetle (Coleoptera: Silphidae) fauna of southern Ontario: ecological and evolutionary considerations. *Can. J. Zool.* 60: 1314-1325.
- Bartlett, J. 1987. Filial cannibalism in burying beetles. *Behav. Ecol. Sociobiol.* 21: 179-183.
- , and C.M. Ashworth. 1988. Brood size and fitness in *Nicrophorus vespilloides* (Coleoptera: Silphidae). *Behav. Ecol. Sociobiol.* 22: 429-434.
- Beninger, C.W. 1994. Phenology, reproductive biology, and habitat associations of *Nicrophorus* Fab. (Coleoptera, Silphidae) of the Mer Bleue Bog area (Ottawa, Canada). *Mem. Entomol. Soc. Can.* 169: 135-143.
- , and S.B. Peck. 1992. Temporal and spatial patterns of resource use among *Nicrophorus* carrion beetles (Coleoptera: Silphidae) in a *Sphagnum* bog and adjacent forest near Ottawa, Canada. *Can. Entomol.* 124: 79-86.
- Campbell, N.A. 1996. *Biology* (4th edition). Benjamin-Cummings, Menlo Park, California.
- Eggert, A.-K. and J.K. Müller. 1992. Joint breeding in female burying beetles. *Behav. Ecol. Sociobiol.* 31: 237-24.
- , and J.K. Müller. 1997. Biparental care and social evolution in burying beetles: lessons from the larder, p. . In: J.C. Choe and B.J. Crespi (eds.). *Social Behavior in Insects and Arachnids*. Cambridge University Press, Cambridge.
- Judziewicz, E.J. and R.G. Koch. 1993. Flora and vegetation of the Apostle Islands National Lakeshore and Madeline Island, Ashland and Bayfield Counties, Wisconsin. *Mich. Bot.* 32: 43-135.
- Kozol, A.J., M.P. Scott, and J.F.A. Traniello. 1988. The American burying beetle, *Nicrophorus americanus*: studies on the natural history of a declining species. *Psyche* 95: 167-176.
- MacArthur R.H. and E.O. Wilson. 1967. *The theory of island biogeography*. Princeton Univ. Press, Princeton, N.J.
- Milne, L.J. and M. Milne. 1976. The social behavior of burying beetles. *Sci. Am.* 235: 84-89.
- Müller, J.K., A.-K. Eggert. and E. Furlkröger. 1990. Clutch size regulation in the burying beetle *Nicrophorus vespilloides* Herbst (Coleoptera: Silphidae). *J. Ins. Behav.* 3: 265-270.
- Otronen, M. 1988. The effect of body size on the outcome of fights in burying beetles (*Nicrophorus*). *Ann. Zool. Fennici* 25: 191-201.
- Pukowski, E. 1933. Ökologische untersuchungen an *Nicrophorus* F. *Zeit. Morph. Okol. Tiere*, 27: 518-586.
- Robertson, I.C. 1992. Relative abundance of *Nicrophorus pustulatus* (Coleoptera: Silphidae) in a burying beetle community, with notes on its reproductive behavior. *Psyche* 99: 189-198.
- Scott, M.P. 1994. The benefit of paternal assistance in intra- and interspecific competition for the burying beetle, *Nicrophorus defodiens*. *Ethol. Ecol. Evol.* 6: 537-543.

- . 1998. The ecology and behavior of burying beetles. *Ann. Rev. Entomol.* 43: 595–618.
- , and S.M. Williams. 1993. Parentage in a communally breeding beetle determined by randomly amplified polymorphic DNA. *Proc. Natl. Acad. Sci., U.S.A.* 90: 2242–2245.
- Shubeck, P.P., N.M. Downie, R.L. Wenzel and S.B. Peck. 1977. Species composition of carrion beetles in a mixed-oak forest. *William L. Hutcheson Mem. For. Bull.* 4: 12–17.
- Sikes, D.S. 1996. The natural history of *Nicrophorus nigrita*, a western Nearctic species (Coleoptera: Silphidae). *Pan-Pac. Entomol.* 72: 70–81.
- Smith, R.J. and B. Heese. 1995. Carcass selection in a high altitude population of the burying beetle, *Nicrophorus investigator* (Silphidae). *Southwest. Nat.* 40: 50–55.
- Trumbo, S.T. 1990a. Interference competition among burying beetles (Silphidae, *Nicrophorus*). *Ecol. Entomol.* 15: 347–355.
- . 1990b. Reproductive success, phenology and biogeography of burying beetles (Silphidae, *Nicrophorus*). *Am. Midl. Nat.* 124: 1–11.
- . 1990c. Regulation of brood size in a burying beetle, *Nicrophorus tomentosus* (Silphidae). *J. Ins. Behav.* 3: 491–499.
- . 1992. Monogamy to communal breeding: exploitation of a broad resource base by burying beetles (*Nicrophorus*). *Ecol. Entomol.* 17: 289–298.
- , and A.G. Fernandez. 1995. Regulation of brood size by male parents and cues employed to assess resource size by burying beetles. *Ethol. Ecol. Evol.* 7: 313–322.
- Wilson, D.S. and J. Fudge. 1984. Burying beetles: intraspecific interactions and reproductive success in the field. *Ecol. Entomol.* 9: 195–203.
- , W.G. Knollenberg, and J. Fudge. 1984. Species packing and temperature dependent competition among burying beetles (Silphidae, *Nicrophorus*). *Ecol. Entomol.* 9: 205–216.
- Wilson, E.O. 1971. *The Insect Societies*. Belknap Press of Harvard University Press, Cambridge, MA,