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A STUDY OF THE ECOLOGY AND REPRODUCTIVE BIOLOGY OF THE CARRION BEETLE
ASSEMBLAGE IN THE MER BLEUE BOG AREA WITH SPECIFIC REFERENCE TO THE
HABITAT ASSOCIATIONS OF *NICROPHORUS VESPILLOIDES* HERBST
AND *N. DEFODIENS* MANNERHEIM (COLEOPTERA: SILPHIDAE)

by

CLIFFORD W. BENINGER, B.Sc.

A thesis submitted to
the Faculty of Graduate Studies and Research
in partial fulfillment of
the requirements for the degree of
Master of Science

Department of Biology

Carleton University

Ottawa, Ontario

May 12, 1989

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the degree of Master of Science

Thesis Supervisor

Chair, Department of Biology

Carleton University

May 12, 1989

Abstract

The reproductive biology, seasonality and habitat associations of *Nicrophorus* were studied in the Mer Bleue bog area in order to determine the relative importance of competition in structuring this assemblage. Among scavenging groups, vertebrates acquired the most small mammal carrion, but *Nicrophorus* beetles were the most successful group of invertebrates. Patterns of resource use among *Nicrophorus* differ spatially and temporally. *N. vespilloides* is reproductively active and occurs only in Sphagnum bog, while *N. defodiens* is found only in the mixed forest of the nearby sand ridge. *N. sayi*, *N. orbicollis*, and *N. tomentosus* are caught infrequently in the bog, and are unable to reproduce there. These species reproduce on the ridge. *N. sayi* is spring breeding and univoltine. *N. orbicollis* and *N. defodiens* are probably multivoltine and reproduce throughout the summer. *N. tomentosus* is an autumn breeder and is univoltine. The reproductive segment of the *Nicrophorus* population is underrepresented in baited pitfall traps. Substrate type and reproductive behavior may account in part for the habitat specificity of *N. vespilloides*, but past competition with *N. defodiens* cannot be disregarded. Changes in oviposition behavior and infanticide are two strategies to optimize resource utilization in *N. vespilloides*.

Two of four species of phoretic mite associated with *Nicrophorus* exhibited carrier site preference. Two new species of mite were identified which are related to species found in Japan and Europe. Adult females of *P. carabi* were found to be predaceous on *Nicrophorus* eggs in culture. This feeding behavior is described and its relevance to the relationship between mite and beetle discussed.

Acknowledgements

Many individuals have contributed directly or indirectly to this paper. I would first like to thank S. B. Peck for introducing me to a fascinating area of study, and for his comments on this paper. I would also like to thank G. Umphrey for his good humour and unending patience during the summer I reared beetles. E. E. Lindquist and V. E. Behan-Pelletier of the Biosystematics Research Institute deserve special mention for their encouragement and help with mite identifications. I thank also L. Ling for his excellent S.E.M. photos, and H. Damman and T. Arnason for their helpful comments. D. Shutler, K. Metz, M. Mallory and D. Hoysack also deserve thanks for their friendship and for giving me a slightly different ecological perspective. Finally, and most importantly, I would like to thank J. Cearn's and my son Christopher, without whose support and friendship I could not have completed this project.

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Scope of Thesis

I undertook this study to examine competitive interactions within the genus *Nicrophorus*, with specific reference to the habitat associations of the sister species pair, *N. vespilloides* and *N. defodiens* in the Mer Bleue bog. The study was later broadened to include the *Nicrophorus* fauna of the forests on the sand ridges in the bog area. In addition to field work carried out in the summer of 1988, both of the above species were reared in the lab to determine clutch size, growth rates and substrate specificity.

Also, with the help of the staff at Biosystematics Research Institute (Agriculture Canada, Ottawa) four species of phoretic mites were identified, two of which are new. Mites were examined to determine carrier site preference, and the feeding behavior of the adult of *P. carabi* described.

communication and are species-specific (Niemitz 1972, Schumacher 1973). Another less specific form of stridulation is defensive, and is produced when the beetles are disturbed or handled (Bredohl 1984). The buzzing sound and movement of the abdomen, may mimic a disturbed, but torpid bumble bee (Lane and Rothschild 1965). The beetles have a foul smelling fluid which may be expelled from the anus. They are conspicuously coloured and this may be aposematic.

Geographic Survey of *Nicrophorus* Studies

Spicarova (1971, 1972, 1974) studied size variation in relation to the amount of larval food for *N. vespillo* in eastern Europe. Recent work in Germany has focused on clutch size and optimal resource utilization for *N. vespilloides* (Müller 1987). In Great Britain Springett (1968) initiated study into the relationships between *Nicrophorus* and their phoretic mites. Also in Great Britain, Bartlett (1987b, 1988) has provided additional evidence for the use of a sex attractant and that males of *N. vespilloides* participate actively in the rearing of the brood. In addition, Bartlett (1987a) has shown that male and female *N. vespilloides* practice infanticide when large numbers of first instar larvae survive the egg stage. Halffter et al. (1983) have detailed the reproductive biology of a Mexican species of *Nicrophorus*.

The distribution and habitat associations of the carrion beetle fauna in Japan have been studied by Katakura and Fukuda (1975), Katakura and Ueno (1985) and Katakura et al. (1986). These studies have shown that there are significant differences in resource use among *Nicrophorus*

3) *Can physical and behavioral factors account for the habitat associations of N. vespilloides and N. defodiens?*

To address the three questions outlined above, over 300 CO₂ killed *Mus musculus* were placed along transects in the bog and ridge forest. The relative success of invertebrate and vertebrate scavengers in obtaining mice was recorded by examining each mouse 3 times in the two week period prior to placement of freshly killed mice. A combination of baited pitfall trapping and small mammal placement determined spatial and reproductive isolation for *N. vespilloides*. Lab rearing examined physical and behavioral aspects that might determine habitat preference. In addition to the answering the above questions, the following hypotheses were tested.

- 1) *Reproductively active Nicrophorus concentrate their search efforts toward locating small mammal carrion.*
- 2) *Female Nicrophorus beetles assess the size of the food resource and lay clutches that will optimize brood size.*
- 3) *If regulation of clutch size is not observed, but brood size is optimized under field conditions, then there is some other means of optimizing resource utilization.*

- 4) *Adults of P. carabi* are predaceous on *Nicrophorus* eggs in culture.

To test the first hypothesis, the frequency of adult *Nicrophorus* species caught at baited pitfall traps was compared to the number of mice buried by *Nicrophorus* species. Reproductively active *Nicrophorus* should concentrate their search for small carcasses and be underrepresented in pitfall traps with large carrion as bait.

The second hypothesis was tested by lab-rearing the sister species *N. vespilloides* and *N. defodiens* and comparing clutch size to amount of larval food (mouse weight). This determined whether females can assess the size of the larval food resource and lay an initial clutch which will optimize brood size.

To test the third hypothesis, brood sizes and weights were recorded from field collected broods. Two other strategies for optimizing brood size are infanticide (large first clutch, small resource) or oviposition of a second clutch (small or normal first clutch but large resource).

The final hypothesis was tested by giving eggs of *Nicrophorus* beetles to adults and deutonymphs of *Poecilochirus carabi* removed from beetle cultures.

CHAPTER ONE

GENERAL INTRODUCTION

Reproductive Biology of *Nicrophorus*

Carrion beetles of the family Silphidae are adapted in a number of ways to locate and utilize carrion, a patchily distributed and ephemeral resource. There are two subfamilies of Silphidae, the Silphinae and the Nicrophorinae, and member species of each has its own pattern of resource use. Members of the Silphinae reduce their interactions with flies and *Nicrophorus* species by utilizing large carcasses for feeding and reproduction (Anderson 1982a). Adult Silphinae arrive at the carcass when decay is well underway, and their eggs do not hatch for several days. By this time fly larvae have consumed most of the carcass and the larval Silphinae feed on what flesh remains (Anderson 1982a, Johnson 1974). Adult *Nicrophorus* are also known to be attracted to large carcasses but only to feed. They may feed on the carrion itself (Jaques 1915) but also consume fly larvae (Clark 1895, Steele 1927). All species in the genus *Nicrophorus* use small carcasses for reproduction (but see also Peck 1986), and therefore competition for larval food provisions is assumed to be intense (Putman 1983) because of the scarcity of small vertebrate carrion.

Pukowski's (1933) study of European *Nicrophorus* was the first to detail aspects of the reproductive biology of these beetles. Milne and Milne (1944, 1976) have since summarized much of what is known of the biology of carrion beetles. Beetles use olfaction rather than visual cues to orient to carrion (Shubeck 1975). They follow odor gradients in the air with the help of olfactory sensillae located primarily on the apical antennal segments (Dethier 1947, Ernst 1969). *Nicrophorus* beetles are sensitive to hydrogen sulfide, mercaptans and amines released in the decay process (Schneider and Steinbrecht 1968, Waldow 1973). Since olfaction is the primary sense involved in the location of carrion, foraging success may be affected by the direction of the prevailing winds (Petruska 1976).

Once a suitable carcass is located, phoretic mites associated with *Nicrophorus* pierce and feed on deposited Diptera eggs (Springett 1968), a behavior which removes flies from competition with beetle larvae. Carcasses often are located by more than one species of *Nicrophorus*, and fighting occurs until a single conspecific pair monopolizes the carcass. If a single male finds a carcass he releases a sex pheromone to attract a conspecific female (Pukowski 1933, Bartlett 1987b). The male and female then bury the carcass to a depth which varies according to species. In the process of burial the carcass is moulded into a sphere, and the fur or feathers are stripped off (Pukowski 1933). Burial of the carcass acts as a stimulant for the female to mature her ovaries, a process which may take several days (Scott and Tranfiello 1987). The female lays one or more clutches of eggs in the substrate near the brood

ball (Müller 1987). Pukowski (1933) described a specialized gallery in which the eggs were laid, but I could not confirm her results with *Nicrophorus vespilloides* and *N. defodiens*. Embryological development is completed in slightly more than two days, and first instar larvae make their way to the food source. Often the female stridulates when the eggs hatch. Pukowski (1933) thought that the sounds produced by the female directed the first instar larvae to the brood ball.

Once larvae locate the brood ball the female feeds them from a pool of liquified food at the top of the carcass. The larvae pass through three larval instars, and usually maximum larval weight is reached in less than five days (Pukowski 1933, pers. obs.). The male generally leaves before the brood matures, but *N. vespilloides* males often remain with the female (Bartlett 1988, pers. obs.). The larvae are fed intensively by the male or female immediately after a molt, because their mouthparts at these times are too soft for self feeding (Pukowski 1933). After reaching maximum weight, the larvae enter a pre-pupal period which lasts for a week to ten days and during which the third instar larvae become increasingly quiescent. Development is complete after a pupal period of approximately two weeks. The emergence of adults from the soil is determined by daylength for some species (Spicarova 1972).

Nicrophorus beetles are known to stridulate under certain conditions. Sound is produced by rubbing the base of an elytron against one of the two stridulatory files on the fifth abdominal tergite, and is produced when the female is in copula, feeding the larvae, or burying the brood ball (Bredohl 1984). These types of stridulation may be for

communication and are species-specific (Niemitz 1972, Schumacher 1973). Another less specific form of stridulation is defensive, and is produced when the beetles are disturbed or handled (Bredohl 1984). The buzzing sound and movement of the abdomen, may mimic a disturbed, but torpid bumble bee (Lane and Rothschild 1965). The beetles have a foul smelling fluid which may be expelled from the anus. They are conspicuously coloured and this may be aposematic.

Geographic Survey of *Nicrophorus* Studies

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The distribution and habitat associations of the carrion beetle fauna in Japan have been studied by Katakura and Fukuda (1975), Katakura and Ueno (1985) and Katakura et al. (1986). These studies have shown that there are significant differences in resource use among *Nicrophorus*

species. In particular, *N. vespilloides* is predominant in forests or grasslands in northern Japan, depending on the locale. Katakura et al. (1986) suggest that *N. vespilloides* changes habitat types because of interactions with other sympatric species of the carrion community.

In North America the study of carrion beetles has concentrated on a number of different ecological parameters. Early studies such as those of Hatch (1927) and Leech (1934) were descriptive, and provided some information on the reproductive biology of Nearctic *Nicrophorus*. Leech (1934) described an interesting behavior for *N. defodiens* in which the mature larvae are guided by the female across open ground to a pupation site removed from the food supply. This behavior has yet to be confirmed in field studies.

Shubek (1969, 1971, 1975) studied the population dynamics and activity patterns of the Silphidae of the eastern United States. Also in the United States, Wilson and Fudge (1984) have examined intraspecific competition in *Nicrophorus* and Wilson et al. (1984) discussed the dependence of temperature on competition between *N. defodiens* and *N. orbicollis*. Wilson and Knollenberg (1984) have found that females with mature ovaries tend to avoid baited pitfall traps and concentrate on the location of small carcasses for reproduction. In addition to reproductive biology, Wilson has also studied the relationships between the phoretic mite *Poecilochirus carabi* (Vitz) and *Nicrophorus* beetles. From two extensive field studies, Wilson (1983) and Wilson and Knollenberg (1987) conclude that the mites generally do not benefit the beetles in the short term, but they do have long term beneficial effects on the reproductive success of the beetles.

In the eastern United States, Davis (1980) and Schweitzer and Master (1987) have documented the decline of the large American burying beetle, *N. americanus*. *Nicrophorus americanus* was once widespread in the United States, but now the only known population is on an island off the coast of New England. Anderson (1982b) suggested that the loss of primary forest habitat caused the extinction of *N. americanus* across most of its ancestral range. However, Schweitzer and Master (1987) do not believe habitat destruction to be the main reason because this species is still collected, and once was common in areas where there was little or no primary forest. At present the cause for the decline of *N. americanus* is unknown, and the species has been listed as endangered in the U.S.A. (Hecht 1988).

Workers in Canada, such as Anderson and Peck (1985) and Peck and Kaulbars (1987), have summarized the identification and distribution of the carrion beetles of North America. Anderson (1981, 1982a) studied competition and partitioning of resources among the carrion beetle fauna in southeastern Canada, and created the first key to identify all Nearctic *Nicrophorus* larvae to species (Anderson 1982c). He also noted that two sister species, *N. vespilloides* and *N. defodiens*, were habitat specific; the former was found in swamps and marshes, while the latter occurred in forest habitat.

Field studies were conducted in the Mer Bleue bog area in eastern Ontario during the summer of 1988 to determine whether *N. vespilloides* was restricted to this bog habitat. It was hypothesized that competition with *N. defodiens* resulted in the restriction of *N. vespilloides* to bog and marsh habitats. Interspecific competition has been interpreted as

determining the seasonal and daily activity patterns for other species of *Nicrophorus* as well. Temporal and spatial patterns of resource use among *Nicrophorus* were examined to see if these were consistent with the hypothesis that competition has been important in structuring the carrion feeding guild in the Mer Bleue bog area. In addition, two species were reared in the laboratory to examine clutch size, growth rates and substrate requirements. Finally, carrier site preferences for three species of mite were determined, and the feeding behavior of the adult mite *Poecilochirus carabi* described.

Study Site

Location

The study site is located in the Mer Bleue bog and adjacent area 8.0 km to the east of Ottawa, Ontario, Canada (Figs 1 & 2). Most of the bog is now owned by the federal government as part of the National Capital Commission (NCC) greenbelt. The NCC monitors development on land that it owns in the Ottawa (Ontario) area. The bog is approximately 5 km at its greatest width and is bordered by mixed deciduous and conifer forest composed primarily of maple and poplar species. Two raised sand ridges penetrate the bog from the west. These are partially cultivated, and produce hay, corn and dairy products. Large areas of second growth forest are present, and are reserved for public recreational use. The presence of forest on the ridge tops in close proximity to *Sphagnum* bog provided a unique opportunity to study the habitat associations and reproductive dynamics of the carrion beetles in this area.

Geologic History

A brief description of the geologic history follows, much of which has been condensed from Proceedings of the Mer Bleue Seminar (1974). However, specific papers will be referred to where appropriate. The following geologic history of the bog is taken from Bikk's (1974) paper.

The Mer Bleue bog is located in what was once the Ottawa River channel system (Camfield 1969). Originally, these channels were eroded into the floor of the Champlain Sea Basin some 12,000 - 9,500 years B.P. The Champlain Sea extended into the Ottawa area when the Wisconsin ice sheet withdrew to the north, and the land had not yet rebounded from the weight of the ice. Once isostatic rebound began to raise the level of the land the sea withdrew and river channels formed over the abandoned sea bed.

After several phases of erosion and sedimentation, the active river channels moved to the north and organic deposits of *Typha* and *Carex* were laid down. Due to the relative impermeability of the Champlain Sea clay and underlying Billings Shale, drainage of the basin is poor.

Formation

The following summary of the formation of the bog is condensed from Small (1974). Formation of the bog began with an undrained basin of water that became stagnant and poorly aerated. The lack of oxygen greatly reduced the growth of decomposers, allowing undecayed organic

material to fill the basin. The partly decayed material became compressed due to the overlying weight of deposited organic debris. This compressed material formed peat, and could eventually form soft coal if compression continues. The bog became acidic because of colonization of the bog by species of the moss genus *Sphagnum*. *Sphagnum* mosses not only secrete acidic materials but decay of their dead remains form acidic compounds such as sulphuric acid. Increase in acidity of the bog due to these processes further retarded the growth of decay organisms and resulted in accelerated peat accumulation.

Low pH levels in the bog have three consequences: 1) higher concentrations of substances toxic to plants such as aluminum, manganese and iron; 2) bacteria which convert ammonium compounds to nitrates are inhibited (most plants utilize nitrates); 3) bog trees adapted to growing in a low pH substrate are usually coniferous, needles of which contain toxic phenolics which are eventually released into the soil when they are shed.

Sphagnum moss grows best in the center of the bog, and more undecayed organic material accumulates in this area. Therefore the center becomes raised, and mineral rich drainage water cannot reach this area. Peat is very poor in nutrients and the only influx of nutrients for this central area is through rainfall. Due to the extreme shortage of nutrients, only a few hardy plants are able to grow there.

Vegetation

Three well-represented families of vascular plants are found in the

Mer Bleue bog: Ericaceae (heaths), Orchidaceae (orchids), and Cyperaceae (sedges). Due to the low availability of nutrients, several insectivorous plant species are also found in the bog. Two common species are *Sarracenia purpurea* L. (pitcher plants) and *Drosera rotundifolia* L. (sundews). Shallow-rooted trees such as *Larix laricina* (tamarack) and *Picea mariana* (black spruce) are able to colonize dry areas raised above the water table. However, the bog is dominated by *Sphagnum* sp moss (Small 1974).

The ridge top vegetation and soils differ greatly from the bog. The following are dominant on nearby Dolman ridge: northern white cedar (*Thuja occidentalis*), white sugar maple (*Acer saccharum*), beech (*Fagus grandifolia*) birch (*Betula lutea*), jack pine (*Pinus banksiana*), poplar (*Populus balsamifera*), white pine (*Pinus strobus*), and several oak (*Quercus*) species. Undergrowth is dominated by ferns, mosses and grasses. Identification of the many grasses and shrubs was not attempted.

Fauna

Mammals that occur in the bog include *Sorex cinereus* (the masked shrew), *Lepus americanus* (snowshoe hare) *Tamiasciurus hudsonicus* (red squirrels) and *Zapus hudsonius*, (meadow jumping mouse) (Smith 1974). Many species of birds are found in the bog (Ouellett 1974), and some species may be important scavengers.

Unfortunately, little is known of the insects that inhabit the bog.

but it is the only known locality for some species. Flies of the families Tachinidae, Tabanidae (numerous), Chironomidae, and Muscidae are represented (Munroe 1974). Many species of Odonata (Corbett and Walley 1969) as well as Lepidoptera (Freeman 1969) have been collected in the bog. I have collected Orthopteroid insects, in particular Nemobiine crickets and katydids. In addition, several species of carrion beetles in the two sub-families Silphinae and Nicrophorinae, are found in the bog. *Oiceoptoma noveborensis* and *Necrophila americanus* are the two members of the Silphinae that were collected in the bog during the summer of 1988. All species of Nicrophorinae collected belong to the genus *Nicrophorus*, and in decreasing order of abundance are: *N. vespilloides*, *N. orbicollis*, *N. sayi*, and *N. defodiens*. In addition to being the most abundant species, *N. vespilloides* was the only species to successfully reproduce in the bog.

Fig. 1. Location of Mer Bleue

Fig. 2. The Bog and Environs

CHAPTER 2

SEASONALITY, HABITAT ASSOCIATIONS AND FORAGING STRATEGIES OF *NICROPHORUS* IN THE MER BLEVE BOG AREA

Introduction

In the past, baited pitfall trapping has been used to examine the species composition of Silphidae attracted to carrion (Shubeck 1969), the daily activity patterns of *Nicrophorus* (Shubeck 1971), and the ability of *Nicrophorus* to orient to carrion (Shubeck 1968). This type of trapping has also proven useful in the study of ecological interactions among closely related species of Silphidae (Anderson 1982a). Anderson's study was the first to examine aspects of resource partitioning among the Silphid beetle fauna of southern Ontario (Canada).

Nicrophorus are known to be attracted to large carcasses, but only to feed and not for reproduction. They feed on the carrion itself and are also predaceous on fly larvae (Clark 1895, Steele 1927). All species in the genus *Nicrophorus* bury small vertebrate carcasses for reproduction. Since carrion is an ephemeral resource and patchily distributed, competition for larval food provisions is expected to be intense (Putman 1983). However, species of *Nicrophorus* have definite

daily and seasonal activity patterns that reduce competitive interactions among congeneric species (Anderson 1982a).

Two closely related species, *N. vespilloides* and *N. defodiens* appear to reduce interactions by spatial partitioning of resources. In North America, *N. vespilloides* and *N. defodiens* are said to be habitat specific, the former occurring only in swamps, marshes and sphagnum bogs, while the latter is found in forests (Anderson 1982a). In Japan *N. vespilloides* occurs in forest and grassland habitats (Katakura and Fukuda 1975, Katakura and Ueno 1985), but in Europe it is found in a variety of habitats (Horion 1949, Pukowski 1933). The sister species, *N. defodiens*, is not found in the Palearctic and is morphologically more primitive than *N. vespilloides*. Anderson (1981) speculated that the ancestral form was widespread in North America and dispersed into the Palearctic across the Bering land bridge in the Miocene. The ancestral range became divided when the land bridge was inundated at the end of the Miocene. The two forms diverged in morphology prior to re-emergence of the land connection in the late Pleistocene. During the Pleistocene the Palearctic form dispersed across Beringia into the Nearctic, and found its ancestral habitat occupied by *N. defodiens*. After they became sympatric, competition or other interactions between *N. defodiens* and *N. vespilloides* resulted in the restriction of *N. vespilloides* to bog habitats in North America.

The Mer Bleue bog in Ottawa is an ideal site in which to examine the relationship between this sister species pair. In the Mer Bleue bog area, open bog and mixed forest grow adjacent to one another. Raised sand ridges penetrate the bog from the west and support a mixed

broadleaf and conifer forest less than three hundred meters away from open sphagnum bog.

The use of baited traps placed both along the ridge and in the bog would allow me to: 1) determine whether *N. vespilloides* and *N. defodiens* forage for large carrion in both habitats. 2) document the phenology and relative abundance of all *Microphorus* in the study area; and 3) test Wilson and Knollenberg's (1984) hypothesis that reproductively active species are underrepresented in pitfall traps. Species that forage for small carcasses may avoid larger carrion such as chicken legs used for bait in pitfall traps. Problems such as male bias and differential trap susceptibility must be considered when analyzing data gathered from pitfall trapping.

Methods

Baited pitfall traps. I placed traps at two sites along the Dolman Ridge at one location in the Mer Bleue bog (Figs. 3-5). A fourth trap was located in a woodlot near Carleton University, approximately 15 km. from the bog. Putrefied chicken legs were used as bait in the traps. The chicken was wrapped in cheesecloth and fixed by a string to hardware cloth at the top of the trap (Newton and Peck 1975). Pitfall traps were made from #10 metal cans (14 cm in depth with a diameter of 12 cm) and buried in the ground until the soil was level with the outside lip of the container. Holes drilled in the bottom of the cans provided drainage. Tops of the traps were covered with hardware cloth (1/2 inch mesh) held in place by two large rocks. A flat rock was placed on top

to protect the traps from rain. Traps were checked every three to five days after placement of the bait, and the live *Nicrophorus* were identified to species, sexed, and then released. Used bait was collected and disposed of far from the trap sites. Initial attempts to identify the sexes based on relative size of tarsal segments were abandoned because this character is variable (Bliss 1949). Instead, sexes were identified according to relative size of the final abdominal segment (Easton 1980), a character which I found very reliable. Early spring captures of *N. sayi* are not included in the totals given for trapping bias because of the unreliability of characters used at that time to sex the beetles.

Transects Twenty galvanized steel enclosures 18.0 cm in depth and 14.0 cm. in diameter were placed along north-south transects in the bog and on the ridge (figs 4 & 5). Enclosures were separated from each other by a distance of 20 meters. They were sunk into soil or moss to their rims and their inside was filled with soil or moss to within 3 cm. of the top. The bottom of each enclosure was covered with aluminum screen to prevent escape of burrowing beetles or brood. Baits were previously frozen, CO₂ killed *Mus musculus*. From inside, the protruding lip of the enclosure was a barrier against relocation of the bait by *Nicrophorus*. Mice discovered by *Nicrophorus* were therefore buried within the circumference of the enclosure. Mice were checked after an overnight discovery period, and again after one week. At the end of two weeks broods and adult beetles (if present) were collected.

Fig. 3. Pitfall Trap Sites

Fig. 4. Ridge Transect Site

Fig. 5. Bog Transect Site

Site Characteristics

Site 1 - Locality: Dolman Ridge, off Anderson Road on NCC land
approx. 3.0 km west of site 3.

Habitat Type: mature mixed broadleaf and conifer forest.

Soil: sand over clay, varying in depth from one to several
meters.

Vegetation: northern white cedar (*Thuja occidentalis*),
white sugar maple (*Acer saccharum*), beech (*Fagus
grandifolia*) birch (*Betula lutea*), jack pine (*Pinus
banksiana*), poplar (*Populus balsamifera*), white pine
(*Pinus strobus*), Several oak (*Quercus*) species.

Undergrowth is dominated by ferns, mosses and
grasses.

Site 2 - Locality: Dolman Ridge, near Dewberry trail on NCC land
approx. 2.0 km west of site 3.

Habitat Type: mixed broadleaf and conifer forest.

Soil: sand over clay, in low-lying areas sand is entirely
absent, in other areas it may reach a depth of several
meters.

Drainage: generally well drained, but lower areas poorly
drained, accumulating rain and meltwater.

Vegetation: very similar to site 1 except fewer mature hardwoods and conifers such as oak and white pine.

Site 3 - Locality: Mer Bleue bog, approx. 200 metres north of the tip of Dolman Ridge.

Habitat Type: *Sphagnum* bog, highly acidic and nutrient poor.

Soil: *Sphagnum* peat.

Drainage: very poor, normally the bog is water saturated to the surface or a few centimeters from the surface.

Vegetation: Open bog: *Sphagnum sp* moss is predominant but sheep laurel (*Kalmia angustifolia*), labrador tea (*Ledum groenlandicum*), leatherleaf (*Chamaedaphne calyculata*) and bog rosemary (*Andromeda glacophylla*) are also common.

Treed bog: all of the above plants but also black spruce (*Picea mariana*) and tamarack (*Larix laricina*).

Site 4 - Locality: Large woodlot near Carleton University, approx. 15 km SW of Site 3.

Habitat Type: fragmented broadleaf forest.

Soil: sand and bedrock overlain by an organic soil layer of several cm. to one meter.

Vegetation: similar to site 1 but lacking conifers. Sugar maple, beech, birch and elm are the dominant tree species.

Results

Phenology and habitat associations.

Species composition of collected *Nicrophorus* varied temporally at each site and between sites (Figs 6a-d). *Nicrophorus vespilloides* predominated at Site 3 in the bog throughout the spring, summer and autumn but rarely occurred on the ridge at sites 1 and 2 during the same period. In linear distance the ridge pitfall trap sites were no more than 300 meters from open bog, yet *N. vespilloides* was very infrequently trapped at these locations. Similarly, *N. defodiens* was only collected once in the bog early in May. It is associated with the mixed forest habitat on the ridge. These data indicate that *N. vespilloides* and *N. defodiens* rarely forage for large carrion outside their own particular habitat. The flight ability of *Nicrophorus* has not been examined in detail but they are known to be strong fliers, and marked individuals have been recaptured up to 300 meters from the release point (Sanborne 1977). Therefore it is likely that they have the potential to easily traverse the distance between ridge and bog habitats. *N. defodiens* and *N. vespilloides* were not trapped at site 4.

The seasonal activity pattern for *N. defodiens* resembled that of *N. vespilloides*. Both species remained active throughout the summer, but *N. vespilloides* began to breed earlier, in mid to late May (figs. 7a & 8a). Teneral adults of *N. defodiens* and *N. vespilloides* appeared at traps from July to September. Since both *N. vespilloides* and *N. defodiens* are

Figs. 6a-d. Relative species composition of *Microphorus* collected at four sites located in bifacial traps, from May to September 1983. (absolute numbers available in Appendix 1).

active throughout the summer, they have the potential to raise more than one brood. Laboratory rearing indicates that *N. vespilloides* develops from egg to reproductively competent adult in about four weeks. Therefore *N. vespilloides* and *N. defodiens* are likely both multivoltine, the adults of the final generation in late summer probably overwinter.

Among other *Nicrophorus*, *N. sayi* was active at sites 1 and 2 in early spring and summer. However, it was rarely found at site 4 and was completely absent at site 3 (figs. 6a-d). *N. sayi* therefore is generally associated with forest habitats and does not occur in bogs. Teneralis of *N. sayi* appear at pitfall traps in August and September but do not bury mice (figs 7a-b). *N. sayi* is therefore univoltine, the progeny from the spring breeding season likely overwinter as adults.

Except for site 3, *N. orbicollis* was active throughout the study period at all sites, differing only in its relative abundance between habitats (figs; 6a-d). *N. orbicollis* was captured at site 3 only in July and September, but was active at sites 1 and 2 throughout the collection period. Except for July and September, *N. orbicollis* was the most abundant species at site 4, and was the only species caught there in the spring and early summer. Teneralis of *N. orbicollis* appear in August, so it is probable that *N. orbicollis* has two generations per year.

N. tomentosus appeared at all sites in July and was active until pitfall trapping terminated in September. However, the transect study results indicate that *N. tomentosus* was still reproductively active in early October. Teneralis of *N. tomentosus* first appear in August.

Therefore, the second generation probably overwinters. *N. tomentosus*, like *N. orbicollis*, was found at all trapping sites and in a variety of habitats.

Comparison Between Baited Pitfall and Transect Studies

At sites 2 and 3 the two trapping methods were combined in an attempt to differentiate which beetles came to carrion to feed (using pitfall traps) and those which were attempting to reproduce (using mice along transects).

Site 2 - Ridge

There were considerable differences between the species of *Nicrophorus* caught at baited traps and those that were reproductively active. In May, *N. sayi* was the most abundant species at the traps, but was also the only reproductively active species of *Nicrophorus*. *Nicrophorus orbicollis* and *N. defodiens* were caught at pitfall traps in May but did not bury mice (figs. 7 & 8) . It is probable that since *N. sayi* breeds exclusively in the spring, *N. orbicollis* and *N. defodiens* were unable to obtain mice for reproduction because of interactions with this species. The baited traps attracted few *N. orbicollis* and no *N. defodiens* in June and July, yet these two species were very active in

Ridge

7a - Transect

7b - Pitfall

Figs. 7a-b. Comparison of *Nicrophorus* attracted to large carcasses (pitfall) and small carcasses (transect) at the ridge site.

Bog

8a - Transect

Figs. 8a-b. Comparison of Microphonus attracted to large carcasses (pitfall) and small carcasses (transect) at the bog site.

burying mice in this period.

Other discrepancies are apparent between the pitfall trap and transect study. Pitfall trapping indicated that *N. tomentosus* was active in July and August, and not in September. This was in conflict with the transect study which showed that *N. tomentosus* buried mice almost exclusively in September and October.

Site 3 - Bog

The pitfall traps did accurately sample the reproductively active segment of the *Microphorus* population in the bog for the months of May and June. However, in July, August and September *N. orbicollis* and *N. tomentosus* were overrepresented in the traps. These two species rarely found and buried mice in summer and early fall. In addition, neither *N. orbicollis* or *N. tomentosus* were successful in raising a brood in the bog.

Similarly, *N. vespilloides* was well represented in the pitfall traps throughout the spring and summer, but not in September. This is in contrast to the transect study which indicates that *N. vespilloides* was still actively burying mice in late August and early September. *N. sayi* was never caught in the pitfall trap at this site.

Trapping Bias

Over the entire collection period more females (N = 366) than males (N = 312) were caught at the pitfall traps.

Discussion

Phenology and Habitat Associations

This study confirms the observations of Anderson (1982a) and Wilson et al. (1984) that *N. vespilloides* is restricted to marshes and bogs in the Nearctic. *N. vespilloides* forages for large carrion almost exclusively at site 3, in open *Sphagnum* bog, and was caught very rarely at sites 1 & 2 on the ridge. Significantly, it was never trapped at site 4 which was removed by a distance of 15 km. from the bog. It is surprising that the habitat preferences of *N. vespilloides* and *N. defodiens* are so pronounced that within a distance of several hundred meters only one or the other species is captured. In addition, the transect study (Chapter 3) indicates that neither species reproduces outside its particular habitat.

N. vespilloides varies geographically in habitat associations. Pukowski (1933) and Horion (1949) found that *N. vespilloides* occurred in a variety of habitats in Europe. In Japan Katakura and Ueno (1975, 1985) indicate that *N. vespilloides* is predominantly a grassland species that may also be abundant in mixed forests, depending on locality.

Since *N. defodiens* does not occur in the Palearctic, the plasticity in habitat associations observed for *N. vespilloides* in Europe and Japan cannot be explained by interactions, past or present, with *N. defodiens*. Katakura and Ueno (1985) propose that interactions with sympatric members of the carrion community cause *N. vespilloides* to alter habitat associations. This interpretation is consistent with my findings. The existence of two distinct habitats within the Mer Bleue area allows *N. vespilloides* to concentrate its reproductive efforts in a specific habitat and to therefore avoid competition for small carcasses with *Nicrophorus* on the ridge. In this respect it is significant that neither *N. vespilloides* nor *N. defodiens* are reproductively active outside of their specific habitats. Consequently, past competition with other *Nicrophorus*, and perhaps *N. defodiens* in particular, may account for the restriction of *N. vespilloides* to bog habitats (Chapter 3). However, as den Boer (1987) points out, microclimate and other physico-chemical factors must also be considered. The effect of physical factors (Chapter 4), such as the nature of the substrate, may also play an important role in the habitat specificity of *N. vespilloides*.

Nicrophorus defodiens and *N. orbicollis* continue to reproduce throughout the summer. Wilson et al (1984) did not find teneralis of *N. defodiens* in the summer even though they breed earlier and have a shorter generation time. They suggest that competition with *N. orbicollis* restricts the breeding season of *N. defodiens* to two periods in late spring and perhaps late summer. However, on the ridge area of the Mer Bleue, *N. defodiens* and *N. orbicollis* were the most active

species of *Nicrophorus* throughout the summer and were equally successful in securing carcasses for reproduction (Chapter 3). The decline in reproductive activity of *N. orbicollis* and coincident increase in the activity of *N. defodiens* in late summer does seem to imply a degree of interference competition. However, unlike Wilson and Knollenberg's findings, *N. defodiens* is not completely prevented from reproducing in the summer.

Among other *Nicrophorus*, the absence of *N. sayi* at site 3 may result from interactions with *N. vespilloides*, which is also active early in the season. Anderson (1982a) noted that *N. sayi* was primarily a forest species, and this tends to reduce interactions with other species that are active early in the spring. However, other factors cannot be ruled out. The absence of *N. sayi* at site 4 may be due to the isolated nature of the forest. This woodlot is surrounded by residential developments. Therefore it may not be large enough to permit the co-existence of two large species such as *N. sayi* and *N. orbicollis*. At site 3 *N. orbicollis* and *N. tomentosus* are abundant in pitfall traps during the summer and fall but were unable to raise broods. It is uncertain why these two species were unable to reproduce in the bog, but considering the overwhelming success of *N. vespilloides*, competition may be a determinant in reproductive success.

At site 2 *N. defodiens* did not appear to be active in the months of June and July, yet the transect study indicates that these were times when it was very active in obtaining mice for reproduction. The same is true for *N. orbicollis* which was reproductively active on the ridge during these two months but was rarely caught at the pitfall trap in the

same interval.

The trapping data for *N. sayi* and *N. tomentosus* also support Wilson and Knollenberg's (1984) findings. *Microphorus sayi* breeds early in the spring, and teners appear at pitfall traps in August and September. Results from the transect study indicate that adult beetles that were probably the progeny of the overwintered generation did not bury mice in late summer. These adults may therefore overwinter and reproduce in the spring of the following year.

Unlike *V. sayi*, *N. tomentosus* breeds in the late summer and into the autumn. However, the greatest number were captured at pitfall traps in early July; but at this time *N. tomentosus* only succeeded in burying a single mouse along the transect. This indicates that the reproductive segment of the population of *N. tomentosus*, like *N. sayi* was not accurately sampled by pitfall trapping. It also confirms Wilson and Knollenberg's (1984) finding that *N. tomentosus* appears at pitfall traps long before it is found with mice.

Trapping Bias

The fact that discrepancies exist between the two sampling methods for all five species of *Microphorus* found in the Mer Bleue area strongly supports Wilson and Knollenberg's (1984) conclusion that females of three species with well developed ovaries tended to avoid baited pitfall traps, searching instead for small carcasses. However, Wilson and Knollenberg's experimental design differed in some respects from my own. For example, I used four pitfall traps located in four different

habitats, whereas they used a combination of eight pitfall traps in one locale. It is uncertain how this affects comparisons between my study and Wilson's, but it is notable that reproductively active species are underrepresented in pitfall traps in both our studies.

Wilson and Knollenberg (1984) also indicate that males reach reproductive maturity earlier, and therefore traps will be female-biased. Dupuis (1987) found that her traps were slightly female biased, but these were located some distance above the ground and therefore bias may have been introduced in the trapping method. When all the data were combined for the traps placed in the Ottawa area a slight female bias was observed. However, as Wilson and Knollenberg (1984) point out, the situation is complicated by the fact that females generally stay underground longer than males, therefore the above ground population is male-biased. In addition, large carcasses provide males with an opportunity to mate. Clearly, more work is needed on the relative importance of these factors.

Summary

- 1) The sister species *N. defodiens* and *N. vespilloides* are habitat specific.
 - 2) Other *Microphorus* vary in relative abundance seasonally, and between sites.
- N. sayi* is univoltine and is associated with mixed forests and does

N. sayi is univoltine and is associated with mixed forests and does not occur in bog habitats.

N. orbicollis is active at all sites throughout the summer and is multivoltine.

N. tomentosus is bivoltine and is also found in all habitats. It is reproductively active in late summer and into the autumn.

- 3) Baited pitfall trapping does not accurately sample the reproductively active segment of the population.

CHAPTER 3

COMPETITION FOR AND UTILIZATION OF CARRION RESOURCES IN THE MER BLEUE BOG AREA

Introduction

Since Pukowski's (1933) study of the European *Microphorus* there has been continued interest in the ecology and reproductive biology of these beetles. *Microphorus* beetles, their carrion food source, and phoretic associates are a model system for the study of species interactions. Recently, Wilson and Fudge (1984) and Wilson et al (1984) studied aspects of intra- and inter-specific competition within *Microphorus*. *Microphorus* beetles must also compete with other invertebrates such as Diptera larvae for carrion. Wilson (1983) found that shallowly buried brood balls were more likely to fail due to fly oviposition. In addition, Dupuis (1987) found that the presence of calliphorid larvae may affect the mean weight of the larvae in a brood. Vertebrates are other scavengers that remove carcasses that represent potential resources for *Microphorus* reproduction. Rates of vertebrate removal range from about 35% (Wilson and Fudge 1984, Dupuis 1987) to 63% (Hendrycks 1984, Putman 1983). The relative importance of competition

in the structuring of communities has been the subject of considerable debate in the recent of literature (Connor and Simberloff 1979, 1986; Wiens 1977).

Competition among congeners may be reduced if they have different activity patterns or habitat preferences (Schoener 1974). Anderson (1982) found that *Nicrophorus* species reduce competition by partitioning resources spatially. *Nicrophorus vespilloides* is a species restricted to swamps and *Sphagnum* bogs in the Nearctic (Chapter 1). However, in Europe and Japan *N. vespilloides* occurs in a variety of habitats (Pukowski 1933, Katakura and Fukuda 1975). Anderson suggested that competition with the sister species *N. defodiens* resulted in the restriction of *N. vespilloides* to bog and marsh habitats in North America.

The purpose of this study was to determine whether the pattern of resource use among scavengers such as flies and vertebrates in general, and among *Nicrophorus* in particular, was similar for ridge and bog sites. In addition, the transect study determined whether *N. vespilloides* and *N. defodiens* are reproductively isolated to bog and ridge habitats respectively. This information was needed to support (or reject) the hypothesis that competition may explain the habitat specificity of *N. vespilloides*. Data from broods collected at two week intervals from the bog area would also determine whether *N. vespilloides* and *N. defodiens* can optimize brood size in the field.

Methods

Transect sites:

Twenty galvanized steel, open enclosures 18.0 cm in depth and 14.0 cm. in diameter were placed 20 meters apart along a north-south transect in the bog and on the ridge. Each enclosure was filled with soil or moss to within 3 cm of the lip of the container. The bottom of each enclosure was covered with aluminum screen to prevent escape of burrowing beetles or brood. At two week intervals a single dead CO₂ killed mouse, freshly thawed was placed in the center of each enclosure. The protruding lip of the enclosure prevented relocation of the mice by *Nicrophorus*. Mice discovered by *Nicrophorus* were therefore buried within the circumference of the enclosure.

Mice were weighed at the site prior to placement with a Pesnel hand held spring balance scale (accurate to 0.5 gms.). Following a 24 hour period for the discovery of mice, the transect was examined and mice classified as discovered or undiscovered. If discovered by scavengers, they were classed as vertebrates, invertebrates, or *Nicrophorus*. If discovered by *Nicrophorus*, then species, sex, size and depth of burial were recorded.

After one week the mice were checked again and again classed as above. At the end of two weeks the enclosures were examined for a final time. Broods (if present), and their mice were collected from each site. New, previously frozen mice were then placed in the center of

enclosure. Broods and adults were placed in sealed plastic bags and each frozen upon return to the university. If adults were not present with the brood, larvae were identified to species using Anderson's (1982c) keys. Size of broods was recorded, and blotted wet weights of individual larvae were measured on a Mettler P1200 balance (accurate to 0.001 gm.). Weight of the mouse remains, if present, were also recorded.

Results

Resource Acquisition By Scavengers. The number of mice acquired by different types of scavenger during the study period is summarized in figs. 9a & b. There is no significant difference in the pattern of resource use between ridge and bog sites for the three scavenging groups ($\chi^2 = 3.60$, $p = 0.166$). Vertebrate scavengers were the most successful of groups at both sites, obtaining a total of 99 mice (58.6%) from the ridge and 94 mice (49.4%) from the bog. The relative success of vertebrates changed with time at both locations. Monthly removal rates on the ridge were a relatively constant 40% (fig. 10), but removal peaked at 60% in June. Rates were more variable in the bog, but reached 100% in early August. The next most successful group were *Nicrophorus* beetles, which utilized a total of 47 mice (29.4%) on the ridge and 56 mice (27.8%) in the bog. However, as indicated below, the successful species within *Nicrophorus* differed between the two sites. The least successful scavengers were the Diptera which garnered only 23 and 38 mice in ridge and bog habitats respectively.

Resource Acquisition Within *Nicrophorus*. Although a similar fraction of the mice in the bog and on the ridge were found and used for reproduction by *Nicrophorus*, there was a dramatic difference in the success of *Nicrophorus* species at the two sites (figs. 11a & b). On the ridge *N. defodiens* is the most successful species in locating mice overnight, but loses a small portion of the mice to vertebrates and other *Nicrophorus* species. In the bog *N. vespilloides* is the most successful species in overnight location of, and in maintaining possession of mice for reproduction. It is notable that *N. vespilloides* never found or buried a mouse on the ridge (Fig. 11a), while *N. defodiens* did not find or bury a mouse in the bog (Fig. 11b). The difference in the pattern of resource acquisition within *Nicrophorus* between the two sites is highly significant ($\chi^2 = 101.3$, $p < 0.001$).

N. vespilloides is so successful within the bog that no other species of *Nicrophorus* managed to raise a brood of larvae in that habitat. In contrast, every species of *Nicrophorus* on the ridge except *N. vespilloides* successfully reproduced.

Temporal Change in *Nicrophorus* Reproduction. The baited pitfall study (Chapter 2) provided information on the phenology and distribution of *Nicrophorus* species, but did not indicate which of the collected species were reproductively active. Since mice were placed along transects both on the ridge and in the bog, it was possible to determine temporal changes in the reproductive activity of *Nicrophorus* species. Mice

Figs. 9a–9b Utilization of carrion resource by different scavenger groups at ridge and bog sites ($\chi^2 = 3.60$ $p = 0.166$).

10 - Removal by Vertebrate Scavengers

Fig. 10 Temporal change in the success of vertebrate scavengers: ridge and bog habitats.

Figs. 11a-b. *Nicrophorus* species associated with food resource at intervals of one day, one week, and two weeks for ridge and bog sites ($\chi^2 = 101.3$, $p < 0.001$).

placed in the bog and on the ridge were examined overnight, after one week and for a final time at the end of two weeks. Almost all mice were either found and buried by *Nicrophorus* or removed by vertebrates within one week. Therefore, the species of *Nicrophorus* associated with buried mice one week after placement was a good indication of which species were reproductively active.

Figures 12a & b indicate the change in *Nicrophorus* species associated with buried mice one week after placement throughout the study period. On the ridge *N. sayi* buried mice in late May but by early June it was no longer reproductively active (Fig. 12a). The decline of *N. sayi* on the ridge coincided with an increase in the reproductive activity of *N. orbicollis* and *N. defodiens*, both of which predominate until the beginning of September. By late August *N. orbicollis* stopped burying mice, coincident with a peak in the reproductive activity of *N. defodiens*. It was not until late September, when *N. orbicollis* and *N. defodiens* were not reproductively active, that *N. tomentosus* acquired a substantial fraction of the mice for reproduction.

In the bog *N. vespilloides* was active from May until October. *Nicrophorus orbicollis* buried some mice in June and July, but no successful broods were recorded.

Parental Care. In the Mer Bleue bog a large amount of data on parental care was available for *N. vespilloides*. Figs. 13a-c outline the number and sex of beetles associated with carcasses at intervals of one day, one week and two weeks. After a period of overnight discovery

a large number of mice were possessed by single conspecific pairs. However, an even greater number of mice were found by females or males only, and it was not uncommon to find more than two beetles at a single mouse (Fig. 13a). After one week, many mice were found with 3 or more conspecific adults but there were also mice buried by conspecific pairs, single females, and single males (Fig. 13b). At the end of two weeks, when broods and adults were removed from the field, only two mice had more than two *N. vespilloides* adults associated with them. All the remaining carcasses were found with both parents, females only, or with only the brood present (Fig. 13c). The number of brood balls found with females only is close to the number found with conspecific pairs. This indicates that males often remain with the brood until maturity and may therefore actively participate in the rearing of larvae.

Temperature Dependant Competition. Wilson (1984 et al) found that *N. defodiens* was more successful at locating carcasses at low temperatures and that the nocturnal activity pattern of *N. defodiens* did not overlap with that of *N. orbicollis*. Minimum ground temperatures were recorded at the ridge and bog sites for the duration of the study period (fig. 17). Minimum overnight temperatures are plotted against the overnight discovery of mice for *N. defodiens* and *N. orbicollis* (fig 14). The number of mice located overnite by either species is not significantly different ($p = 0.46$ ANCOVA).

Figs. 12a-b: Microphorus species associated with mice one week after placement, for the duration of the study period. Dates coinciding with complete vertebrate removal of mice are not included.

Figs. 13a-c Relationship between number and sex of adult *N. vespilloides* associated with mice at intervals of one day to two weeks

Temperature and Competition
Between *N. defodiens* and *N. orbicollis*

Fig. 14. The effect of temperature on the overnight location of mice for *N. defodiens* and *N. orbicollis*

Resource Utilization. Brood information was gathered for all species of *Nicrophorus* found in the study area, but sufficient data for statistical analysis was available for only three species: *N. vespilloides*, *N. defodiens* and *N. orbicollis*. In determining which broods were suitable for analysis the following criteria had to be met: 1) The burial chamber was not disturbed in any way by vertebrate scavengers. 2) Larvae were in the third instar. 3) Broods were not damaged in transport, or in freezing.

N. vespilloides: The largest amount of data was available for this species (28 broods). The number of larvae in a brood and the weight of mouse are positively correlated ($r = 0.558$, $P < 0.01$, fig. 15a). When the negative partial correlation between brood size and mean offspring weight is removed, the correlation between brood size and mouse weight is more significant ($r = 0.624$, $p = 0.001$). There is no relationship between mean individual larval weight and mouse weight when the effect of brood size is removed.

N. defodiens: 14 successful broods were collected for this species. There is no significant partial correlation between brood size and weight of mouse ($r = 0.34$, $p > 0.05$), or between mean weight of individual larvae and mouse size ($r = 0.345$, $p > 0.05$) when the effect of brood size is removed.

N. orbicollis: Only 9 broods were suitable for analysis with this species. No significant correlation exists between number of larvae in a brood and mouse weight ($r = 0.32$, $p > 0.05$), or between mean individual larval weight and mouse weight when the effect of brood size is removed.

Comparison of Broods Between *Nicrophorus* Species

There is no relationship between mean larval weight and the number of larvae in a brood within a species. However, between species it is apparent (fig. 18) that the trend is for species with smaller larvae to produce larger broods. There is no statistical difference in the mean size of broods between species (ANOVA $p = 0.172$ n. s.). However, the mean individual larval weight for *N. orbicollis* is significantly different from the other three species (ANOVA $p < 0.001$).

Interspecific Interactions

Ridge: A summary of two species interactions (there were no three species interactions) is presented in (Table 1). Generally, the larger *N. orbicollis* and *N. sayi* were successful in displacing *N. defodiens* from carcasses it had buried.

Bog: Two species interactions at this site were not as common as on the ridge. On two of three occasions *N. orbicollis* was successful in displacing *N. vespilloides* from carcasses (Table 2), but failed to reproduce.

Fig. 15. Relationship between brood size and mouse weight for *N. vespilloides*.

Brood Characteristics for Four Species of *Nicrophorus*

Figs. 16a-b. Relationship between mean number of larvae in a brood and mean weight of individual larvae for four species of *Nicrophorus*. Total number of larvae weighed are indicated on the x-axis for each species.

Figs. 17a-b. Maximum and minimum temperature readings taken at intervals of one day to one week for bog and ridge sites.

Discussion

Relative Success of Scavenging Groups

The relative success of *Nicrophorus* in the utilization of carrion as a reproductive resource was overshadowed by the success of vertebrate scavengers. Vertebrates removed 58.6 % and 44.8 % of the mice placed on the ridge and bog respectively. Frequently the enclosures were excavated to depths as great as 15.0 cm. indicating prior burial by *Nicrophorus*. Wilson and Fudge (1984) found that overnight removal by vertebrates varied between two sites, but could reach 35 %. Dupuis (1987) reported that removal of carcasses reached 40% in a four day period following placement and that learning may have been involved. The rate of removal in the Mer Bleue study area was higher than the above, but close to Putnam's (1983) figure of 63%. Hendrycks (1984) also recorded removal rates of slightly more than 60%. The large number of mice obtained by vertebrates, both before and after interment by *Nicrophorus*, suggests that vertebrates are the beetles' most serious competitor for carrion.

The July peak in removal of mice by vertebrates is difficult to explain. It may be, as Dupuis (1987) indicated, that one or several vertebrates learned to associate food with the traps or flagging tape. Over a two week period all of her mice were removed because the vertebrate had learned to key in on the traps. Further study on the

amount of introduced error caused by vertebrate learning is necessary.

Nicrophorus beetles were the second most successful group of scavengers; the total numbers of mice utilized by this group at the ridge and bog sites were similar. However, there was a dramatic difference in the success of *Nicrophorus* species at the two sites. *Nicrophorus vespilloides* was the only species to reproduce in the bog, and never found or utilized a mouse on the ridge. In contrast, *N. defodiens* was the most successful of the four species on the ridge, yet did not reproduce in the bog. The fact that these two closely related species concentrate their reproductive efforts exclusively in two different habitat types supports Anderson's (1981) suggestion that past competition resulted in the observed habitat separation. However, as mentioned previously there may be physical and environmental conditions which keep these two species isolated. Some of these are dealt with in the following chapter.

Spatial and Temporal Aspects of *Nicrophorus* Reproduction

The temporal change in reproductive activity for *Nicrophorus* species agrees generally with Anderson (1982a) and Wilson et al (1984). *N. sayi* may minimize interactions with *N. defodiens* and *N. orbicollis* by breeding in the spring. The fact that *N. sayi* lost mice to *N. orbicollis* but not to *N. defodiens* seems to indicate that *N. sayi* stops burying mice in mid-summer because of the increase in activity of *N. orbicollis*. *Nicrophorus tomentosus* does not interact with other *Nicrophorus* species because it breeds in the autumn, when *N. defodiens*

and *N. orbicollis* are no longer active. *Microphorus defodiens*, *N. orbicollis*, and *N. vespilloides* are all species which have similar seasonal activity patterns. *N. vespilloides* may avoid possible competition with *N. defodiens* by reproducing only in bog habitats. It is uncertain why *N. orbicollis* is unable to successfully reproduce in the bog but interactions with *N. vespilloides* may be a factor.

Microphorus defodiens and *N. orbicollis* occur in the same habitat, and have a similar seasonal activity pattern. Since *Microphorus* beetles are distasteful to birds (Jones 1932) and are nocturnal, predation pressure is probably low. Therefore these beetles are abundant relative to their food supply and are said to compete directly for reproductive resources (Wilson et al. 1984). As mentioned in Chapter 2, the decline in reproductive activity of *N. orbicollis* and coincident increase in the activity of *N. defodiens* in late summer seems to imply that *N. defodiens* does not realize its full reproductive potential when *N. orbicollis* is active. However, unlike Wilson et al.'s (1984) findings, *N. defodiens* is not completely prevented from reproducing in the summer. Wilson et al. (1984) present convincing evidence that *N. defodiens* is not able to reproduce in mid-summer because *N. orbicollis* is more successful at finding or siezing carcasses at higher temperatures. In addition *N. defodiens* and *N. orbicollis* have distinct, non-overlapping nocturnal activity periods: *N. defodiens* is active until 22.00 hrs. and *N. orbicollis* is active from 22.00 to 7.00 hrs (Wilson et al. 1984).

Wilson et al. (1984) point out that in the Nearctic the relative abundance of *N. defodiens* increases to the north while the relative abundance of *N. orbicollis* decreases. According to their data *N*

defodiens and *N. orbicollis* should be competitively equal at a latitude close to 46 degrees (Ottawa is situated at 45 20 ' N.) The present study supports Wilson et al (1984). Both *N. defodiens* and *N. orbicollis* were more successful in overnight location of mice at higher temperatures, but the difference in success rate at a given temperature was not significant.

Resource Utilization

Among the three species of *Nicrophorus* examined, there was a surprising lack of significance in the relationship between brood size and mouse weight. A significant positive correlation between brood size and mouse weight was found for only one species, *N. vespilloides*. Since *N. vespilloides* cannot control first clutch size on a mouse of given weight (Chapter 4), the increase in brood size with large food provisions is difficult to account for. However, it is known that *N. vespilloides* will often lay a second clutch of eggs on large carcasses to optimize resource utilization (Müller 1987), and this may account for the increase in brood size in relation to larger food resource. As discussed in Chapter 4 the intraspecific variability in size of adults is influenced by the size of the larval food source, and also by the laying of replacement clutches (Spicarova 1971, 1973). In addition, Bartlett (1987a) found that both parents will consume first instar larvae if clutch size is large and the resource is small. The data from my field study confirm the fact that *N. vespilloides* is able to optimize brood size in the field. When few eggs are laid on a large resource

then the female will lay a second clutch (Möller 1987, Spicarova 1971, 1973).

While there was a lack of significance in relation to size of larvae and the food source within a given species, there is a trend for the smallest species, *N. defodiens*, to have the largest brood size, and the largest species, *N. orbicollis*, to have the smallest brood size. Since all species of *Nicrophorus* must breed on a limited resource, it is possible that at some level there is selection for smaller species to rear more larvae. However, only the mean weight of *N. orbicollis* was significantly different from the other species. Perhaps with larger sample sizes the specific relationship between brood size and larval weight will become clearer.

Parental Care

Pukowski (1933) noted that the male was capable of feeding the brood in the absence of the female, but often left the burial chamber shortly after the larvae hatched. She also found that for *N. vespilloides* both parents often remained with the brood until the larvae were mature. Dupuis (1987) found that male *N. tomentosus* voluntarily left the crypt within a week after a carcass was buried.

In the present study of *N. vespilloides*, both male and female parents were found associated with a large number of the broods collected at the end of two weeks. The presence of the male with mature, or nearly mature larvae may indicate that males of *N. vespilloides* participate in the rearing of the brood. Pukowski (1933) noted that

adult males of several species were rarely (27 % of all cases) found in the crypt, regardless of maturity of the brood. However, in those cases where adult males were found in the crypt, 62.5 % of these were males of *N. vespilloides*. She also observed males of *N. vespilloides* and *N. germanicus* feeding the immature larvae. Bartlett (1988) found that males of *N. vespilloides* fed the larvae just as often as the females did, and that males stayed with the brood until the larvae were mature (eighth or ninth day). If males actively defend the brood then differences in the degree of paternal care among *Nicrophorus* may be explained if predation pressure differs between habitats (Bartlett 1988). Scott (1989) found that when males of *N. orbicollis* remained with the brood, overculling of the first instar larvae led to reduced offspring survival. She suggested that the survival value of parental care is in protection of a valuable resource from conspecifics. The evolution of this behavior will undoubtedly be an active area of research in the future.

Summary

- 1) *Nicrophorus* beetles were less successful than vertebrate scavengers but obtained more carcasses for reproduction than the *Diptera*.
- 2) *Nicrophorus vespilloides* is the only species of five broadly sympatric *Nicrophorus* to reproduce in the Mer Bleue bog. The sister species *N. defodiens* breeds only in the mixed forest surrounding the bog.

- 3) Males of *Nicrophorus vespilloides* remain with the brood until the larvae are near maturity. Males may therefore participate in brood care.
- 4) A significant positive correlation between brood size and amount of larval provisions exists for *N. vespilloides*. This species probably optimizes brood size by infanticide and the laying of a second clutch of eggs on large resources.
- 3) *Nicrophorus sayi* and *N. tomentosus* do not interact with *N. defodiens* and *N. orbicollis* because they breed in the spring and autumn respectively.
- 4) *Nicrophorus defodiens* and *N. orbicollis* are equally successful in the overnigh't location of mice but *N. defodiens* does lose some mice to *N. orbicollis*

CHAPTER 4

RESOURCE UTILIZATION AND THE IMPORTANCE OF REPRODUCTIVE BEHAVIOR IN HABITAT SELECTION FOR THE BURYING BEETLES *NICROPHORUS VESPILLOIDES* AND *N. DEFODIENS* (COLEOPTERA: SILPHIDAE)

Introduction

Burying beetles of the genus *Nicrophorus* are carrion feeders that have adapted in remarkable ways to utilize an ephemeral resource. Carcasses of small mammals are located by the beetles and usually monopolized by a conspecific pair. The carcass is then buried to varying depths depending on the species and nature of the substrate. Once buried, the fur is removed from the carcass and it is moulded into a sphere and prepared for the brood (Pukowski 1933). The female then lays the eggs in the substrate near the carcass, and after several days the first instar larvae make their way to the food source. In some species both the male and female feed the brood (Bartlett 1988), while in others the male leaves shortly after the brood hatches (Pukowski 1933). This degree of parental care is rare in the Coleoptera. The behavior of carrion beetles of the genus *Nicrophorus* has been studied intensively by Pukowski (1933), Spicarova (1971, 1972, 1974) and summarized by Milne and Milne (1976). However, little is known of the

phenology and reproductive dynamics of these beetles or the behavior of any species not studied in Europe.

The reproductive biology of the sister-species pair, *N. vespilloides* and *N. defodiens* has been studied in the Mer Bleue bog area (Ottawa, Canada). *Microphorus defodiens* occurs only in the United States and Canada (Peck and Kaulbars 1987), apparently only in forest habitats with sand or loam soils. *Microphorus vespilloides* is a species which appears to be restricted to swamps, marshlands, and sphagnum bogs in the Nearctic (Anderson and Peck 1985) but in Japan occurs in forest and grassland habitats (Katakura and Ueno 1985), and in Europe is common in a variety of habitats (Pukowski 1933, Horion 1949). Anderson (1982a) suggested that competition between *N. defodiens* and *N. vespilloides* resulted in the restriction of *N. vespilloides* to bog habitats in North America. Work in the Mer Bleue area has shown that *N. vespilloides* is habitat specific, rarely occurring at sites less than a kilometer from open bog, and is not reproductively active outside of the bog (Beninger in prep.). Conversely, *N. defodiens* is not found in the bog, and does not reproduce outside of mixed forest habitat.

These two species were reared in the laboratory to address the following specific questions: Is the habitat specificity of the two species related to the type of substrate found in each habitat (sand or *Sphagnum* moss)? Is clutch size related to the size of the food resource (can females regulate brood size and larval weight)? Are growth rates and size of mature larvae the same for both species? Do adult *Poecilochirus carabi* mites feed on *Microphorus* eggs in laboratory cultures?

Materials and Methods

Establishment of cultures. Conspecific pairs of male and female *N. vespilloides* were allowed to locate and bury a CO₂ killed, previously frozen, mouse (*Mus musculus*) in the Mer Bleue bog overnight. Beetles were then removed to the laboratory and placed in plastic rearing containers (16 cm in height and 12 cm in diameter). The bottom of each container held moistened sand to a depth of 6.0 cm. The sand was sifted through a fine screen (1.0 mm² mesh) to a uniform consistency and then moistened with tap water before being placed in the containers. A fresh dead mouse of pre-determined weight was placed on the surface of the sand, and a male and female pair placed in each container. An aluminum screen, held in place by a strong elastic, covered the open end of the container and prevented escape of the beetles.

Cultures of *N. defodiens* were established in a similar manner. To duplicate the natural state as closely as possible, mites associated with the beetles were not removed prior to culturing. Later, mite-free cultures were established to examine the effect of mite predation. Cultures were watered at intervals to prevent desiccation.

Effect of substrate. *N. vespilloides*, would not breed in sand alone, but required moss on the surface of the cultures. Cultures of *N. vespilloides* therefore contained sand to a depth of 5 cm. covered by a 5 cm. deep layer of *Sphagnum* moss. Females of both species showed a

preference for oviposition in the sand rather than the moss, and this facilitated counting of the eggs; in nature *N. vespilloides* lays eggs at varying depths around and beneath the mouse in *Sphagnum* sp. moss. Cultures of the two species were divided into two sets: one set to rear larvae and the other to examine clutch size ($N = 5$ for each) .

Larval Rearing. Larvae were reared with adults ($N = 5$ cultures for each species). Eggs laid in these cultures were returned to the containers after counting. Cultures were examined every 24-h. and the weight of individual larvae in each brood recorded. At maturity, larvae were permitted to burrow into the sand. Over the following weeks some of these were examined to determine their stage of development (prepupa, pupa, teneral, adult).

Oviposition behavior. To determine clutch size the sand was initially examined for the presence of eggs at 24-h intervals. However, when we found that more than 48-hr were required for embryological development, cultures were examined every 48-hr to minimize disturbance.

To count eggs, beetles and moss were temporarily placed into separate containers and the sand placed on a clean sheet of cardboard. The sand was examined carefully, and eggs were counted, measured, weighed and placed in covered dishes with a small amount of moist sand from the original culture. Removed eggs were allowed to hatch to determine time to complete embryological development, but the first instar larvae were not fed. The sand and moss in all cultures were changed at two week intervals. Mice were replaced if the female stopped

ovipositing for two consecutive days. A clutch of eggs is therefore defined as the total number of eggs laid in this interval.

Mite predation. It was observed that *Poecilochirus carabi* (= *P. necrophori*) mites were feeding on *Nicrophorus* eggs in dishes that contained sand and eggs removed from the cultures. These mites consumed two *Nicrophorus* eggs, and were present in dishes from which eggs disappeared. It then became necessary to establish mite-free cultures to examine the effect of mite predation.

Establishment of mite-free cultures Five male and female pairs of *N. vespilloides* were selected for mite-free cultures. Three of these pairs were teneral males and females that had been laboratory reared. The other two pairs were tenerals caught later in the season. All *Poecilochirus* mites were removed with a fine brush while beetles and mites were anaesthetized on a plate perfused with CO_2 . The sand in these cultures was autoclaved, and the moss immersed in boiling water.

Many *Macrocheles* mites were attached underneath the elytra and could not be removed without endangering the life of the beetle through prolonged exposure to CO_2 . To minimize any effect of these remaining mites, the sand and moss were replaced daily with autoclaved sand and moss for one week. After this time the sand and moss were replaced weekly, and the cultures kept in trays filled with water to prevent re-contamination.

Mite-free cultures of *N. defodiens* were established in a similar manner with five pairs caught in the field.

Results

Burial behavior. Burying behavior differs between the two species. *N. defodiens* buried mice in sand to the maximum depth allowed by the containers, (6.0 cm) and bred freely with only sand in the cultures. In contrast, *Nicrophorus vespilloides* did not bury mice in the sand of the culture containers, and did not breed with only sand as a burial substrate. Only one of 10 initial cultures containing sand alone produced larvae. The mouse remained unburied even in this one successful culture. However, when moss obtained from the bog was laid on top of the sand, 4 of 5 later cultures produced larvae. *N. vespilloides* is known to bury mice deeply in *Sphagnum* sp. moss found in its natural habitat (up to 28.0 cm, pers. data).

Oviposition behavior. Females which were given fresh mice usually began to oviposit within a week and continued to oviposit for two to three days. After this there was a pause of two days to a week, during which no eggs were laid. The number of eggs laid by individual females for a given weight of mouse did not show a significant correlation with mouse size for *N. vespilloides* or *N. defodiens* (Figs. 18a-b). Mite-free and mite-contaminated cultures had insignificant correlation coefficients for clutch size and mouse weight.

Clutch Size. The first clutch size (mean = 30.7, S.D. = 10.8, N=12) was slightly larger than the second (mean = 27.8, S.D. = 10.3, N=12) for *N.*

Figs. 18a-c. Relationship between clutch size and amount of larval and adult food provision for *N. vespilloides* and *N. N. defodiens*.

Figs. 19a--b Larval growth rates for *N. vespilloides* and *N. defodiens*. Symbols represent different cultures.

vespilloides (mite and mite-free cultures combined) but this difference was insignificant ($p = 0.49$). For *N. defodiens* first and second clutch sizes did not differ significantly (mean = 23.0 and 23.4 respectively, $N=5$, $p = 0.963$). During the 3 month culture period the total number of eggs laid by an individual female *N. vespilloides* ranged from 33 to 175 eggs (mean = 86). Clutches ranged in size from only 2 eggs to over 50 for a single mouse, with a mean of 30.

Eggs recovered from *N. vespilloides* cultures varied in size from 1.9 to 2.5 mm in length, and from 0.77 mm to 0.96 mm in diameter and were off-white in colour ($N=20$). Eggs of *N. defodiens* were slightly smaller, 1.46 to 1.86 mm in length and 0.80 to 0.91 in width ($N=10$).

Growth Rate. The most striking result was the rapid growth of the larvae in the first few days after eclosion. *Nicrophorus vespilloides* reaches maximum larval weight in only five days at 21 C (approx 0.23 gms, Fig. 19), after which there is a small weight loss. The loss may be due to the energy expended when the larvae burrow into the soil after leaving the carcass (Fig. 19a) but more probably is caused by voiding of the gut prior to pupation (Pukowski 1933). There are three larval instars. Since the average weight of an egg for *N. vespilloides* is 0.0022 gms ($N = 60$) this represents a one-hundred fold weight-gain in only five days! The cultured *N. defodiens* show a similar pattern of larval weight gain, with exponential growth continuing into the third instar (Fig. 19b). However, mature larval weight is less for *N. defodiens*, averaging 0.12 gms compared to 0.23 gms for *N. vespilloides*.

One culture of *N. vespilloides* produced twelve teneral adults. Three male and female pairs of teneral adults were given mice and began to lay viable eggs within one week after removal from the sand. Based on this culture, the non-feeding third instar larval period is estimated to last from one week to ten days, and the pupal period is approximately the same. Time for development from egg to reproductively competent adult therefore averages 24 days for *N. vespilloides*.

Brood Size. Brood sizes for *N. vespilloides* were 22, 20, 10 and 11 larvae. There was some larval mortality in each brood, (2-4 individuals), but it is difficult to say whether these were natural or caused by stress when larvae were removed for weighing. The percentage of eggs that hatched is also uncertain, since only first instar larvae were observed for *N. vespilloides*. However, eggs were observed and counted for 3 cultures of *N. defodiens* in which larvae were reared. Many of these eggs did not hatch, probably because they became damaged during the time in which they were removed and counted. For example 8, 8, and 28 eggs hatched from cultures in which 23, 22, and 28 eggs were laid respectively.

Discussion

The two sister species prefer different substrates for burial of mice and reproduction. *Nicrophorus vespilloides* made no attempt to bury the carcass in sand and (with one exemption) did not breed except in the presence of a substrate layer of moss. The fact that *N. vespilloides*

will not breed without prior burial of a brood ball may be related to behavioral cues that stimulate ovary maturity (Wilson and Knollenberg 1984, Scott and Traniello 1987). However, the single case in which larvae were reared from an unburied mouse indicates that prior burial is not absolutely essential for reproduction in this species. In contrast *N. defodiens* readily buries the carcass in sand, and breeds in the absence of moss.

In Europe *N. vespilloides* buries mice only shallowly, underneath leaf litter in mesic forests (Pukowski 1933). Field studies indicate that *N. vespilloides* does not bury mice in the forest surrounding the Mer Bleue bog, but will bury mice as deep as 28 cm in *Sphagnum* sp. moss within the bog (Beninger in prog.). When enclosures were fitted with screens that limited the depth of burial to 15 cm, mice were invariably buried to the maximum depth allowed by the screen. This indicates that *N. vespilloides* can bury mice to considerable depths in its Nearctic habitat.

Two explanations can account for the difference in depth of burial between European and North American *N. vespilloides*. First, *N. vespilloides* may require yielding substrates, such as moss or leaf litter to bury mice. *Sphagnum* moss provides little resistance to burial, and in some areas of the Mer Bleue bog it can extend to considerable depths before becoming water saturated. This hypothesis is supported by the fact that this species does not bury mice in a sand substrate provided in the lab. However, it fails to explain why *N. vespilloides* does not bury mice (even under leaf litter), in the mixed forest habitat surrounding the bog.

Second, Nearctic *N. vespilloides* may bury mice deeply due to an adaptive change in behavior as it became sympatric with *N. defodiens*. The yielding substrate found in bogs may have initiated a behavioral change allowing *N. vespilloides* to bury mice deeply. Deeply buried brood balls are less subject to disturbance by invertebrates and vertebrates (Wilson 1983). Deep burial of mice was possible only in bogs, therefore this behavior removed *N. vespilloides* from interacting with forest inhabiting congeners such as *N. defodiens*.

The habitat preference shown by *N. vespilloides* in North America may therefore be directly related to the type of substrate found in bog habitats, or indirectly substrate related because of an adaptive change in behavior in response to competition with *N. defodiens*. This latter hypothesis is most tenable since it explains the absence of *N. vespilloides* in the forest around the bog, and also because in Japan *N. vespilloides* is known to vary in habitat association through interactions with other Silphid species (Katakura and Ueno 1985). In addition, *N. vespilloides* is not a bog specialist in the Palearctic where *N. defodiens* is absent.

Other aspects of the reproductive biology of *N. vespilloides* and *N. defodiens* do not contribute to an understanding of the habitat associations of these species, but provide useful data on resource utilization for comparison with other *Nicrophorus*.

The time for both species to reach maximum larval weight is remarkable, but not unexpected because of the nature of the food resource. *Nicrophorus* larvae must compete with decay bacteria, and

other invertebrate decomposers such as fly larvae. Therefore, very rapid development of the early larvae should be intensely selected for, particularly since fly larvae only require a few days to reach maturity (Putnam 1983). Pukowski (1933) also noted that the larvae of *N. vespillo* developed rapidly, although she only weighed three individual larvae at regular intervals and not the broods of several females. The rapid initial growth is followed by a period of rest in the third instar that lasts approximately one week. During this period of time the larvae become increasingly lethargic and lose a small amount of weight.

The number of larvae that eventually utilize a mouse may be reduced because of egg predation by the adult females of the mite *P. carabi*. Laboratory results suggest that mite predation is not significant, but more work is needed on the relationship between *P. carabi* and *Nicrophorus* beetles. *P. carabi* is known to breed freely on carcasses in the absence of *Nicrophorus* (Springett 1968), and has been found to enhance the reproductive success of *N. tomentosus* in the field (Wilson 1983) by preying on fly eggs. These mites may also have long term, indirectly beneficial effects on the fitness of *Nicrophorus* beetles (Wilson and Knollenberg 1987). It is also probable that *P. carabi* is a species complex rather than a single species (Wilson 1982, and E. Lindquist pers. com.). Another phoretic mite, *M. merdarius* may also prey on *Nicrophorus* eggs since it too is known to feed on eggs and first instars of fly larvae (Halliday and Holm 1987).

Females of *N. vespilloides* and *N. defodiens* do not regulate the number of eggs laid in relation to the size of the mouse. This result was unexpected because large food resources tend to favour large

clutches in models of insect oviposition (Parker and Courtney 1984). However, these models do not consider parental care of the brood. *Nicrophorus* beetles have evolved some K - selected strategies such as adult acquisition of larval food resources, and parental care. In addition, *Nicrophorus* beetles appear to optimize resource use by laying a second clutch on large resources, or culling the brood when the resource is small.

Müller (1987) found that if only a few larvae are allowed to utilize the food, or if the first clutch is removed, female *N. vespilloides* will optimize their resource use by laying smaller "replacement" clutches. In the present study *N. vespilloides* and *N. defodiens* did not lay smaller replacement clutches, probably because they were given fresh mice after each period of oviposition; the food source was therefore of high quality. Spicarova (1971) noted that dwarf individuals of *N. vespillo* are progeny derived from a second clutch of eggs laid by the female on the same food source. The food had been degraded by the first brood of larvae and also by bacterial decay. Therefore, the second brood lacked food of adequate nutritional content and developed into smaller larvae and adults. She also found that smaller adults resulted when many larvae from the first clutch competed for food. However, she did not rear larvae in isolation to more accurately determine the effects of this competition.

Bartlett (1987a) found that adults of *N. vespilloides* will eat some of the first instar larvae if a large clutch is laid on a small resource and most (or all) of the eggs hatch. Bartlett (1987a) believes that infanticide is practiced rather than oophagy because predation by

staphylinids may reduce egg survival. This behavior may not be restricted to *N. vespilloides*, and the presence of males may even result in overculling of the brood (Scott 1989).

In summary, clutch size is not correlated with size of the resource probably because *Nicrophorus* optimize resource use through infanticide and laying of second clutches.

Summary

- 1) *Nicrophorus defodiens* buries mice in sand and breeds in the absence of moss.
- 2) *Nicrophorus vespilloides* buries mice deeply and breeds in moss substrates, not sand. Substrate type alone can not account for the habitat specificity of *N. vespilloides*. Other ecological factors such as past competition with *N. defodiens* must also be considered.
- 3) The number of eggs laid by females of both species is not related to the amount of larval provisions.
- 4) The larvae of both species reach maximum weight within five days of hatching.
- 5) *Nicrophorus vespilloides* larvae weigh approximately twice as much as *N. defodiens* larvae at maturity.
- 6) Adult females of the mite *Poecilochirus carabi* (G&R Canestrini) were predaceous on the eggs of *N. vespilloides* in culture.

CHAPTER 5

PHORETIC MITES (ACARI) ASSOCIATED WITH *NICROPHORUS* BEETLES (COLEOPTERA, SILPHIDAE) OF THE MER BLEUE BOG AREA, WITH NOTES ON ADULT FEEDING BEHAVIOR OF *POECILOCHIRUS CARABI* G. & R. CANESTRINI (- *P.* *NECROPHORI* VITZTHUM) SENSU HYATT 1980 (MESOSTIGMATA, PARASITIDAE)

Introduction

Mites associated with beetles of the genus *Nicrophorus* form part of a unique ecological community that includes decomposer organisms such as bacteria, nematodes and fly larvae. *Nicrophorus* beetles re re competition with decomposers and scavengers by burying small carcasses which will serve as a larval food source (Pukowski 1933). The male and female both participate in feeding the brood and protect them from invertebrate predators (Pukowski 1933, Bartlett 1988). Mites associated with these beetles are generally phoretic, with most simply using the beetles as transport to new feeding and breeding sites. In the course of a study of the reproductive biology of *Nicrophorus* in the Mer Bleue area it was observed that mite infestations of collected beetles were extreme in some cases, and appeared to have adverse affects on their carrier's flight capabilities. It was therefore of interest to study the

relationships between these mites and their carriers. Some mite species were found to exhibit preference for attachment sites on the bodies of the beetles. The site preferences for three species of mites were photographed and described.

The deutonymph of *Poecilochirus carabi* G. & R. Canestrini (= *P. necrophori* Vitzthum sensu Hyatt 1980) is phoretic on *Nicrophorus* and is known to consume fly eggs and first instar larvae on carcasses located by *Nicrophorus* (Springett 1968). The consumption of fly eggs and larvae by the deutonymph is thought to benefit the beetles because fly larvae are then removed from competition with the beetles' brood for utilization of the food resource. The relationship between *P. carabi* and *Nicrophorus* beetles has therefore been described as mutualistic (Wilson 1983, Wilson and Fudge 1984a). In laboratory cultures of the current study female adults of *P. carabi* were observed to feed on the eggs of cultured *Nicrophorus*. This suggested that the adults are general in their feeding habits, and that the relationship between the mite *P. carabi* and *Nicrophorus* beetles may be more complex than previously believed.

Methods

Preparation of specimens. Beetles prepared for scanning electron micrographs were collected from the carcasses of mice in the field, preserved in 70% ethyl alcohol, air dried and placed in a humidor for 24 hours. Low voltage scanning electron micrographs were taken of uncoated specimens. Representative mites were also cleared and mounted

in Hoyer's medium on slides for examination.

Culturing of beetles. Laboratory cultures of two species of *Nicrophorus* beetles; *N. vespilloides* Herbst and *N. defodiens* Mannerheim were established from conspecific pairs which had each buried a mouse in the field. Mites associated with the beetles were not removed prior to culturing. Neumann (1943) was used to identify adults and deutonymphs of *P. carabi*. Identifications of other mite species were made by E. E. Lindquist and V. M. Behan-Pelletier of the Biosystematics Research Centre (Agriculture Canada) in Ottawa.

Feeding behavior of *P. carabi*. Adult females of *Poecilochirus carabi* were present in the sand of containers in which there was a known amount of egg mortality. Adults of this species were hypothesized to feed on *Nicrophorus* eggs. To test this hypothesis four small petri dishes (5.5 cm. diam.) containing moistened plaster of paris were prepared and an adult female *P. carabi* placed in each. The female *P. carabi* were removed from underneath or on top of the bodies of dead mice in the beetle cultures. A single *Nicrophorus* egg, layed less than 24 hrs previously, was placed in the center of each petri dish and the mites were observed continuously for 60-90 min in each trial. A final observation was made at the end of 24 hrs, and the trial was then terminated. Four deutonymphs of *P. carabi* cultures were also given a *Nicrophorus* egg in the same procedure described above.

Results

Mite species associated with *Nicrophorus*. Four species of mites were found to be associated with *Nicrophorus* beetles in the lab and field; *Pelzneria* nr. *crenulata* Scheucher, *Uroobovella* nr. *novasimilis* Hiramitsu, *Macrocheles merdarius* Berlese and *Poecilochirus carabi* G. & R. Canestrini (= *P. necrophori* Vitzthum).

Carrier site preference. The non-feeding, phoretic deutonymph (hypopus) of the mite *Pelzneria* nr. *crenulata* was found on the intersegmental area beneath the posterior lip of the pronotum. However, large infestations in lab cultures (Fig. 20c) and field specimens (Figs. 20a,b,d) indicate that this mite prefers to attach to intersegmental areas anywhere on the beetle.

Adults of *Macrocheles merdarius* were attached underneath the hind wing and on the dorsal surface of the abdomen of *N. vespilloides* recovered from the field (Figs 21a,b). In heavy infestations the entire surface underneath the wing was covered with these mites. It was not possible to remove these mites without damaging the beetle. The anterior extremities of the mites are attached firmly, probably by the chelicerae to the beetle. Figure 21b is a close-up of a single *M. merdarius* that appears to be using its chelicerae to grasp the intersegmental membrane of the fourth and fifth abdominal tergites. *M. merdarius* is known to feed on the eggs and first instar larvae of dung-breeding post flies (Halliday and Holm 1987). The feeding behavior

of this mite was not examined in this study, but since it feeds on fly eggs it may also feed on eggs of *Nicrophorus*.

The deutonymph of an undescribed species of *Uroobovella* attaches by an anal stalk to the legs of *N. orbicollis* (Fig. 22a). This mite most closely resembles *U. novasimilis* which is associated with *Nicrophorus* beetles in Japan. Its feeding habits are not known. The anal stalk consists of an extremely strong, yet flexible substance (Fig. 22d arrows) that makes removal of the mites extremely difficult.

The deutonymphs of *P. carabi* were not site specific, and did not have any special means of attachment to their beetle carrier. Individual mites were observed to move rapidly and often leave the beetle and then climb back on. The mites do not remain attached to the beetles after death.

Detrimental Phoresy. Deutonymphs of *P. carabi* are phoretically associated with *N. vespilloides* and *N. defodiens* beetles in the lab and field. In the field, the male beetle leaves the brood chamber shortly after the brood hatches but the female remains with the brood, feeding the early larval instars and defending them from predators (Pukowski 1933, but see also Bartlett 1988). Since the mites also breed underground on the carcass (Springett 1968), the departing male, and later female beetles, often carry with them large numbers of deutonymphs. The flying ability of the beetles sometimes appeared to be hindered by the large numbers of mites (pers. obs.). I have observed this with *N. vespilloides* and *N. defodiens* both in the lab and field. One male *N. defodiens*, which was captured near the soil surface

Figure Captions

Figure 20a-b. Lateral view of *Nicrophorus vespilloides* collected in the field showing heavy infestation of *Pelzneria* nr. *crenulata* hypopodes under the pronotal area.

Figure 20c. Lateral view of *Nicrophorus vespilloides* reared in the laboratory, demonstrating infestations of *Pelzneria* nr. *crenulata* hypopodes similar to 20a-b.

Figure 20d. *Pelzneria* nr. *crenulata* hypopodes found at intersegmental boundaries on abdomen of *Nicrophorus vespilloides* from the field.

for transport to carrion. Springett (1968) did not find reproduction of *Nicrophorus* to depend on the presence of these mites in the absence of *Calliphora* eggs. However, in cultures where *Calliphora* eggs were present and the mites absent, *Nicrophorus* failed to breed. Deutonymphs of *P. carabi* have been observed to feed on Diptera eggs laid on the carcasses prior to burial by the beetles (Springett 1968). Fly larvae are therefore removed as possible competitors with the beetle larvae for the food resource. Wilson (1983) was unable to confirm this behavior in his study. However, Wise et al. (1988) have observed deutonymphs and adults of another species of *Poecilochirus* preying on eggs and first instar fly larvae. Wilson (1983) also found, in field experiments, that the reproductive success of *Nicrophorus* increased in the presence of the mite. He therefore suggested that a mutualistic relationship exists between *Nicrophorus* and *P. carabi*.

In the present study adult female *P. carabi* fed on *Nicrophorus* eggs removed from culture containers. This suggests that egg feeding is not confined to the deutonymph stage and that eggs other than those of Diptera are subject to mite predation. Korn (1982a) found that adult females of *P. carabi* are so oophagous that they conceal their eggs from females of their own species. It is uncertain whether male adults also feed on *Nicrophorus* eggs. When adults of *P. carabi* were sampled, adult females were readily available but males were not observed. Female *P. carabi* are not parthenogenic (Korn 1982a) but there may be an artificial sex-ratio bias because of sex-related differences in developmental times. The development time from deutonymph to adult is shorter for males (Korn 1982b) but adult

Figure Captions

Figure 21a. Adults of *Machrocheles merdarius* attached to abdominal tergites 1,2 and 3 of *Nicrophorus vespilloides*.

Figure 21b. Adult female of *Machrocheles merdarius* attached to membranous area between fourth and fifth abdominal tergites of *Nicrophorus vespilloides*. Three of the smaller *Pelzneria* nr. *crenulata* hypopodes are also visible in the image.

Figure 22a. Deutonymphs of *Uroobovella* nr. *novasimilis* attached to underside of mesothorax and legs of *Nicrophorus orbicollis*.

Figure 22b. Close up of 22a. Arrows indicate anal stalks.

above a buried brood ball with a female and third instar larvae, was found to be carrying 355 deutonymphs of *P. carabi*. Similar infestations have been observed for *N. vespilloides* in the field. This number of phoretic *P. carabi* is even higher than those found among infested beetles (*N. defodiens*) in the laboratory (2 males carried 97, and 158 deutonymphs while 1 female carried 120).

Feeding Habits of *P. carabi*. Adult *P. carabi* were observed on the surfaces of mouse carcasses in the laboratory, and were also found on *Nicrophorus* eggs in the sand of culture containers. In four trials single adult female *P. carabi* were given *Nicrophorus* eggs. In two of these trials the *Nicrophorus* eggs were pierced and fed on by the adult *P. carabi* within five minutes. After locating the egg the mite moved over and around it, of legs using its most anterior pair of legs as feelers. Every second to two seconds the mite paused and applied its mouthparts to the egg. During each pause the gnathosoma remained in one position on the egg while the chelicerae executed rasping movements. About 2 min after locating the egg the mite pierced it near one of its poles, and the egg contents gushed over the anterior extremities of the mite. The mite then removed itself from the egg, and began to consume the egg contents from its underside and front legs. The chelicerae and front legs were employed as scoops to move material into the mouth. The mite returned twice to feed on the egg during the following 15 min., until about half of the egg was consumed. Finally, its body distended, the mite began to search for an escape

from the dish.

In the two trials in which adult female *P. carabi* did not consume an egg, they exhibited behavior similar to that described above. Once the mites located the egg they moved over and around it, pausing to apply the mouthparts as described above. They manipulated the eggs so much as to move them from the centre of the dish to the perimeter in both cases. However, despite what appeared to be repeated attempts to feed, the mites left the egg unconsumed after 24 hrs.

Attempts were made to photograph an adult mite feeding at a *Nicrophorus* egg using a polaroid camera mounted on a Nikon dissecting microscope. However, a high level of illumination was necessary and the mite avoided the illuminated area. Alternatively, if suddenly illuminated while probing the egg, the mite ceased this activity and retreated from the illuminated area before a photograph could be taken.

Deutonymphs of *P. carabi* removed from cultures did not exhibit the same behavior as adults when placed in petri dishes that contained a *Nicrophorus* egg. Deutonymphs actively explored the area of the dish and paused only for a second or two when they encountered the egg. After 24 hrs only one egg in the four dishes had been consumed. In this case the deutonymph had moulted to an adult female during the 24 hr experimental period, and the cast nymphal exoskeleton was found close to the remnants of the egg.

Discussion

Hypopodes of *Pelzneria* nr. *crenulata* were the smallest and most numerous form of mite found on *Nicrophorus* beetles. They are very difficult to remove because they attach to the beetle by means of adhesive organs on their anal plate. This mite prefers intersegmental areas as sites of attachment, but is not as site specific as *Machrocheles mordarius*. Yoder (1972) found that three species of *Nicrophorus*, *N. tomentosus*, *N. vespilloides* and *N. americanus* carried hypopodes of *P. crenulata* in Michigan. It is uncertain whether this species of *Pelzneria* is the same as that associated with *N. vespilloides* in the Mer Bleue area.

Machrocheles mordarius was one of two species of mite associated with the beetles that was site specific. Adults of both sexes of this mite were most often found underneath the wings on abdominal tergites one to three, but occasionally were attached to the intersegmental membranes of the upper abdomen. Site preference is probably dictated by the absence of sclerotization in these areas. Soft, membranous surfaces allow this mite to grasp firmly with its chelicerae, reducing the likelihood of dislodgement during flight. Borchers (1968) also noted that *Macrocheles* sp. preferred tergites one to three as attachment sites but also attached to spiracular openings. Yoder (1972) found that *Machrocheles vespillo* Berlese and *Machrocheles necrophoraphila* Yoder also attached to spiracular openings, perhaps because of the high humidity. These are probably the species of

Macrocheles which Borchers (1968) found attached to spiracles of *N.orbicollis*

The deutonymph of *Uroobovella* nr. *novasimilis* attaches by a strong anal stalk that makes removal of the mite almost impossible without damage to the beetle. It is not as site specific as *M. merdarius* but prefers the basal area of the legs, and underside of the pro- and meso-thorax. When the beetle locates a new carcass this mite may be able to disengage itself by molting to an adult (Lindquist pers. com. 1988).

The deutonymph of *Poecilochirus carabi* does not have special means of attachment, and moves freely over all surfaces of the beetle. As suggested by Wilson (1982) and Lindquist (pers. com. 1988) *P. carabi* may actually represent a species complex. Deutonymphs of *P. carabi* are phoretic on many species of *Nicrophorus* and utilize carcasses found by the beetles in which to reproduce.

Adult male and female *Nicrophorus* beetles in both laboratory and field frequently become so infested with the deutonymphs of *P. carabi* that flight seems difficult. Since *N. vespilloides* and *N. defodiens* are multivoltine (Anderson 1982a, and personal data) large numbers of phoretic mites may hinder them in their search for new carcasses to raise brood. Springett (1968) found that in the laboratory some beetles were infested with as many as 800 *P. carabi* mites, but most of the mites became dislodged within five minutes of flight. A similar case of detrimental phoresy has been described by Elzinga and Broce (1988) for house flies.

Korn (1983) found that *P. carabi* reproduced successfully in the absence of *Nicrophorus*, so the mites are dependant on the beetles only

for transport to carrion. Springett (1968) did not find reproduction of *Nicrophorus* to depend on the presence of these mites in the absence of *Calliphora* eggs. However, in cultures where *Calliphora* eggs were present and the mites absent, *Nicrophorus* failed to breed. Deutonymphs of *P. carabi* have been observed to feed on Diptera eggs laid on the carcasses prior to burial by the beetles (Springett 1968). Fly larvae are therefore removed as possible competitors with the beetle larvae for the food resource. Wilson (1983) was unable to confirm this behavior in his study. However, Wise et al. (1988) have observed deutonymphs and adults of another species of *Poecilochirus* preying on eggs and first instar fly larvae. Wilson (1983) also found, in field experiments, that the reproductive success of *Nicrophorus* increased in the presence of the mite. He therefore suggested that a mutualistic relationship exists between *Nicrophorus* and *P. carabi*.

In the present study adult female *P. carabi* fed on *Nicrophorus* eggs removed from culture containers. This suggests that egg feeding is not confined to the deutonymph stage and that eggs other than those of Diptera are subject to mite predation. Korn (1982a) found that adult females of *P. carabi* are so oophagous that they conceal their eggs from females of their own species. It is uncertain whether male adults also feed on *Nicrophorus* eggs. When adults of *P. carabi* were sampled, adult females were readily available but males were not observed. Female *P. carabi* are not parthenogenic (Korn 1982a) but there may be an artificial sex-ratio bias because of sex-related differences in developmental times. The development time from deutonymph to adult is shorter for males (Korn 1982b) but adult

longevity is similar for both sexes (Korn 1982a). Males will therefore initially predominate, but females may be more abundant later in the reproductive cycle. The failure to obtain males may therefore be related to the time when the cultures were sampled.

The results of this study are not conclusive but pose questions for further research. Future study should determine whether feeding on *Nicrophorus* eggs by adults of *P. carabi* occurs under natural conditions and if so, how this behavior affects fecundity of the beetles. Do deutonymphs and adults exhibit a preference for fly or beetle eggs? Are the effects of detrimental phoresy on individual beetles outweighed by oophagous behavior of the mites? Recent work by Wilson and Knollenberg (1987) suggest that while short term benefits are few, there may be adaptive long term benefits for the beetles. The symbiosis between *P. carabi* and *Nicrophorus* may therefore be more complex than previously believed. Answers to these questions will lead to a better understanding of the relationship that exists between *P. carabi* and *Nicrophorus* beetles.

Summary

- 1) Two of four species of mites phoretically associated with *Nicrophorus* exhibited carrier site preference.
- 2) Hypopi of *Pelzneria nr crenulata* are frequently found at intersegmental boundaries of the thorax and abdomen.

- 3) Adults of *Macrocheles merdarius* occur beneath the wings and on the dorsal surface of the abdomen.
- 4) The deutonymph of a new species of *Uroobovella* attaches by an anal stalk to the legs and ventral surface of *N. vespilloides*.
- 5) Deutonymphs of *P. carabi* are phoretic on *Nicrophorus* beetles and do not site specific on their carrier.
- 6) Adult females of *P. carabi* feed on the eggs of *N. vespilloides* in culture. This implies that these mites may have detrimental effects on beetle fecundity in laboratory culture.

CHAPTER 6

IS COMPETITION IMPORTANT IN STRUCTURING THE CARRION FEEDING GUILD OF THE MER BLEUE?

This final chapter is intended to summarize the findings of this study and to place them in the context of current thinking on the relative importance of competition in structuring natural communities. Some laboratory experiments were done in the present study, but these were not undertaken to directly observe the outcome of two species interactions. Rather, their purpose was to determine whether physical factors and reproductive behavior could shed light on the habitat associations of *N. vespilloides* and *N. defodiens*. I will therefore concentrate primarily on the field data in chapters one and two of the thesis.

As mentioned in a previous chapter, the relative importance of competition in the structuring of communities is an area of debate and intense research in ecology (Connor and Simberloff 1979, 1986, Strong et al 1979). Connell (1983) and Schoener (1983) reviewed the available literature and concluded that competition is present in the majority of studies. However Schoener's review was more exhaustive and he found competition to exist in a higher percentage of studies (see also Schoener 1985). In controlled laboratory experiments it has been

possible to demonstrate competitive exclusion (Gause 1934), or coexistence through resource partitioning (Ayala 1971). However, in field studies it has been extremely difficult to unambiguously demonstrate interspecific competition. Also, field studies tend to be descriptive, rather than experimentally manipulative and therefore are not predictive (Gaudet and Keddy 1988, Keddy 1989). In the following pages I will discuss how my results contribute an understanding of the importance of competition in the structuring of the carrion feeding community of the Mer Bleue.

The competitive structuring of communities is likely to be confined to smaller community units known as "guilds" (Arthur 1987). A modified definition of a guild is "any group of species that exploit the same type of resource". This is a functional, rather than taxonomic definition, therefore very different species may be grouped together to form a guild (Arthur 1987). Therefore, the carrion feeding guild of the Mer Bleue bog area is composed of two large groups, vertebrates and invertebrates. Carrion feeding vertebrates are probably not specialists on carrion and more likely are general scavengers or omnivores. In my study I did not attempt to identify the different subgroups of vertebrates, but I did find that the only two successful groups of invertebrate carrion feeders were *Nicrophorus* beetles and Diptera larvae. These two groups are unique in that carrion serves as a larval food source for them and is therefore essential for reproduction.

I have shown that vertebrates are the most successful scavenger group in two distinct habitats within the Mer Bleue area. The pattern of resource use among vertebrates, invertebrates, and *Nicrophorus* is not

statistically different between bog and ridge sites. However, among invertebrates, *Nicrophorus* beetles obtained more units of small mammal carrion for reproduction than Diptera. When a resource unit used by one group removes it from potential use by another group, the type of competition may be defined as exploitive (Arthur 1987). This definition therefore applies to carrion feeders of the Mer Bleue. However, the evidence for competition among these groups is indirect because the resource is not known to be limiting. Evidence for competition among *Nicrophorus* beetles and the problem of limiting resources will be discussed fully below.

The five *Nicrophorus* species of the Mer Bleue comprise a guild of closely related species that bury small vertebrate carrion for reproduction. It is within this guild that possible competitive interactions were examined in detail. The idea that competition is strongest between congeners because of their similar ecological requirements dates to Darwin (1859), and is still central to ecological thinking. I have shown that the five *Nicrophorus* species of the Mer Bleue area have definite spatial and temporal activity patterns of reproductive resource use that reduce interactions with congeners. However, this does not address the question of whether *Nicrophorus* beetles actually compete for their common reproductive resource. I will therefore define the conditions necessary for competition and determine whether the conditions are satisfied in this study.

Two conditions are necessary for two-species competition: both species must require the same resource, and that resource must be scarce

(limiting) (Pianka 1983). An alternate, and perhaps more useful formulation of the necessary conditions is: "overlapping unidimensional RUFs + resource limitation = competition" (Arthur 1987). "RUF" stands for "resource utilization function" and is defined as a plot of utilization against a quantitative resource variable. This definition is based on MacArthur's (1968) statistical treatment of the niche.

If competition presently occurs among *Nicrophorus* in the bog area, then individual species must overlap in their resource use, and the resource must be limiting. I will discuss below whether these conditions are met first for the sister species *N. vespilloides* and *N. defodiens*, and then for *Nicrophorus* species found on the ridge.

In this study I found that *N. vespilloides* rarely forages for large carrion on the ridge, and is reproductively isolated to its bog habitat. *N. defodiens* rarely forages for large carrion in the bog, and reproduces only on the ridge. Therefore these two species do not interact for a common reproductive resource (have non-overlapping RUFs) and consequently do not, at present, compete for that resource. I have implied that because these are closely related species, the observed habitat associations are the result of spatial partitioning of resources due to past competition.

The evidence in favour of past competition between *N. vespilloides* and *N. defodiens* is as follows. In Europe and Japan *N. vespilloides* varies in habitat preference through interactions with other species of *Nicrophorus* (Katakura and Ueno 1985) but is not a habitat specialist. The sister species, *N. defodiens*, is not found in Europe or Japan.

However, in North America *N. vespilloides* is broadly sympatric with the sister species *N. defodiens* but is highly habitat specific (Anderson 1982a, and personal data). In addition, both species concentrate their reproductive efforts exclusively in different habitat types in the Nearctic. Replacement over a short distance by congeneric species is not evidence in itself of competitive exclusion, and there may be other possible explanations such as food preference and physico-chemical tolerances (den Boer 1987). Since the reproductive resource (small vertebrates) is the same for both species in each habitat, food reference can be disregarded. Physical factors such as the substrate type available for burial may be part of the answer, but this does not explain why *N. vespilloides* does not bury mice on the ridge where the leaf litter layer is deep.

Perhaps, referring to "the ghost of competition past" (Connell 1980) removes the question from the realm of science (den Boer 1987). However, this is a reasonable interpretation of the data. Suggestions for further research include mark and recapture experiments where large numbers of one species are removed from one habitat and released in the other. Alternatively, it would be interesting to see whether *N. vespilloides* will expand its niche by trapping and removal of ridge species. These experiments would be relatively complex and require more than a single field season.

Microphorus species that occur on the ridge have definite daily and seasonal activity patterns that reduce interactions with other species. *N. sayi* and *N. tomentosus* are spring and fall breeders respectively, and

therefore interact minimally with *N. defodiens* and *N. orbicollis*. However, both of these species have been found in association with either *N. defodiens* or *N. orbicollis* on the same mouse carcass. In all cases with a definite outcome, the larger *N. orbicollis* was successful in taking over carcasses located by other species. Similarly, *N. orbicollis* and *N. defodiens* have the same seasonal activity pattern, but have distinct, non-overlapping nocturnal activity periods (Wilson et al 1984b). In Ottawa *N. defodiens* and *N. orbicollis* are equally successful in their overnight location of mice, but a portion of the carcasses located by *N. defodiens* are lost to *N. orbicollis*. The above species therefore overlap in their resource use to some extent, despite temporal resource partitioning. How great this overlap is remains to be seen. Therefore the first condition necessary for competition between species (overlapping resource use) is satisfied for *Nicrophorus* of the ridge.

The second condition, that the resource be limiting, is more difficult to address. Pukowski (1933) and Wilson et al (1984b) argue that the fighting behavior and abundance of *Nicrophorus* relative to their food source are indirect evidence of competition. Clearly, this evidence does not 'prove' the existence of competition because there is no quantitative data on the amount of resource available to *Nicrophorus*.

However, we may have to be satisfied with indirect evidence because of the logistic difficulties in trying to obtain accurate information on the amount of small vertebrate carrion available at any given moment in time. For example, small mammal populations are one source of carcasses for *Nicrophorus*. However, population estimates for these animals have extremely large variances due to the combined effects of emmigration,

immigration, natality, mortality etc. (Merriam 1988 pers. com.). What is needed is an extremely accurate picture of the population dynamics of a number of small vertebrate species in order to obtain an estimate of how many carcasses are available to *Nicrophorus* during a given study period. At present this information is lacking, and is unlikely to be obtained in the future.

Since the second condition for competition, resource limitation, has not been satisfied, I cannot state with certainty that competition, past or present, has been important in structuring the carrion feeding guild in general, or the burying beetle guild in particular. However, I can suggest that the pattern of resource partitioning within *Nicrophorus* is consistent with the hypothesis that competition has been important in structuring this guild. I cannot, however, validate the hypothesis.

In conclusion I would like to quote from Arthur (1987), who, I believe, best describes the difficulties encountered in the study of competition:

"As usual in ecology, laboratory experiments give us clear conclusions whose relevance to nature may be debatable, while field studies can hardly fail to be relevant in nature, but are rarely conclusive. Given such a situation, it is unwise to neglect either approach."

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APPENDIX

Table 1: Results From Baited Pitfall Traps

		Trap Site							
		1		2		3		4	
		# of indiv.	%	# of indiv.	%	# of indiv.	%	# of indiv.	%
May 06-10									
<i>N. sayi</i>		29	90.6	40	88.9	00	0.0	-	
<i>N. defodiens</i>		02	6.3	04	8.9	01	33.3	-	
<i>N. vespilloides</i>		01	3.1	01	2.2	02	66.7	-	
<i>N. orbicollis</i>		00	0.0	00	0.0	00	0.0	-	
May 29-30									
<i>N. sayi</i>		18	21.2	05	16.1	00	0.0	00	0.0
<i>N. defodiens</i>		04	4.7	05	16.1	00	0.0	00	0.0
<i>N. vespilloides</i>		00	0.0	01	3.2	12	100.0	00	0.0
<i>N. orbicollis</i>		63	74.1	20	64.6	00	0.0	00	0.0
June 10-14									
<i>N. sayi</i>		15	40.5	01	100.0	00	0.0	00	0.0
<i>N. defodiens</i>		11	29.7	00	0.0	00	0.0	00	0.0
<i>N. vespilloides</i>		00	0.0	00	0.0	01	100.0	00	0.0
<i>N. orbicollis</i>		11	29.7	00	0.0	00	0.0	03	100.0
July 8-10									
<i>N. sayi</i>		02	5.6	00	0.0	00	0.0	00	0.0
<i>N. defodiens</i>		01	2.7	00	0.0	00	0.0	00	0.0
<i>N. vespilloides</i>		05	13.9	00	0.0	19	55.8	00	0.0
<i>N. orbicollis</i>		18	50.0	01	8.3	12	35.3	00	0.0
<i>N. tomentosus</i>		10	27.8	11	91.7	03	8.8	06	100.0
Aug. 18-24									
<i>N. sayi</i>		00	0.0	02	22.0	00	0.0	00	0.0
<i>N. defodiens</i>		13	30.0	03	33.0	00	0.0	00	0.0
<i>N. vespilloides</i>		00	0.0	00	0.0	08	53.0	00	0.0
<i>N. orbicollis</i>		26	59.0	01	11.0	00	0.0	15	50.0
<i>N. tomentosus</i>		05	11.0	03	33.0	07	47.0	15	50.0
Sept. 20-24									
<i>N. sayi</i>		106	70.6	06	4.0	00	0.0	03	6.1
<i>N. defodiens</i>		04	2.6	01	6.7	00	0.0	00	0.0
<i>N. vespilloides</i>		00	0.0	00	0.0	00	0.0	00	0.0
<i>N. orbicollis</i>		14	9.3	08	53.0	02	100.0	16	32.6
<i>N. tomentosus</i>		26	17.2	00	0.0	00	0.0	30	61.3

Table 2: Ridge: Summary of Two Species Interactions

OVERNIGHT (June 1)	ONE WEEK (June 8)	TWO WEEKS (June 15)
species width	species width	species width
1 sayi f = 4.5 + 1 orbic f = 8.0	2 orbic m = 7.5 f = 6.5	1 orbic m = + f = 7.0 brood
1 defod m = f = 4.0	? ?	2 sayi m = 5.0 f = 5.5
(July 14)	(July 20)	(July 27)
1 defod f = 4.5	2 orbic m = 5.0 f = 7.0	Abandoned maggots
3 defod m = 4.0 f = 4.5 f = 4.5	1 orbic m = f = 6.5	orbic Brood
1 orbic f = 5.5	2 orbic m = 6.5 f = 7.0 1 defod m = 4.5	Removed verts
(Aug. 26)	(Sept. 1)	(Sept 08)
1 orbic f = 6.5	2 defod m = 5.0 + f = 4.0 1 orbic m = 7.0	Abandoned maggots
1 defod m = f = ?	2 orbic m = 6.5 f = 7.0	Removed verts
undiscovered	1 defod f = 3.5 + 1 tomen f = 6.0	Abandoned maggots
undiscovered	2 orbic m = 6.5 + f = 6.5 1 tomen m = 4.5	orbic brood

defod = *N. defodiens*
 orbic = *N. orbicollis*
 vesp = *N. vespilloides*

sayi = *N. sayi*
 toment = *N. tomentosus*

m = male f = female
 width = pronotal
 width

Table 3: Bog: Summary of Two Species Interactions

OVERNIGHT (June 15)	ONE WEEK (June 21)	TWO WEEKS (June 28)
species width 2 orbic f = 7.5 m = 7.0	species width 2 vesp m = 7.0 f = 6.0	species width 1 vesp f = 6.0 + brood
2 vesp m = 6.5 f = 6.0	1 orbic f = 8.0	Abandoned maggots
2 vesp m = 6.0 f = 5.0	2 orbic m = ? f = 7.0	Abandoned maggots
(Aug. 25) undiscovered	(Aug. 31) 2 tomen m = 5.5 f = ? + 1 vesp m = 6.0	(Sept 7) Removed verts
(Sept. 15) undiscovered	(Sept. 20) 5 toment m = 5.5 f = 6.5 f = 7.0 2f = ? + 1 vesp f = 6.0	(Sept 28) Abandoned maggots

Table 5: Summary of Data for Field-Collected Broods

<i>N. vespilloides</i>	N	Mean	STD	Min	Max	SE
Brood size	29.0	14.69	8.56	2.00	44.00	1.590
Mean wt.	27.0	0.201	0.049	0.128	0.309	0.009
Mouse wt.	29.0	24.10	4.624	18.50	38.00	0.859
<i>N. defodiens</i>						
Brood size	14.0	19.36	7.64	9.00	36.00	2.040
Mean wt.	14.0	0.142	0.036	0.087	0.232	0.009
Mouse wt.	14.0	24.54	4.834	18.00	33.00	1.292
<i>N. orbicollis</i>						
Brood size	9.0	12.22	4.41	7.00	19.00	1.470
Mean wt.	9.0	0.393	0.086	0.261	0.519	0.029
Mouse wt.	9.0	27.44	6.464	18.00	36.00	2.155
<i>N. tomentosus</i>						
Brood size	9.0	12.22	4.41	7.00	19.00	1.470
Mean wt.	9.0	0.393	0.086	0.261	0.519	0.029
Mouse wt.	9.0	27.44	6.464	18.00	36.00	2.155

Table 6: Brood Data for *N. vespilloides*

Culture 4					
Date	# Brood Recovered	Weight Smallest (gms)	Weight Largest (gms)	Weight of Brood (gms)	Mean Weight of Brood (gms)
June 17	22	0.0025	0.018	0.257	0.011
18	22	0.014	0.129	2.300	0.105
19	24	0.062	0.242	4.410	0.183
20	24	0.083	0.242	4.450	0.185
21	24	0.079	0.195	3.800	0.158
23	23	-	-	3.530	0.153
Culture 6					
June 12	20	0.008	0.030	0.45	0.023
13	22	0.055	0.123	2.80	0.127
14	22	0.055	0.205	4.13	0.188
15	23	0.071	0.200	4.95	0.215
20	23	0.090	0.246	5.00	0.217
Culture 7					
June 10	7	-	-	0.037	0.005
11	10	0.012	0.048	0.225	0.023
12	9	0.098	0.220	1.430	0.158
13	10	0.180	0.240	2.330	0.233
14	9	-	-	2.050	0.227
15	9	0.197	0.235	2.000	0.222
17	8	-	-	1.600	0.200
18	6	-	-	1.100	0.183
19	8	-	-	1.480	0.185
Culture 10					
June 10	11	-	-	0.185	0.017
11	10	0.105	0.175	1.130	0.113
12	10	0.213	0.271	2.410	0.241
13	10	0.224	0.291	2.690	0.269
14	10	-	-	2.250	0.225
15	10	-	-	2.300	0.230
17	6	-	-	1.400	0.233
18	6	-	-	1.350	0.225
19	6	-	-	1.420	0.236

Table 7 Clutch data Culture #1
N. vespilloides

Clutch data Culture #2
N. vespilloides

Egg Length (mm)		Egg Width (mm)		Egg Length (mm)		Egg Width	
1.9		0.9		1.8	2.1	0.5	0.8
2.5		1.0		1.5	2.1	0.3	0.8
2.2		0.9		2.0	0.9	0.5	0.8
2.2		1.0		2.3	1.6	0.8	1.0
2.0		0.9		2.0	1.9	0.6	0.9
2.0		1.0		2.0	2.1	0.8	0.8
2.0		1.0		2.0	2.1	0.8	0.8
2.0		1.0		2.0	1.8	0.9	0.9
2.5		0.9		2.0	1.9	1.0	1.8
2.1		1.0		2.0	2.1	0.9	0.6
<hr/>		<hr/>		<hr/>		<hr/>	
Mean	2.140		0.960	Mean	1.910		0.765
SD	0.212		0.052	SD	0.299		0.179
Min	1.900		0.900	Min	0.900		0.300
Max	2.500		1.000	Max	2.300		1.000
SEM	0.670		0.016	SEM	0.067		0.040
Total # eggs laid = 17				Total # eggs laid = 41			
Total weight = 0.042 gms				Total weight = 0.078 gms			
Mean weight = 0.0022 gms				Mean weight = 0.0021 gms			

Table 8: Brood Data for *N. defodiens*

Culture 1D					
Date	# Brood Recovered	Weight Smallest (gms)	Weight Largest (gms)	Weight of Brood (gms)	Mean Weight of Brood (gms)
June 17	28 eggs	-	-	-	0.0027
18	18	0.0065	0.019	0.233	0.013
19	21	0.010	0.112	1.700	0.081
20	20	0.073	0.146	2.300	0.115
22	20	-	-	2.050	0.103
Culture 2D					
June 16	22 eggs	-	-	0.050	0.0023
17	3	all approx. same		0.010	0.0033
18	8			0.245	0.0310
19	4			0.498	0.125
20	7			0.750	0.107
21	7			0.670	0.096
22	7			0.715	0.102
23	6			0.650	0.108
Culture 3D					
June 17	23 eggs			0.051	0.0022
18		a few eggs hatched			
19	8	0.013	0.037	0.210	0.026
20	8	0.023	0.085	0.580	0.073
21	8	0.033	0.110	0.780	0.098
23	7	-	-	0.650	0.093

Table 9: Clutch Data for *N. defodiens*

Egg Length (mm)			Egg Width (mm)		
1.74	Mean	1.66	0.83	Mean	0.86
1.56	SD	0.12	0.87	SD	0.12
1.67	Min	1.46	0.91	Min	1.46
1.67	Max	1.86	0.83	Max	1.86
1.74	SE	0.04	0.80	SE	0.01
1.63			0.87		
1.56			0.83		
1.46			0.87		
1.67			0.83		
1.86			0.91		

END

1|8|09|90

FIN