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Resource partitioning in the carrion beetle (Coleoptera:Silphidae) fauna of southern Ontario: ecological and evolutionary considerations

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Resource partitioning in the silphid fauna of southern Ontario is examined in detail, using baited pitfall traps placed in four different habitats. During 1979 and 1980, a total of 9549 specimens of Silphidae were collected, representing 12 species, of which 5 were in the subfamily Silphinae and 7 in the subfamily Nicrophorinae. The roles of different seasonal patterns, habitat specificity, and food type and size in resource partitioning are discussed for all species. At the subfamilial level, resource partitioning is accomplished through selection of different sizes of carcasses, while at the specific level, seasonal patterns and habitat specificity appear to be the primary means permitting coexistence.

In the Silphidae, competition for food resources appears to be the primary factor inducing ecological character displacement. The possible origins of patterns of resource use in this assemblage are discussed in an ecological and geological time framework.

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Le partage des ressources entre les membres de la faune silphidienne du sud de l'Ontario a été étudié en détail à l'aide de pièges à fosse appâtés placés dans quatre habitats différents. En 1979 et 1980, 9549 spécimens de Silphidae ont été capturés; parmi les 12 espèces représentées, 5 étaient de la sous-famille des Silphinae et 7 de la sous-famille des Nicrophorinae. Pour toutes les espèces, on discute du rôle de la distribution saisonnière, de la spécificité de l'habitat ainsi que du type et de la grosseur des carcasses, comme facteurs impliqués dans le partage des ressources. Au niveau de la sous-famille, les ressources sont partagées grâce au choix de carcasses de différentes tailles, alors qu'au niveau de l'espèce, des différences dans la distribution saisonnière et la spécificité de l'habitat semblent être les principaux moyens de coexistence.

Chez les Silphidae, la compétition pour les sources de nourriture semble être le facteur primordial produisant les divergences de traits écologiques. On discute des origines possibles des patrons d'utilisation des ressources chez ces insectes à l'échelle des temps écologique et géologique.

Introduction

Past studies of carrion communities have been concerned with such questions as faunal succession (e.g., Johnson 1974; Bornemissza 1957; Payne 1965; Howden 1950), general ecological interactions among all taxa (e.g., Pirone 1974; Cornaby 1974; Putman 1978; McKinnerney 1978) and faunal surveys (e.g., Payne and King 1969, 1970; Payne and Mason 1971; Payne et al. 1968). Walker (1957) has examined how certain environmental conditions affect the distribution of carrion-feeding arthropods in different habitats. Few works have been concerned with ecological interactions among closely related taxa or members of a specific taxon. Exceptions are studies by Denno and Cothran (1975, 1976) on the necrophagous calliphorid and sarcophagid flies, by Young (1978) on neotropical necrophagous scarab beetles, and by Shubeck (1968, 1969, 1971, 1976) on some of the Nearctic Silphidae.

Ecological interactions among European Silphidae, especially *Nicrophorus*, have been examined by Pukowski (1933), Mroczowski (1949), Théodoridès and Van Heerdt (1950), Paulian (1946), and Cantonnet and Lecordair (1947). The ecology of Japanese silphids has been well treated by Katakura and Fukuda (1975).

None of these studies, however, addresses the specific question of resource partitioning, even though the data are in many studies indicative of such a principle, probably resulting in reduced ecological interactions among closely related, coexisting taxa.

Recently, Schoener (1974) has reviewed literature on resource partitioning by both vertebrates and invertebrates, noting significant niche dimensions along which coexisting taxa usually space themselves such that competition is reduced. These dimensions are available habitat types, available food types and sizes, and possible patterns of seasonal and temporal activity (see also Pianka 1974). Little, however, is mentioned as to how the evolutionary history of assemblages can be inferred from present patterns of resource use.

The present study thus was undertaken to ascertain how the species of Silphidae in the eastern North American carrion feeding guild fill the available niche dimensions and whether the resultant patterns are

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indicative of resource partitioning. How these present patterns of resource use could be used to infer evolution of the species assemblage as a whole, when data are available on phylogenetic relationships of constituent taxa, is also discussed.

Area of Study

The area chosen was located northeast of Metropolitan Toronto, Ontario (Fig. 1). Four sites were selected on the basis of habitat differences and two baited pitfall traps were installed at each locality. Some characteristics of the four sites chosen were as follows.

Site No. 1: deciduous forest

This area was a lowland forest with rich, moist soil, high in humus content owing to abundance of leaf litter. The dominant tree species was *Acer saccharum*. Ferns were abundant in the early part of the season and the herb layer had a continuous moderate cover. There was a patchy distribution in the shrub layer, with most being *Cornus* or *Acer* saplings. The forest was situated in a river valley, with slopes having some *Tsuga canadensis* and less of a herb cover. On the slopes, soil was better drained and ferns were absent.

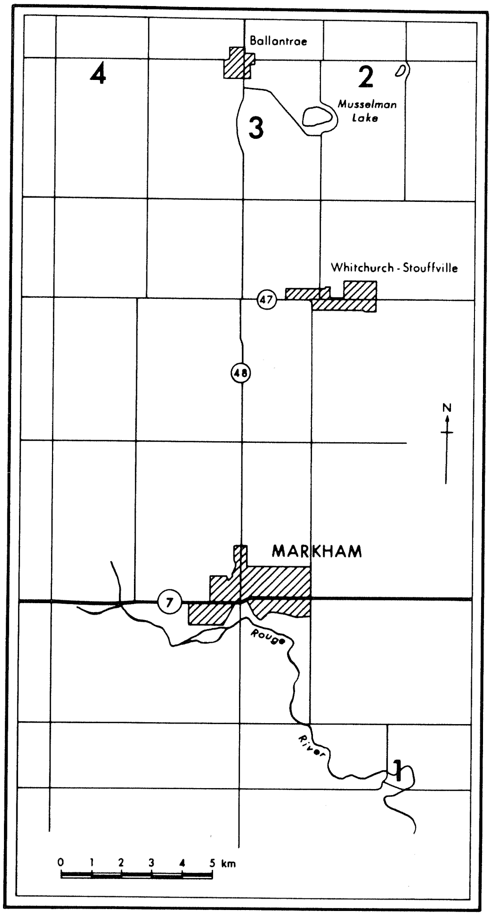


FIG. 1. Map of study area. Circled numbers indicate major highways. 1-deciduous forest site, 2-old field/meadow site, 3-marsh site, 4-coniferous forest site.

Site No. 2: old field and meadow

This area was an old field and a grassy meadow separated by a hedgerow approximately 4 m wide and extending the length of the field. The field was typical of a successional assemblage invading a cultivated lot that had been left unused for 4–5 years. There was a continuous herb cover which averaged about 1 m in height. *Solidago* spp. were common as were *Asclepias syrica*, *Verbascum thapsis*, *Daucus carota*, and *Linaria vulgaris*. Various grasses were present in the field and were the dominant, if not the sole, plants in the meadow. Identification of these grasses was not attempted.

Site No. 3: marsh

This area was a typical *Typha* marsh, which underwent a seasonal inundation, with water accumulating in the spring or after heavy rainfall. The cover was nearly 100% *Typha* spp. with scattered individuals of other herbs also being present. *Salix* sp. and *Populus tremuloides* were present deeper in the marsh, as were some scattered *Sambucus canadensis*.

Site No. 4: coniferous forest

This area was a red pine plantation with an extremely dry litter layer covering a very sandy soil. The understory was open and included scattered *Acer saccharum* and *Fraxinus americanus* seedlings. Herb cover was low and confined to the open canopy areas, which were either initially unplanted or were areas where trees had fallen.

Materials and methods

Beetles were collected in baited pitfall traps, 14 cm in diameter and 17 cm deep, with a 50:50 solution of water and ethylene glycol in the bottom into which the insects fell (Newton and Peck 1975; Southwood 1978). Each trap was baited with approximately 200 g of fish (white sucker, *Catostomus commersoni*) and serviced at weekly intervals, with the old bait being removed and replaced with fresh bait. The insects in the solution were sieved through a tea strainer and placed in formalin – acetic acid – alcohol (FAA) solution (Norris and Upton 1974, p. 11) to preserve the internal reproductive systems. The glycol was then poured back into the trap and the trap was reset. The same solution of glycol was used until it became noticeably diluted, whereupon it was replaced.

Silphids were sorted and removed from the trap residues and placed in a fresh solution of FAA. The residues were then discarded.

Sampling was begun on May 7, 1979 and terminated November 3, 1979. In 1980, the sampling was started earlier, since the traps of May 7 of the previous year were already capturing beetles. Sampling in 1980 began on April 12 and continued until May 24, thus providing the early season data which were lacking and enough of an overlap between the yearly sampling periods to permit year-to-year comparisons.

After 7 days in the FAA solution, the beetles were transferred to an 80% ethanol solution, wherein they were maintained until they were examined. Examination, following the methods of Barlow (1970, 1973), consisted of identification and enumeration of the adults and larvae of each species found in each trap, sexing of the adult individuals, enumeration of teneral individuals, and dissection of the females in order to ascertain their reproductive state.

These data were recorded on tables for each species collected and are presented here as graphs of the life history of each species (Figs. 2–18). Data used in the construction of these graphs represent pooled samples (two) from each site for each weekly period.

Classification of the taxa collected follows Portevin (1926) and Peck (1982).

Results

During the study, 9549 adult specimens representing 12 species of Silphidae were collected. Of these 12 species, 5 were members of the subfamily Silphinae and 7 members of the subfamily Nicrophorinae.

The most numerous species of silphine collected was *Oiceoptoma noveboracense*, followed by *Necrophila americana* and *Thanatophilus lapponicus*. The other two species, *Oiceoptoma inaequale* and *Necrodes surinamensis* were collected in small numbers.

The most commonly collected species of *Nicrophorus* was *N. tomentosus*, followed by *N. orbicollis*, and then *N. sayi*. *Nicrophorus marginatus* was also quite numerous, while *N. pustulatus*, *N. defodiens*, and *N. vespilloides* were rarely captured.

Relative abundance of all Silphidae collected is summarized in Table 1. The ecological attributes of all species collected are summarized in Tables 2 and 3.

TABLE 1. Relative abundance of the species of silphidae trapped during 1979 and early 1980

Silphinae	
Oiceoptoma noveboracense (Forster)	1908
Necrophila americana (Linnaeus)	1477
Thanatophilus lapponicus (Herbst)	616
Oiceoptoma inaequale (Fabricius)	51
Necrodes surinamensis (Fabricius)	11
Nicrophorinae	
Nicrophorus tomentosus Weber	2306
Nicrophorus orbicollis Say	1849
Nicrophorus sayi Laporte	1123
Nicrophorus marginatus Fabricius	125
Nicrophorus vespilloides Herbst	32
Nicrophorus defodiens Mannerheim	27
Nicrophorus pustulatus Herschel	26

Seasonal development and phenology

The most numerous silphine, *O. noveboracense*, was active very early in the season, with the first adults appearing in early to mid-April (Fig. 2). Many females carried eggs, indicative of reproductive activity. This was further evidenced by presence of larvae in the traps in early May (Fig. 14). Numbers of adults declined in June, with a subsequent peak of adult activity occurring throughout July. Many of these were teneral and thus probably the progeny of the early season generation. Activity declined into September and no eggs were laid or larvae noted at this time.

Necrophila americana exhibits a cycle similar to *O. noveboracense* except that emergence of overwintering adults began in mid-May, 2–3 weeks after emergence of the latter (Fig. 3). Egg-carrying females were numerous at this time and were present until early July. Throughout this same time larvae were numerous, but their initial appearance occurred noticeably later than for any other species for which larvae were recorded (Fig. 14). In late July through August, tenerals were present, indicative of emergence of the first brood of larvae. No eggs or larvae were noted at this time.

The other common silphine, *Thanatophilus lapponicus*, does not show a pattern similar to those already discussed. This species emerges early in the season, with the first adults appearing in mid- to late April (Fig. 4). The larvae are found in early May, the earliest silphine larvae to appear (Fig. 14). Egg-carrying females are also present at this time and continue to be present into early June. Tenerals first appear in mid-June and are present throughout the duration of adult activity which lasts until mid-September. The appearance of more egg-carrying females in late June and early July, along with the increased presence of larvae, is indicative of a second period of reproductive activity. Continued presence of tenerals, as well as occasional late season activity, is indicative of an overwintering adult stage.

The remaining two species of silphines were rarely collected, and thus patterns of development are difficult to document clearly. It appears that *O. inaequale* follows a pattern very similar to that of *O. noveboracense* (Fig. 5), with emergence of overwintering adults early in the season. Reproductive activity takes place at this time, with the emergence of the new brood of adults in July and August. *Necrodes surinamensis* was very rarely collected and little can be elucidated except that it is summer active (Fig. 6). The presence of tenerals among the first individuals to appear may be indicative of overwintering in a stage other than the adult.

Among nicrophorines, *N. tomentosus* emerges late in the season, with the first adults appearing in mid- to late June (Fig. 7). Tenerals were present at this time and continue through July and into August. Peak numbers of adults appear in mid- to late August, with activity continuing into September.

Nicrophorus orbicollis, in contrast to *N. tomentosus*, emerges early in the season with the first adults appearing in mid- to late May (Fig. 8). Peak numbers occur in early June through July, with tenerals appearing in early August and continuing into September.

The other common species, *N. sayi*, appears very

TABLE 2. Ecological charcteristics of eastern Canadian Silphinae

Species	Carcass size	Reproductive period	Habitat
Oiceoptoma noveboracense	Medium to large	Early spring	Primarily forests
Necrophila americana	Medium to large	Late spring to early summer	Primarily marsh
Thanatophilus lapponicus	Medium to large	Early spring and late summer	Primarily meadow or field
Oiceoptoma inaequale	Medium to large	Early spring	Primarily deciduous forest
Necrodes surinamensis	Large	Early summer	All types

TABLE 3. Ecological charcteristics of eastern Canadian *Nicrophorus* species

Species	Carcass size	Reproductive period	Habitat
Nicrophorus tomentosus	Small	Mid- to late summer	All types
Nicrophorus orbicollis	Small	Late spring to early summer	Primarily forests
Nicrophorus sayi	Small	Early to late spring	Primarily coniferous forests
Nicrophorus marginatus	Small	Early to late spring	Primarily meadow or field
Nicrophorus vespilloides	Small	Early to late spring	Marsh
Nicrophorus defodiens	Small	Early to late spring	Coniferous forests
Nicrophorus pustulatus	Small	Early to late spring	All types

early in the season, with the first adults appearing in mid-April (Fig. 9). Peak numbers occur soon afterward, followed by decline in activity into June. Tenerals appear in July, with activity increasing, continuing into October and November.

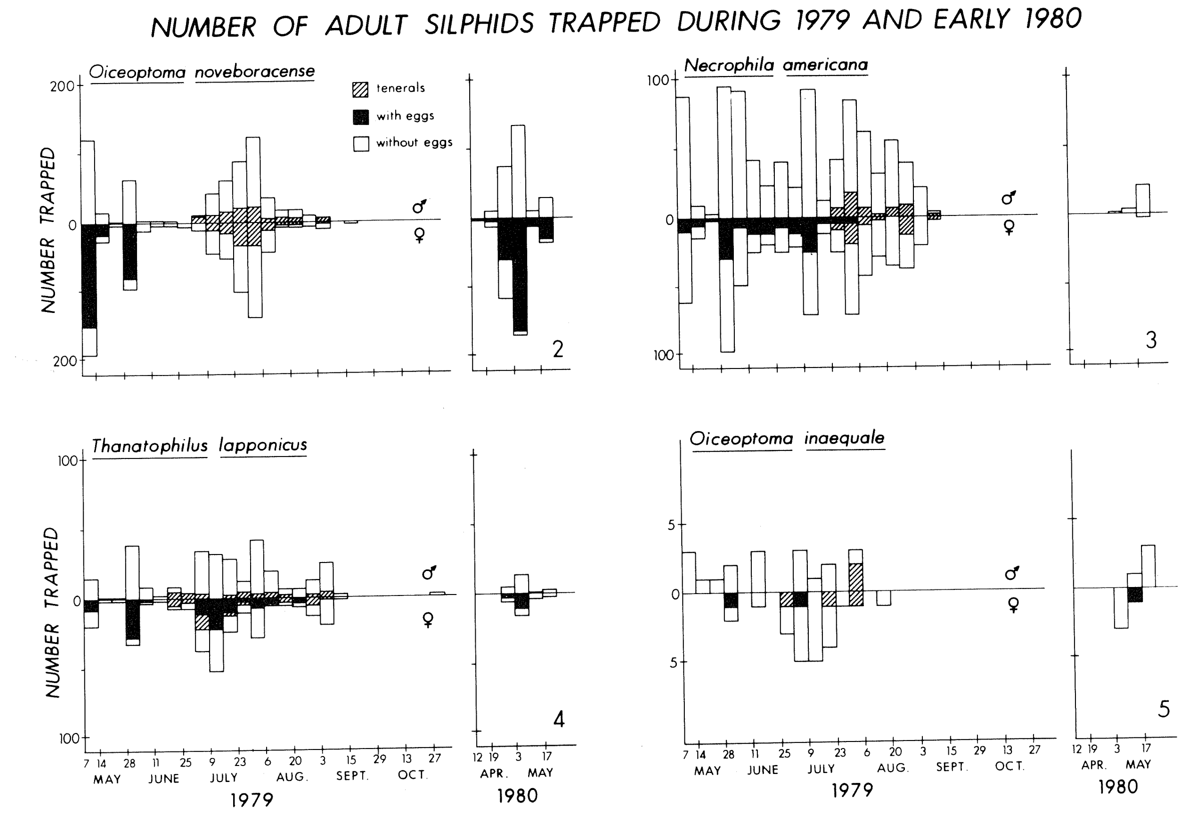
Nicrophorus marginatus is also an early emerger, with the first adults appearing in mid- to late May (Fig. 10). Activity declines throughout June, but increases in July and August. Tenerals are present in mid-July and in late August.

Of the rarer species, *N. pustulatus* first appears in early May (Fig. 11). Activity is initially sporadic but increases from mid-July through mid-September. Tenerals are present from mid-August through early September. Both *N. defodiens* and *N. vespilloides* appear to have similar patterns of activity. They are both active early in the season, however, *N. defodiens* (Fig. 12) appears later than *N. vespilloides* (Fig. 13). The former first appears in late May while the latter first appears in early May. They are both active throughout the summer although apparently sporadically. No tenerals were recorded for either species.

In all *Nicrophorus* females caught and examined, none were found to possess eggs.

Habitat associations

Among silphines, *O. noveboracense* was found in all habitats sampled (Fig. 15), although it was more common in the coniferous forest area. It was not commonly found in the marsh and was slightly more common in the deciduous forest than in the meadow. *Necrophila americana* was also found in all habitats sampled (Fig. 16), although in this instance it was much more common in the marsh. It is rare in the meadow and



FIGS. 2–5. Number of adult silphids trapped during 1979 and early 1980. Fig. 2. *Oiceoptoma noveboracense*. Fig. 3. *Necrophila americana*. Fig. 4. *Thanatophilus lapponicus*. Fig. 5. *Oiceoptoma inaequale*.

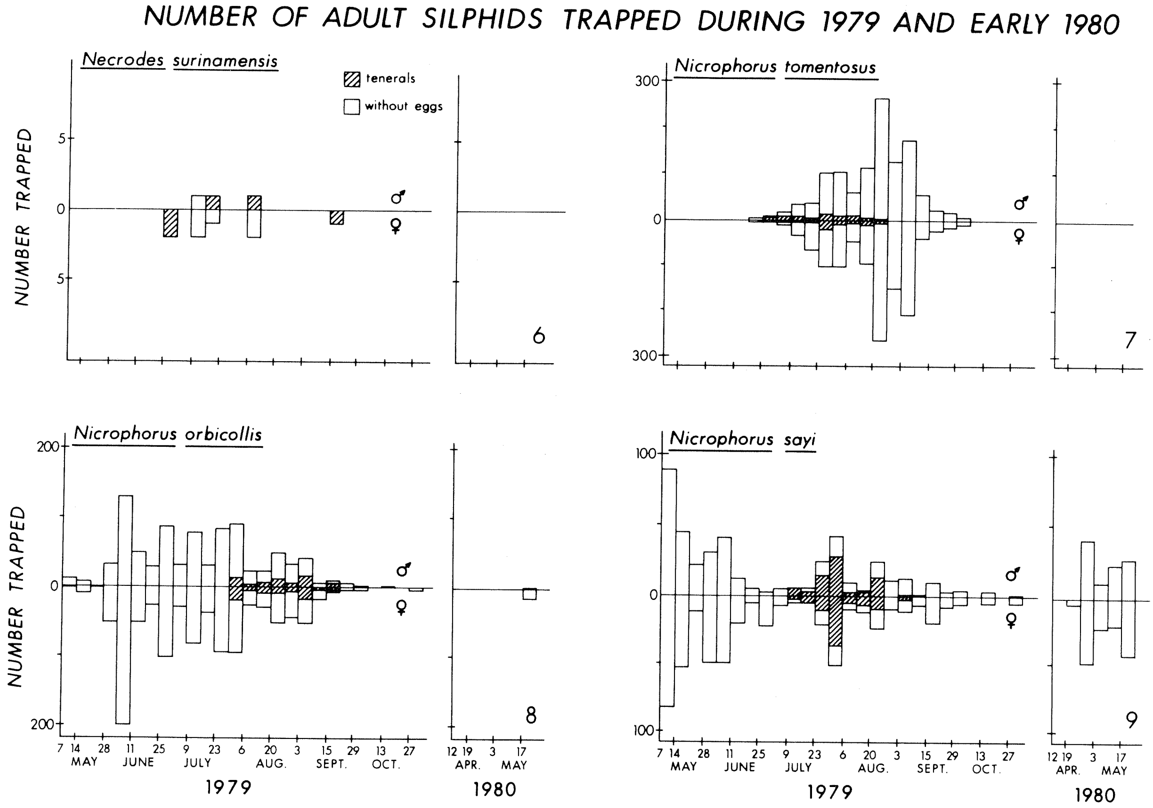
about equally abundant in the two forested areas. *Thanatophilus lapponicus* is found only in the open habitats (Fig. 15), being more common in the meadow than in the marsh. *Oiceoptoma inaequale* is found in the deciduous forest and in the marsh, however very rarely in the latter habitat (Fig. 15). *Necrodes surinamensis* is found in both the coniferous forest and the meadow (Fig. 16).

Among nicrophorines, *N. tomentosus* is found commonly in all habitats (Fig. 16), being more common in the coniferous forest and the meadow. In contrast to this is the pattern shown by *N. orbicollis* (Fig. 18). This species, although found in all habitats, is more common in the two forested areas. *Nicrophorus sayi*, like *N. orbicollis*, is more common in the forested areas (Fig. 18), although much more so in the coniferous forest. It is much less common in the open habitats than *N. orbicollis*. *Nicrophorus marginatus* is very habitat specific (Fig. 17). It is found only in the open habitats, with only very few individuals occurring in the marsh, as it was late in the season when the marsh dries up. Both *N. defodiens* and *N. vespilloides* are highly habitat specific. The former is found only in the coniferous forest (Fig. 17) and the latter only in the marsh (Fig. 18). *Nicrophorus pustulatus* is found in approximately equal numbers in the two forested areas (Fig. 17). It is also present in the meadow although not abundantly.

Discussion

In contrast to carabids,the subjects of previous phenological studies (e.g., Barlow 1970, 1973), the Silphidae possess acrotrophic ovarioles and thus the absence of a corpus luteum after eggs have been laid made it impossible to detect spent females. Thus, only three reproductive states could be recognized; teneral, nonteneral lacking eggs, and nonteneral possessing eggs. In *Nicrophorus*, only two of these states could be recognized, teneral and nonteneral, since no females of any species collected were found to possess eggs. This can be attributed to the life cycle and reproductive habits of these beetles.

Unlike the silphine females which lay their eggs in the soil around a food source that is exposed on the soil surface and used by many individuals, *Nicrophorus* adults bury the food source, and females lay eggs in a specially constructed underground chamber (Pukowski



FIGS. 6–9. Number of adult silphids trapped during 1979 and early 1980. Fig. 6. *Necrodes surinamensis*. Fig. 7. *Nicrophorus tomentosus*. Fig. 8. *Nicrophorus orbicollis*. Fig. 9. *Nicrophorus sayi*.

1933). After the carcass is buried, a period of inactivity precedes egg laying. During this period, when the adults can be seen to feed on the food source, eggs are probably matured. Since only a single pair of beetles will use a carcass, should more than a single pair find the same carcass, fighting takes place to determine possession of the resource. As in many anautogenous insects (e.g., mosquitoes and other blood-feeding groups), delayed maturation of eggs may be due to insufficient food reserves in the female which can only be replenished when a suitable food resource is acquired. Indirectly, this would ensure that a female, should she have to fight for possession of a carcass or forage extensively, would not have valuable energy prematurely stored in the eggs.

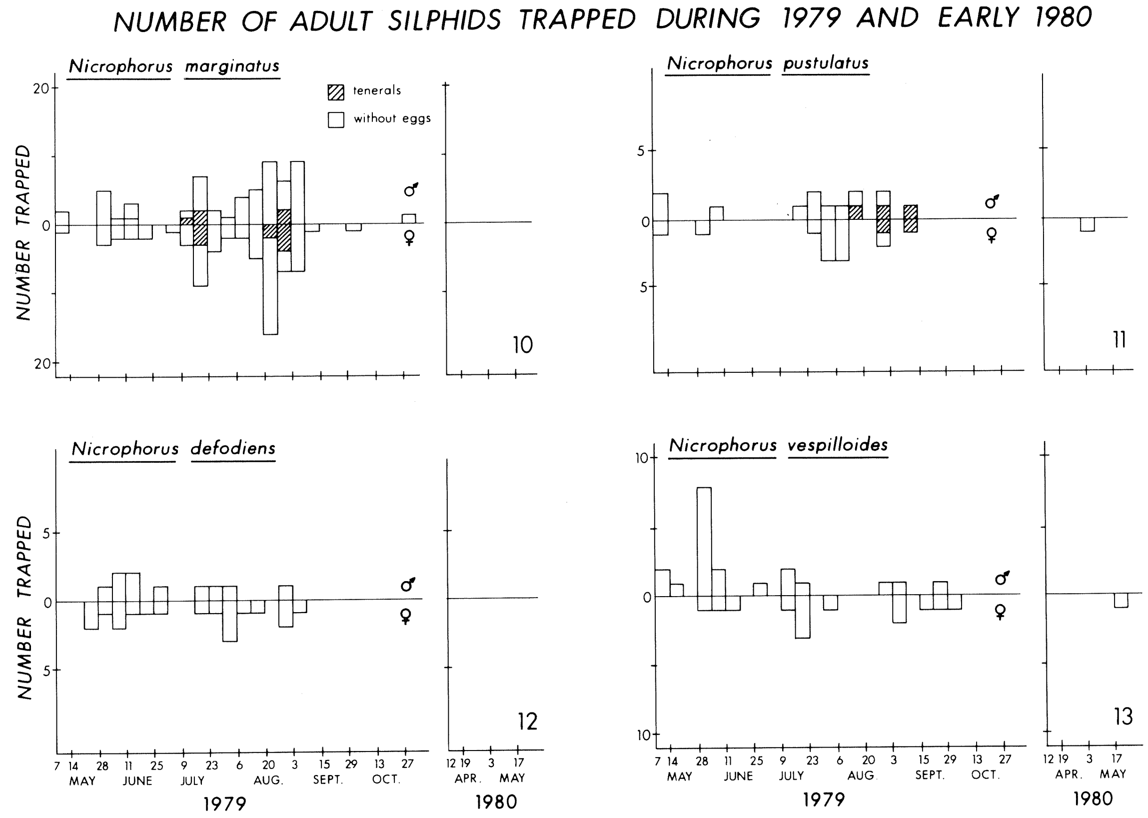
Niche dimensions of the assemblage

Schoener (1974) outlined the various niche dimensions commonly exhibiting variation such that coexistence can occur between closely related species. Closely related means that the taxa under study are in the same genus, family, and order and with no reference made to phylogenetic relationships among these taxa. Although the present study has only examined in detail the roles of seasonal patterns and habitat associations, discussions based on literature and my observations concerning the other niche dimensions are also included.

Food type and size

In the Silphidae, two patterns of resource use pertaining directly to the use of food for reproductive purposes have been developed. Both appear primarily concerned with minimizing interactions between the numerically dominant flies and the beetles.

Adults of the Silphinae arrive at a carcass during its early or middle stages of decay (Payne 1965; Johnson 1974). Eggs, which hatch in 4–5 days, are then laid in soil around the carcass. During this period flies also arrive and oviposit on the carcass. Fly eggs hatch almost immediately (Denno and Cothran 1975, 1976) and the larvae, often present in great numbers, begin to feed. These larvae digest their food externally, liquifying the decaying material with a digestive enzyme released through the mouth. This fluid is subsequently reingested by the larvae. They complete development rapidly, migrating from the carcass to pupate in 3–5 days, the time at which the silphid larvae are hatching. These



FIGS. 10–13. Number of adult silphids trapped during 1979 and early 1980. Fig. 10. *Nicrophorus marginatus*. Fig. 11. *Nicrophorus pustulatus*. Fig. 12. *Nicrophorus defodiens*. Fig. 13. *Nicrophorus vespilloides*.

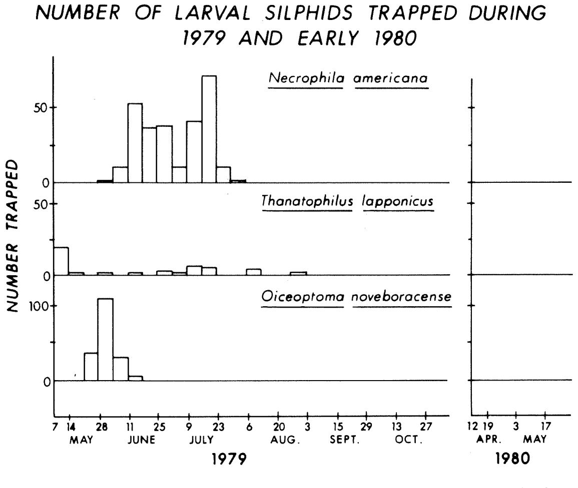


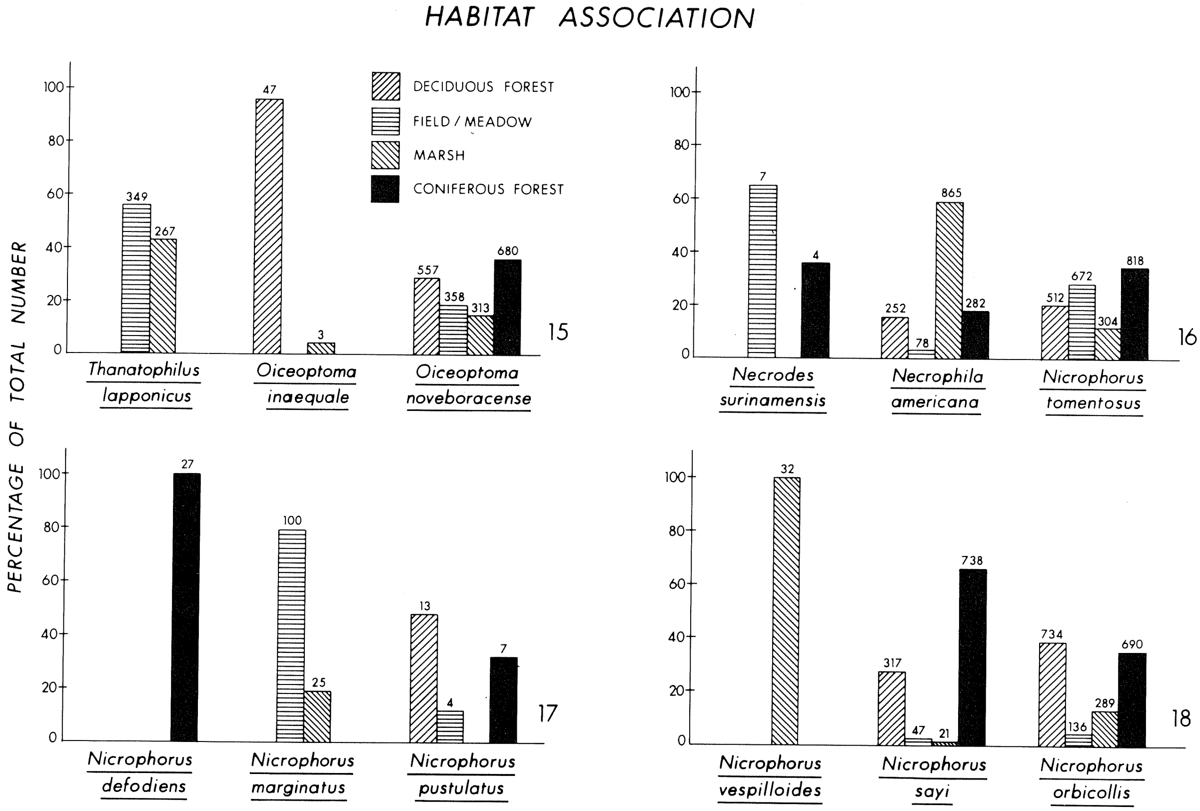
FIG. 14. Number of larval silphids trapped during 1979 and early 1980.

newly emerged larvae then feed only on that part of the resource not eaten by fly larvae, namely small pieces of flesh left on the bones and on the moist inside face of the skin (Dorsey 1940; Johnson 1974).

Silphines, especially *Necrodes surinamensis*, appear most commonly on large carcasses. This is due undoubtedly to the availability of food as smaller carcasses (e.g., mice or shrews) tend to have little useful material left after flies have finished feeding. Larger carcasses provide sufficient food resources for the large numbers of beetles that are usually present.

In contrast to the Silphinae, *Nicrophorus* adults avoid direct competition with the flies by getting to the food source before or concurrently with the flies. They then bury the carcass in the soil or under leaf litter, and at the same time they kill and eat any fly larvae that may be present (Steele 1927; Clark 1895). They also carry a load of phoretic mites which eat or destroy fly eggs and thus aid the beetles in providing a competition free environment in which to rear their larvae (Springett 1968). Once the carcass is buried, eggs are laid and the larvae, when they hatch, feed upon the carrion. Smaller carcasses are the only food resources capable of being used by the beetles, since larger carcasses would be impossible for the beetles to bury.

Within the higher taxa, there appears to be no resource partitioning with regard to food type or stage of



FIGS. 15–18. Habitat association. Fig. 15. *Thanatophilus lapponicus*, *Oiceoptoma inaequale*, *Oiceoptoma noveboracense*. Fig. 16. *Necrodes surinamensis*, *Necrophila americana*, *Nicrophorus tomentosus*. Fig. 17. *Nicrophorus defodiens*, *Nicrophorus marginatus*, *Nicrophorus pustulatus*. Fig. 18. *Nicrophorus vespilloides*, *Nicrophorus sayi*, *Nicrophorus orbicollis*.

decay. Shubeck (1976) has examined the possible existence of selection for poikilothermic or homeothermic carrion in the Silphidae. He found that there was little evidence to suggest selection was taking place, and that the beetles were probably using what was available. Similarly, work on succession of beetles on carrion (Johnson 1974; Payne 1965; Howden 1950) shows no differences between stage of decay at which specific species of silphids occur.

Patterns of seasonal and temporal activity

Most insect species reproduce seasonally, with peak periods of adult activity occurring only at certain times of the year. The results from the present study indicate that these periods are spaced along a seasonal niche dimension, a pattern that may permit coexistence.

In the Silphinae, *Necrophila americana*, *Oiceoptoma noveboracense*, and *Thanatophilus lapponicus* are reproductively active at different times of the year (Figs. 2–4, Table 2). This is especially evident for larvae (Fig. 14). *Thanatophilus lapponicus* adults are also reproductively active during a second period later in the year, a characteristic exhibited by no other species in this assemblage. This may be the result of the unpredictable and highly limited resource characteristics of the northern environments where most populations of this species live. Insects which survive there must be opportunistic and adapted for rapid reproduction. Other silphid species, most of which have distributions primarily centered in southern areas (Table 4), have only one generation per year.

Of the other two species, *O. inaequale* also appears to be an early season breeder (Fig. 5), a pattern supported by studies of Howden (1950) and Reed (1958), while the limited data about *Necrodes surinamensis* tend to demonstrate that it is active later in the season. In fact, Ratcliffe (1972) states that *N. surinamensis* is active throughout the entire summer season in most areas where it has been collected, probably breeding in spring and again later in the season. *Necrodes surinamensis* is rarely found on moderately sized carcasses such as raccoon, skunk, or groundhog, but is more often found in large numbers on large carcasses such as deer or bear, thereby probably avoiding competition with other sil-

TABLE 4. Distribution within North America of the species of Silphidae trapped during 1979 and early 1980*

Silphinae	
Oiceoptoma noveboracense	SE United States into SE Canada, west to Alberta
Necrophila americana	SE United States into SE Canada, west to Manitoba
Thanatophilus lapponicus	Canada and the montane areas of the western United States
Oiceoptoma inaequale	SE United States into extreme SE Canada
Necrodes surinamensis	Widely distributed, but only locally common in western United States and Canada
Nicrophorinae	
Nicrophorus tomentosus	SE United States into SE Canada, west to Saskatchewan
Nicrophorus orbicollis	SE United States into SE Canada, west to Saskatchewan
Nicrophorus sayi	SE United States into SE Canada, west to Alberta
Nicrophorus marginatus	Widely distributed except in northern Canada and the montane areas of the western United States
Nicrophorus vespilloides	Boreal North America, into the extreme NE United States
Nicrophorus defodiens	Boreal North America, the western coastal and montane areas and Appalachian states
Nicrophorus pustulatus	SE United States into SE Canada, west to Saskatchewan

*From Anderson (1981).

phines, which, although also found on the latter, are more frequently found associated with the former.

The distribution of *O. inaequale* (Table 4) and its absence in the study of Pirone (1974) indicates that the present study was carried out near the northern limit of its range. In southern areas, where it is more common, adults emerge earlier in the year than those of any other coexistent species (Howden 1950; Reed 1958). Possibly, environmental conditions associated with increasing latitude place restrictions on its life-history pattern, thus forcing it to occur at the same time as *O. noveboracense*, by which it is competitively excluded.

Past studies (Shubeck 1969, 1976; Pirone 1974) have noted patterns of seasonal development of *O. noveboracense* and *N. americana* to be similar to those recorded here; however, only Pirone briefly mentions the role of such patterns in resource partitioning.

Adults of many species of *Nicrophorus* appear to have reproductive patterns which overlap early in the year (Figs. 8–13, Table 3). Only *N. tomentosus*, which overwinters as a prepupa and not as an adult, is not present at this time. Adults of this latter species emerge later in the year (Fig. 7) when only *N. orbicollis* adults may yet be reproductively active.

Among the early season *Nicrophorus*, *N. sayi* is earliest, with adults becoming active in some instances while there is still snow on the ground. In this manner it appears to avoid competition with the other *Nicrophorus* adults, all of which become active about 2–3 weeks later.

Seasonal data indicate all species with the exception of *N. tomentosus* overwinter as adults.

In other geographical localities, Pirone (1974) and Shubeck (1969, 1976) have demonstrated patterns of seasonal activity for *N. tomentosus*, *N. orbicollis*, and *N. pustulatus* similar to those recorded here.

In short term temporal activity, most species of silphines appear to be diurnal (Shubeck 1971), with the exception of *Necrodes surinamensis*, while most species of *Nicrophorus* with the exception of *N. tomentosus* appear to be nocturnal. Since *Nicrophorus* adults can bury carcasses rapidly and thus reduce the chances of the carcass being found by a competitor, the diurnal habits of *N. tomentosus* may play an important role in resource partitioning.

Habitat associations

Availability of distinct habitats within an area offers another mechanism by which species partition resources and therefore coexist. By concentrating its reproductive activity in a single habitat, a species can minimize interactions with other species should they be associated with a different habitat. Even if they are not, concentration of reproductive efforts in a single habitat places selection pressures on other species to become habitat specific themselves (Atkinson and Shorrocks 1981; Shorrocks *et al* 1979).

Many species of silphids have distinct habitat associations, which when considered in conjunction with the seasonal patterns, eliminate ecological interactions by defining unique, nonoverlapping niches (Tables 2 and 3).

Of silphines, only *N. americana* and *O. noveboracense* occurred in all habitats, although *N. americana* was found more commonly in the marsh and *O. noveboracense* more commonly in the forests. Occurrence of both commonly in the same areas (Pirone 1974; Shubeck 1969, 1976) may be acccounted for by the seasonal differences. *Oiceoptoma inaequale* was also found in forests, although is rare in areas where *O. noveboracense* is common. *Thanatophilus lapponicus* is the only silphine found commonly in open habitats. The habitat associations of *Necrodes surinamensis* are unclear, but for reasons pertaining to food habits it would not appear to be in direct interaction with any of the other species.

Species of *Nicrophorus* also exhibit a high degree of habitat specificity with *N. marginatus*, *N. vespilloides*, and *N. defodiens* being found only in the meadow, marsh, and coniferous forest, respectively. *Nicrophorus marginatus* appears to be a prairie species that has spread eastward as man has provided cleared habitats, a route of dispersal that has been nicely treated by Lindroth (1971) for carabid beetles. *Nicrophorus vespilloides* and *N. defodiens* are primarily boreal in their distributions (Table 4), and appear to coexist throughout their ranges through differential habitat use.

The other four species are found in most habitats. *Nicrophorus tomentosus* is common in all habitats, a fact probably precipitated by its pattern of seasonal development. *Nicrophorus sayi* and *N. orbicollis* are both found primarily in forests, a fact which would reduce interactions with the other early season species.

In general, patterns of habitat association within the area of study appear to be consistent with expectations based on geographical distribution of the respective species (Table 4). Those species with distributions primarily in southeastern United States tend to be forest species, while those with northern distributions tend to be common in open habitats or coniferous forests.

Evolutionary considerations

To my knowledge, no rigorous data are available to demonstrate the abundance of carrion in nature. The fact that large numbers of silphid beetles (and other insects) can be consistently attracted by carrion bait, as was done in this study, indicates that either local populations of carrion beetles are high or that carrion is rare, or both. Regardless, the resultant effect is that food is in high demand and thus can be treated as a factor limiting population growth. Furthermore, like dung, fungi, and fruit, the random distribution in place and time and the ephemeral nature of the food resource would make it highly unpredictable and would necessitate extensive and efficient foraging.

In the silphids and other carrion-feeding insects, competition for these food resources is probably the most important factor responsible for the inducement of ecological character displacement. Predation pressures, which would operate to promote variation by selectively removing individuals of a species at a particular time or in a particular place do not appear to be important. The limited data on silphids indicates that they are avoided by birds in laboratory studies (Jones 1932), and are not known to be important in the diets of other vertebrate predators. Similar diel patterns and similar food habits of most species would also appear to expose all species equally to predation and thus exclude a predator from becoming species specific.

Similarly, the role of pressures acting to maintain or establish reproductive isolation does not appear to play a role in the present assemblage since only one pair of species, *N. defodiens* and *N. vespilloides*, appear to share a direct common ancestor in the strict phylogenetic sense.

These preceeding discussions center upon proximal factors that may determine structure of the silphid assemblage. They do not explain the origin of these factors. Notions about the latter must be developed in terms of a detailed reconstructed phylogeny of silphid beetles. Such is not currently available, but comparison of the distribution patterns of extant silphids with distribution patterns of various groups with which silphids are sympatric permits development of at least a general historical framework.

Preliminary phylogenetic analysis (Hennig 1966; Eldredge and Cracraft 1980) of silphid species whose distributions are consistent with the boundaries of the eastern deciduous forest region of North America (Table 4) reveals that many have their closest extant relatives in southeastern Asia or Europe (Anderson 1981). This pattern of relationship has been widely noted for other taxa as well, most notably angiosperms (Wolfe 1975, 1981). The most recently and widely accepted explanation of this vicariant pattern (Nelson and Platnick 1980) is that the vicars are isolated remnants of an ancestral assemblage of taxa or community which was widely and uniformly distributed far to the north during Eocene time (Wolfe 1975; Matthews 1979). Subsequent cooling trends led to divergence in the constituent taxa as environmental characteristics changed. Such changes also caused extinction of many populations, and brought about the vicariance that is now seen. It seems unlikely that the highly congruent pattern demonstrated by these assemblages of isolates could have resulted purely from random dispersal within Holarctica.

Thus, possibly the assemblage of silphids of temperate eastern North America has exhibited phyletic consistency for an extended period (i.e., at least since the Eocene). Similar ecological interactions among the taxa may also have been maintained for this period; however, such an inference could only be made if the European and (or) southeast Asian assemblages of silphids should demonstrate similar patterns of resource use among similarly related taxa to those studied in North America. These similarities, if found, would further serve to support the hypothesis of an early origin of the assemblage because the extant patterns would have already evolved prior to time of vicariance, and would not have been recently, independently derived in each extant assemblage.

Long duration of association of the eastern deciduous forest species would also support the concept of a closely associated, coevolved complex of species (Rosenzweig 1975) rather than a random association where the constituent taxa would each exhibit close relationships in geographically and ecologically different areas (MacArthur and Wilson 1967).

Although the deciduous forest complex of species may have been assembled long ago, other species now occurring in the east were probably not part of this assemblage as evidenced by their diverse habitat associations and widespread distributions. Contact between these species and those of the eastern assemblage has been made more recently, probably as a result of colonization as Pleistocene ice retreated, and so the resulting ecological relationships must have developed more recently also. I believe, therefore, that part of the ecological relationships among silphids in eastern North America is to be explained by events that happened during geological time, and another part by events that happened in recent ecological time.

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