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The Silphidae (Coleoptera) of the Maritime Provinces of Canada

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ABSTRACT

The carrion beetle (Silphidae) fauna of the Maritime Provinces of Canada is surveyed. Eleven species are found in the region, and they are all present in all three provinces and on Cape Breton Island. As a result of this survey, five new provincial records are reported; *Necrophila americana, Thanatophilus lapponicus, Nicrophorus pustulatus,* **and** *Nicrophorus sayi* **are newly recorded in Prince Edward Island, and** *Nicrophorus investigator* **is newly recorded in New Brunswick. Additionally,** *N. sayi* **is newly recorded from the Îles de la Madeleine,** *Nicrophorus orbicollis* **is newly recorded from Cape Breton Island, and** *N. investigator* **is newly recorded from the mainland of Nova Scotia. Historical reports of one species, the endangered** *Nicrophorus americanus*, **are reviewed with the conclusion that there is no verifiable evidence that it has ever occurred in Nova Scotia.**

Although all species feed and breed on carrion, there are nevertheless substantial differences in their developmental biology, behavior, seasonality, diel activity, habitat preferences, the particular carrion resources they utilize, and other aspects of their biology that allow them to differentially utilize this resource. The general features of the biology of the two subfamilies, the Silphinae and Nicrophorinae are reviewed, and in individual species accounts, particular aspects of each species are highlighted. The distributions of all species are mapped, and the relative abundance and seasonal distribution of species are graphed. Aspects of resource partitioning, competition, and niche width of the species are discussed. To assist in identification, a key to species found in the region is provided, as are colour habitus photographs of all the species.

RÉSUMÉ

Les silphidés (Silphidae) des Provinces Maritimes du Canada sont recensés. Onze espèces sont trouvées dans la région et toutes sont présentes dans les trois provinces et sur l'Île du Cap Breton. Par cette étude, cinq additions à la faune provinciale sont rapportées; *Necrophila americana*, *Thanatophilus lapponicus*, *Nicrophorus pustulatus*, **and** *Nicrophorus sayi* **sont nouvellement signalée dans l'Île du Prince Édouard, et** *Nicrophorus investigator* **est nouvellement signalée en Nouveau Brunswick. Aussi,** *Nicrophorus sayi* **est nouvellement signalée en l'Île de la Madeleine,** *Nicrophorus orbicollis* **au Cap Breton, et** *Nicrophorus investigator* **en Nouvelle-Écosse continentale. Les données historiques sur** *Nicrophorus americanus*, **une espèce en voie de disparition, sont passées en revue pour conclure qu'il n'y a aucune évidence vérifiable que ce phénomène se soit produit en Nouvelle-Écosse.**

Bien que toutes les espèces s'alimentent et se reproduisent sur des charognes, des différences

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substantielles existent néanmoins au niveau de leur biologie développementale, leur comportement, leur saisonnalité, leur activité diurne, leur préférence en termes d'habitat, le type de charogne qu'elles utilisent, ainsi qu'au niveau d'autres aspects de leur biologie qui leur permettent d'utiliser cette ressource. Les caractéristiques générales de la biologie de deux sous-familles, les Silphinae et les Nicrophorinae, sont passées en revue et des aspects particuliers à chaque espèce sont soulignés. La distribution de chaque espèce est cartographiée et l'abondance relative, de même que la distribution saisonnière des espèces sont illustrées. Différents aspects du partage de la ressource, de la compétition et de l'étendue de la niche des espèces sont discutés. Pour faciliter l'identification, une clé des espèces de la région est fournie, de même que des photographies couleurs de l'habitus de l'ensemble des espèces.

INTRODUCTION

The Silphidae (carrion beetles) is a widely distributed family consisting of 15 genera and about 180 species worldwide. The Silphinae, with 12 genera and 111 species, occur primarily in the Northern Hemisphere. The Nicrophorinae include the Asian genera *Eonecrophorus* and *Ptomascopus*, and the widely distributed genus, *Nicrophorus*, which includes 68 species worldwide (Sikes 2008). In North America 30 species in eight genera have been recognized (Peck 2000). Campbell (1991) reported 25 species in Canada, including ten from New Brunswick, 11 from Nova Scotia, and seven from Prince Edward Island.

The biology of the Silphidae exhibits many complex and fascinating features, differing substantially between members of the two subfamilies, the Silphinae and the Nicrophorinae. The life cycle of species in the Silphinae is generally less complex. When adults find suitable carrion they mate and females oviposit in surrounding soil. Larvae hatch in 2–7 days and begin to feed on the carcass. There are three instars lasting 3–10 days. Larvae then pupate in the surrounding soil and adults emerge in 14–21 days (Anderson and Peck 1985). They avoid competition with Diptera larvae on carrion by waiting until the majority of fly larvae move into the soil to pupate, approximately 5 days after oviposition (Anderson and Peck 1985). The silphine larvae then feed on the remaining carrion. There are no documented larval-parental interactions (in contrast to *Nicrophorus* spp.), and phoretic mites are largely absent. Adults are sometimes found in association with dung or garbage but seldom breed there. Different species partition food resources through differential use of habitats and different seasonal patterns of development (Anderson and Peck 1985).

The biology of *Nicrophorus* spp. is significantly more complex. The following account is largely based on Anderson and Peck (1985), Trumbo (1992), Scott (1998), and Trumbo and Bloch (2000). Adults generally seek out smaller carrion (4–300+ gm, the size range varying from species to species), typically small mammals such as mice and voles, or small passerine birds. When a male-female pair (or sometimes more individuals) finds such a carcass they either attempt to bury it, or move it to a substrate suitable for burial (hence the common British name of "sexton beetles"). They do so by burrowing underneath the carcass and pushing the soil out on one side. In this way the dead animal slowly sinks into the ground, later to be covered by displaced soil. Some species only partially excavate a carcass, leaving it in a trench, which is then covered, by leaves and other debris.

A principal objective of such behavior is to hide the carcass from potential competitors such as dipteran larvae, other carrion beetles, and vertebrate scavengers. Phoretic mites are invariably present on adult beetles. These mites, in the families Parasitidae, Anoetidae, Uropodidae, and Macrochelidae, and particularly *Poecilochirus* spp. in the Parasitidae, feed on fly eggs and are involved in a symbiotic relationship with the beetles (Springett 1968). The mites destroy eggs that would otherwise hatch into maggots; competitors for the carrion resources, while the *Nicrophorus* beetles transport the mites to spatially and temporally scattered food sources that would otherwise be unavailable to the mites.

On smaller carcasses, intra-sexual fighting commences until only a single male-female pair remains. On sufficiently larger carcasses, where the amount of carrion exceeds the maximum brood potential of a single female, more than one pair of beetles may succeed in utilizing the carcasses for breeding. Trumbo (1992) described this breeding system as facultatively quasisocial. Displaced females may linger near the carcasses for some time and attempt brood parasitism whereas displaced males may also linger adopting a satellite strategy and attempting to mate with the dominant female.

Once buried, the victorious beetles excavate a brood chamber around the carcass, strip it of hair or feathers, shape it into a sphere, and deposit oral and anal secretions on this brood ball which help delay decomposition. The

female then excavates a lateral passage from the brood chamber where she lays eggs. The clutch size varies from species to species, and also depends upon the size of the carcass. A smaller number of eggs are laid when carcasses are smaller. Non-dominant females, of the same or even different species, may attempt brood parasitism since newly hatched larvae (even of different species) are accepted by brooding females during a specific time window.

When the altricial larvae hatch they are initially fed by trophallaxis by one or both parents with a liquid regurgitated by the adults. After several hours the larvae begin to feed on their own entering the carrion ball through a hole chewed in the exterior by the female. Larvae are also sporadically fed by adults following their first and second moults. Parents regulate their brood size according to the size of the carcass, both by limiting the number of eggs that are oviposited, and also through selective infanticide so that larvae reared on carcasses of different sizes disperse from it at maturity at equivalent weights. Mature larvae (after three instars) disperse from the brood chamber into the surrounding soil and either pupate, emerging as adults in 13–15 days, or else hibernate as pre-pupae, pupating and emerging the following spring.

The breeding systems of *Nicrophorus* beetles have been extensively investigated. There are other aspects of this complex biology and variation amongst species. Different species vary their developmental biology, behavior, seasonality, diel activity, habitat preferences, the particular carrion resources they utilize, and other aspects of their biology, in such way as to partition this resource into a variety of spatial and temporal niches that each species exploits with differential efficiency.

In the Maritime Provinces, there are 11 species of silphids, four in the Silphinae and seven in the Nicrophorinae (Table 1). Six of these (*Necrodes surinamensis* (F.), *Necrophila americana* (L.), *Oiceoptoma noveboracense* (Forster), *Nicrophorus orbicollis* Say, *Nicrophorus tomentosus* Weber, and *Nicrophorus vespilloides* Herbst) were reported from Nova Scotia as early as Kirby (1837) and *Thanatophilus lapponicus* (Herbst) was recorded by both Jones (1869) and Evans (1899), an indication of the early prominence of this group of beetles. By the time of Anderson and Peck's (1985) survey of the carrion beetles of Canada and Alaska, all 11 species were known from the region, however, in the past 26 years more information has been amassed about the composition, distribution, abundance, and phenology of silphids in the region. This study, reports on these new findings.

METHODS AND CONVENTIONS

The taxonomy and nomenclature employed in this study follows that of Anderson and Peck (1985). Specimens of Silphidae originating from Atlantic Canada were examined and identified. A total of 3,287 specimens were examined; 2,810 from Nova Scotia, 328 from New Brunswick, 147 from Prince Edward Island, and 2 from the Îles de la Madeleine, Québec. Abbreviations of collections (largely following Evenhuis 2011) referred to in the accounts below are:

The seasonal distribution of species records (Figures 4 & 10) was compiled by summing all the records for which there was sufficiently precise data on collection date. This includes records collected by many investigators from across the region and collected by many different techniques (pitfall traps, carrion traps, flight intercept traps, at lights, by hand, etc.) over more than a century. The figures are an approximation of true phenology, but suffer from the vagaries of the collecting record. Despite these limitations, the results are the best information specifically available for the Maritime Provinces region, and the seasonal distribution patterns derived from these data closely parallel the seasonality of each species as reported by Anderson and Peck (1985). Similarly the relative abundance figures (Figures 3 & 7) derive from a summation of all historical and contemporary data from throughout the region and also suffer from the vagaries of the collecting record and the techniques used to collect specimens.

ACNS	Agriculture and Agri-Food Canada, Kentville, Nova Scotia, Canada
ACPE	Agriculture and Agri-Food Canada, Charlottetown, Prince Edward Island, Canada
CBU	Cape Breton University, Sydney, Nova Scotia, Canada
CGMC	Christopher G. Majka Collection, Halifax, Nova Scotia, Canada
CNC	Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, Ontario, Canada
DHWC	David H. Webster Collection, Kentville, Nova Scotia, Canada
FNP	Fundy National Park Collection, Alma, New Brunswick, Canada
GSC	Gary Selig collection, Bridgewater, Nova Scotia, Canada
JCC	Joyce Cook Collection (now at the New Brunswick Museum, Saint John, New Brunswick, Canada)
JOC	Jeffrey Ogden Collection, Truro, Nova Scotia, Canada
MTC	Martin Turgeon collection, Saint-Basile, New Brunswick, Canada
NBM	New Brunswick Museum, Saint John, New Brunswick, Canada
NSAC	Nova Scotia Agricultural College, Bible Hill, Nova Scotia, Canada
NSMC	Nova Scotia Museum, Halifax, Nova Scotia, Canada
NSNR	Nova Scotia Department of Natural Resources Insectary, Shubenacadie, Nova Scotia, Canada
RWC	Reginald Webster Collection, Charters Settlement, New Brunswick, Canada
SMU	St Mary's University, Halifax, Nova Scotia, Canada
STFX	St Francis Xavier University, Antigonish, Nova Scotia, Canada
UMNB	Université de Moncton, Moncton, New Brunswick, Canada
UPEI	University of Prince Edward Island, Charlottetown, Prince Edward Island, Canada

Table 1. Silphidae found in the Atlantic Canada region

	NB	PE	IM	NS	NF	LB	Distribution in NE North America
Silphinae							
Necrodes surinamensis (Fabricius)	1	1		1	1		CT, MA, ME, NB, NF, NH, NS, NY, ON, PE, QC, RI, VT
Necrophila americana (Linnaeus)	1	1		1			CT, MA, ME, NB, NH, NS, NY, ON, PE, QC, RI, VT
Oiceoptoma noveboracense (Forster)	1	1		1			CT, MA, ME, NB, NH, NS, NY, ON, PE, QC, RI, VT
Thanatophilus lapponicus (Herbst) *	1	1	1	1	1	1	LB, ME, NB, NF, NH, NS, ON, PE, QC, RI
Nicrophorinae							
Nicrophorus defodiens Mannerheim	1	1		1	1		MA, ME, NB, NF, NH, NS, NY, ON, PE, QC, VT
Nicrophorus investigator (Zetterstedt) *	1	1		1	1	1	LB, ME, NB, NF, NS, ON, PE, QC
Nicrophorus orbicollis Say	1	1		1			CT, MA, ME, NB, NH, NS, NY, ON, PE, QC, RI
Nicrophorus pustulatus Herschel	1	1		1			CT, MA, ME, NB, NH, NS, NY, ON, PE, QC, RI
Nicrophorus sayi Laporte	1	1	1	1	1		CT, MA, ME, NB, NF, NH, NS, NY, ON, PE, QC, RI, VT
Nicrophorus tomentosus Weber	1	1		1			CT, MA, ME, NB, NH, NS, NY, ON, PE, QC, RI
Nicrophorus vespilloides Herbst *	1	1		1	1	1	CT, LB, MA, ME, NB, NF, NH, NS, NY, ON, PE, QC, RI
Total	11	11	2	11	6	3	

Notes: Newfoundland and Labrador species and distributions are included as a base of comparison for the Maritime Provinces fauna; NB = New Brunswick; PE = Prince Edward Island; IM = Îles de la Madeleine, QC; NS = Nova Scotia; NF = insular Newfoundland; LB =Labrador; * = Holarctic species.

Northeastern North America is taken to consist of the following jurisdictions: ON = Ontario; QC = Québec; PM = Saint-Pierre et Miquelon; CT = Connecticut; MA = Massachusetts; ME = Maine; NH = New Hampshire; NY = New York; RI = Rhode Island; and VT = Vermont.

IDENTIFICATION

A key to species of Silphidae [adapted from Anderson and Peck (1985)] found in the Maritime Provinces of Canada is provided on page 87. An excellent guide to the Silphidae of North America, complete with illustrated keys and colour habitus photos of all species was provided by Hanley and Cuthrell (2008). Although there is no verifiable evidence that the endangered *Nicrophorus americanus* has ever occurred in Nova Scotia (see below) the species is included in the key to assist investigators who may be interested in looking for it.

RESULTS

As a result of an examination of specimens of Silphidae from the Maritime Provinces of Canada, five new provincial records are reported. *Necrophila americana*, *Thanatophilus lapponicus*, *Nicrophorus pustulatus*, and *Nicrophorus sayi* are newly recorded in Prince Edward Island; *Nicrophorus investigator* in New Brunswick; *Nicrophours orbicollis* from Cape Breton Island; *Nicrophorus investigator* from mainland Nova Scotia; and, *Nicrophorus sayi* from Îles de la Madeleine. Additionally, Specific details follow.

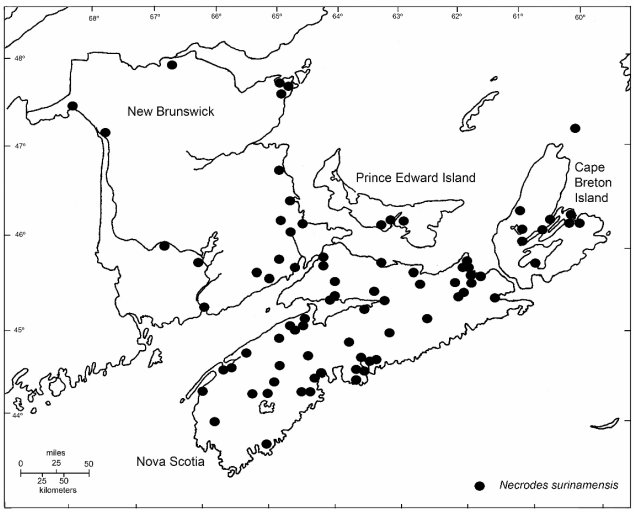
Silphinae

Necrodes surinamensis (Fabricius, 1775)

Necrodes surinamensis (Figure 1j) is widely distributed in the Maritime Provinces, including St. Paul Island off the northern tip of Cape Breton Island (Figure 2). It was first reported from Nova Scotia by Kirby (1837), Jones (1869), and Evans (1899), and from all three Maritime Provinces and insular Newfoundland by Anderson and Peck (1985), Campbell (1991), and Peck and Miller (1993). It is an abundant species in the region (Figure 3). Adults (n = 439) have been collected between 8 May and 17 October. The seasonal distribution of records indicates that the first (overwintering) cohort of adults is most frequently found between the middle of May and the third week of June. There is a secondary peak between the middle of July and the middle of August corresponding to the second (newly emerged) annual cohort (Figure 4). Second cohort adults subsequently overwinter (Anderson and Peck 1985).

Ratcliffe (1972) studied the natural history of *Necrodes surinamensis* and reported that it is frequently found on carcasses of larger mammals (i.e., dog, bear, moose, deer) and these larger carcasses appear to be solely used for reproductive purposes. Anderson (1982) categorized it as a eurytopic species found in all habitats. In the Maritime Provinces they have been found on dead cow (*Bos primigenius* Bojanus), pig (*Sus scrofa* L.), common crow (*Corvus brachyrhynchos* Brehm), fish, and on a minke whale (*Balaenoptera acutorostrata* Lacepede). Many specimens have been collected with light traps.

Figure 2. Distribution of *Necrodes surinamensis* in the Maritime Provinces of Canada.



Key to the Silphidae of Atlantic Canada

1. Elytra truncate, exposing three or four abdominal tergites, usually with red or orange maculations (Nicrophorinae) 2
– Elytra usually not truncate, at most exposing one or two abdominal tergites; usually without red or orange maculations (Silphinae) 9

2(1). Frons and pronotal disk red [25-35 mm] ..... *Nicrophorus americanus*
– Frons and pronotal disk black 3

3(2). Pronotum with dense yellow pubescence [12–18 mm] (Figure 1a) ..... *Nicrophorus tomentosus*
– Pronotum glabrous, or with sparse hair on anterior or lateral margins 4

4(3). Metatibia curved; anterior black band of elytron not reaching epipleuron [15–23 mm] (Figure 1b) ..... *Nicrophorus sayi*
– Metatibia straight; anterior black band of elytron usually reaching epipleuron 5

5(4). Elytral epipleuron unicolorous, black or orange 6
– Elytral epipleuron bicoloured, black and orange 8

6(5). Elytral epipleuron black 7
– Elytral epipleuron orange [13–18 mm] (Figure 1c) ..... *Nicrophorus investigator*

7(6). Dorsal surface of elytron with long, fine hairs; epipleural ridge short, reaching only to level of tip of scutellum [15–22 mm] (Figure 1d) ..... *Nicrophorus orbicollis*
– Dorsal surface of elytron without long hairs; epipleural ridge long, reaching almost to level of base of scutellum [15–20 mm] (Figure 1e) ..... *Nicrophorus pustulatus*

8(5). Base of elytral epipleuron orange, with pre-basal black spot [12–16 mm] (Figure 1f) ..... *Nicrophorus vespilloides*
– Base of epipleuron entirely black [12–18 mm] (Figure 1g) ..... *Nicrophorus defodiens*

9(1). Pronotum with disk black, margins yellow [15–20 mm] (Figure 1h) ..... *Necrophila americana*
– Pronotum entirely black, or with disk black and margins orange-red 10

10(9). Head and pronotum covered in dense yellow pubescence [10–14 mm] (Figure 1i) ..... *Thanatophilus lapponicus*
– Head and pronotum glabrous or with sparse hairs 11

11(10). Pronotum with disk entirely black [15–25 mm] (Figure 1j) ..... *Necrodes surinamensis*
– Pronotum with disk black and margins orange-red [13–15 mm] (Figure 1k) ..... *Oiceoptoma noveboracense*

Figure 1. Dorsal habitus photographs of *Nicrophorus tomentosus (a), Nicrophorus sayi (b), Nicrophorus investigator* (c), *Nicrophorus orbicollis (d), Nicrophorus pustulatus (e),* ***Nicrophorus vespilloides (f), Nicrophorus defodiens (g) Necrophila americana*** (h), *Thanatophilus lapponicus (i), Necrodes surinamensis* (j), *Oiceoptoma noveboracense (k).* **Photo credit***: Guy Hanley, Minot, North Dakota, USA (a, b, c, d, e, f, g, h, j, k); Jim Moore, Westwood, California, USA. (i)*

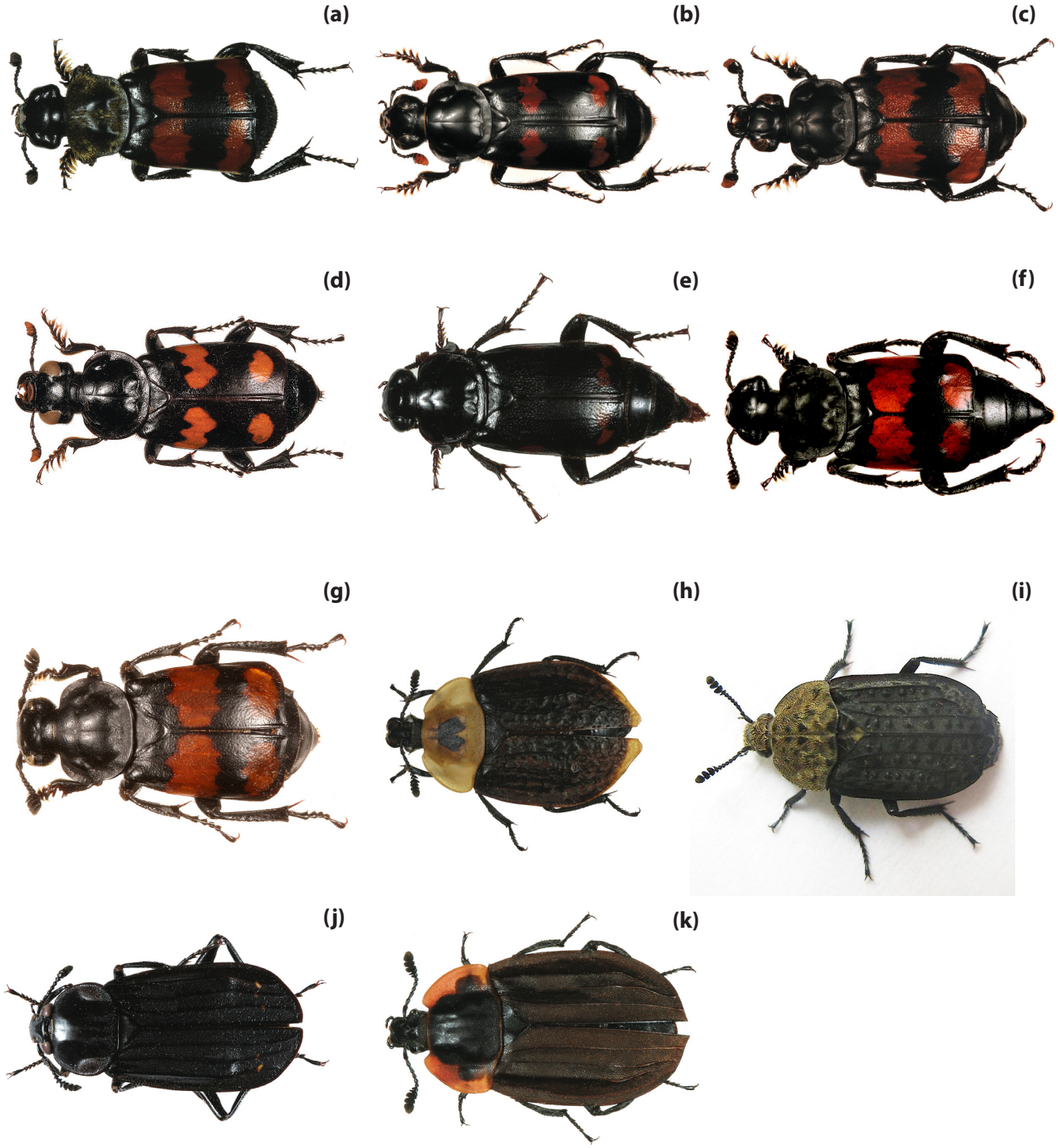


Figure 3. Relative abundance of Silphinae in the Maritime Provinces of Canada.

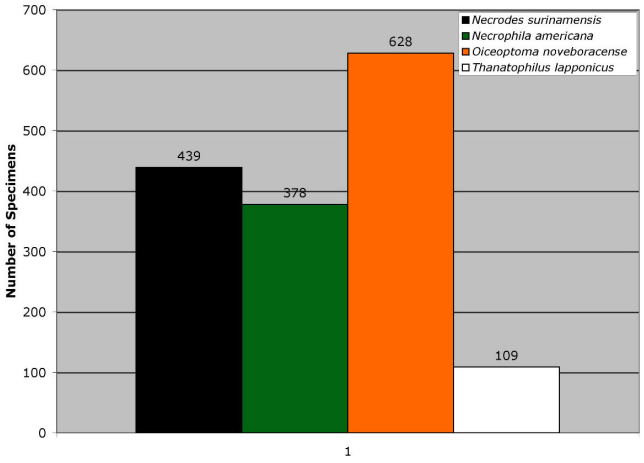
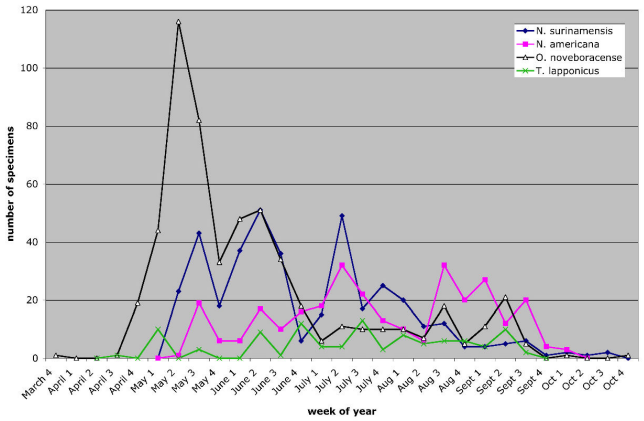


Figure 4. Seasonal distribution of Silphinae in the Maritime Provinces of Canada.



Necrophila americana (Linnaeus, 1758)

PRINCE EDWARD ISLAND: **Kings County**: Montague, 13 September 1981, L.S. Thompson (1, ACPE); **Prince County**: Enmore, 1 June 1981, T. Power (1, UPEI); Miscouche, 10 July 1996, J.G. Stewart (1, ACPE); Summerside, 4 September 2011, C.G. Majka, wet meadow (1, CGMC); **Queens County**: Charlottetown, 22 July 1974, S. Favier (1, UPEI); Charlottetown, 25 September 1980, L.S. Thomson, lawn (1, ACPE); Millvale, Trout River, 25 June 2003, C.G. Majka, along river (1, CGMC); Mount Herbert, 1920-1924, J.R. Mutch (1, UPEI); Southport, 21 September 2000, M.E.M. Smith, under house trailer (8, ACPE); St. Patricks, 15 June 2002, 25 June 2003, C.G. Majka, old field, in compost (3, CGMC); St. Patricks, 31 August 2009, C.G. Majka, spruce forest, in moss (1, CGMC); Vernon River, 3 June 1970, R. Wenn (1, UPEI); Fullerton's Marsh, 16 June 1970, W. Coulson, eating rotten egg (5, UPEI); no locality indicated, 1974-83 (14, UPEI).

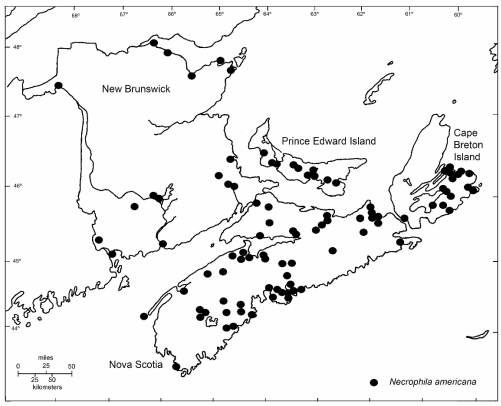
Necrophila americana (Figure 1h) is newly recorded from Prince Edward Island. It is widely distributed in the Maritime Provinces, although it appears to be absent from northern and western Cape Breton Island (Figure 5). It was reported from Nova Scotia by Kirby (1837) and Jones (1869); and from New Brunswick and Nova Scotia by Anderson and Peck (1985) and Campbell (1991). It is an abundant species in the region (Figure 3). Adults (n = 378) have been collected between 12 May and 5 October. The seasonal distribution of records shows considerable variation; the first cohort of emerging adults is most frequently found between the third week of May and the middle of July (Figure 4). This corresponds with the period of reproductive activity noted in Anderson and Peck (1985). A secondary peak in adult numbers is then found from the third week of August to the third week of September (Figure 4) corresponding to a second annual cohort that then overwinters (Anderson and Peck 1985).

Anderson (1982) and Anderson and Peck (1985) reported that *Necrophila americana* is found primarily in open, mesic habitats, but also in forested areas, and that adults are primarily diurnal. In the Maritimes Provinces *Necrophila americana* has been found in a variety of open and forested habitats, including marshes, blueberry fields, and old fields on dead raccoon (*Procyon lotor* L.), pig, common crow, herring gull (*Larus argentatus* Pontoppidan), and a wood turtle (*Clemmys insulpta* (LeConte)), and in compost, chicken manure, and on rotten eggs. Specimens have been collected with pitfall traps, carrion-baited traps, and flight intercept traps. Adults are believed to be mimetic of bumble bees (Fisher and Tuckerman 1986).

Oiceoptoma noveboracense (Forster, 1771)

Oiceoptoma noveboracense (Figure 1k) is widely distributed throughout the Maritime Provinces (Figure 6). It was reported from Nova Scotia by Kirby (1837) and Jones (1869), and from all three Maritime Provinces by Anderson and Peck (1985) and Campbell (1991). It was also reported from Cape Breton Island by Campbell et al. (1987). Together with *Nicrophorus defodiens*, they are the most abundant silphids in the region (Figures 3 & 7). Adults (n = 628) have been collected between 26 March and 28 October. The seasonal distribution of records indicates the first cohort of adults is most frequently found between the end of April and the

Figure 5. Distribution of *Necrophila americana* in the Maritime Provinces of Canada.



end of June. Thereafter, numbers decrease with a secondary, smaller peak between the third week of August and the middle of September corresponding to the second annual cohort (Figure 14). These adults subsequently overwinter (Anderson and Peck 1985). *Oiceoptoma noveboracense* is found in substantial numbers earlier in the spring than other silphids (Figure 14; Anderson and Peck 1985).

The diurnal adults are most commonly found in forested habitats (Anderson 1982; Anderson and Peck 1985). In the Maritime Provinces they have been found on dead cow, white-tailed deer (*Odocoileus virginianus* Zimmerman), pig, coyote (*Canis latrans* Say), bobcat (*Lynx rufus* Schreber), cat (*Felis catus* L.), great black-backed gull, herring gull, common crow, robin (*Turdus migratorius* L.), and on a painted turtle (*Chrysenys picta* Schneider) as well as in compost. Specimens have been collected with carrion baited traps and flight intercept traps.

Figure 6. Distribution of *Oiceoptoma noveboracense* in the Maritime Provinces of Canada.

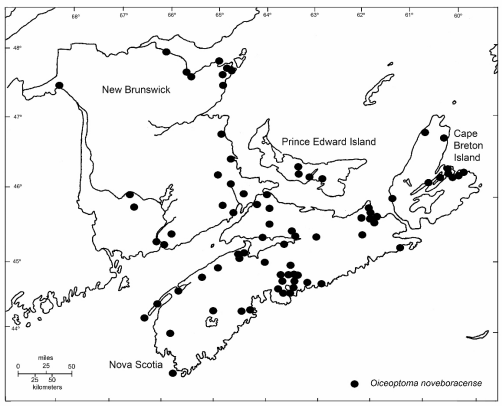
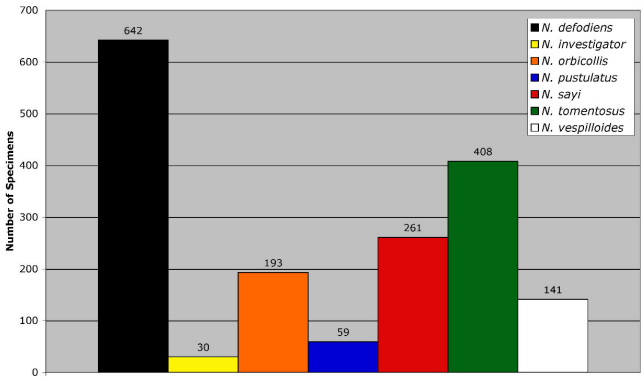


Figure 7. Relative abundance of Nicrophorinae in the Maritime Provinces of Canada.



Thanatophilus lapponicus (Herbst, 1793)

PRINCE EDWARD ISLAND: Queens County: Mt. Stewart, 16 June 1936, no collector indicated (1, UPEI); Stanhope, 25 June 1937, no collector indicated (1, UPEI); Wood Islands, 30 June 2003, C.G. Majka, seashore (1, CGMC).

Thanatophilus lapponicus (Figure 1i) is newly recorded from Prince Edward Island. It is widely distributed in the Maritime Provinces including Sable Island and the Îles de la Madeleine of Québec (Figure 8). It has not been recorded in northwestern New Brunswick and M. Turgeon (personal communication) reports that he has not found it in Madawaska County in this portion of the province. It was reported from Nova Scotia by Jones (1869) and Evans (1899); and from New Brunswick, Nova Scotia, insular Newfoundland, and Labrador by Anderson and Peck (1985) and Campbell (1991). This is a Holarctic species is also found in Iceland, Sweden, Norway, Finland, and northern Russia (Ruzicka 2011).

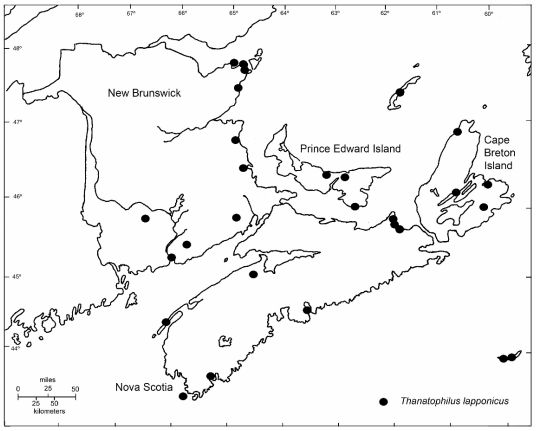
Thanatophilus lapponicus is the least abundant species in the Silphinae in the Maritime Provinces (Figure 3). Adults (n = 109) have been collected between 23 April and 23 September. Anderson (1982) found that *Thanatophilus lapponicus* had two generations (i.e., three cohorts) each year. The first period of reproductive activity occurs between late April and late May which corresponds to early records in the Maritime Provinces (Figure 4). A second cohort of adults appears in early June and is reproductively active until late July. Subsequently, a third cohort appears to be present in the Maritimes from late August to late September (Figure 4). This third cohort (i.e., the second generation of the season) overwinters as adults (Anderson and Peck 1985).

Anderson and Peck (1985) reported *Thanatophilus*

lapponicus as the dominant species of open habitats, throughout its range, particularly in northern regions. It is a cold-adapted species occurring at high elevations in western North America. In the Maritime Provinces, it is most frequently found in open areas at coastal sites (beaches, sand dunes, seashores, heathy areas) where it has been recorded on dead cow, horse (*Equus ferus* L.), red fox (*Vulpes vulpes* L.), herring gull, common tern (*Sterna hirundo* L.), rock eel (*Pholis gunnellus* (L.)), and other dead fish.

An interesting report is that in Miller (1996) of a *Thanatophilus* specimen excavated from late Pleistocene deposits in Mabou, Nova Scotia dating between 10,900 and 10,500 years BP. Anderson and Peck (1985) point out that *Thanatophilus lapponicus* is absent from the late Pleistocene fossil record in Canada, and that the only silphids recorded in excavations from this period are *Thanatophilus sagax* (Mannerheim) and *Thanatophilus trituberculatus* (Kirby), two currently rare silphids found in northern and western portions of North America. Thus, it is probable that the West Mabou late Pleistocene record represents *Thanatophilus sagax* or *Thanatophilus trituberculatus*. Anderson and Peck (1985) posit that the absence of *Thanatophilus lapponicus* at that time may be the result of qualitative changes in the tundra ecosystem of the late Pleistocene as proposed by Matthews (1974, 1982).

Figure 8. Distribution of *Thanatophilus lapponicus* in the Maritime Provinces of Canada.



Nicrophorinae

Nicrophorus americanus Olivier, 1790

Majka (2010) reviewed the history of publications (Hatch 1928; Blackwelder 1939; Madge 1956; Davis 1980; Peck and Anderson 1985; Peck and Miller 1993; Raithal 1991; Ratcliffe 1997; Bedick et al. 2004) that have referred to *Nicrophorus americanus* as occurring in Nova Scotia. No voucher specimens of this species originating from Nova Scotia or an original source for this report were found. The paper concluded that there is no evidence that this species ever occurred in the province.

One reference missed in this review was Jones (1869) which does report "Necrophorus Americanus, Oliv." from Nova Scotia stating *"Common in putrid carcasses of animals."* J. Matthew Jones, F.L.S., was then president of the Nova Scotia Institute of Natural Science. He was not an entomologist, and in his paper he credits the Rev. C.J.S. Bethune with the identification of "nearly" all his specimens. Bethune, one of the founders of the Entomological Society of Ontario and the first editor of the Canadian Entomologist, was an entomologist who was knowledgeable on Coleoptera. What, then, can one deduce from this report?

In addition to reporting *Nicrophorus americanus*, Bethune also identified *Nicrophorus orbicollis, Nicrophorus tomentosus* (as *Nicrophorus velutinus*), and two other unidentified species of *Nicrophorus*. Could Bethune have been mistaken in his identification of *Nicrophorus americanus* and have attributed this name to another *Nicrophorus* species found in Nova Scotia? Possibly, although *Nicrophorus americanus* is a distinctive species. Could *Nicrophorus americanus* have been "common" in Nova Scotia in 1869 and have subsequently been extirpated? Possibly, although this seems very improbable. *Nicrophorus americanus* was not included by Kirby (1837) amongst the three species of *Nicrophorus* (*Nicrophorus tomentosus, Nicrophorus vespilloides,* and *Nicrophorus orbicollis*) collected by Captain Basil Hall and Rev. Thomas McCulloch in Nova Scotia in the 1820's, nor was it mentioned by Evan (1899) who collected Coleoptera (including Silphidae) in Halifax in 1897. It seems unlikely that a species listed as a common *Nicrophorus* in Nova Scotia by Jones (1869) would have completely failed to have been detected by both Kirby (1837) some 30 years earlier and Evans (1899) some 30 years later, both of whom recorded carrion beetles from the province.

Furthermore, in the course of this study, 1,517 voucher specimens of *Nicrophorus* species collected in Nova Scotia between 1922 and the present were examined. No specimens of *Nicrophorus americanus* were found amongst these. Although it is well known that *Nicrophorus americanus* has disappeared from approximately 90% its historical range (Sikes and Raithel 2002), this decline appears to have taken place largely over the past 40+

years (Anderson 1982). In the 1940's it was still considered common and was found in 35 states in the USA and two Canadian provinces (Lomino et al. 1995). It would therefore seem improbable that the disappearance of this species would have commenced in Nova Scotia a century earlier.

What is the identity of the specimens referred to as *Nicrophorus americanus* by Bethune? It may not be possible to answer this question. The disposition of his collection of beetles is not mentioned by Jones (1869). It is certainly not present in any existing reference collection in Nova Scotia, or indeed in Atlantic Canada. In extensive research over the past decade on the Coleoptera of Atlantic Canada, no voucher specimens from this collection were found. Also, in a thorough review of the literature related to the Coleoptera of northeastern North America, no reference to any specimen Coleoptera collected by J.M. Jones (aside from Jones 1869 itself) was located. Whatever their disposition, they would appear to have been lost. Therefore, despite the report in Jones (1869), it nevertheless seems prudent to conclude that this report was in error, and that there is no verifiable evidence that *Nicrophorus americanus* has ever occurred in Nova Scotia.

Nicrophorus defodiens Mannerheim, 1846

PRINCE EDWARD ISLAND: 1974-1983, locality and collector information lost (5, UPEI); **Prince County**: Tryon, 15 August 2001, C. Noronha, potato field, pitfall trap (1, ACPE); **Queens County**: Victoria, 6 August 1981, V. Friesen, pitfall trap (3, UPEI).

Nicrophorus defodiens (Figure 1g) was not recorded from Prince Edward Island in Anderson and Peck (1985), although Campbell (1991) and Peck and Miller (1993) did record it from the Province without providing specific locality records. It was recorded from New Brunswick, mainland Nova Scotia, and the extreme southwest of insular Newfoundland by Anderson and Peck (1985) and from Cape Breton Island by Campbell et al. (1987). It is widely distributed in the Maritime Provinces (Figure 9). *Nicrophorus defodiens* is by far the most abundant silphid found in the region (Figures 4, 7). Adults (n = 642) have been found between 19 May and 5 October. The seasonal distribution of records shows a bimodal pattern corresponding to the two annual cohorts. Overwintering adults appear in early June and increase to a peak in numbers by mid-July; a secondary peak in the middle of August represents newly emerged adults of the second cohort (Figure 10). Overwintering takes place in the adult stage (Anderson and Peck 1985).

It is found primarily in dry boreal, coniferous forests throughout its range (Anderson 1982; Anderson and Peck 1985). On a Newfoundland island with a seabird colony, all specimens of *Nicrophorus defodiens* collected were in a coniferous (*Abies balsamaea - Picea mariana*) forest (Wilhelm et al. 2001). Adults do not bury carcasses, but conceal them under leaf litter or debris (Leech 1934). In the Maritime Provinces, they have been recorded in a wide variety of coniferous and deciduous forests as well as in sphagnum bogs and blueberry fields. Adults have been collected on dead cow, pig, mouse, chicken (*Gallus domesticus* (L.), and sparrow as well as on dung. Specimens have been collected with pitfall traps, carrion-baited traps, flight intercept traps, malaise traps, and light traps.

Figure 9. Distribution of *Nicrophorus defodiens* in the Maritime Provinces of Canada.

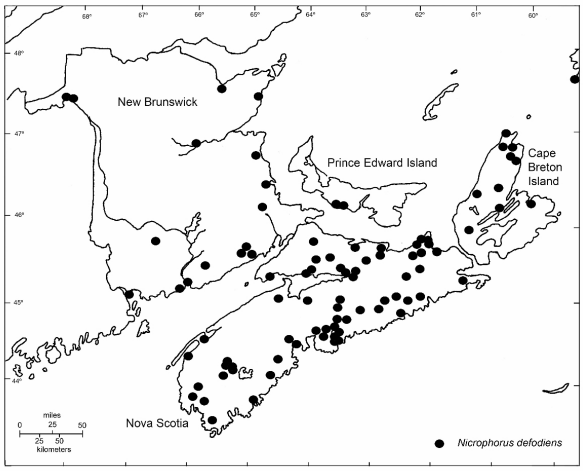
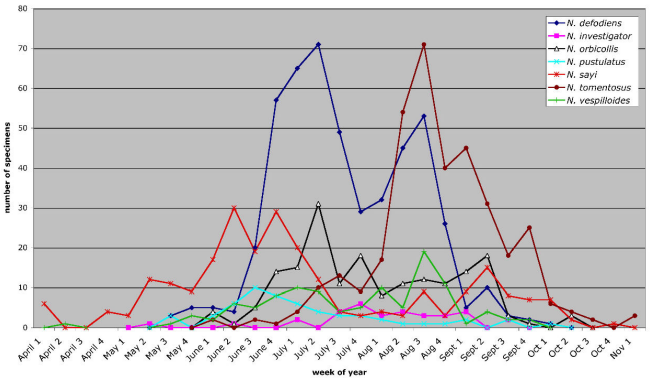


Figure 10. Seasonal distribution of Nicrophorinae in the Maritime Provinces of Canada.



Nicrophorus investigator (Zetterstedt, 1824)

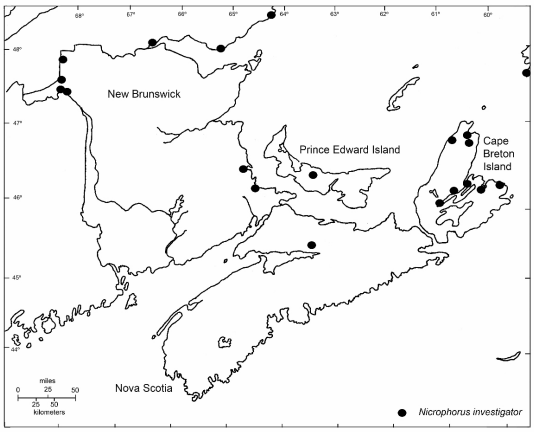
NEW BRUNSWICK: **Kent County**: Bouctouche, 2007-2008, J.-P. Michaud [Michaud et al. (2010)]; **Madawaska County**: East Iroquois River, 20 July 1992, 19 September 1992, M. Turgeon (2, MTC); Edmundston, 22 September 1991, C. Plourde (1, UMNB); St. Basile, 8 August 1992, 6 July 1993, 2 August 1993, 14 August 1994, 17 August 1995, 25 July 1996, M. Turgeon (7, MTC); **Restigouche County**: Left Hand Belone Brook, 18 August 1991, M. Turgeon (1, MTC); **Westmorland County**: Shediac, August 1978, E. Ouellette (1, UMNB). **NOVA SCOTIA**: **Colchester County**: Debert, 15 June 1993, J. Ogden (1, JOC). **PRINCE EDWARD ISLAND**: **Queens County**: St. Patricks, 20 August 2002, C.G. Majka, compost (1, CGMC).

Nicrophorus investigator (Figure 1c) is newly recorded in New Brunswick and on the mainland of Nova Scotia. It was not recorded from Prince Edward Island in Anderson and Peck (1985), although Campbell (1991) did record it from the province without providing specific locality records. It was reported from Cape Breton Island by Davis (1980), and from insular Newfoundland, and Labrador by Anderson and Peck (1985) and Peck and Miller (1993). It was also reported from Cape Breton Island by Campbell et al. (1987). Michaud et al (2010) reported it from Bouctouche, New Brunswick, however without indicating that it had not previously been reported from the province. Although found in all three Maritime Provinces, it has a localized distribution in the region (Figure 11). *Nicrophorus investigator* is a Holarctic species found throughout much of Europe except for Iceland, the southern Balkans (Albania, Macedonia, Greece, European Turkey), Portugal, and the Mediterranean islands (Ruzicka 2011). It is also found in the eastern Palaearctic, across Siberia to the Russian Far East, south through Mongolia, Korea, Japan, China, the Central Asian republics, Kashmir, Pakistan, Iran, Transcaucasia, and Turkey (Sikes et al. 2002).

Nicrophorus investigator is the rarest sexton beetle found in the region (Figure 7). Adults (n = 30) have been recorded between 9 May and 22 September. Small numbers of adults have been found throughout this time period (Figure 10). These presumably represent adults of a single reproductively active cohort since Anderson and Peck (1985) indicated that the new seasonal brood overwinters in the pre-pupal stage. Anderson and Peck (1985) noted that little had been published on the biology of this species in North America but that there was some evidence of competitive exclusion between this species and *Nicrophorus tomentosus* and *Nicrophorus hybridus*. There is some evidence that this may be true in this region. The two principal populations of *Nicrophorus investigator* in the Maritime Provinces – in Madawaska County in northwestern New Brunswick, and in the northern and western areas of Cape Breton Island – are in areas where *Nicrophorus tomentosus* is rare or absent.

In a study conducted in Germany, 76% of adults were captured in forested (oak, beech, birch and pine) habitats; 24% in open habitats (meadows and arable land) (Kolianos and Schwarz 2000). In another study on a Newfoundland island, 83% of *Nicrophorus investigator* specimens were collected in open habitats; 17% in a coniferous forest (Wilhelm et al. 2001). In the Maritime Provinces adults have been found on a dead chicken and on compost. A number of specimens were collected with light traps. It has been recorded as a sound and visual mimic of the bumblebee *Bombus lucorum* L. (Lane and Rothschild 1965).

Figure 11. Distribution of *Nicrophorus investigator* in the Maritime Provinces of Canada.



Nicrophorus orbicollis Say, 1825

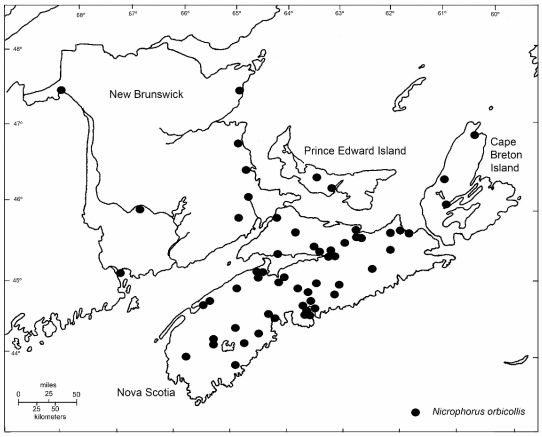
NOVA SCOTIA: **Inverness County**: Margaree Forks, 27 July 1986, E. Georgeson, light trap (1, NSNR); Whycocomagh, 23 September 1987, E. Georgeson, light trap (1, NSNR); **Victoria County**: Cape North, 17-25 July 1998, R.F. Lauff, dead chicken (2, STFX).

Nicrophorus orbicollis (Figure 1d) is newly recorded on Cape Breton Island, Nova Scotia. It was first recorded from Nova Scotia by Kirby (1837) and Jones (1869); and from New Brunswick and Prince Edward Island by Anderson and Peck (1985) and Campbell (1991). It is widely distributed throughout the Maritime Provinces (Figure 12). It is moderately abundant in the region (Figure 7).

Adults (n = 193) have been collected between 2 June and 14 October. The seasonal distribution of records indicates adults first appear in early June and increase to the middle of July, representing the reproductively active, first cohort. A secondary peak in mid-September represents the second cohort of newly emerged adults (Figure 10). Overwintering takes place in the adult stage (Anderson and Peck 1985).

Nicrophorus orbicollis is found in both open and forested habitats, but more commonly in the latter; adults are nocturnal and are often caught at lights (Anderson 1982; Anderson and Peck 1985). In the Maritime Provinces they have been found in coniferous and deciduous forests and in blueberry fields, on dead pigs, chickens, and on compost. Specimens have been collected with pitfall traps, carrion-baited traps, flight intercept traps, and light traps.

Figure 12. Distribution of *Nicrophorus orbicollis* in the Maritime Provinces of Canada.



Nicrophorus pustulatus Herschel, 1807

NEW BRUNSWICK: **Albert County**: Mary's Point, R.P. Webster (1, RWC); **Kent County**: St. Charles, July 1977, D. Robichaud (1, UMNB); **Madawaska County**: East Iroquois River, 25 June 1995, 13 June 1995, M. Turgeon (2, MTC); St. Basile, 30 June 1993, 6 July 1993, M. Turgeon (2, MTC); **Restigouche County**: Left Hand Belone Brook, 13 June 1992, M. Turgeon (2, MTC); Balmoral, 26 July 1978, G. Chouinard (1, UMNB); **Westmoreland County**: Canaan, 12 June 1978, Y. Bossé (1, UMNB). **PRINCE EDWARD ISLAND**: **Kings County**: Upton, 16 July 1955, F.M. Cannon (1, ACPE); **Queens County**: Cornwall, 17 June 1993, M.E.M. Smith (1, ACPE); Mount Herbert, 29 August 1923, J.R. Mutch (1, UPEI).

Nicrophorus pustulatus (Figure 1e) is newly recorded on Prince Edward Island. It was not recorded from New Brunswick in Anderson and Peck (1985), although Campbell (1991) did record it from the province without providing specific locality records. It is widely distributed throughout the Maritime Provinces, although records from southwestern New Brunswick are lacking (Figure 13). It is apparently relatively scarce in the region (Figure 7) in keeping with its apparent general rarity throughout Canada (Anderson and Peck 1985). Adults (n = 59) have been collected between 19 May and 6 October. There are two annual cohorts. The seasonal distribution of records indicates that adults reach a peak in the latter half of June (Figure 10). Anderson and Peck (1985) indicate that adults are reproductively active upon spring emergence, with teneral adults emerging later in the season; overwintering takes place in the adult stage. The limited data available for this species in the Maritime Provinces does not indicate a secondary peak in numbers corresponding to a second cohort.

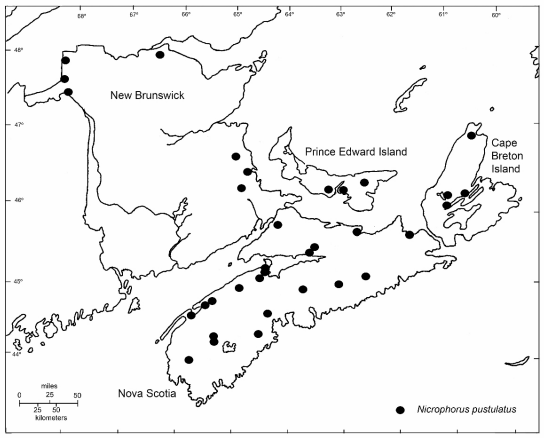
Adults are nocturnal, found in forested habitats, and commonly collected at lights (Anderson and Peck 1985). In Nova Scotia, most specimens for which there is habitat information were collected in forested environments; 38% were collected with light traps. Anderson and Peck (1985) wrote "*The common occurrence of adults at lights, yet their apparent rarity in pitfall traps, may indicate that the species posses a different natural history than other* Nicrophorus." Under natural conditions, *Nicrophorus pustulatus* has only been observed to breed in the nests of black rat snakes (*Elaphe obsoleta* (Say)) and possibly fox snakes (*Elaphe vulpine*) (Baird and Girard) where it is a parasitoid of snake eggs (Blouin-Demers and Weatherhead 2000; Keller and Heske 2001).

In the Maritime Provinces, rat and fox snakes are absent and the only two oviparous snakes found are the northern ringneck snake (*Diadophis punctatus edwardsi* (Merrem)) and the eastern smooth green snake (*Opheodrys v. vernalis* (Harlan)) (Gilhen 1984). Blouin-Demers and Weatherhead (2000) suggested that in parts of its range *Nicrophorus pustulatus* may exploit vertebrate carcasses, or alternatively turtle eggs, in areas where oviparous snakes are absent or rare. John Gilhen (Nova Scotia Museum (NSM), personal communication) has never found sexton beetles in association with nests of either snakes or turtles in Nova Scotia. An interesting feature of the biology of *Nicrophorus pustulatus* is the high fecundity of females; Trumbo (1992) recorded up to 187 offspring from a female, triple the normal number for other species of *Nicrophorus*. Blouin-Demers and Weatherhead (2000)

suggested that this feature of their biology may be related to their evolution as nest parasitoids of snakes, and the large average clutch mass of communally nesting snakes. A high fecundity would allow *Nicrophorus pustulatus* to take advantage of the large biomass of such resources.

In Georgia, Ulyshen et al. (2007) found *Nicrophorus pustulatus* was abundant high (15 m) in the forest canopy, in contrast to *Nicrophorus orbicollis,* which was much commoner and was abundant at ground level. They did not know what food sources *Nicrophorus pustulatus* was using, but suggested that they might utilize tree cavities (i.e., bird nests?). In a study examining the nests of boreal owls (*Aegolius funereus richardsoni* (Bonaparte)) and northern saw-whet owls (*Aegolius acadicus acadicus* (Gmelin)) in Nova Scotia, Majka et al. (2006) found 14 species of beetles, but no species of Silphidae. In Nova Scotia, one specimen of *Nicrophorus pustulatus* was collected on a dead moose (*Alces alces* Gray). A number of specimens were collected with light traps.

Figure 13. Distribution of *Nicrophorus pustulatus* in the Maritime Provinces of Canada.



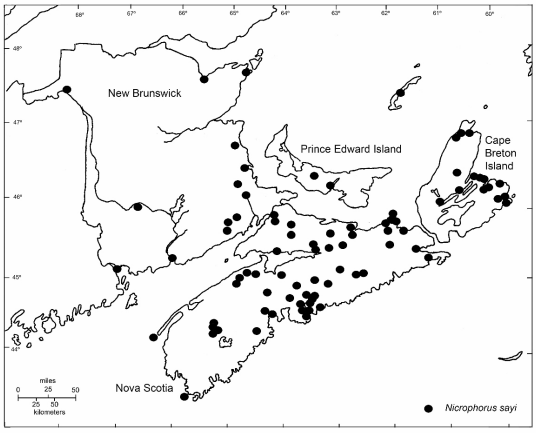
Nicrophorus sayi Laporte, 1840

PRINCE EDWARD ISLAND: **Queens County**: 13 June 1978, L.S. Thompson (1, ACPE); St. Patricks, 20 August 2002, 25 June 2003, 27 June 2003, C.G. Majka, old field, compost (3, CGMC); West Royalty, 9 July 1970, R. Wenn, light trap (1, UPEI). **QUÉBEC**: **Îles de la Madeleine**: no date records, E.J. B. (1, NSAC).

Nicrophorus sayi (Figure 1b) is newly recorded on Prince Edward Island and on the Îles de la Madeleine, Québec. It was recorded from New Brunswick, Nova Scotia, and southwestern insular Newfoundland by Anderson and Peck (1985) and Campbell (1991). It is widely distributed throughout the Maritime Provinces (Figure 14) and is a relatively abundant species throughout the region (Figure 7). Adults (n = 261) have been collected between 4 April and 31 October. It is certainly the most active and abundant of *Nicrophorus* species in the spring, with substantial numbers of adults present from late April to mid June when other species are absent or only present in small numbers (Figure 10). This is also true across Canada. Anderson and Peck (1985) wrote *"Adults of* N. sayi *are the first adults of any species of* Nicrophorus *to become active in the spring. They are often present while snow is still on the ground."* Numbers of first cohort adults reach a peak between mid-June and early July; a second peak between the third week of August and mid-September represent the second cohort of emerging adults (Figure 10). Overwintering takes place in the adult stage (Anderson and Peck 1985).

Nicrophorus sayi is found in both open and forested areas, showing a preference for the latter (Anderson and Peck 1985). In the Maritime Provinces they have been collected in a wide variety of coniferous and deciduous forests, blueberry fields, and an old-field ecosystem. Adults have been found on dead cow, pig, mouse, porcupine (*Erethizon dorsatum* (L.)), and chukar (*Alectoris chukar* (Gray)) and on compost. Specimens have been collected with pitfall traps, carrion-baited traps, flight intercept traps, Malaise traps, and light traps.

Figure 14. Distribution of *Nicrophorus sayi* in the Maritime Provinces of Canada.



Nicrophorus tomentosus Weber, 1801

Nicrophorus tomentosus (Figure 1a) was first reported from Nova Scotia by Jones (1869) and from New Brunswick, Nova Scotia, and Prince Edward Island by Anderson and

Peck (1985) and Campbell (1991). It is widely distributed through the Maritime Provinces, although records from northern and western Cape Breton are sparse (Figure 15). It is a common species throughout the region (Figure 7). Adults (n = 408) have been collected between 2 June and 6 November. The seasonal distribution data indicates that numbers of adults begin to increase relatively late in the season (mid-July), reaching a peak from the middle of August through the end of September (Figure 10). Anderson and Peck (1985) observed that *Nicrophorus tomentosus* was summer-active with a single cohort of adults present. Mature (third-instar) larvae move into soil surrounding their feeding locality and remain quiescent during the fall and winter, pupating the following spring.

Unlike most other Nearctic sexton beetles, adults of *Nicrophorus tomentosus* do not bury the carcasses they feed on. They make a shallow excavation beneath it, into which it sinks, and then cover it with leaf litter and other debris (Anderson and Peck 1985). They occur in many habitat types. Anderson and Peck (1985) conjectured that these eurytopic habitat preferences could be due to their late summer emergence when adults of other sympatric species of *Nicrophorus* are not reproductively active. *Nicrophorus tomentosus* has been recorded as mimetic of adult bumble bees (*Bombus* spp.) which they greatly resemble when in flight (Milne and Milne 1944).

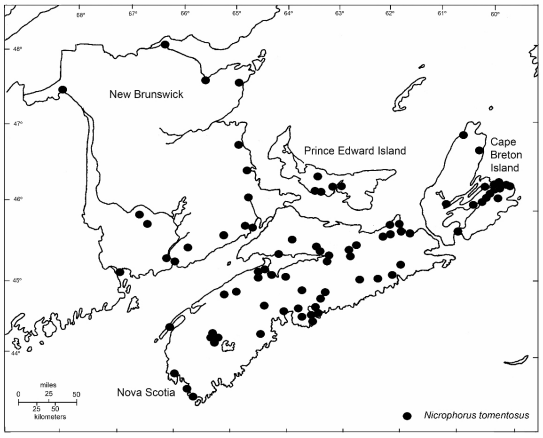
In the Maritime Provinces *Nicrophorus tomentosus* has been collected in a wide range of coniferous and deciduous forests, in sphagnum bogs, blueberry fields, and in old-field ecosystems. Individuals have been collected on a dead short-tailed shrew (*Blarina brevicauda* (Say)), pig, mouse, decomposing fish heads, and in compost. Specimens have been collected with pitfall traps, flight intercept traps, and carrion baited traps.

Nicrophorus vespilloides Herbst, 1783

PRINCE EDWARD ISLAND: 1974-1983, locality and collector information lost (4, UPEI); **Queens County**: Mount Herbert, 8 September 1952, M. Jenkins (1, UPEI).

Nicrophorus vespilloides (Figure 1f) was not recorded from Prince Edward Island in Anderson and Peck (1985), although Campbell (1991) did record it from the province without providing specific locality records. It was first reported from Nova Scotia by Kirby (1837) and from New Brunswick, mainland Nova Scotia, southwestern insular Newfoundland, and Labrador by Anderson and Peck (1985), Peck and Miller (1993), and Campbell (1991); the latter neglecting to mention

Figure 15. Distribution of *Nicrophorus tomentosus* in the Maritime Provinces of Canada.



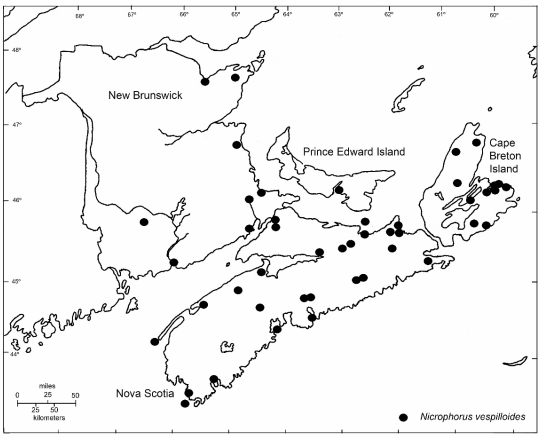
records from Labrador. It was recorded from Cape Breton Island by Campbell et al. (1987). This is a Holarctic species that has been recorded throughout Europe with the exception of Iceland, Portugal, the Mediterranean islands, and European Turkey (Ruzicka 2011); and in the eastern Palaearctic in Siberia, Korea, Japan, Mongolia, China, Iran, Kazakhstan, and Turkey (Sikes et al. 2002).

It is widely distributed throughout the Maritime Provinces, although it has not been recorded in northwestern New Brunswick and M. Turgeon (personal communication) reports that he has not found it in Madawaska County in this portion of the province (Figure 16). *Nicrophorus vespilloides* is a relatively uncommon species in the Maritime Provinces (Figure 7). Adults (n = 141) have been collected between 9 April and 27 September. There are two cohorts annually, a reproductively active spring cohort, and a late summer to early fall cohort that subsequently overwinters (Anderson and Peck 1985). The seasonal distribution data from the Maritime Provinces provides some indication of this pattern with one peak of adult numbers in late June and early July, and a second peak in late August (Figure 10).

Unlike most other sexton beetles, adult *Nicrophorus vespilloides* do not bury the carcasses they feed on. They make a shallow excavation beneath it, into which it sinks, and then cover it with leaf litter and other debris (Pukowski 1933). In North America, *Nicrophorus vespilloides* is found exclusively in swampy or boggy areas in boreal forests. In Europe, by contrast they are found only in dry coniferous forests, a difference that Anderson and Peck (1985) indicate may be due to competitive interactions with the North American *Nicrophorus defodiens*. In the Maritime Provinces, most specimens for which there is habitat data have been

found in barrens, bogs, and blueberry fields; occasionally in old-growth red spruce (*Picea rubens* Sarg.) forests. One specimen was collected on a dead great black-backed gull, another on a decomposing mushroom. Another specimen, together with five larvae, were collected on a brood ball comprised of a juvenile garter snake (*Thamnophis sirtalis pallidula* Allen). Specimens have been collected with pitfall traps, Malaise traps, flight intercept traps, and light traps.

Figure 16. Distribution of *Nicrophorus vespilloides* in the Maritime Provinces of Canada.



DISCUSSION

As previously noted, in the context of Maritime entomology, the Silphidae provide a excellent opportunity to investigate a relatively small family (11 species) that exploit a single food resource (carrion), but individually vary their developmental biology, behaviour, seasonality, diel activity, habitat preferences, the particular carrion resources they utilize, and other aspects of their biology, in such way as to partition this resource into a variety of spatial and temporal niches that each species exploits with differential efficiency. Table 2 provides a brief summary of some of the salient aspects of the bionomics of these species that helps provide insights into the spatial and temporal resource partitioning of the Silphidae in the Maritime Provinces.

As noted in the Introduction, the Silphinae utilize large and medium sized (i.e., 300+ gm) carrion items, delaying their utilization of the carrion until the initial pulse of dipteran maggots have left to pupate in the soil. Amongst the Silphinae found in the Maritime Provinces, *Oiceoptoma noveboracense* is active significantly earlier in the season than other species (Figure 4). The other three species are active during the middle of the season, however, *Necrodes surinamensis* is nocturnal and utilizes large carrion, whereas the other two species are diurnal and utilize medium to large-sized carrion items. Of the two mid-season diurnal species, *Necrophila americana* is found primarily in marshes and other mesophytic habitats, whereas *Thanatophilus lapponicus* is found in open, more xeric habitats, and in the Maritime Provinces, is particularly frequent in coastal environments such as sand dunes and ocean beaches (Table 2). It is also the only silphid in the region that has three annual cohorts, in other words it reproduces twice in the span of a season.

Amongst species of *Nicrophorus*, *Nicrophorus sayi* is active early in the season (and is restricted to coniferous forests), *Nicrophorus tomentosus* is active late in the season, whereas all other species are active during the mid-season (Figure 10). Of the mid-season species, two are diurnally active (*Nicrophorus investigator* and *Nicrophorus vespilloides*), although these are differentiated by habitat preferences and number of annual cohorts; while three are nocturnally active (*Nicrophorus defodiens, Nicrophorus orbicollis* and *Nicrophorus pustulatus*), although the exceptional *Nicrophorus pustulatus* is not generally found on carrion in the field and in natural environments has been reported as an egg parasitoid in snake nests. Two species (*Nicrophorus defodiens* and *Nicrophorus sayi*) are restricted to coniferous forests; two others (*Nicrophorus orbicollis* and *Nicrophorus pustulatus*) are found in coniferous and deciduous forests, and two more (*Nicrophorus investigator* and *Nicrophorus tomentosus*) are eurytopic and are found in a variety of open and forested habitats. Additionally, differences in body sizes of the species have some bearing on the size of carcasses that they are able to utilize, and in situations of inter-specific competition, smaller species can be displaced by larger ones in fights for carrion.

It is of interest to note that only two species of *Nicrophorus* have a single cohort each season (i.e., the mature larvae hibernate as pre-pupae) and pupate the following season – *Nicrophorus investigator* and *Nicrophorus tomentosus*. There is some evidence that there is competitive exclusion between these two species, and in the Maritime Provinces *Nicrophorus investigator* is only found frequently in areas where *Nicrophorus tomentosus* is absent or rare. There is also evidence of competition between the similarly-sized *Nicrophorus defodiens* and *Nicrophorus vespilloides*, with the result that the latter species, which in Europe is found in forested habitats, in North America is frequently displaced to marshy environments (Anderson and Peck 1995). Even this brief examination of some of the most evident features that differentiate species of silphids, makes clear important elements of how they differentially partition spatial,

Table 2. Bionomics of Maritime Provinces Silphidae

	Body size	Annual cohorts	Reproductive seasonality	Diel activity	Carcass size	Habitat
Silphinae						
Necrodes surinamensis	large (15-25)	2	mid-season	nocturnal	large	eurytopic
Necrophila americana	medium (15-20)	2	mid-season	diurnal	medium-large	marshes
Oiceoptoma noveboracense	small (13-15)	2	early	diurnal	medium-large	eurytopic
Thanatophilus lapponicus *	small (10-14)	3	mid-season	diurnal	medium-large	open habitats
Nicrophorinae						
Nicrophorus defodiens	small (12-18)	2	mid-season	nocturnal	small	coniferous forests
Nicrophorus investigator *	small (13-18)	1	mid-season	nocturnal & diurnal	small	eurytopic
Nicrophorus orbicollis	large (15-22)	2	mid-season	nocturnal	small	deciduous & coniferous forests
Nicrophorus pustulatus	medium (15-20)	2	mid-season	nocturnal	small	deciduous & coniferous forests
Nicrophorus sayi	large (15-23)	2	early	nocturnal	small	coniferous forests
Nicrophorus tomentosus	small (12-18)	1	late	diurnal	small	eurytopic
Nicrophorus vespilloides *	small (12-16)	2	mid-season	nocturnal & diurnal	small	marshes & coniferous forests

Notes: Body size in mm; * = Holarctic species.

temporal, and other resources; although species do co-occur, and there are areas of niche overlap, even though the group as a whole is dependant on one food resource, carrion.

The differences in relative abundance between species (Figures 3 & 7) may be related to both the ecological width of the niches they occupy (*sensu* Roughgarden 1972), and also how widespread and frequent this ecological niche is within the land area of the Maritime Provinces. For example, although eurytopic species such as *Necrodes surinamensis* and *Oiceoptoma noveboracense* are very abundant, the eurytopic *Nicrophorus investigator* is the most infrequently collected species in the region. The most abundant silphid, *Nicrophorus defodiens*, is restricted to coniferous forests, and this habitat is extremely widespread in the region. On the other hand, the atypical biology of *Nicrophorus pustulatus* may mean that it is collected far less frequently than are other silphids, so its apparent scarcity may instead reflect the fact that conventional collecting techniques for this group frequently fail to detect its presence.

It is likely that the inventory of Maritime Provinces Silphidae is complete. All 11 species found in the region have been recorded in all three provinces and on Cape Breton Island. Although both *Nicrophorus americanus* and *Nicrophorus marginatus* Fabricius have been recorded in both Québec and Maine, it is unlikely that the former has ever occurred in the region [see above and Majka (2010)] and the latter appears to be a more southern species (Anderson and Peck 1985), which is not apt to be found in the Maritimes. *Oiceoptoma inaequale* (Fabriciuis) is found in southwestern Québec and *Thanatophilus sagax* (Mannerheim) has been found in western Québec (Anderson and Peck 1985), however, neither of these species is apt to range into the Maritime Provinces.

From a zoogeographic perspective it is interesting to note that the full suite of Maritime silphid species is found on both Prince Edward Island and Cape Breton Island. In general, the proportion of beetles found on both of these islands is diminished in comparison with that of the neighbouring mainland areas of New Brunswick and Nova Scotia. For example, of the Carabidae, only 52% of Maritime provinces species are found on Prince Edward Island; 57% on Cape Breton Island (Majka et al. 2007). The large proportion of Silphidae found in both areas may be reflective of the excellent flight and dispersal abilities of silphids.

Although the Silphidae are a comparatively well known family of Coleoptera in the Maritime Provinces, more remains to be learned about these beetles in the region, an important subject given their ecological importance in recycling carrion in a large spectrum of habitats, and the interest that they have received in regard to forensic entomology (Michaud et al. 2010).

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