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Research Article

Arboreal Burials in *Nicrophorus* spp. (Coleoptera: Silphidae)

Amanda J. Lowe[1] and Randolph F. Lauff[2]

[1] *Department of Biology, Saint Mary's University, 923 Robie Street, Halifax, NS, Canada B3H 3C3*
[2] *Department of Biology, St. Francis Xavier University, 2320 Notre Dame Avenue, Antigonish, NS, Canada B2G 2W5*

Correspondence should be addressed to Randolph F. Lauff, rlauff@stfx.ca

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Nicrophorus beetles are well known for interring small vertebrates below ground for the purpose of rearing their young. However, the *arboreal* use of carrion has not been previously investigated. Nest boxes were suspended in the canopy of two forest habitats in Nova Scotia, Canada, to determine if this microhabitat fostered the same behaviour. Although four species of *Nicrophorus* as well as *Oiceoptoma noveboracense* (Forster) were recorded in association with carrion, *arboreal* reproduction was recorded exclusively and for the first time in *N. tomentosus* Weber and *N. defodiens* Mannerheim. Both *N. sayi* Laporte and *N. pustulatus* Herschel were associated with the arboreal carrion but did not reproduce on it during these experiments.

1. Introduction

Carrion found on the forest floor is a sporadic and ephemeral resource causing rigorous competition among scavengers. This competition is especially intense between the many species of scavenging insects [1, 2]. Other than flies, the most likely insects to arrive at a carcass within the first 24 hours are the burying beetles (Coleoptera: Silphidae: *Nicrophorus*; [3]). Their common name refers to how they inter small vertebrate carcasses in order to use them as a brood-rearing resource.

These beetles invest extensive energy into carrion burial and the care of the larvae [4, 5]. Typically, both parents regurgitate flesh from the brood ball for the begging, early instar larvae, while preventing competing flies from ovipositing in the carrion [6]. This brooding behaviour is unparalleled by any other social interaction seen in the Coleoptera [7, 8] and is essential for larval development [9, 10].

Carrion burial, although essential and well-studied for most *Nicrophorus* life cycles, is variable among the species. Pukowski [5] and L. J. Milne and M. H. Milne [4] were among the first to document the extensive burial process which took pairs of beetles 5–8 hours to completely entomb a small vertebrate carcass under a few centimetres of soil. Since these early observations, researchers have shown that differences in the size of both the beetle and the carrion can affect how efficiently carcasses are buried. Smaller species have more difficulty securing larger resources from competitors and keeping them free from fly infestation [11]. As a result, multiple beetles can be observed cooperatively burying larger carcass and providing joint parental care for the brood [12, 13].

The smaller nicrophorines do not completely bury carrion according to the process described in L. J. Milne and M. H. Milne [4]. *Nicrophorus tomentosus* and *N. vespilloides* dig shallow pits and make use of leaf litter and debris as cover [5, 14]. *Nicrophorus defodiens* may not bury carrion at all but simply conceals the resource under leaf litter [15]; Wilson and Fudge [7] report this species also digging a shallow pit prior to covering the carcass with leaves.

Carrion beetles have been traditionally caught using ground-based methods, such as carrion-baited pitfall traps and ground-level carrion [7, 16, 17]. Neither the use of eggs as a brood-rearing resource (recently demonstrated for *N. pustulatus* in Ontario [18] and Illinois [19]) nor the collaborative use of salmon carcasses by *N. investigator* Zetterstedt [20] could have been predicted using the traditional ground-level carrion techniques.

Additionally, studies over a vertical gradient in the forest reveal patterns of species' distribution which would have gone unnoticed using the traditional, ground-based techniques [21, 22]. Shubeck [23] was the first to compare the response of burying beetles between ground-level carrion and carrion suspended 1.5 m above the ground. Vertical preferences at heights greater than a couple of metres have only been recently investigated [21, 24–26]. The authors suggested that *N. pustulatus* might preferably search for carrion in the canopy to avoid the competition of the larger *N. orbicollis* on the ground. Using traps at several heights above the ground, Ulyshen and Hanula [25] showed that the vertical distribution of beetles, even within a family, can be diverse. Schroeder et al. [22] recorded carrion beetles over 3–25 m, the greatest vertical gradient investigated so far. The evidence from these studies lend insight into which species can be caught in the canopy, but studies investigating why some beetles occur in the canopy have yet to be conducted.

Nicrophorus spp. have been found within the cavity nests of two raptors, the Northern Saw-Whet Owl (*Aegolius acadicus*, [Gmelin]) [27] and the American Kestrel (*Falco sparverius* L., RFL unpublished data). Whether their presence in raptor nests simply reflects an attraction to uneaten prey or deceased nestlings is unknown. Although the extensive work by Krištofík et al. [28] and Majka et al. [29] found several dozen beetle species in almost 100 Boreal (Tengmalm's) Owl (*A. funereus*) and Northern Saw-whet Owl nests, no nicrophorines were among them.

Despite the diversity of burying behaviour among *Nicrophorus* being well documented, field studies of carrion beetle burials have been limited to ground-based carrion. Foraging in the canopy may be preferred by some species [24, 25], but reproduction on arboreal carrion remains undocumented. With evidence of a height preference in some species and a documented presence in raptor nests, it is possible that of the multiple strategies used by burying beetles, arboreal reproduction is included. The current study will focus on the use of this understudied microhabitat for reproduction in *Nicrophorus* species found on mainland Nova Scotia, Canada.

2. Materials and Methods

2.1. Study Sites. This study was located on Crown Land along the Beaver River at The Keppoch, 14 km southwest of Antigonish, NS. The mixed woods site (centered at N 45° 32′ 4.5′′, W 62° 8′ 13.6′′) was made up of 50% tolerant hardwoods (yellow birch (*Betula alleghaniensis* Britt), sugar maple (*Acer saccharum* Marshall)), 30% eastern hemlock (*Tsuga canadensis* (L.) Carr.), 10% other hardwood, 10% other conifer (GIS data obtained from NS Department of Natural Resources); the trees at the site averaged 16 m in height. The hemlock site (centered at N 45° 31′ 57.9′′, W 62° 8′ 19.9′′), approximately 250 m upstream from the mixed wood site, was dominantly eastern hemlock with 10% tolerant hardwood, 10% spruces (*Picea* spp.), and 10% other conifer; the average tree height was 15 m. There were approximately 150 m between the closest traps of the two sites.

2.2. Nest Box Design and Placement. The nest boxes were made from inverted 2 L milk jugs which were cut into equal top and bottom sections; the sections were then nested together with about two centimetres of overlap. The halves were hinged together using two wire loops, one of which was permanent, the other was removable to allow access to the inside of the nest box (Figure 1).

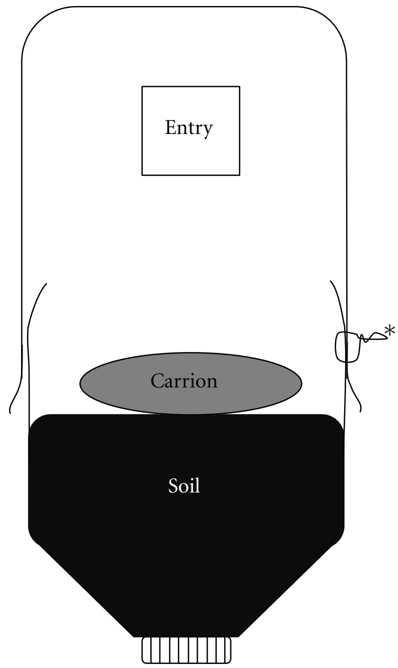

Figure 1: A nest box with soil and carrion in place. Only one of two wire hinges (∗) holding the two halves in place is shown; the other was affixed to the diagonally opposite corner, not visible in this diagram. Not to scale.

The bottom half of the nest box (i.e., the top of the jug) was filled with potting soil (Premium Nature Mix, Hortibec) up to 2 cm below the cut. Although soil is not frequently expected in the canopy, the occurrence of natural, mineral-reduced, canopy soil is typical of old rot holes or woodpecker cavities. This soil comes from the use of the cavity for purposes such as the nesting of small owls, whose young regurgitate and defecate in the cavity. The wastes build up for over a month and with time that organic matter composts into a mineral-free soil. We sought to mimic this largely mineral-free organic matter by using the potting soil which is also mineral-free.

A small passerine or other similarly sized bird with an average mass of 24.1 ± 10.1 g (mean ± standard deviation, see Section 2.3) was placed on the soil surface before wiring the nest boxes shut (Figure 1). Beetles accessed the carrion through a 3×3 cm entry cut on one side of the nest box. Small holes were punctured into the jug caps to allow for drainage.

The nest boxes were individually strung from large tree branches near the bottom of the canopy layer. At the mixed woods site, the boxes were hung at an average height of 9.5 ± 0.6 m above the forest floor, and, at the hemlock site, the boxes were at 9.7 ± 0.5 m; the nest box heights at the two sites were not significantly different from each other ($P > 0.05$; Student's t-test). Care was taken to ensure the nest boxes were at least a metre from both the trunk and the branch from which it was hung; this was done to reduce scavenging by vertebrates, predominantly raccoons (*Procyon lotor* [L]).

The nest boxes at the mixed woods site were spaced 21.4 ± 6.9 m from each other. Five of six trees containing nest boxes were yellow birch; the remaining box was hung in a white spruce (*Picea glauca* (Moench) Voss). Five of six nest boxes at the hemlock site were strung in eastern hemlock; the remaining was in a yellow birch. The average distance between neighbouring nest boxes at this site was 22.0 ± 9.2 m. The spacing of nest boxes at the two sites were not significantly different from each other ($P > 0.05$; Student's t-test).

2.3. Bait Animals. Most birds used for this study were collected from community members as window kills or from a rehabilitation centre. As such, the majority were species typical of bird feeders in the area. The species and weight of each bird used were recorded (see Table 2).

2.4. Nest Box Inspection and Analysis. The nest boxes were erected on 23 May 2009. Observations from the nest boxes were then made twice weekly for eight consecutive weeks between May 26 and August 28, 2009.

The status of the bird was recorded as being with or without larvae or pupae, buried or unburied. The soil was only replaced if infested with maggots; birds were replaced based on the same criterion, or if they had been consumed. Once a burial was established, it was necessary to carefully dig for adults, larvae, or pupae during checks. Burying beetles were identified to species [14] and quantified during each check. The carrion, along with its inhabitants, was reburied.

Nest boxes containing final instar larvae or pupae were brought into the lab (at approximately 21°C) if no parent beetles were found. Nest box exits were then covered with 6 mm hardware cloth to allow for air flow but prevent escape of newly eclosed adults. The broods were checked periodically, and eclosed adults were identified. All specimens were preserved in 70% isopropanol or pinned and deposited into the collection of RFL. A nesting was considered successful if at least one adult eclosed.

2.5. Statistical Analysis. The comparisons made between the use of the two habitats for burial were tested for significance using a Pearson's Chi-squared test with $k = 1$ degrees of freedom and a P value of 0.05.

3. Results

Four *Nicrophorus* species (*N. sayi*, *N. pustulatus*, *N. tomentosus*, and *N. defodiens*), as well as *Oiceoptoma noveboracense*, were observed in the nest boxes (Table 1). No adult beetle was observed in a nest box which contained pupae. No species had a significant forest habitat preference (Chi-squared analyses, $P > 0.05$ in all cases).

Of the 160 beetle observations within nest boxes, *N. tomentosus* was the most frequently found, with almost 70% of all the observations being of this species. *Nicrophorus tomentosus* was found in nest boxes with either unburied or buried carcasses, with or without larvae. Just over half were observed in nest boxes of the mixed woods site (Table 1).

Nicrophorus defodiens was represented by 10% of the observations and was associated with the same stages of carrion burial as was *N. tomentosus*. Ten of the sixteen *N. defodiens* (62.5%) were found at the hemlock site.

The 24 specimens of *N. sayi* were associated with unburied carrion in 87% of the observations and were never found in nests containing larvae or pupae of burying beetles. This species was distributed between the two forest types almost evenly, in a pattern very similar to that of *N. tomentosus*.

The least recorded burying beetle, *N. pustulatus*, was recorded in nest boxes six times, representing less than 4% of encounters. The observations were distributed between both forest types. Most were in nests that did not have brood balls, except on August 25, 2009, when one *N. pustulatus* was found in the presence of four adult *N. tomentosus* and a partially buried carcass. There were unidentified nicrophorine larvae on the carcass.

The only Silphid found which was not from the genus *Nicrophorus* was *O. noveboracense*; the six specimens were equally divided between habitats and were only observed with unburied carcasses (Table 1).

Nicrophorus defodiens and *N. tomentosus* each had single successful broods in the hemlock site, while the latter was also successful in the mixed woods site. The bait bird was discovered buried for the successful *N. defodiens* nest on June 30, 2009. The bait birds were discovered buried on August 7, 2009 and August 11, 2009, for the successful *N. tomentosus* nests in the mixed woods and hemlock woods site, respectively. The carcasses in each of the three successful nest boxes had all been completely buried. The only burying beetles found in successful nest boxes prior to the eclosion of the next generation were of the same species which eventually eclosed.

The other local burying beetles, *N. orbicollis* Say and *N. vespilloides* Herbst, were not found in any of the canopy nest boxes.

4. Discussion

Oiceoptoma noveboracense is expected to be attracted to carrion, though it was not found in association with buried carcasses. *Oiceoptoma noveboracense* is not a burying beetle and does not bury carcasses. The purpose of carcass burial by nicrophorines is to hide the resource from competitors [30] such as *O. noveboracense*; the absence of this beetle from the nest boxes at postburial stages suggests the nicrophorines' strategy is successful.

It is likely that two local nicrophorines, *N. vespilloides* and *N. orbicollis,* were not recorded in the nest boxes for different reasons. *Nicrophorus vespilloides* is a specialist of open habitats such as bogs [14, 31] and is therefore not expected in the forest. *Nicrophorus orbicollis* is uncommon in the study area and, when found, avoids the canopy [23]. Additionally, it was expected that no adult beetles of any species would be observed in nests with next-generation pupae since pupae no longer need care.

Although not likely as rich in carrion as the ground, the canopy still has the potential to provide significant amounts

Table 1: Observations of adult beetles in nest boxes at the different carcass stages. The adults may or may not have been parents of offspring, if any, from a nest; however, these adults were not next-generation beetles. Since adult beetles were not marked, the values represent maxima. H: hemlock woods; MW: mixed woods.

	Unburied		Buried, no larvae		Buried, with larvae		Buried, with pupae		
	H	MW	H	MW	H	MW	H	MW	Totals
N. tomentosus	28	45	15	11	5	4	0	0	108
N. defodiens	0	6	4	0	6	0	0	0	16
N. sayi	8	13	3	0	0	0	0	0	24
N. pustulatus	3	2	0	0	1	0	0	0	6
O. noveboracense	3	3	0	0	0	0	0	0	6
Totals	42	69	22	11	12	4	0	0	160

Table 2: Bait birds.

Species		Mean mass (g)	*n*
Duckling	*Anas* sp.	27.6	1
Spotted sandpiper	*Actitis macularius*	17.5	1
Downy woodpecker	*Picoides pubescens*	25.7	1
Yellow-bellied flycatcher	*Empidonax flaviventris*	12.5	1
Flycatcher	*Empidonax* sp.	13.4	1
Black-capped chickadee	*Poecile atricapillus*	13.6	7
Blue-headed vireo	*Vireo solitarius*	22.0	1
Red-eyed vireo	*Vireo olivaceus*	18.9	1
Cedar waxwing	*Bombycilla cedrorum*	35.0	2
Swainson's thrush	*Catharus ustulatus*	35.8	2
Hermit thrush	*Catharus guttatus*	34.5	1
Ovenbird	*Seiurus aurocapilla*	20.9	4
Yellow-rumped warbler	*Setophaga coronata*	14.0	1
Savannah sparrow	*Passerculus sandwichensis*	25.8	1
White-throated sparrow	*Zonotrichia albicollis*	24.6	2
Dark-eyed junco	*Junco hyemalis*	22.6	8
Purple Finch	*Carpodacus purpureus*	29.6	18
White-winged crossbill	*Loxia leucoptera*	26.8	1
Common redpoll	*Acanthis flammea*	21.4	1
Pine siskin	*Spinus pinus*	13.0	4
American goldfinch	*Spinus tristis*	13.5	6
Evening Grosbeak	*Coccothraustes vespertinus*	58.2	2
Finch sp.	Carduelinae	24.9	1
Unknown chick		29.0	4

of carrion. There are many species of cavity nesting, altricial birds including small raptors (e.g., American Kestrel and Northern Saw-whet Owl), seven species of woodpecker (Piciformes), and more. Two species of cavity-nesting squirrels are also in the study area, Red Squirrel (*Tamiasciurus hudsonicus* (Erxleben)) and Northern Flying Squirrel (*Glaucomys sabrinus* (Shaw)). In all of the birds, the rearing of the nest-bound young is the responsibility of both parents. If a predator kills either parent, the nestlings are destined to perish as well. If the female squirrel is depredated, the milk-dependant young will die. Should either of these scenarios happen, burying beetles are one of several canopy-foraging groups of carrion exploiters to potentially use the newly available resource.

Terrestrial-based work has revealed that burying beetles may take advantage of abandoned cavities and burrows rather than dig a new crypt for a carcass [31, 32]. Therefore, using an existing tree cavity may simply be an extension of a behaviour first utilized on the ground.

Nicrophorus tomentosus was the most abundant species found in the canopy nest boxes and was a confirmed breeder there. Although this species has one of the widest foraging niche breadths of all *Nicrophorus* species [33], their frequent presence in elevated traps [23] alluded to life history aspects beyond what was known. Complete burial of carcasses which is typical of most nicrophorines is not characteristic of *N. tomentosus* [14]. Normally, they only dig a shallow pit and cover the carcass with leaves. In the current study, no leaves were provided which may have obligated the beetles to completely bury the carcass.

Smaller species of burying beetle, such as *N. defodiens*, are often out-competed for breeding resources by larger species

[34]. Wilson et al. [3] showed a decrease in the proportion of successful broods on the ground for *N. defodiens* during mid July, correlating with an increased ambient temperature facilitating searches by the larger *N. orbicollis*. As the number of intrageneric competitors increase with midsummer [14, 35], the decreased ability of *N. defodiens* to produce successful broods on the ground may have stimulated a shift in breeding habitat [3, 16] and provided pressures favouring canopy search behaviour and breeding.

Only one brood was produced by *N. defodiens* in this study. Similar to the unconventional burial noted for *N. tomentosus*, the carcass used for the *N. defodiens* brood was also completely buried. Although this has been documented as a rare occurrence, normally, this species simply covers its carcasses with leaf litter [7].

The two other beetles recorded in canopy nest boxes, *N. sayi* and *N. Pustulatus,* may reproduce in the canopy, although they were not confirmed as breeders in this study. Both species were associated with brood balls in the nest boxes at least once, but this association was less common than observations with unburied carrion. Sexually mature beetles are differentially attracted to small vertebrate carcasses [36], like those used in this study, which supports the potential for breeding by *N. sayi* and *N. pustulatus*. The timing of this study was initiated towards the end of the breeding season for *N. sayi*, which may account for the small number of observations and lack of confirmed breeding for this species.

Carcass use has never been documented for *N. pustulatus* in the wild, despite hundreds of bait animals being placed out [7, 31] though Smith et al. [37] and others have documented *N. pustulatus* breeding on mice in the lab. This species is infrequently caught in conventionally baited pitfall traps [38], suggesting it is either truly uncommon or has a different life history which does not involve carrion at ground level. Serendipitous discoveries of *N. pustulatus* rearing its young on ground-nesting snake eggs [18, 19] has solved part of the conundrum surrounding this beetle's unusual life history. Other apparently contradictory data show *N. pustulatus* routinely in the canopy [25, 26, Table 1], suggesting the canopy as a foraging habitat, or an as yet undocumented alternate breeding habitat.

The novel observation of one *N. pustulatus* and four *N. tomentosus* found together in association with larvae of a partially buried carcass suggests brood parasitism, even though the identity of the species responsible for the burial could not be determined. Although Trumbo [13] was unable to record brood parasitism in the field, he did document the ability of *N. pustulatus* to parasitically lower the brood size of *N. orbicollis* in lab [39]. However, parasitism is a common behaviour among most genus members and occurs both inter- and intraspecifically, [38, 40–43].

Previous canopystudies used either unbaited flight intercept traps [25] or rat-baited window traps [26] and dominantly caught *N. pustulatus* in the elevated traps. No previous study has provided *N. pustulatus* with both carrion and a nest for brood rearing in its apparently preferred canopy microhabitat. This documented canopy preference [25, 26] and occurrences of *N. pustulatus* in the nest boxes from this study, combined with previous findings of this species in the nest cavities of a Northern Saw-Whet Owl [27] and an American Kestrel (Lauff unpublished data), provide compelling evidence that *N. pustulatus* may reproduce in the canopy.

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