AERIAL FORAGING AND SEXUAL DIMORPHISM IN BURYING BEETLES (SILPHIDAE: COLEOPTERA) IN A CENTRAL ONTARIO FOREST

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Abstract

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Burying beetles (Coleoptera: Silphidae) are commonly sampled on the ground using pitfall traps. Recent work has shown that these beetles also respond to aerial traps baited with carrion. In this study, we sampled the Silphidae of Algonquin Park using traps baited with mouse and bird carrion, and set at 2, 4, and 6 m heights. The most abundant species caught was *Nicrophorus tomentosus*, followed by (in order) *N. defodiens, N. sayi, Oiceoptoma noveboracense, N. pustulatus, Necrophila americana,* and *Necrodes surinamensis.* Only *N. tomentosus* showed bait preference, with higher than expected catches at traps baited with mice. Catches differed based on trap height for two species, with most *N. defodiens* being caught in the lower traps (2 m), and all *N. pustulatus* caught at the high traps (6 m). *Nicrophorus tomentosus* males caught in the 6 m traps were significantly larger than males caught in the lower traps, and females caught at all heights. Possible reasons are discussed.

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Introduction

The carrion beetles (Family Silphidae) have long been a favourite group with collectors and naturalists in North America. There are 30 species of these in North America, and individual species specialize in carrion types based on size and source, ranging from large carcasses such as black bears (Watson and Carlton 2003) (e.g. subfamily Silphinae), to small rodent sized carcasses such as mice and song birds (subfamily Nicrophorinae, the burying beetles; Anderson and Peck 1985). Burying beetles use olfactory cues to locate carcasses, and are able to locate fresh squirrel carcasses several metres distant in a few minutes (Dethier 1947).

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In spite of the attention that this group has attracted in the past, basic life history and niche information is still lacking. For example *Nicrophorus pustulatus* Herchel was only recently determined to be a parasitoid on snake eggs (Blouin-Demers and Weatherhead 2000; Keller and Heske 2001). Regional surveys of extant *Nicrophorus* species do report catching *N. pustulatus* in low numbers (e.g., Anderson 1982; Shubeck et al. 1981), and outside of the range of the black rat snake (Smith et al. 2007). It appears that *N. pustulatus* must utilize some other unknown source of carrion.

What this is may be consistent with the recently observed vertical distribution of *N. pustulatus* in Georgia, where *N. pustulatus* were almost exclusively caught several metres above ground (Ulyshen and Hanula 2007a) in the forest canopy. The canopy habitat includes tree cavities, and these could offer a specialized niche of carrion such as dead nestlings, e.g. squirrels, birds, or bats. Any species differences in how this habitat is exploited should be reflected in catches obtained using carrion baited traps placed at various heights.

In this study, we report on the species composition of Silphidae caught in carrion baited traps placed at three different heights above the ground in Algonquin Park, a large forested region of central Ontario. We also compared trap catches at traps with avian and mammalian baits.

For burying beetles, there are reproductive advantages to size, with larger species and individuals winning fights over carcasses (Otronen 1988; Trumbo 1990). Body size is also related to flight capability. During flight, beetles lose heat due to convection (Merrick and Smith 2004), so that conserving heat would enable longer flights, for example, flight associated with searching or localized dispersal. Such flights would take place at higher levels (Taylor 1974), so we would expect elevated traps to catch these individuals. For the most numerous species caught, *N. tomentosus*, we tested for differences in the size of males and females at each height, reasoning that such size differences might indicate sex biased flight capability associated with dispersal from natal sites.

Materials and Methods

Silphid beetles were collected during August 2008, in Algonquin Provincial Park, Ontario, Canada. The study site was located along Highway 60, at kilometre 20, Found Lake, Peck Township on the Canadian Shield. The forest was composed of mature trees: maple (predominantly *Acer saccharum* Marsh.), beech (*Fagus grandifolia* Ehrh.), hemlock (*Tsuga canadensis* (L.) Carr.), and birch (*Betula papyrifera* Marsh and *Betula allegheniensis* Britton). The understory was shaded, was easily accessible by foot, and composed mainly of bracken (*Pteridium aquilinum* (L.) Kuhn) with some low density shrubs.

Twenty-four traps were deployed for seven day periods beginning 1, 7, and 14 August 2008, for a total of 72 samples. During sampling, many traps were destroyed by wildlife (bears and raccoons) and wind. If damage occurred early in the sampling week, traps were re-installed for later collection, so that the length of a trapping period varied for some traps. Fourteen ruined traps could not be replaced. For each sampling week, traps were positioned in a grid or block comprised of three rows of eight traps per row. The rows were spaced 15 m apart, with traps in each row spaced 10 m. Traps were placed at 2, 4, and 6 m above ground, with 6 m traps placed in the upper trunk zones but just below the canopy level. Trap height and bait type were randomized over the 24 possible locations in each block (there were eight possible X and three possible Y coordinates), so that there were four traps for each bait type at each height in the block.

Traps were constructed from 2 L plastic soda pop bottles with a 6 cm diameter hole cut into the middle of one side to allow beetles to enter the traps. Bait was wrapped in cheese cloth and hung in each bottle by a piece of wire pushed through the lid. The bottom of each trap had a 1.5 cm deep layer of killing solution consisting of 5% dish soap and water (Larsen 2005). A sling shot was used to send a weighted rope over a tree branch to raise and lower traps.

Half the traps were baited with chicken wings and the other half with mice. Frozen domestic mice (*Mus musculus*) were obtained from a reptile feed supply store. The mean weight per mouse was ~ 25 g. Frozen chicken wings were obtained in bulk from the grocery store (mean weight ~ 30 g). Baits were frozen until placed in traps without any prior aging or ripening.

Trapped beetles were preserved in 70% isopropyl alcohol. A sub-sample of 320 *Nicrophorus tomentosus*, about 100 specimens from each height, were sexed and measured for total body length.

Because of the missing data, ANOVA could not be used to test the effects of bait type and trap height on trap catches. Instead, we used a chi-square test (Sokal and Rohlf 1995) to compare the observed to expected total catch frequencies of each species for bait type and trap height. The expected frequencies were determined from the number of trapping days for each category. For example, if 140 individuals of a species were caught over 50 trapping days at traps baited with mice, and 220 were caught over 100 trapping days at traps baited with birds, then the expected frequencies would be (140+220) x (50/150) =120 for mouse traps and (140+220) x (100/150) = 240 for bird traps. Because several comparisons were performed for each test, the critical values of chi-square at a significance level of $\alpha = 0.05$ were adjusted using the Bonferroni method by which $\alpha' = \alpha/k$ (Sokal and Rohlf 1995). For the bait tests and the trap height tests we used k = 7 (number of species tested). Our adjusted critical values for chi-square were 9.94 for 2 degrees of freedom (three trap heights), and 7.33 for 1 degree of freedom (two bait types).

We tested whether there were differences in body length of *N. tomentosus* between males and females at each height using a 2-way ANOVA with trap height and sex as treatments. Statistical tests were done using an Excel spreadsheet and STATISTICA 7 (Statsoft Inc. 2004).

Results

We caught 2388 Silphidae from 7 species in the traps (Table 1). The most abundant species was *Nicrophorus tomentosus*, accounting for 81% of the total catch. The rarest species was *Necrodes surinamensis*, of which only a single individual was caught, this at 4 m. Members of each species were more abundant in the 2 m traps except for *N.*

TABLE 1. Number of each species of Silphidae captured in carrion baited aerial traps at three different heights in Algonquin Park, Ontario, in August 2008.

	Trap height			
Species	2m	4m	6m	Total
Nicrophorus tomentosus	863	497	585	1945
Nicrophorus defodiens	191	76	42	309
Nicrophorus sayi	43	22	25	90
Oiceoptoma noveboracense	21	7	5	33
Nicrophorus pustulatus	0	0	6	6
Necrophila americana	4	0	0	4
Necrodes surinamensis	0	1	0	1
Total	1122	603	663	2388

pustulatus, which was only found in 6 m traps (Table 1). *N. tomentosus* was the only species for which trap catches differed by bait types, with slightly more caught at mouse baited traps than expected (observed = 856, expected = 791.9; Table 2).

More *N. defodiens* were caught in the lowest traps and more *N. pustulatus* in the higher traps (Table 2). For the other species, observed trap catches at the three heights did not differ from the expected proportions.

The biggest male *N. tomentosus* were caught in the 6 m traps; these were significantly larger than females caught at all heights (Duncan's Multiple Range post-hoc test, 2 metres: p=0.003; 4 metres: p=0.024; 6 metres, p=0.025) and males at 2 metres (2 metres: p=0.012; 4 metres, p=0.07) (Table 3, Fig. 1).

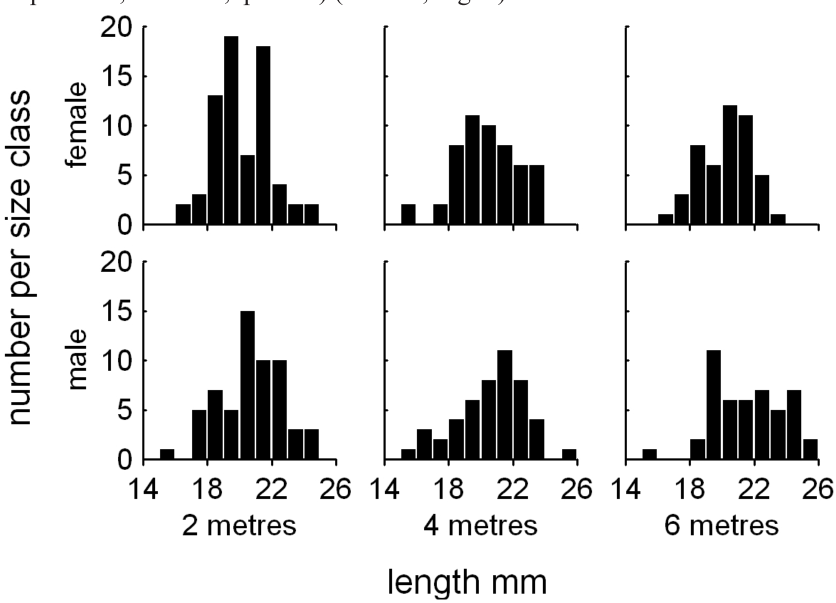

FIGURE 1. Frequency distribution of body lengths of female and male *N. tomentosus* at 2, 4, and 6 metre traps.

TABLE 2. Seasonal totals, per trap means and standard deviations, for each species of Silphidae captured, by bait type (bird and mouse), and trap height (2 m, 4 m, 6 m), in Algonquin Park, Ontario, in August 2008. Treatments were tested using a chi-square test with the critical value based on a Bonferroni adjusted α. Expected frequencies were based on the sum of trapping days for each category (Days).

			Total catch (Mean, SD) by species						
Category	(Days)	N	*N. defodiens*	*N. pustulatus*	*N. sayi*	*N. tomentosus*	*N. americana*	*N. surinamensis*	*O. noveboracense*
bird	(249)	33	179 (5.4, 6.3)	4 (0.1, 0.55)	46 (1.4, 2.4)	1089 (33.0, 36.9)	0	1 (0.03, 0.2)	26 (0.8, 1.2)
mouse	(171)	23	130 (5.7, 5.7)	2 (0.1, 0.29)	44 (1.9, 2.6)	856 (37.2, 45.5)*	4 (0.2, 0.7)	0	7 (0.3, 0.9)
2m	(176)	23	191 (8.4, 7.5)*	0	43 (1.9, 2.5)	863 (37.6, 48.2)	4 (0.2, 0.7)	0	21 (0.9, 1.4)
4m	(116)	16	76 (4.8, 4.2)	0	22 (1.4, 2.4)	497 (31.1, 27.0)	0	1 (0.1, 0.3)	7 (0.4, 0.8)
6m	(128)	17	42 (2.4, 2.9)	6 (0.4, 0.79)*	25 (1.5, 2.7)	585 (34.3, 41.0)	0	0	5 (0.3, 0.5)

*significant at $\alpha = 0.05$, chi-square$_{crit.}$ = 7.33 (1 df) for bait type and 9.94 (2 df) for trap height.

TABLE 3. Mean lengths (mm) of *N. tomentosus* caught in carrion baited aerial traps at three different heights in Algonquin Park, Ontario, in August 2008.

	Mean (SD) N, by sex	
Trap height	Males	Females
2m	20.25 (2.00) 59	19.71 (1.73) 70
4m	20.21 (2.17) 48	19.96 (1.93) 53
6m	21.20 (2.24) 47	19.84 (1.62) 47

Discussion

Nicrophorus tomentosus and *N. defodiens* were the most common species captured in this study. Work done in North Carolina has shown that these species are frequently encountered late in the warm season (Trumbo 1990). In southern Ontario, *N. tomentosus* breeds from mid to late summer (Anderson and Peck 1985), with trap catches peaking in late August (Anderson 1982); *N. defodiens* is active from May to early September and has been trapped at similar levels during this period (Anderson 1982). *Nicrophorus sayi*, a spring breeder in Ontario (Anderson 1982) was the third most common species captured, consistent with a previously reported peak in early and late August of teneral adults (Anderson 1982).

Only *N. tomentosus* showed any bait preference, with a minor preference for traps with mice. For the *Nicrophorus* spp., small carrion would include dead fledglings as well as dead rodents. In terms of possible tree hole exploitation, both types of carrion would be present. Generally, Silphinae are attracted to larger carrion (Anderson and Peck 1985).

Height Preference

Nicrophorus were caught at all heights except *N. pustulatus* and *N. defodiens*. *Nicrophorus defodiens* is a small species, and it compensates for this competitive disadvantage by being able to locate carcasses quicker than its larger competitors, such as *N. orbicollis* Say (Trumbo and Bloch 2002). That it was caught less often in the higher traps may reflect a possible decreased flight height due to its smaller size rather than its inability to find the bait.

Our results support our initial reasoning that carrion in the forest canopy might be a suitable specialized niche for exploitation for *N. pustulatus*. Our low catch of 6 individuals is similar to low catches reported in previous studies (Anderson 1982; Robertson 1992). *Nicrophorus pustulatus* does not appear to respond to traps baited with fresh carcasses (Trumbo 1990). However, it has been caught in pitfall traps baited with well-rotted carrion (Trumbo 1990; Anderson 1982).

Catching *N. pustulatus* at elevated traps is consistent with earlier work (Ulyshen and Hanula 2007b). In Ontario, Robertson (1992) caught *N. pustulatus* at 1 m to 2 m. Low catches of *N. pustulatus* at ground level could be due to this species specializing in canopy or nest-cavity habitats rather than specific carrion sources; *N. pustulatus* will breed on dead rodents in lab settings (Robertson 1992).

Nevertheless, black rat snake eggs are the only known wild breeding medium (Smith et al. 2007; Blouin-Demers and Weatherhead 2000), which may explain the generally low numbers caught using mammalian or avian baits. Because of this, the presence of *N. pustulatus* is relevant to the conservation of regionally rare or endangered snake species (Smith et al. 2007) e.g. the black rat snake *Elaphe obsoleta* (Say) in Ontario, a species not found in Algonquin Park (Logier 1970). Our results suggest that surveying for *N. pustulatus* should include aerial traps.

Sex and Size Dimorphism in *Nicrophorus tomentosus*

For *N. tomentosus*, because males and females both remain with their brood after covering a carcass, it is unlikely that there is a size advantage for one sex or the other in terms of contests over carcasses. However, there may be a size advantage in terms of flight capability. During flight, beetles lose heat due to convection (Merrick and Smith 2004), so that conserving heat would enable longer flights, for example flight associated with local dispersal. *Nicrophorus tomentosus* is a bumble bee mimic (Fisher and Tuckerman 1986), and is covered in yellow hairs (Milne and Milne 1944), which can contribute to conserving heat and regulating body temperature in *Nicrophorus* spp. (Merrick and Smith 2004).

The female *Nicrophorus tomentosus* we caught were the same size at all trap heights, whereas males caught on 6 m traps were significantly larger than both females and males from lower traps (Table 3). Trumbo (1990), found no difference in the size of male and female *Nicrophorus tomentosus*, nor did we in our lower traps. The larger males were largely present in 6 m traps only (Fig. 1). Sampling at the higher traps would over-represent this group.

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