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Note

A case of a Pustulated Carrion Beetle (*Nicrophorus pustulatus*, Coleoptera: Silphidae) burying live Tree Swallow (*Tachycineta bicolor*, Passeriformes: Hirundinidae) nestlings under the nest

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Abstract
The ecology of Pustulated Burying Beetle (*Nicrophorus pustulatus*, Coleoptera: Silphidae) appears distinct among *Nicrophorus* species, with evidence of it parasitizing snake eggs and foraging primarily above the ground and into the forest canopy. Here we document an extension of its aberrant ecology and behaviour: a case of *N. pustulatus* burying 2-day-old live and dead nestlings of Tree Swallow (*Tachycineta bicolor*, Passeriformes: Hirundinidae) under the nest, behaviour consistent with the early stages of breeding in *N. pustulatus*. Based on different levels of decomposition, we suspect that *N. pustulatus* responded to one dead swallow nestling in the brood of five and went on to bury all of the nestlings at the bottom of the nest box. The observation provides the first evidence, to our knowledge, of *Nicrophorus* burying live vertebrates.

Key words: Burying beetle; *Nicrophorus pustulatus*; Tree Swallow; *Tachycineta bicolor*; evolutionary ecology

Pustulated Carrion Beetle (*Nicrophorus pustulatus* Herschel, Coleoptera: Silphidae) has a broad distribution across the eastern United States and Canada (Anderson and Peck 1985; Ringrose *et al.* 2019), and yet its ecology has remained puzzling. Early observations suggested that this species was rare throughout its range because few were captured in ground traps that typically attract burying beetles (Wilson *et al.* 1984; Anderson and Peck 1985; Trumbo 1990; Robertson 1992). However, observations of *N. pustulatus* coming in to lights at night hinted that it may be more common than ground trapping has revealed (Anderson and Peck 1985; Robertson 1992; Lingafelter 1995).

In captivity, *N. pustulatus* readily bred on vertebrate carcasses >100 g, suggesting that this species may specialize in larger carcasses, unlike many other *Nicrophorus* species that typically use small vertebrate carrion for breeding (Trumbo 1990; Robertson 1992). Experiments in the lab further demonstrated that *N. pustulatus* was unique among coexisting *Nicrophorus* in its ability to raise up to 187 young in a single reproductive bout (one female) on larger carcasses (up to 260-g Black Rat [*Rattus rattus*]), sometimes even rejecting smaller carcasses (<20 g) for breeding (Trumbo 1992). The scarcity of *N. pustulatus* captured in the field, even on larger carcasses, was perplexing (Wilson *et al.* 1984; Trumbo 1992). Also, observations of *N. pustulatus* acting as a brood parasite of Roundneck Sexton Beetle (*Nicrophorus orbicollis* Say) in captivity provided evidence of more complexity in its breeding biology (Trumbo 1994).

The discovery of *N. pustulatus* regularly parasitizing oviparous snake eggs (Blouin-Demers and Weatherhead 2000; Keller and Heske 2001; Smith *et al.* 2007; LeGros *et al.* 2010) documented a remarkable evolutionary shift for burying beetles. *Nicrophorus* were only known to reproduce on the carcasses of vertebrates (Scott 1998), and thus larvae entering and parasitizing live, developing vertebrate eggs and causing their mortality was unique (Blouin-Demers and Weatherhead 2000). The suggestion that

N. pustulatus could be a snake egg specialist, however, was at odds with (i) its capture at traps baited with rat (Trumbo 1990; Ulyshen *et al.* 2007), chicken (Wettlaufer *et al.* 2018), goose (Ringrose *et al.* 2019), fish (White Sucker [*Catostomus commersonii*]; Anderson 1982), and ground beef (Robertson 1992); (ii) its willingness to breed on vertebrate carcasses in captivity (Robertson 1992; Rauter and Moore 2002; Trumbo 2007; Rauter and Rust 2012); (iii) its similarity to other *Nicrophorus* in terms of breeding biology in the lab, including burying, removing fur, and preparing mouse carcasses (Robertson 1992); and (iv) its occurrence outside of the range of oviparous snakes (Ringrose *et al.* 2019), although beetles could potentially parasitize turtle eggs in some of these areas (Blouin-Demers and Weatherhead 2000; Smith *et al.* 2007). Although the use of vertebrate carcasses could represent an ancestral trait that had not yet been lost (Blouin-Demers and Weatherhead 2000; Smith *et al.* 2007), evidence suggested that *N. pustulatus* would still likely use vertebrate carrion as a resource for reproduction in nature.

The capture of *N. pustulatus* in passive insect traps in the forest canopy (Ulyshen *et al.* 2007), followed by repeated successful trapping of this species using baited traps set above the ground (Ulyshen *et al.* 2007; LeGros and Beresford 2010; Low and Lauff 2012; Dyer and Price 2013; Brown and Beresford 2016; Wettlaufer *et al.* 2018), provided new evidence that this species could be a specialist on vertebrate resource opportunities above the ground. In most populations, *N. pustulatus* was more common in traps set above the ground than on it (Ulyshen *et al.* 2007; LeGros and Beresford 2010; Dyer and Price 2013; Wettlaufer *et al.* 2018) and represented the only carrion beetle species to be more abundant in the canopy than on the ground (Ulyshen *et al.* 2007; LeGros and Beresford 2010; Wettlaufer *et al.* 2018).

If *N. pustulatus* is uniquely common above the ground, then what resources does it use for breeding, and how does it prepare or bury its resources for breeding? One hypothesis is that *N. pustulatus* specializes in nesting vertebrates, such as birds, snakes, and mammals, taking advantage of mortality associated with reproduction, in addition to live snake eggs (LeGros and Beresford 2010; Wettlaufer *et al.* 2018). Observations of *N. pustulatus* in the nests of cavity-nesting birds, including cases of it burying dead nestlings in the nests, are consistent with these ideas (Phillips *et al.* 1983; Low and Lauff 2012; Wettlaufer *et al.* 2018).

Here we report an extension of these observations: a case of *N. pustulatus* burying nestlings of the cavity-nesting Tree Swallow (*Tachycineta bicolor*, Hirundinidae), including at least one live nestling, under the nest.

At 1440 on 10 June 2019, K.V.B.D. was checking nests of Tree Swallows at the Massassauga Tree Swallow nest box grid at the Queen's University Biological Station in southeastern Ontario (44°34′38.9″N, 76°23′07.9″W, 150 m elevation), where 54 artificial nest boxes were part of a long-term Tree Swallow monitoring project (Cox *et al.* 2019). Nest checks are conducted every three days throughout May and June and into July, to monitor the progress of nest building and record information on important breeding events, such as first egg, incubation start, and hatch. During nest checks, K.V.B.D. came across a failed nest, ~35 m from the forest, and ~1.5 m above the ground, that had contained five eggs on 7 June. The first egg in this nest was laid on 21 May, and the female Tree Swallow began incubating on 25 May, the day she laid the final egg. The estimated hatch date was 8 June (calculated as 14 days after the beginning of incubation).

On 10 June, the nest was expected to contain two-day old nestlings; however, K.V.B.D. found the nest empty. When a nest that is expected to contain eggs or nestlings is empty, it usually means that it has been subject to predation. In such cases, the nest is removed from the box by researchers so that a new pair of birds can use it. When K.V.B.D. lifted the nest to remove it, she found five nestlings on the wooden floor of the nest box: four dead and one alive. One large *N. pustulatus*, identified later in photos and video by P.R.M. (following Anderson and Peck 1985; voucher photographs deposited in the Canadian National Collection of Insects, Arachnids and Nematodes, https://cnc.agr.gc.ca/taxonomy/Specimen.php?id=2520115), was also present in the box, carrying or pulling two of the nestlings across the bottom of the box. The *N. pustulatus* then went to the back corner of the box and attempted to hide under some of the nest material that was still present. Photos and videos of *N. pustulatus* and the nestlings, as well as the nest and nest box, are archived in the Macaulay Library, Cornell Lab of Ornithology, and are available online (https://macaulaylibrary.org/asset/173174091, 173174111, 173174121, 488626, 488627, 488628). The live nestling (far right in the photos and video) had a fresh faecal sac stuck to its cloaca and was moving. Three of the four dead nestlings looked fresh, with normal colouration and no signs of decomposition. The fourth dead nestling (far left in photos and video) was yellowish, with a darker colouration of the abdomen under the skin, consistent with decomposition. No odour of decomposition was noticed by K.V.B.D. The developmental stage of the nestlings (see Gates 2019) was consistent with their having hatched on 8 June. We did not weigh the nestlings, but a Tree Swallow nestling of similar age and developmental stage typically weights 2–5 g (Zach and Mayoh 1982; Quinney *et al.* 1986).

The adult Tree Swallows did not appear to be active at the nest. When a nest is being cared for by adults, they typically become agitated when someone approaches the nest and will dive-bomb (Winkler *et al.* 2011; K.V.B.D. pers. obs.). Because this did not occur during the several minutes that K.V.B.D. observed the nestlings, it is likely that the adults had already abandoned the nest. The cause of death of the nestlings is unknown, and there was no mortality at any of the other 53 boxes at the site in the days leading up to or following the death of these nestlings. The nestlings showed no signs of damage or physical trauma, and the faecal sac stuck to the live nestling is consistent with recent feeding by the adults.

Following the observation, K.V.B.D. left the nestlings and the beetle in the box (with the nest); when she returned to the grid on 13 June 2019, the nestling carcasses had decayed, suggesting that the beetle had abandoned them.

We provide evidence of *N. pustulatus* burying live Tree Swallow nestlings under the nest, consistent with the early stages of preparation for breeding on vertebrate carrion in this species (Robertson 1992). We suspect that the beetle was attracted to the nest by one dead nestling in the nest box, and that it proceeded to bury the remaining live nestlings as well. Although we did not witness *N. pustulatus* burying the nestlings, we surmise that this occurred because (i) *N. pustulatus* regularly bury vertebrate carcasses in captivity (Robertson 1992), (ii) the *N. pustulatus* was observed moving two dead nestlings in the nest box suggesting that it was treating the nestlings as a resource, (iii) adult Tree Swallows have never been recorded burying nestlings despite extensive study (Winkler *et al.* 2011), (iv) nestling Tree Swallows at that developmental stage have little coordinated movement beyond raising their heads during begging (Winkler *et al.* 2011), (v) Tree Swallow nestlings have never been recorded burrowing into the nest on their own (Winkler *et al.* 2011), and (vi) the Tree Swallow nest was composed of densely interwoven grasses and other materials (https://macaulaylibrary.org/asset/173174121), making the passive movement of all nestlings to the bottom of the nest box almost impossible, even while *N. pustulatus* was burying a dead nestling. Given their developmental stage, the nestlings would likely be unable to resist being moved by *N. pustulatus*. We saw no evidence that the beetle injured or killed the dead nestlings; however, once buried, the nestlings would not be fed or retrieved by the adult Tree Swallows, and thus would likely starve. The faecal sac present on the one remaining live nestling suggests that it had been fed by the adults sometime earlier that day. *Nicrophorus pustulatus* are typically nocturnal when foraging (Anderson 1982; Anderson and Peck 1985) and, thus, likely entered the nest box the previous night when adult females usually brood young nestlings (Winkler *et al.* 2011).

Nicrophorus pustulatus has been found previously in Tree Swallow nest boxes at our study site, always associated with dead nestlings. In 2017, *N. pustulatus* was found in a nest box with a brood of Tree Swallow nestlings that had all died when they were 8–12 days old (A. Cox pers. comm. August 2019). On 14 June 2016, a male–female pair of *N. pustulatus* was found with five, week-old dead nestlings buried at the bottom of a nest box, suggesting that the pair was beginning to breed (A. Schizkoske unpubl. data 2016 as cited in Wettlaufer *et al.* 2018). Before 2016, researchers on the Tree Swallow grids had also noticed carrion beetles in boxes associated with nestling mortality (both American Carrion Beetle [*Necrophila americana* L.] and *Nicrophorus* spp.); however, the beetles were not identified to species (F. Bonier pers. comm. August 2019).

Tree Swallows are extremely sensitive to cold and rainy weather because they rely on flying insects for food, and insects are less likely to fly during poor weather (Winkler *et al.* 2011, 2013; Cox *et al.* 2019). When cold, rainy weather events coincide with the nestling period for Tree Swallows, nestlings suffer high mortality (Winkler *et al.* 2013; Cox *et al.* 2019) creating a potentially abundant resource for burying beetles. This resource may be limited by adult Tree Swallows removing dead nestlings in response to partial brood mortality (Chek and Robertson 1991) and by researchers removing dead nestlings during nest checks. In addition to Tree Swallow nests, *N. pustulatus* has also been found in the nests of two other cavity-nesting birds: Northern Saw-whet Owl (*Aegolius acadicus*; Phillips *et al.* 1983) and American Kestrel (*Falco sparverius*; Low and Lauff 2012). Both of these species will accumulate excess prey remains in the nest (Smallwood and Bird 2002; Rasmussen *et al.* 2008) that could be food for *N. pustulatus*, and American Kestrels often suffer nestling mortality and partial brood loss when prey is scarce (Smallwood and Bird 2002).

The burying of live vertebrates has not, to our knowledge, been described previously in the genus *Nicrophorus* (Anderson and Peck 1985; Scott 1998). Although we suspect that the behaviour was accidental, associated with a beetle responding to a dead nestling, it represents an interesting intermediate step between scavenging and predation that might be expected in the evolution of predatory behaviour. Such a transition was suggested for the origins of snake egg parasitism, which may have begun with *N. pustulatus* responding to ruptured or spoiled eggs that failed to hatch, and progressed to parasitoid behaviour (Blouin-Demers and Weatherhead 2000; Smith *et al.* 2007). Although burying live nestlings may be a rare occurrence, most nest box researchers clean out the nest boxes after the end of the nesting season (Gates 2019), and, thus, cases of live burial would not likely be discovered. Also, any nestling alive at the time of burial would likely starve soon after and would, therefore, be dead on discovery by researchers.

The burial behaviour of *N. pustulatus* in this and previous nests suggests that dead nestlings of birds are used for breeding, adding new perspectives to *N. pustulatus* ecology. Overall, *N. pustulatus* appears most common off the ground and in the canopy and seems extremely flexible in its ability to use different resources, including resources of different sizes (Trumbo 1992). The use of snake eggs, particularly in cavity nests above the ground (Blouin-Demers and Weatherhead 2000), has parallels with observations of *N. pustulatus* in bird nests. Collectively, carrion and other sources of food arising from vertebrate reproduction may provide an important resource for *N. pustulatus* largely ignored by ground-breeding burying beetles.

Author Contributions

Discovery, Observations, Photos, and Video: K.V.B.D.; Investigation: K.V.B.D. and P.R.M.; Writing – Original Draft Preparation: K.V.B.D. and P.R.M.; Writing – Review & Editing: K.V.B.D. and P.R.M.

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