A Review of Hypotheses of Decline of the Endangered American Burying Beetle (Silphidae: Nicrophorus americanus Olivier)

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A review of hypotheses of decline of the endangered American burying beetle (Silphidae: *Nicrophorus americanus* Olivier).

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Abstract

The largest species of North American *Nicrophorus* (Coleoptera: Silphidae), *N. americanus*, was placed on the US federal list of endangered species in 1989. This paper reviews literature bearing on eight hypotheses that attempt to explain the dramatic decline of this species over 90% of its former range. What is known regarding each hypothesis is separated from what remains to be investigated. We find that although progress has been made during the past 12 years, even the most well supported hypothesis requires a number of important studies to be completed or extended before we can confidently explain the decline of this species and predict the success of conservation efforts.

Introduction

The American burying beetle, *Nicrophorus americanus* Olivier, was first listed as endangered in 1989 by the US Fish and Wildlife Service (Federal Register 54(133): 29652–55), after museum and field surveys in the early 1980s discovered it was absent from most of its historic range (Davis 1980; Anderson 1982). This species has been the subject of intense study and speculation since its decline was announced in 1980. We have found 46 papers published during the first 200 years before 1980 that referred to this species (usually providing minimal ecological information), but in the last twenty years an additional 78 publications have appeared, most of which focused on this species (Sikes et al. 1999), but none of which answered the central question of what caused this species' decline.

In North America north of Mexico, and exclusive of the West Indies, there are 15 species of *Nicrophorus* (Peck and Kaulbars 1987; Sikes and Peck 2000). These beetles are popular among biologists because,

in addition to their large size and colorful markings, they exhibit complex reproductive behaviors, including biparental care, which is extremely rare in the order Coleoptera. They derive their common name, burying beetles, from their habit of burying small vertebrate carcasses, on which they raise their offspring. The ecology and behaviors of over 20 *Nicrophorus* species have been well studied (Pukowski (1933) and Trumbo (1992), Scott (1998), Sikes et al. (1999) and references therein). Kozol et al. (1988) were the first to publish a detailed life history of *N. americanus*.

As recently as the 1920s, *Nicrophorus americanus* was considered common across most of the eastern half of North America and was known from 35 states and three Canadian provinces (Davis 1980; Anderson 1982). However, it now occurs in less than 10% of its former range (Figure 1). Populations are restricted to Block Island, Rhode Island, an island off the Atlantic coast, and the western periphery of the historic range (western Arkansas, eastern Oklahoma, central and southern Nebraska, southeastern Kansas, and southcentral South Dakota). Wells et al. (1983) stated
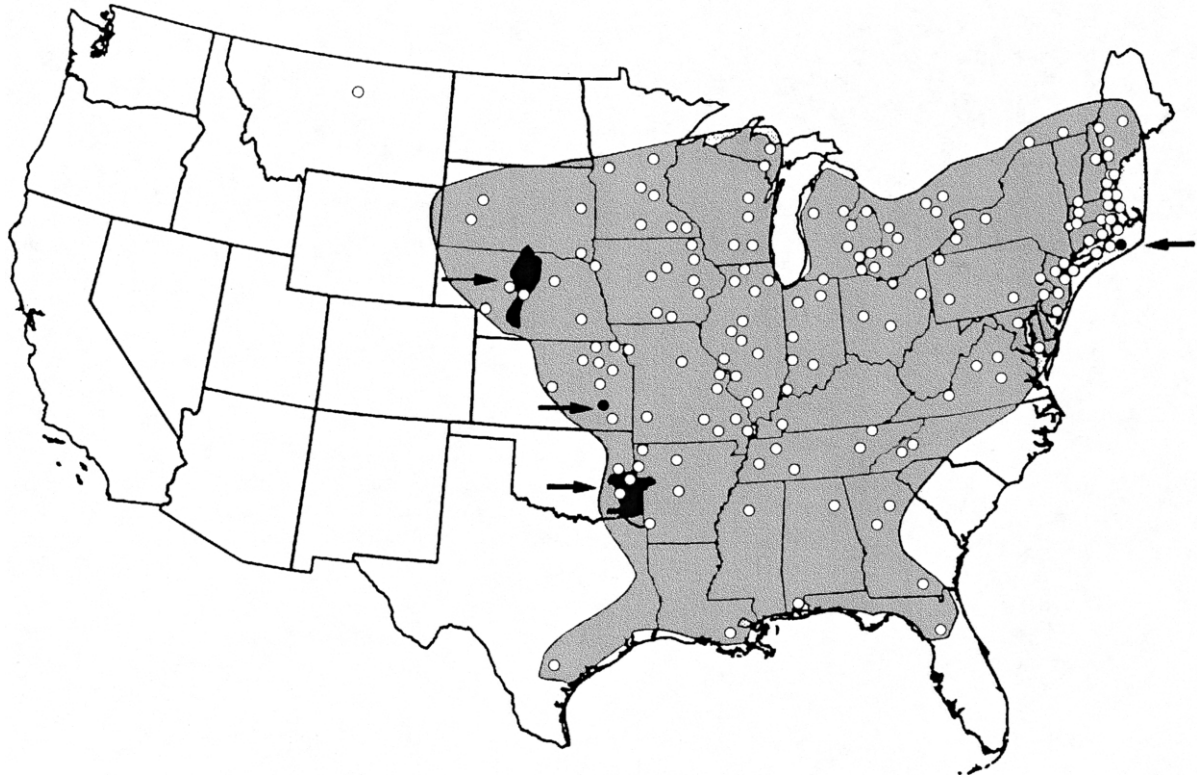
Figure 1. Current (black) and historic (gray shade and white dots) range of *N. americanus* (modified from Lomolino et al. (1995) and Holloway and Schnell's (1997), US Fish and Wildlife Service (1991).

that this species' case "*must represent one of the most disastrous declines of an insect's range ever to be recorded.*" This dramatic example of species endangerment is unusual in that it is difficult to imagine a scenario that would drive *N. americanus*, which is physically dominant within its guild, to the brink of extinction yet leave its eight sympatric congeners untouched.

Many hypotheses for this decline have been suggested; only some of which have been explored empirically, and none exhaustively (Table 1). The determination of why this species has declined depends to some extent on knowing what factors predict its presence. However, the factors that led to the decline of *N. americanus* may not all still be present. If former limiting factors no longer occur, then we might expect *N. americanus* to gradually expand back into its historic range, but there is no evidence that this is happening. If the factors that led to the decline of this species continue to shape its current distribution and prevent recolonization of former habitats, then we should be able to determine precisely what these factors are. Although there is a large body of circumstan-

tial evidence, much of which has been cited in prior discussions of this species' decline, there remain numerous questions to be answered and suppositions to be supported by empirical evidence. Without this information firmly in hand, conservation efforts are handicapped.

Herein we will briefly present the hypotheses of decline for *N. americanus* and discuss what has been learned during the last twelve years about each.

It should be mentioned that each hypothesis in Table 1 is not exclusive of the others. In fact, it is likely that multiple effects interacted, perhaps synergistically, to influence the decline of *N. americanus* (Myers 1987; Ratcliffe 1995; Amaral et al. 1997). However, any explanation for the decline of *N. americanus* must at least address why the sympatric congeners, which feed and breed on similar resources, have apparently remained unaffected.

DDT/pesticide use

Kozol (1995), and Raithel (in US Fish and Wildlife Service (1991)), presented a clear argument against

Table 1. Hypotheses of decline for *Nicrophorus americanus*. See text for detailed description of each hypothesis. **Accounts for congeners**: does the hypothesis explain why sympatric congeners are unaffected? **Accounts for pattern**: does the hypothesis explain the geographic pattern (Figure 1).

Hypothesis	source	accounts for congeners?	accounts for pattern?
DDT/pesticide use	(Kozol et al. 1988)	no	no
Artificial lighting	(Ratcliffe 1995)	no	no
Pathogen	(US Fish and Wildlife Service 1991)	yes	yes
Habitat alteration hypotheses:			
Old growth specialist	(Anderson 1982)	yes	no
Prairie specialist	(herein)	yes	yes
Vertebrate competition	(US Fish and Wildlife Service 1991)	yes	no
Loss of ideal carrion	(US Fish and Wildlife Service 1991)	yes	no
Congener competition	(US Fish and Wildlife Service 1991)	yes	no

the DDT hypothesis, pointing out that the American burying beetle had disappeared from areas where DDT was never sprayed, that some recent (since 1960) populations were in areas that had been sprayed with DDT, and that most populations were gone 25 years before DDT, or other organochlorine pesticides, were used. Raithel (US Fish and Wildlife Service 1991) pointed out, however, that several *N. americanus* populations in the Midwest did disappear during the period that DDT was applied (1940 to 1972). Also, in a controlled study of the effects of DDT on forest invertebrates, Hoffmann et al. (1949) showed that DDT spraying eliminated populations of three *Nicrophorus* species (*Nicrophorus orbicollis* Say, *Nicrophorus sayi* Weber, and *Nicrophours defodiens* Mannerheim). Irrespective of the pattern and timing of decline, for DDT, or any man-made toxin, to be a significant factor in this puzzle we would have to evoke *ad hoc* hypotheses to account for the lack of equivalent impact on the sympatric congeners of *N. americanus*. Unfortunately, there are few historical data (e.g., Trumbo and Thomas (1998)) regarding *Nicrophorus* community structure with which to assess effects of past DDT spraying or other contaminants. Although this hypothesis is rejected as the primary explanation, it remains possible that some *N. americanus*, and presumably other *Nicrophorus*, populations may have been extirpated by DDT use.

Artificial lighting

Artificial lighting as an explanation of decline (e.g., Ratcliffe (1995, 1996)) is less easily dismissed. Several extant populations of the American burying beetle do occur in remote, relatively lightless areas. The

responses of silphids to artificial lights vary among species. Backlund and Marrone (1997) captured 13 species of silphid in baited pitfall traps in south-central South Dakota, but only three species were common at black lights. They captured no *N. americanus* at lights during their sampling but did catch this species in pitfall traps. In the Northeast, *N. americanus* (US Fish and Wildlife Service 1991), as well as *N. orbicollis*, *N. pustulatus* Herschel, and *Necrodes surinamensis* (Fabricius), consistently come to lights (Anderson and Peck 1985). However, *N. americanus* is attracted less frequently to lights than to carrion baited traps. Even in the areas of Block Island where the American burying beetles are most common, it is typical to see only a few (0–3) individuals per night at a blacklight.

There are few empirical data that quantify light captures for this species. Circumstantial support for artificial lights as a factor in the decline could be derived from the fact that most extant populations of *N. americanus* occur in relatively remote, lightless areas, and electric lighting was becoming widespread during the late 1800s (Bright 1949), concurrent with the beginning of *N. americanus*' disappearance from the Northeast. However, fluorescent lights (including blacklights like those used in "Bug Zappers") are considerably more attractive to night-flying insects, and these are a relatively recent feature of the landscape. Additionally, the *N. americanus* population on Block Island has coexisted with artificial light for over 50 years and both *N. orbicollis* and *Necrodes surinamensis*, other light-attracted silphids, remain abundant there.

This hypothesis could be carefully addressed through studies that quantify the amount of artificial

light near the extant populations, and examine the mortality of *N. americanus* and congeners due to these lights. It remains at least possible that artificial lights, if they are responsible for a chronic, albeit low, level of adult attrition, could be affecting *N. americanus* populations. Nevertheless, it presently seems that if artificial lighting has had a negative effect on *N. americanus*, it has been minor relative to other influences.

Pathogen

In addition to accounting for the health of sympatric congeners, a good hypothesis should also explain the unusual geographic pattern of the remaining populations (Figure 1). It is a widely held belief that species' ecological requirements are best met toward the centers of their distributions. However, *N. americanus* disappeared from its range core and persists only on the very edge of its historic range.

A pathogen hypothesis readily accounts for such a geographic pattern of decline. Any pathogen that could be transmitted among adult burying beetles, and was non-fatal to congeners of *N. americanus*, would eliminate all contiguous *N. americanus* populations, leaving only peripheral isolates untouched. Raithel (in US Fish and Wildlife Service (1991)) suggested this hypothesis and also pointed out that no evidence of a disease or pathogen has been found. However, we know of no investigation that expressly attempted to test this hypothesis. Consistent with this theory is the phylogenetic analysis of Peck and Anderson (1985) in which *N. americanus* was not found to belong to any of the *Nicrophorus* species groups of the New World, *i.e.*, it was phenotypically, and presumably evolutionarily, distant. *Nicrophorus americanus*, therefore, could be physiologically unique and vulnerable to a pathogen to which its congeners are immune. The numerous *Nicrophorus* symbionts, which include mites and nematodes, could also contribute to the spread of disease. These symbionts rapidly transfer among hosts, both within and among species, when the beetles feed at carcasses too large to bury (Schwarz and Koulianos 1998).

Channel and Lomolino (2000), investigated the geographic pattern of decline in 245 endangered species. Their analysis showed that the remaining populations of many endangered species (98% of their sample), including birds, mammals, fishes, mollusks, arthropods, and plants, are in the peripheries of their former ranges. Therefore, the peripheral isolate pattern noted for *N. americanus* may be the rule rather than the exception. They suggested that this pattern resulted from the "contagion-like spread of extinction forces" (*loc. cit.*), primarily a loss of ideal habitat from the center of a species range. Since this geographic pattern of decline has been observed in cases where pathogens were not involved, an explanation for the observed pattern of decline of *N. americanus* does not necessarily depend on an epizootic event. However, Channel and Lomolino's (2000) investigation certainly does not eliminate the possibility that some sort of pathogen may have affected *N. americanus* populations.

Habitat loss

The remaining hypotheses deal primarily with changes to the habitat of *N. americanus*, including the carrion resource base. However, data that address differences between the central and the peripheral habitats of *N. americanus*' historic range are still lacking. Although these hypotheses are plausible and account for the persistence of sympatric congeners, they do not definitively explain how the current geographic pattern (Figure 1) was created.

Vegetation changes: old growth specialist

The very first hypothesis published to explain the decline of *N. americanus* was that of Anderson (1982), who suggested that the species might be a specialist of old growth forests and require the deeper, looser soils of such habitats. There are indications that *N. americanus* formerly occurred in primary forests. For example, Walker (1952) described a capture site in Tennessee as an open "park-like" forest with thick herbaceous vegetation and Creighton et al. (1993) showed this species to be more common in open, upland forests and grasslands than in densely vegetated lowland forests. However, given the broad historical range of this species (Figure 1), it seems unlikely that *N. americanus* could have been a vegetation specialist. Lomolino et al. (1995) specifically tested and rejected Anderson's old growth hypothesis, concluding that *N. americanus* was a vegetation generalist. There is information to indicate that *N. americanus* tolerates, and may even prefer, open habitats. Most of the historical *N. americanus* collections, at least in the eastern portion of its range, occurred during the period when much of the landscape was highly agricultural. For example, Block Island was a thoroughly

denuded sheep pasture for at least 200 years; today its vegetation consists of maritime shrub communities, coastal moraine grasslands and agricultural pastures. On Block Island, trap transects for *N. americanus* are more successful in open areas (Raithel unpub. data). Western populations also occur in prairie and grazed areas (Bedick et al. 1999), forest edge, open savannah-like forests, and scrublands.

However, Lomolino and Creighton's (1996), in another study designed to test Anderson's hypothesis, found evidence that *N. americanus* preferred mature forests over clearcuts and had greater breeding success in forests relative to grasslands. They thought this result might relate to the difficulty the beetles faced in burying carcasses in the grassland soils. The difference in productivity was due primarily to failure rates in the grasslands; once buried, grassland carcasses produced similar larval complements as forest carcasses. However, their emphasis on vegetation type did not preclude other causes of burial failure such as ants or extreme temperature. A study focusing on vegetation alone may obscure two far more important limiting factors; namely, vertebrate (and invertebrate) competition and the natural carrion prey base. In summary, testing for habitat preferences based on vegetation and soil type while ignoring both the naturally occurring abundance of appropriately sized carrion and the intensity of competition in each habitat type, could be misleading in the process of identifying limiting factors for *N. americanus*. Work done on Block Island (Raithel in press) and in Arkansas (Holloway and Schnell's 1997) suggests that vegetation type might be a less efficient predictor of optimal beetle habitat than the prey base and potential vertebrate competition. Additional work, specifically addressing breeding success, including location success (i.e., where do beetles *find* more carcasses, *sensu* Trumbo and Bloch (2000)) and the naturally occurring prey base rather than trap captures or vegetation type, is clearly required before we can determine what factors describe this species' preferred habitat.

Vegetation changes: prairie specialist

An unpublished hypothesis, nearly opposite to the previous, is that the decline of *N. americanus* may be linked to the *return* of forests in eastern North America. If this species was ancestrally rare or absent in forests and preferred open habitats (as it does to some degree today (Kozol et al. 1988; Lomolino et al. 1995; Bedick et al. 1999)), its range may have ex-

panded during the agricultural deforestation of eastern North America begun by native Americans and greatly expanded by European settlers into the mid 1800s (Askins 1997). Such an invasion of the eastern "neosavanna" has been documented for various grassland associated bird species (US Fish and Wildlife Service 1991). With the shift of agriculture from the east to the west and the ensuing reforestation during the 1900's, one might expect grassland-associated species to disappear from many of the areas they had first invaded perhaps centuries earlier. This pattern of decline and range retraction has been documented for several vertebrates associated with open, early successional habitats. For example, the New England Cottontail (*Sylvilagus transitionalis*) has disappeared from over 80% of its former range in the northeastern United Stattes (Litvaitis et al. 1999), and there are numerous similarly declining birds (e.g., Bell's Vireo [*Vireo bellii*], Painted Bunting [*Passerina ciris*])(*l.c.*). Therefore, the current distribution of *N. americanus* might be closer to its pre-settlement distribution than our collection record of the last 200 years would lead us to believe. An alternative explanation for a current prairie association might involve a habitat switch in which the beetle, which once was abundant in forests, perhaps due to a constant supply of passenger pigeon carcasses, is now only found in open habitats because of a dependence on the ground nesting birds or other suitable carrion producers that prefer these habitats.

Holloway and Schnell's (1997) and Lomolino and Creighton's (1996) work, as with the previous hypothesis, indicate that this species can be captured in forests that contain enough of the correct sized carrion. We should not, therefore, expect this species to be a specialist of any particular vegetation type, neither old growth forests nor prairies. It is logical that the carrion resource base is a significantly more important predictor of healthy *N. americanus* populations than any particular vegetation type.

Vertebrate competition

Raithel (US Fish and Wildlife Service 1991) concluded that the best explanation for the decline of *N. americanus* involved habitat fragmentation, which reduced the carrion prey base and increased the vertebrate scavenger competition for it. Kozol (1995) and Ratcliffe (1996), Amaral et al. (1997), Bedick et al. (1999), and other authors have reiterated this theme.

Nicrophorus americanus is the largest species of *Nicrophorus* in the New World and requires carcasses

of 100–200 g (Kozol et al. 1988) to maximize its fecundity, whereas all other *Nicrophorus* species can breed abundantly on much smaller carcasses, with the smallest species using carcasses of 3–5 g (Trumbo 1992). Potential scavenging, predatory, vertebrate competitors of *N. americanus* include the American Crow (*Corvus brachyrhynchos*), Red Fox (*Vulpes vulpes*), Striped Skunk (*Mephitis mephitis*), Raccoon (*Procyon lotor*), Norway Rat (*Rattus norvegicus*), Feral Cat (*Felis catus*) (Jurek 1994), and two recent additions to the northeastern North American fauna: the Coyote (*Canis latrans*) (Parker 1995) and the Virginia Opossum (*Didelphis marsupialis*). A number of these species, especially the Raccoon and Striped Skunk, have seen dramatic population increases over the last century (Garrott et al. 1993). The Coyote was rarely found outside of grassland habitats prior to the 20th century, but with competitive release due to the extirpation of larger predators, like the Gray Wolf (*Canis lupus*) and the Mountain Lion (*Felis concolor*), the increase in deer population, and changes in habitat usage throughout the northeast, the Coyote expanded its range into the forested northeast, reaching Ontario in 1919 and Newfoundland in the 1990s (Gipson and Brillhart 1995; Parker 1995). Coyotes tend to be more common in open habitats than forests (Whitaker and Hamilton 1998) – the same habitats that are preferred by various large, ground-nesting birds, which are both experiencing population declines and are potential optimally-sized carrion producers for the American burying beetle.

There is evidence to support a direct correlation between edge, or fragment size, and vertebrate scavenger pressure, with much of this work involving nesting bird populations (Paton 1994; Yahner and Mahan 1996; Suarez et al. 1997). Some studies have examined the effects of fragmentation on beetle communities (e.g., Klein (1989) and Trumbo and Bloch (2000)), but more studies of this phenomenon using burying beetle communities are needed. Trumbo and Bloch (2000) investigated the influence of fragment size on *Nicrophorus* species' success (measured as the proportion of mouse carcasses buried and held for seven days). They found that beetles had significantly greater success in larger woodland plots and attributed this result in part to lower vertebrate scavenger success in those areas. Sikes (1996), working with *Nicrophorus nigrita* Mannerheim, found that mouse transects laid > 100 m from a trail or road had 10% or fewer carcasses taken by vertebrates, whereas transects near trails or roads had an average of 85%

of the carcasses taken by vertebrate scavengers. Other workers, such as Wilson and Fudge (1984), have shown that in sites with greater vertebrate scavenger pressure, variation in *Nicrophorus* brood size increased.

Trumbo and Thomas (1998) investigated *Nicrophorus* species composition (lacking *N. americanus*) on several small islands and found that smaller islands were not able to support viable populations of large-bodied species. They suggested that larger species required more carrion resources and were therefore more prone to local extinctions. The extant population of *N. americanus* on Block Island seems to be relatively free of competitive pressures; not only are there unusually large populations of ground-nesting birds, but there are few mammal predators or scavengers (Amaral et al. 1997; Raithel in press). This hypothesis is among those most well supported by the available evidence. However, more studies on the response of silphid communities to habitat fragmentation are needed, especially those that would contrast historic and current habitats, or compare multiple extant sites of *N. americanus*.

Loss of ideal carrion

Raithel (*loc. cit.*) strengthened the explanatory power of the vertebrate competition hypothesis by combining it with another hypothesis–loss of carrion of ideal size. At least one bird species in the ideal weight range and the historical geographic range of *N. americanus*, the Passenger Pigeon (*Ectopistes migratorius*) is extinct. This species was historically one of the most abundant birds in North America, with flocks estimated to contain billions of individuals, (Wenninger 1910) and certainly would have produced a significant amount of necromass during the reproductive season of *N. americanus*. In addition, other bird species of the ideal weight size have declined throughout their ranges during the last century. These include the exotic Ring-necked Pheasant (*Phasianus colchicus*), (Raithel in press) and other gallinaceous birds like the Greater Prairie Chicken (*Tympanuchus cupido*), and the Northern Bobwhite (*Colinus virginianus*), (Guthery et al. 2000). Raithel (in press) demonstrated that Block Island has a greater proportion of potential carrion producers (nesting birds, such as the Ring-necked Pheasant and the American Woodcock [*Scolopax minor*]) than the adjacent mainland. Holloway and Schnell's (1997) study is the only one conducted in the western portion of *N. americanus'*

range that examined the carrion resource base. They found significant correlations between the numbers of *N. americanus* caught in traps and the biomass of mammals, the biomass of mammals plus birds, the number of mammal species, and the number of individual mammals, irrespective of the predominant vegetation.

However, we are terribly ignorant about what factors determine the usefulness of a vertebrate species to *N. americanus*. We know little more than the ideal weight of carrion and the presumed breeding season for beetle reproduction–data regarding the localities for suitable vertebrate populations, their mortality rates, the process of carcass production and its quantity (and variance), and competition for carrion are generally lacking. Such data are required to build a robust population model for *N. americanus*. Educated guess work indicates that ideal vertebrate species for a *N. americanus* prey base would be those that produce ample offspring, many of which die after achieving a mass of 80–200 g due to causes other than predation, during the breeding season of *N. americanus* (mid summer). Bird populations are not the only candidates to be good carrion producers. Certain mammal species, like the Blacktail Prairie Dog (*Cynomys ludovicianus*), have also declined drastically (Miller et al. 1990), and such dense concentrations of mammals may also support *N. americanus* populations. A relevant and recent study by Smith et al. (2000) has documented that *Nicrophorus* adults will use pre-existing vertebrate burrows for burial of carcasses, and those that do so realize significantly greater reproductive success as a result. Another documentation of use of vertebrate burrows, specifically bird burrows, by *Nicrophorus* was made by Wilhelm et al. (2001).

Congener competition

The last hypothesis in Table 1, congener competition, extends from the previous two hypotheses. With both an increase in vertebrate scavenger pressure (exacerbated by habitat fragmentation), and a decrease in carrion of the ideal weight size (due to extinction and population declines), the competition between *N. americanus* and sympatric congeners for sub-optimally sized carcasses would be expected to increase. Trumbo (1992) showed that the potential for *Nicrophorus* congener competition for carrion increased with carcass size. Competitive success of carrion-

feeding flies also increases with carcass size (Scott et al. (1987); *l.c.*).

The historical geographic range, and presumably the ecological tolerances, of *N. americanus* are most similar to its congener *Nicrophorus orbicollis.* This similarity in ecological niche (geographic range, diel periodicity, breeding season, *etc*.), and new phylogenetic information indicating these species may be each other's closest surviving relatives (Szalanski et al. 2000), together suggest that *N. americanus* and *N. orbicollis* may be each other's greatest congeneric competitors. In surveys for *N. americanus*, *N. orbicollis* is almost always trapped and is usually 10, or more, times as abundant (e.g., Lomolino and Creighton's (1996) and Amaral et al. (1997); Carlton and Rothwein (1998); Raithel in press). Although *N. orbicollis* appears to be less successful in using the largest carcasses that *N. americanus* requires for maximum reproductive success (> 100 g) (Kozol et al. 1988; Trumbo 1992), this species could be a formidable competitor for smaller and medium sized carcasses.

Another sympatric congener, *Nicrophorus marginatus* Fabricius, is also often present in traps set for *N. americanus* (*l.c.*). *Nicrophorus marginatus* is on average slightly larger (Sikes unpub. data), and in some portions of its range, such as western Nebraska, is more common, than *N. orbicollis* (Bedick et al. 1999). Backlund and Marrone (1997) reported that *N. marginatus* was the most abundant species collected during their surveys for *N. americanus* in South Dakota. Interestingly, they also reported that in areas in which they caught the most *N. americanus*, they caught the least *N. marginatus*. *Nicrophorus marginatus* is well documented as a specialist of open grassland habitat (Anderson and Peck 1985). If such habitat is used more by *N. americanus* now than historically, perhaps because this species is tracking populations of small mammals or gallinaceous birds that prefer open habitats, then competition between these two *Nicrophorus* species may have increased. This relationship has not been investigated. Additionally, Kozol et al. (1988) showed that *N. marginatus* buried larger carcasses than did *N. orbicollis*. Although still probably less successful with the largest carcasses (> 100 g), *N. marginatus* could, as a result, be a more significant competitor of *N. americanus* than *N. orbicollis* in areas of sympatry.

Although, *N. americanus*, because of its larger size, dominates interference competition events -direct physical battles at carcasses (Kozol et al. 1988),

there are data indicating *N. orbicollis* may dominate exploitative competition events -speed of finding and burying carcasses (Matthews 1995) and thus contribute to the current pressures affecting *N. americanus*. However, to what degree *N. americanus* is losing potential breeding carcasses (albeit of less than optimal size), throughout its range, to *N. orbicollis* and/or *N. marginatus* remains unstudied.

Burying beetle females that lose battles to secure a carcass sometimes oviposit near the carcass, allowing some of their larvae to act as brood parasites (Müller et al. 1990; Trumbo 1994). Mixed-species broods are more common on larger carcasses (Trumbo 1992). Investigations of congener competition should be aware of the potential for brood parasitism by either *N. orbicollis* or *N. marginatus* within *N. americanus* broods.

Suggestions for future research

The research reviewed herein provides clues to the two related and most important questions that remain unanswered: What parameters predict the current presence of *Nicrophorus americanus*? Also, what changes were responsible for the decline of this species? To answer these questions will require numerous corroborative, hypothesis-driven investigations. We suggest the following research as being of the highest priority:

1. Predicting the current distribution: The distribution of a monophagous herbivore is, in comparison to that of *Nicrophorus americanus*, relatively easy to predict. The distribution of the host plant with consideration of competitors, predators and climatic tolerances of the herbivore is usually sufficient to predict where it might occur. However, *Nicrophorus americanus* is neither monophagous nor herbivorous. Few studies have directly addressed the resource-base of this species. Holloway and Schnell's (1997, 1997) are the only studies that did so - by attempting to quantify the carrion prey-base and relate these data to the distribution of *Nicrophorus americanus*. These studies results' support the conclusion that this species persists in areas that have unique vertebrate communities but alone are not sufficient to identify *N. americanus* habitat.

   Future investigations in silphid community structure should quantify the potential carrion prey-base in addition to, as has been typical, the carrion-feeding community. If a standardized protocol for collecting and reporting these data could be developed, investigators would be able to compare habitats according to an index based on the available, ideal carrion and the competitive pressure for that resource. Such a process could lead to the identification, management, and creation of landscapes capable of sustaining *N. americanus* populations.

   Initially, studies would have to be performed within the current *Nicrophorus americanus* populations to enable accurate description of 'ideal carrion'. Such descriptors would include traits such as average size during the breeding season of *Nicrophorus americanus*, quantity of carcasses produced during the breeding season of *Nicrophorus americanus*, and habitat affiliation with appropriate substrate for burial (e.g. nesting gulls usually die on beaches which have unsuitable substrates for burial by *Nicrophorus americanus*). Once we can define quantitatively what constitutes an ideal carrion-producing vertebrate species for *Nicrophorus americanus* we can begin identifying and ranking suitable candidate species within the historic range of *Nicrophorus americanus*. Such a list, with maps of current and past distributions (as best as possible), and the research that would go into quantifying the criteria for inclusion, would be a very valuable step towards predicting the presence of *Nicrophorus americanus*.

   Of course, the potential prey base is only half of the needed data. The other part of the equation must be the intensity of competition for the available, ideal carrion. Areas that see the generation of large quantities of ideal carrion during the breeding season of *Nicrophorus americanus* may be of little value to this species if carcasses are removed by vertebrate scavengers before *Nicrophorus americanus* can use them. Thus, a protocol should be developed to allow standardized comparisons of competitive pressure (broken down by factors such as vertebrate/invertebrate and variability, among others). Obtaining these data, particularly considering the variation that can occur over time, could be quite challenging, but must be considered essential towards understanding this species' requirements for survival.

2. Explaining the decline: One could argue that once we understand the ecological requirements of this species and can predict its persistence, explaining its decline is of little practical importance. For this

reason we consider understanding the causes of decline to be of slightly lower priority than understanding this species' current ecological needs. However, if the causal factors of decline persist throughout the historic range of *Nicrophorus americanus* these would necessarily become understood by efforts to describe the potential niche of *Nicrophorus americanus*. It is likely, therefore, that by accomplishing the primary goal we will go far towards explaining the decline of this species. Additionally, efforts to test hypotheses of decline would likely provide data relevant to predicting this species' current, historic, and potential niche.

Summary

It should be clear that several investigations important to our understanding of the decline of *N. americanus* remain to be done. Unlike the DDT hypothesis, the effects of artificial lighting can be readily studied today. The pathogen hypothesis is less easily tested. However, conservationists working with populations of *N. americanus* for reintroduction or breeding purposes should be alert to the possibility of a species-specific pathogen. The evidence against *N. americanus* being a habitat specialist of old growth forests, and having declined due to the loss of these forests and their deeper soils, is strong. The combination of the last three hypotheses build the most plausible explanation for the decline of this species–a conclusion reached first in Raithel (US Fish and Wildlife Service 1991) and subsequently supported and commented on by numerous other authors; (1) reduction of optimally sized carrion, (2) increased vertebrate scavenger competition for that carrion, and (3) increased congener competition for optimally, and suboptimally sized carrion–due, in part, to extinctions or declines of optimally sized prey populations resulting from habitat changes, overharvesting, and increased vertebrate scavenging and predation. The greater pressure from vertebrate scavengers may have resulted from competitive release after the loss of larger predators (such as the Gray Wolf [*Canis lupus*] and the Mountain Lion [*Felis concolor*]) and an increase in habitat fragmentation and edge habitats. *Nicrophorus americanus* thus may be experiencing greater vertebrate and congener competition for a reduced resource base. Presumably, the extant *N. americanus* populations occur in areas with lower vertebrate and/or congener competition and/or a greater resource base, although after

twelve years of study we have yet to confirm this empirically throughout the range of *N. americanus*. The story of the decline of the American burying beetle appears to be a tale of changes in vertebrate community ecology, both of prey and scavenger competitor species. Yet, many of the published studies have looked at vegetation and abiotic correlates rather than vertebrate ecology.

In summary, after over a decade of research, these conclusions are not very different than those of Raithel a decade ago (US Fish and Wildlife Service 1991). Since the US Fish and Wildlife Service (1991) recovery plan, new data have been brought to support the vertebrate competition (Trumbo and Bloch 2000), and the congener hypothesis (Matthews 1995). And there have been other relevant studies, including Channel and Lomolino (2000) investigation of the geographic pattern of decline. Yet, until we have learned more about this species' ecology and its history, these explanations remain primarily speculative. Of the greatest urgency would be investigations (as detailed above in Suggestions for future research) that contrast multiple portions of the historical center of *N. americanus*' range with the eastern and western extant populations with regards to habitat fragment size, biomass of ideal carrion-resource vertebrates (e.g., Holloway and Schnell's (1997)), vertebrate predation /scavenger pressure, and congener competition.

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