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Distribution, ecology, and population dynamics of the American burying beetle [*Nicrophorus americanus* Olivier (Coleoptera, Silphidae)] in south-central Nebraska, USA

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The endangered American burying beetle, *Nicrophorus americanus* Olivier, was previously widespread throughout eastern North America. In the past century numbers of this beetle have drastically declined and currently remnant populations are known from only six states despite intensive surveying efforts conducted for the last nine years. Efforts aimed at discovering and managing remnant populations have been generally limited by a lack of knowledge concerning *N. americanus* biology. We used baited pitfall traps to define the range of the Gothenburg, Nebraska population of *N. americanus*. Using mark-recapture techniques, we estimate that the annual Gothenburg population consists of more than one thousand individuals, meeting the recovery plan criterion to become the third breeding population in the Midwest region. Beyond estimates of population size and range, we present novel data on seasonal and daily activity, sex ratio, age-grading and foraging distances. In 1995 and 1996, the Nebraska population was univoltine and female biased, with over-wintering mature beetles emerging in early June and teneral beetles emerging in August. Nocturnal activity was highest in the third and fourth hours following sunset but was not strongly correlated with temperature. During foraging, beetles travel up to six kilometers, but the majority of our recaptures occurred at distances of less than 0.5 km, suggesting that distances between traps be increased to ensure independence of sampling units. This information will allow future work on captive breeding, re-introduction and genetic studies.

Keywords: Coleoptera, endangered, pit fall trapping

Introduction

Maintaining species diversity and conservation have become important societal goals but management and recovery plans for threatened species are often hampered by a lack of knowledge concerning the species' biology and life history. Management efforts are further limited by the fact that most threatened and endangered species inhabit very limited geographical areas and have specific habitat requirements. Unfortunately, this has led to the extinction of some of these species despite human intervention aimed at recovery (Ehrlich and Ehrlich, 1981). However, not all extinction has been linked to habitat limitations, and some species with a historically wide distribution are now endangered or have become extinct (Primack, 1993). Once the presence and range of these remnant populations has been established, understanding the biology of the species may be the only mechanism that allows both preservation and eventual recovery.

The American burying beetle, *Nicrophorus americanus* Olivier, is a habitat generalist (Creighton *et al.*, 1993; Lomolino and Creighton, 1996) and was once widespread over the eastern half of North America (from 35 U.S. states and three Canadian provinces (Lomolino *et al.*, 1995)). Throughout this century its range and numbers have declined by as much as 90% (Anderson, 1982; Lomolino *et al.*, 1995) and currently it is known from only six states. Five of these states are found at the western edge, and one (Rhode Island) at the extreme eastern edge, of its former range. Records of *N. americanus* in the five western states form a broken line through southeastern South Dakota, central Nebraska, southeastern Kansas, eastern Oklahoma and western Arkansas. Current data suggest a patchy and localized distribution within these states (Ratcliffe, 1996).

Until 1989, *N. americanus* was little studied apart from initial characterization of its morphology and species description. After designation as an endangered species in 1989, research on *N. americanus* dramatically

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increased. Most of this research focused on finding remnant populations, delineating their range and investigating factors associated with the decline of this species throughout its former range. Determination of the presence and range of *N. americanus* is accomplished by surveying with baited pitfall and light traps. Because the beetle has been eliminated from the majority of its range, repeated surveys may be necessary to discover small remnant populations. For example, from 1992 to 1994, a burying beetle survey was conducted in widely separated locations across Kansas without finding any *N. americanus* (Lingafelter, 1995). Despite the scope of the survey, some areas were not surveyed and in 1996 three *N. americanus* were recovered in extreme southeastern Kansas (Miller and McDonald, 1997). Improved knowledge of the biology of this species may both increase the effectiveness of sampling and improve management of existing populations. However, since its listing in 1989 few studies have attempted to meet this goal, and much about the beetle's biology remains unknown or anecdotal.

Ratcliffe and Jameson (1992) reported the re-discovery of *N. americanus* in Nebraska, and Peyton (1994) discovered a population in south-central Nebraska at a site south of the town of Gothenburg. In 1995 we conducted intensive field surveys to establish the range and approximate density of the Gothenburg population of *N. americanus*. The population surveys established sites for future studies and delineated the range of the Gothenburg population. Sampling centered on the Gothenburg site and other historical sites of *N. americanus* captures in Nebraska, and trapping extended outward from these sites to a distance of 14 km past the discovery of any *N. americanus* (Fig. 1).

After establishing the range of *N. americanus* in Nebraska, we characterized its biology in 1996, focusing on attributes that may be crucial in surveys to find remnant populations and management for this species. Bedick (1997) presented a modified survey protocol for *N. americanus*, and in this paper we present its current distribution in Nebraska and its biology. We tested the hypothesis that the Gothenburg population exceeds 500 individuals, a condition necessary to fulfill the 1991 U.S. Fish and Wildlife Service's criterion to become the third, self-sustaining breeding population in the Midwest Region (Oklahoma and Arkansas are the first and second populations (Lomolino *et al.*, 1995; Holloway and Schnell, 1997)). Unlike previous studies, we also determined the population age structure through age-grading of samples, and measured the sex ratio of the population. Finally, we documented hourly nocturnal activity patterns of *N. americanus*. These new data are necessary for future work on captive breeding, reintroduction, and genetic diversity studies.

Methods

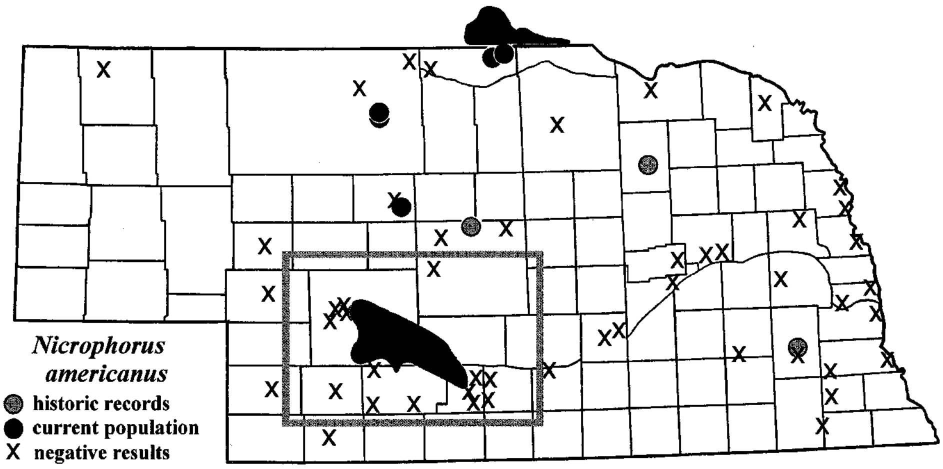
Study area

In 1995 we surveyed for the American burying beetle in central Nebraska to establish the range of the newly-discovered Gothenburg population. The survey was conducted between 6 July and 26 August in five adjacent counties (Dawson, Gosper, Phelps, Lincoln, and Frontier) in south-central Nebraska, centering on the city of Gothenburg. Surveys were also conducted in two counties (Cherry and Keya Paha) in north-central Nebraska. In 1996 additional data were collected between 15 June and 31 August with an intensive survey for *N. americanus* in Lincoln County and limited surveys in Custer and Hayes Counties (Fig. 1).

The study areas encompass an area known as the Loess, or Dissected, Hills that are the eroded remnants of an ancient plain. The soil is composed of a highly erodable loess/sand mixture. Most canyons run north/south and the prevailing summer winds are from the south-southeast. The area has few trees and most of these are concentrated in the canyons and draws while the hilltops remain mostly treeless. Where trees are present, junipers (*Juniperus virginiana* L. and *J. scopulorum* Sarg.) are dominant. Other tree species include box elder (*Acer negundo* L.), hackberry (*Celtis* species), and cottonwood (*Populus sargenti* Marsh or *P. deltoides* Marsh).

The area is sparsely populated and used primarily as grazing land for beef cattle. Corn, alfalfa, sorghum, wheat and prairie hay are grown in a few of the wider canyons, and reservoirs have been constructed at the mouths of several of the canyons. Grazing levels vary throughout the study area due to differing management practices of the landowners resulting in highly variable plant cover. Some native prairie grass species, such as little bluestem (*Schizachyrium scoparius* Michaux), are found throughout the study area while some of the introduced weedy brome species, such as downy, hairy and Japanese *Bromus* species, are found in areas of overgrazing. Woody plants, including yucca (*Yucca glauca* Nutt.), skunk bush sumac (*Rhus aromatic* Ait.), winged sumac (*Rhus copallina* L.), chokecherry (*Prunus virginiana* L.), wild plum (*Prunus americana* Marsh) and western snowberry (*Symphoricarpos occidentalis* Hook), are common in the study area.

The survey area in Keya Paha County is similar to the Loess Hills of south-central Nebraska. The land slopes down to the Keya Paha and Niobrara rivers in a



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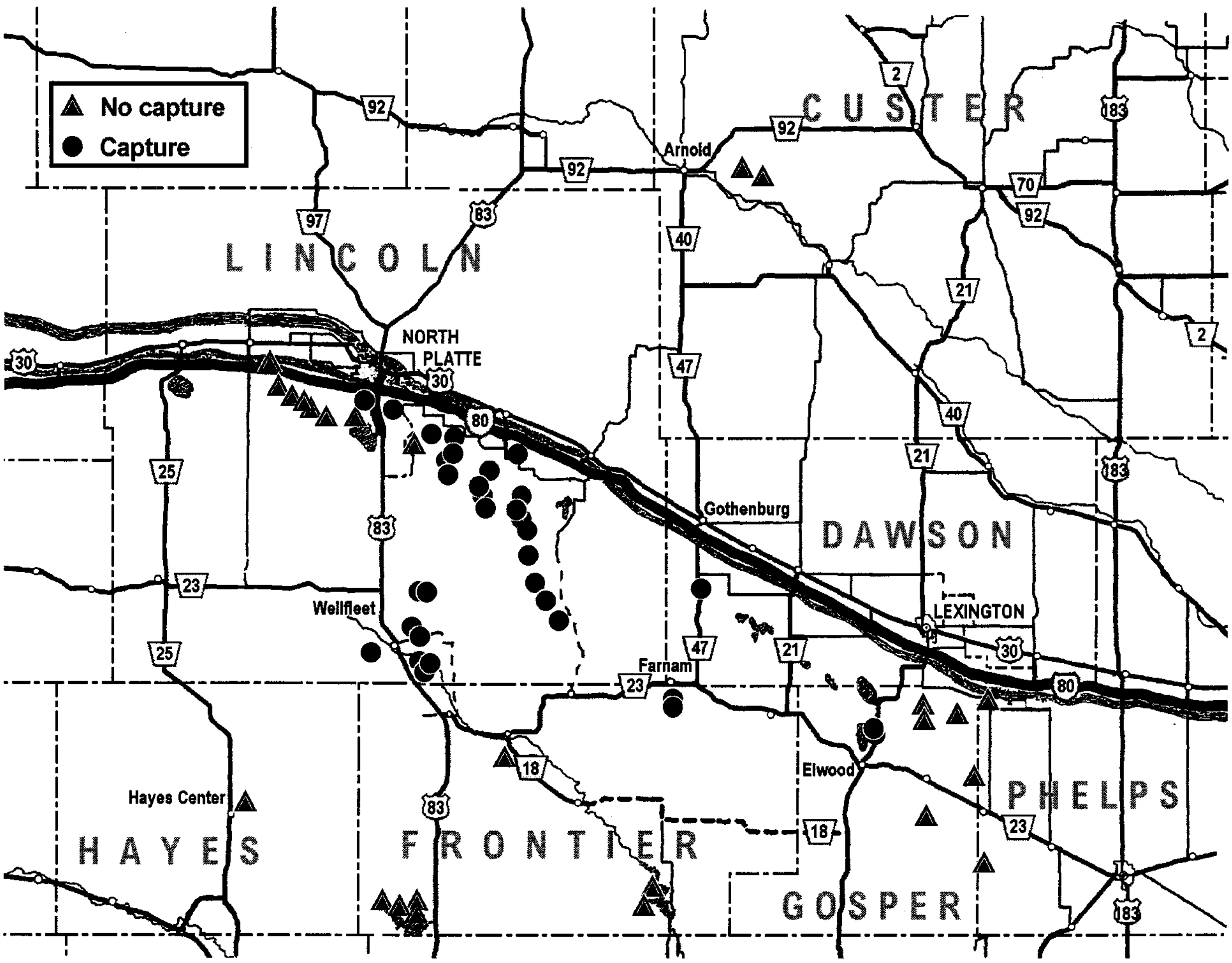

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Figure 1A. The historic records (grey) and present (black) distribution of *N. americanus* in Nebraska. 'X's show all known surveys with negative results from 1991 to 1997. The large polygon shown in the south-central portion of the map represents the Gothenburg population. Map modified from Ratcliffe (1996). The grey rectangle outlines the area of the inset (Fig. 1B).

Figure 1B. Detail of trap locations used to establish *N. americanus* range in Nebraska (triangles) and trap successes (circles).

series of hills. Juniper and cottonwood are numerous in the valleys, but absent from the exposed hilltops, level rangeland and farmland. Small, spring-fed streams are common in many of the side valleys.

Sampling methods

Burying beetles were collected in baited pitfall traps, which consisted of a five-gallon (18.92 l) white plastic bucket (diameter 28.5 cm). All buckets were washed using dish soap and thoroughly rinsed before being used as traps. Buckets were taken to the field and buried in the ground to the bucket lip. Traps were baited with aged carrion placed at the bottom of the bucket. The bait was enclosed in a 0.473 l screen-topped, plastic container to prevent the beetles from coming into contact with the carrion, as prescribed by the U.S. Fish and Wildlife Service (1991) protocol. Bedick (1997) found that a five-gallon bucket was the most appropriate pitfall trap when sampling for *N. americanus* because it provided a larger surface area for each beetle, ventilation was better and beetles could use the soil placed in the bottom of the bucket for escape from other beetles. Additional advantages provided by the large size of the bucket included easy access for clearing the trap, easier monitoring of the bait and the opportunity to observe the beetles before releasing them. A detailed comparison of trap design is provided in Bedick (1997). The pitfall was checked each morning. All beetles were removed from the traps, identified to species and counted. Trapping is expressed as trap-nights, with one pitfall during one night equaling one trap-night.

During our study pitfall traps were baited with found carrion and thawed frozen lab rats. Finding carrion was an opportunistic event and had a high degree of variability. Carrion included mammals, birds, reptiles, amphibians and fish. Kozol *et al.* (1988) found no preference by *N. americanus* for avian or mammalian carrion and, similarly, Bedick (1997) found no preference for carrion type.

Mark and recapture

One method of estimating a population size is to apply permanent marks to individuals, and then subsequently record the number of times these individuals are recaptured and calculate an appropriate index (Southwood, 1978). Although *N. americanus* were marked in the first season during sampling in order to ascertain the range of the Gothenburg population, the trapping sessions were too short (usually three days) for population size estimates.

In the second year we conducted an extensive mark and recapture study in Lincoln County to determine if the *N. americanus* in the Gothenburg area fulfilled the U.S. Fish and Wildlife stipulation as the third self-sustaining population in the Midwest Geographic Recovery Area. We chose the maximum likelihood estimate assuming variation through time to calculate population with a multiple recapture model (Young and Young, 1998). We calculated population estimates for the 1996 over-wintering adult and emergent teneral generations (see aging below). To estimate population size, we chose two sets of trap dates for each generation. Within trapping sets we used equal trap effort (same number of traps) for a six-day period (early season June 23–28 and July 2–7; late season August 14–19 and August 24–29). We calculated the area of attraction for each session by adding the number of traps (assuming a 1 km attraction radius) and excluding areas of overlap between traps. The area of attraction for the early-season traps was 22 km^2. Using the same method, the area of attraction for late-season traps was 18 km^2.

By creating small sub-samples each population was treated as closed to emigration and immigration. By dividing the seasonal activity, birth and death rates had little effect during the periods sampled. During trapping to estimate teneral population, we collected four senescent individuals. These individuals were excluded from analysis when determining estimated population size. The program Ecostat (Young and Young, 1998) was used to calculate population estimates and variability using the M_t Model for closed population mark-recapture data. The M_t model assumes variation through time in capture probabilities and is sensitive to changes in capture number as affected by, for example, changes in weather conditions (Young and Young, 1998).

Within a trapping session we collected summary data by using different colours of enamel paint (Testors model paint) to place a small mark on the posterior portion of the elytra. A different colour or combination of colours was used to mark beetles at each site and additional marks were added each time an individual was recaptured. Paint was found to be a permanent mark on *N. americanus* by Peyton (pers. comm.). Scarring and relative size of beetles (small, medium, large) were recorded along with sex and maturity to confirm recaptures.

To estimate population size we approximated suitable habitat for the Gothenburg population, basing our estimate on the area within a polygon formed by drawing lines between the perimeter captures of *N.*

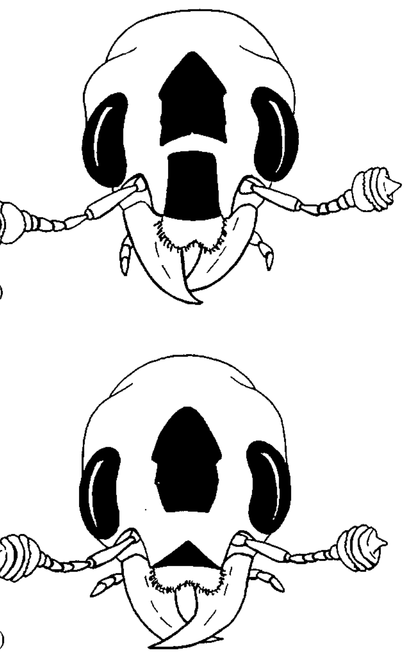
americanus (Fig. 1B) current population in Lincoln, Dawson, Frontier, and Gosper Counties.

Sex determination

Beetles were sexed by examination of the clypeus (Fig. 2). Males have a large, rectangular, red marking and females have a smaller, triangular, red marking. We determined the ratio of female to male *N. americanus* collected during 1995 and 1996 to test whether equal numbers of males and females are attracted to the traps. We used the chi-square goodness of fit statistic (Rees, 1995) to test for a one-to-one sex ratio.

Age grading

All captured *N. americanus* were categorized as teneral, mature, or senescent. Categorization was accomplished by visual examination. The markings of a teneral beetle are brighter and appear more uniform in colour while the exoskeleton is softer and in general more translucent. The pubescence on the elytra is pronounced on teneral individuals and nearly absent on older adults. The pronotum of a mature, second season adult tends to be darker than the markings on its elytra, with the former appearing dark orange to red and the latter appearing orange. The senescent beetle has pale elytral markings, seemingly lacking pigment compared to other age classes. Also, senescent beetles are more scarred, often with pieces missing from the margin of the pronotum or elytra, have cracks in the exoskeleton, and/or appendages are missing (e.g., tarsi, legs or antennae).



(a)

(b)

Figure 2. *Nicrophorus americanus* were sexed by examining the clypeus. Males (a) have a large rectangular area of red marking while females (b) have a reduced, triangular red marking.

Nocturnal activity

Although *N. americanus* is nocturnal (Anderson and Peck, 1985; Kozol, 1989; Ratcliffe, 1996), no research has defined the timing and duration of night-time activity. Kozol (1991) stated that captures of *N. americanus* were unlikely if the overnight low temperature is below 12 °C and that trapping should be done on nights when the expected overnight low is above 15 °C. We tested the validity of this statement by using flight activity to pitfall traps to estimate the foraging times of the beetles while monitoring temperature at the traps during hourly intervals.

Night-time activity for this study was defined as movement to the baited pitfall traps. Three or four buckets were used for each nightly session. The buckets were placed a minimum of 0.5 km apart and baited with similar mammal/snake mixtures. In all cases, the relative proportions and age of the carrion used was comparable for each night. The traps were checked for beetles at 1–1.5 h intervals. The time for checking buckets in a series was staggered by 10–20 min. intervals so that each trap was checked approximately once every hour. The trap series was in place up to three days prior to nocturnal monitoring, which ensured that the nocturnal sessions were conducted in an area of high trapping success.

The monitoring period began close to dusk and lasted until one hour after dawn. For comparative purposes, hour one equaled the time of sunset plus and minus 30 min. Data from all traps in a series were pooled and all captures in a given hour were summed. At each hour, the contents of a trap were removed and all burying beetles identified to species and counted. The *N. americanus* were marked and sexed. The time, temperature and general weather conditions were also recorded at each trap. All temperatures within a sampling period were summed and divided by the total number of readings taken in the period to generate a mean hourly temperature.

Results and discussion

Distribution in Nebraska

The 1995 season Bedick captured *N. americanus* in four of the five south-central counties: Dawson, Lincoln, Gosper, and Frontier (Fig. 1). The captures from Gosper and Frontier constituted new county records for the state of Nebraska. No *N. americanus* were captured at the Niobrara reserve in Cherry County, but three were collected in Keya Paha County near where a single specimen was collected in 1994 (Ratcliffe, 1996).

The 1996 season The limited surveys of nine trap-nights in Custer County, six trap-nights in Cherry County and five trap-nights in Hayes County did not result in the capture of *N. americanus*. Results for these counties should be viewed as tentative because the number of trap sites and trap-nights was low. It is possible that some small populations of *N. americanus* remain in these locations. In 1995 a survey for *N. americanus* in Hayes County by the Nebraska Game and Parks Commission (Dick Nelson, pers. comm.) also had negative results. In 1992, 1994, and 1995, *N. americanus* were reported from the Valentine National Wildlife Refuge in Cherry County (Ratcliffe, 1996). An additional specimen was discovered on the edge of Halsey National Forest in Thomas County in 1995 (Ratcliffe, pers. comm.).

Mark and recapture

During the second year of the study we marked 445 *N. americanus*. We recaptured 118 of these at least once. From the total population we chose four subsets where we had traps in place for at least six days. Two of these periods were used to estimate the population of mature beetles and two periods were used to estimate the population of teneral beetles based on age-grading (see below).

For the early-season mature generation of *N. americanus* we collected a total of 73 beetles from two sites. Calculating that the area of attraction for these traps was approximately 22 km^2, we estimate that the 1996 population of mature beetles at these sites was 293. For the late-season teneral generation of *N. americanus* we collected a total of 131 beetles from two sites. Calculating the area of attraction for these traps was approximately 18 km^2, we estimate that the 1996 population of teneral beetles was 506.

These estimates are not inclusive of the entire Gothenberg population but rather represent the total number of beetles present within the estimated capture-distance (1 km radius; see below) of the subset traps. We estimate that there are 1,943 km^2 of potential habitat for *N. americanus* in the Loess hill region of Nebraska; however, the suitability of this entire habitat area has not been determined. If the entire habitat is suitable for *N. americanus*, we estimate the population of beetles that survived overwintering in 1995 to become the mature generation in 1996 was 1,174. The number of new tenerals in 1996 was 3,046 individuals.

Although it is dangerous to extrapolate from a single year's results, our data suggest that overwintering causes significant mortality. This seems reasonable given that overwintering adults are likely to deplete fat reserves during diapause and require food upon emergence. Alternatively, the Gothenberg population may have increased in 1996 due to high reproductive success.

In addition to obtaining population estimates using marked beetles, we also determined distances covered by individual beetles between captures (all recapture were included (Fig. 3)). Of 158 *N. americanus* recaptured during the 1996 survey, 85% were captured within 0.5 km and 92% were recaptured within 1.0 km of their initial marking. The maximum distance travelled by a recaptured *N. americanus* was 6.1 km. Because these data are for recaptures, the initial distance *N. americanus* travel to find carrion remains unknown. To estimate usable habitat we chose 1 km for the radius of attractiveness for each trap, since this corresponds to a reasonable distance over which beetles will respond to traps (Fig. 3). Using this value probably underestimates the population. We estimate that beetles were sampled from 351.6 km^2 or about one-fifth of the 1,943 km^2 potential habitat.

We captured a large number of *Nicrophorus* beetles during this study (Table 1). Beetle captures are reported as totals and as the average number of *N. americanus*

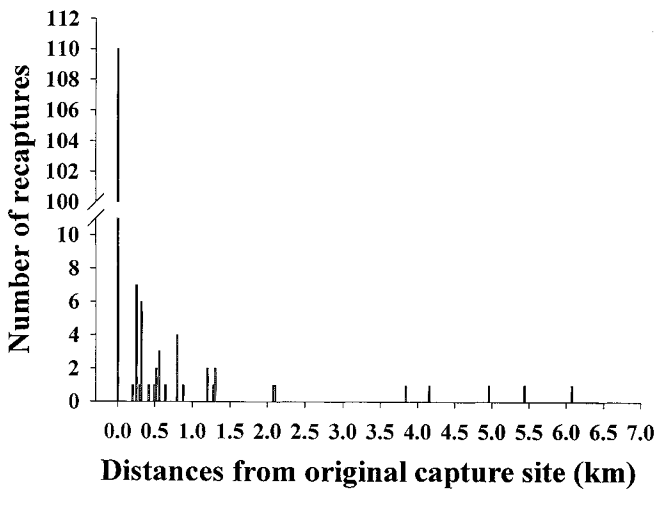


Figure 3. The distance between original capture and recapture of American burying beetles in 1996. Bars represent the total number of beetles recaptured at each distance.

Table 1. Total by species of all *Nicrophorus* beetles collected in 1995 and 1996 using baited pitfall traps in western Nebraska

Species of Silphidae	1995	1996	Total
Nicrophorus americanus Olivier	75	470	545
Nicrophorus carolinus (L.)	158	124	282
Nicrophorus guttula Motschulsky	7	0	7
Nicrophorus marginatus Fabr.	2,591	7,686	10,277
Nicrophorus obscurus Kirby	333	322	655
Nicrophorus orbicollis Say	1,691	2,387	4,078
Nicrophorus pustulatus Herschel	52	84	136
Nicrophorus tomentosus Weber	3,571	1,557	5,128
Total for *Nicrophorus*	8,478	12,630	21,108

caught in a trap-night, excluding recaptures. In 1996 we caught 470 *N. americanus* and a total of 12,630 *Nicrophorus* specimens in 463 trap-nights. In a similar study on the Arkansas–Oklahoma population, Lomilino *et al.* (1995) reported a total of 829 American burying beetles (excluding recaptures) and 4,419 *Nicrophorus* specimens in 5,947 trap-nights. It appears that the Oklahoma–Arkansas study represents a 13 times greater trapping effort resulting in captures of 1.79 times more *N. americanus*, but only 35% as many *Nicrophorus* specimens as we found. This comparison assumes that capture rate of new individuals was similar between the Arkansas–Oklahoma and Nebraska populations. This seems reasonable since trapping took place during a similar period. From this comparison it appears that the Nebraska population of *Nicrophorus* species is greater than that of Arkansas–Oklahoma. It is unclear whether this results in increased competition for resources and thus fewer *N. americanus*, or whether an increased trapping effort in Nebraska would lead to an increase in the number of *N. americanus* captured.

Age grading

The ability to distinguish between the relative age classes of *N. americanus* is important in characterizing population biology. The total catches for each of the three age classes of *N. americanus* is expressed as an average of the total trap effort for each night. The sum of the three age classes is equal to the average number of beetles caught for that night (Fig. 4). Only mature beetles were caught early in the season. The mid-season captures present a clear picture of a transition period where all three-age classes are present. The mature class is partially replaced by the mature pale class, and the two classes are then replaced by the tenerals. A bimodal distribution is seen in the data between the mature and teneral classes.

The mid-season decline in numbers might be a sampling artifact partially explained by a four-day period when traps were not in place within the study

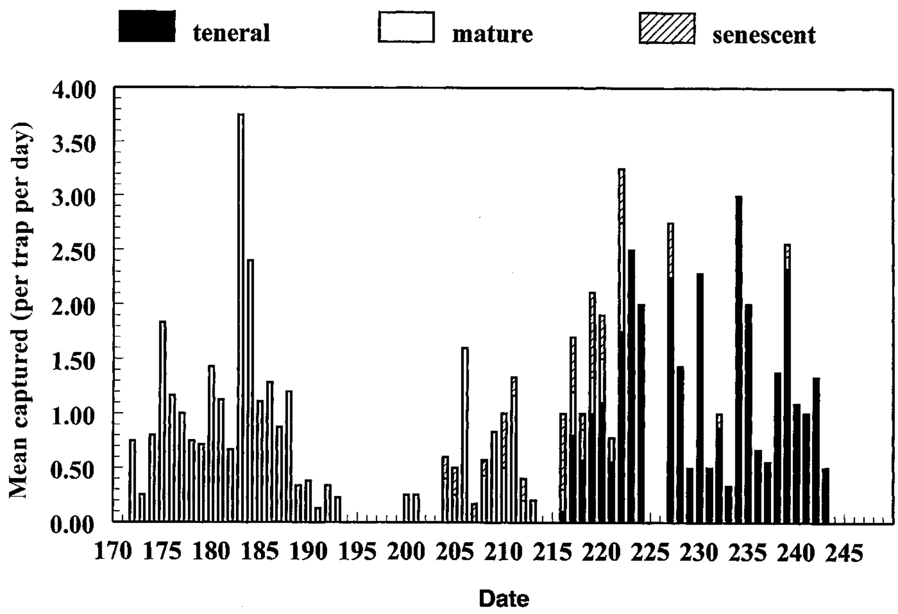


Figure 4. The three age classes of *N. americanus* captured in 1996 versus Julian date (Date 170 = 19 June). The stacked bars represent the mean number of beetles in each age class captured per trap-night.

area. However, age-grading suggests the decline represents a period when many of the beetles were still underground rearing their brood, or when most brood rearing was completed, but the tenerals had not yet emerged from their pupae. It is also probable that some adults died after brood rearing. Of greater interest was the time between the mature and teneral peak. This time (expressed in days) was similar to the 60–79 days for development of *N. americanus* in the laboratory from larvae to emergence (Ratcliffe, 1996). With this interpretation, the first peak corresponded to the maximum breeding period of the beetles, and the second peak was the period of peak emergence.

The peak of mature *N. americanus* observed in the last week of June/ first week of July translates into the time when the beetles were most actively searching for carrion on which to rear their broods. Although the field data demonstrates the suitability of the age grading procedures to differentiate between age classes, more exact estimates of morphological changes and age would be valuable. To develop such estimates it will be necessary to begin with individuals of known age (as is possible with laboratory populations). However, there are probably environmental influences on age-specific changes, so laboratory estimates alone will not provide an adequate time scale. Simultaneous monitoring of individuals in laboratory and field releases from the same brood may possibly be the best approach for assessing age classes. Also, the senescent class of *N. americanus* captured late in the trapping season should be examined in more detail since these beetles are likely to be post-reproductive.

Phenology

Our results indicate that the Nebraska population is univoltine, and it is unlikely that many adults live longer than one year. The identification of different age classes has direct implications for research on *N. americanus*. To establish breeding colonies, it is necessary that beetles chosen from the population are mature rather than senescent as these beetles will probably fail to breed. Conversely, senescent individuals would be good candidates for DNA analysis since their removal would not greatly impact on the population.

In 1996, 3 August was the first date of capture for a teneral *N. americanus*. Using 60 days as the minimum development time, beetle breeding began on 4 June. In Nebraska, *N. americanus* become active in mid-May. Peyton (1996) began trapping near Gothenburg on 15 May 1996 and first captured *N. americanus* on 20 May 1996. Taken together, the results indicate that *N. americanus* begin rearing broods soon after emergence from over-wintering.

Sex ratio

In 1995 we collected significantly more ($P < 0.01$) females than males (46 and 21 respectively). In 1996 we also collected significantly more females (261) than males (207) ($P < 0.05$). We tested sex ratios within each of the three age classes with the expectation that the males emerge from brooding earlier then females, which remain in attendance of the brood (Ratcliffe, 1996). Within each of the three age classes the sex ratio was not significantly different from a one to one ratio ($P > 0.05$), although the power of the test was limited by sample sizes.

Nocturnal activity

We collected a total of 82 *N. americanus* arriving at pitfall traps during the nocturnal observation periods (one night in 1995 and six nights in 1996). The beetles exhibited highest activity (60% of all captures) between the third and fourth hours after sunset (Fig. 5) with no captures occurring immediately after dawn. We tested the hypothesis that beetle activity increases with increasing temperature by regressing number captured versus temperature (Fig. 6). We found that beetle activity was highest between 15 and 20 °C, but exhibited a weakly negative relationship with temperature (number captured = −0.66 °C +17.9 °C; $r^2 = 33.8$). Time after sunset and temperature are strongly correlated, but our data suggest that beetles may delay nocturnal activity when

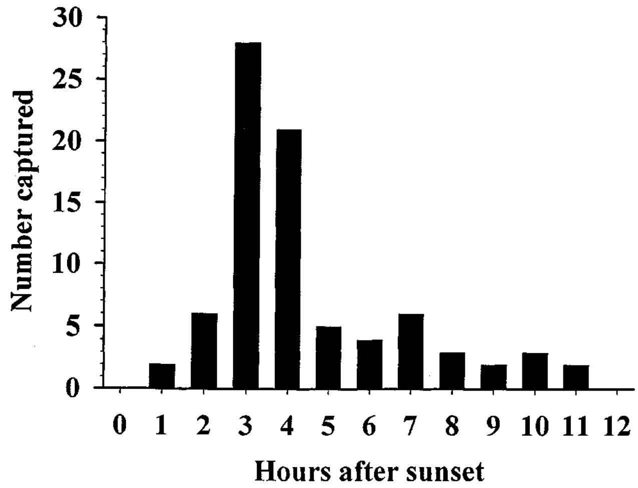


Figure 5. Nocturnal activity of American burying beetles expressed as the sum of beetles captured during each hour over seven nights of observation (N = 82).

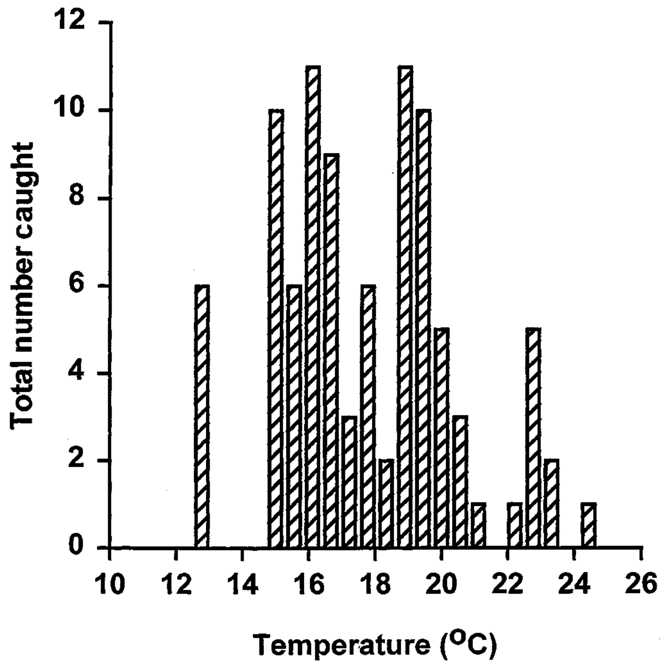


Figure 6. Total number of *N. americanus* versus temperature captured over nine nights of hourly monitoring (N = 92).

temperatures are very warm (> 24 °C). This is further supported by Bedick's (1997) findings that *N. marginatus* is extremely susceptible to desiccation. Although beetle activity was reduced below 15 °C, we collected six beetles at 12.7 °C. These data are generally in agreement with Kozol (1991) but suggest that trapping success is possible at temperatures below 15 °C.

Issues in the decline of *N. americanus*

Competition for limited resources is a major factor in determining a species' habitat use and survival. Competition has been hypothesized as reducing numbers of *N. americanus* because fresh carrion is a patchy and ephemeral resource and because there are a relatively large number of *Nicrophorus* species competing for the same resource (Wilson and Fudge, 1984; Kozol *et al.*, 1988). Indeed, fighting among attracted *Nicrophorus* beetles is severe and often reduces the number of beetles in possession of a carcass to a dominant male–female pair (Ratcliffe, 1996). This fierce competition can lead to injuries and in this study we commonly found *Nicrophorus* species with multiple appendages missing. Work by Kozol *et al.* (1988) showed that competition for carrion was always won by the larger *N. americanus* against the smaller congeners *N. orbicollis* and *N. marginatus*, suggesting that *N. americanus* should not be displaced by competition for resources. However based on size, the conclusion that no serious *Nicrophorus* competitor is present within the range of *N. americanus* may not be true since *N. carolinus* is a large (14–27 mm), robust burying beetle found in prairie habitat (Ratcliffe, 1996). Also, the generality of larger beetle success has not been adequately tested by Kozol *et al.* because *N. marginatus* is diurnal and activity pattern may influence test results (Ratcliffe, 1996).

Despite some potential for competition with *N. americanus* from *N. carolinus*, competition would not account for the decline in *N. americanus* across its eastern range. In disturbed and fragmented habitats around the Gothenburg population we found few *N. americanus*, and thus our findings are consistent with the suggestion that habitat disturbance and fragmentation are associated with the beetle's decline (Lomolino *et al.*, 1995). However, it is noteworthy that in 1996 traps adjacent to cornfields outside the canyon study areas captured *N. americanus*. Therefore, agricultural practices *per se* may not limit *N. americanus*, although the influence of agriculture on carrion availability clearly has an impact. If habitat disturbance is associated with the beetle's decline, related factors such as an increase of vertebrate scavengers and a decrease of appropriate carrion (Phillips, 1936) for *N. americanus* may be the proximate cause of the decline (Klein, 1989; Holloway and Schnell, 1998). In considering these possibilities, the recognition of a large, new population of *N. americanus* in the Gothenburg area provides new opportunities to study the beetle's biology and ecology, which may one day allow the recovery of this species.

Conclusions

We found a large population of *N. americanus* in south-central Nebraska. Based on our samples, the Gothenburg population is among the largest remaining population of *N. americanus* known. Regarding conservation status, with a population size of at least 1,600 (and reasonably much larger) individuals, the Gothenburg population greatly exceeds the 500 individuals standard set by the U.S. Fish and Wildlife Service (1991) to represent a new, self-sustaining population in the Midwest Region.

Population and behavioural studies on the Gothenburg population demonstrate that *N. americanus* is univoltine in Nebraska and is active throughout the summer months. The age grading methods used in this study have great utility in describing age structure and delineating generations, and may be valuable when capturing mature beetles for breeding and senescent beetles for DNA studies. Additionally, the nocturnal activity study indicates that beetle activity follows a circadian rhythm with greatest activity occurring two to four hours after sunset. Although no clear relationship with temperature was observed, a minimum night-time temperature of 12–13 °C seems necessary for activity, while temperatures that are warmer than 24 °C may depress activity.

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