Biological Conservation 81 (1997) 145–152

0006-3207/97 $17.00 + 0.00
PII: S0006-3207(96)00158-9

RELATIONSHIP BETWEEN NUMBERS OF THE ENDANGERED AMERICAN BURYING BEETLE *Nicrophorus americanus* OLIVIER (COLEOPTERA: SILPHIDAE) AND AVAILABLE FOOD RESOURCES

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(Received 10 May 1995; accepted 23 September 1996)

Abstract

The American burying beetle Nicrophorus americanus *Oliver (Coleoptera: Silphidae), designated in the United States as an endangered species, requires vertebrate carcasses for feeding, breeding and rearing young (optimally 80–200 g for breeding, but beetles readily feed on smaller carcasses). Previous studies at the 29 000 ha Fort Chaffee Military Reservation, Arkansas and the 20 000 ha Camp Gruber Training Site, Oklahoma have shown that with habitat defined based on vegetation, the species is a habitat generalist when feeding. Given that the species was not selective relative to habitat type at Fort Chaffee, we investigated whether there was a relationship between numbers of beetles and measures of vertebrate abundance. For beetles, eight baited pitfall traps were set for three nights in 1992 and 1993 along each of the 52 transects where, in previous years, birds and mammals had been censused. Birds were counted using a modified point-count technique (five counts during May–June 1989–1991), and mammals were sampled with 'museum special' snap traps and rat traps (three two-day trapping periods during May–June 1989–1991). In analyzing 0–200 g mammals trapped and birds counted on the transects, significant correlations were found of the number of American burying beetles caught with biomass of mammals; biomass of mammals plus birds; numbers of species of mammals; and numbers of individual mammals. American burying beetles frequented sites where small vertebrates (particularly mammals) were relatively abundant, irrespective of the predominant habitat at that site. © 1997 Elsevier Science Ltd.*

Keywords: American burying beetle, *Nicrophorus americanus*, feeding, endangered species, small mammal abundance.

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INTRODUCTION

The largest North American member of the beetle family Silphidae is the American burying beetle *Nicrophorus americanus* Oliver (Coleoptera: Silphidae), which as adults range in length from 30 to 35 mm (Anderson, 1982; Ratcliffe, 1996). American burying beetles are easily distinguished from other North American *Nicrophorus* by their large size, red to orange frons and red to orange pronotum (Anderson, 1982; Ratcliffe, 1996). *Nicrophorus americanus* use vertebrate carcasses, predominant of birds and mammals, when feeding, breeding and rearing young. On Block Island, Rhode Island they were shown to prefer 80–100 g carcasses for breeding, but readily fed on smaller carcasses and used carcasses up to 300 g (Kozol *et al.*, 1988).

Nicrophorus americanus was included on the endangered species list in July 1989 by the United States Department of the Interior (Federal Register 54:29652–29655). Cause for concern stemmed from the disappearance of *N. americanus* from over 90% of its historic range (Lomolino *et al.*, 1995), which included much of the eastern half of the conterminous US (Fig. 1). The remaining populations of *N. americanus* are known from: (1) Block Island, Rhode Island; (2) eastern Oklahoma and western Arkansas; and (3) central Nebraska and southern South Dakota (Kozol *et al.*, 1988; Ratcliffe & Jameson, 1992; Ratcliffe, 1996). These populations survive on the periphery of the species' historic range (Lomolino *et al.*, 1995).

Several attempts have been made based on vegetation to assess the habitats in which *N. americanus* is most successful. Creighton *et al.* (1993*b*) postulated that oak–hickory forests, the habitat in which their records indicated that *N. americanus* were most commonly found in eastern Oklahoma, are most similar to the preferred habitat before the decline of the beetle. Anderson (1982) assumed that the decline of the American burying beetle was due to deforestation of old-growth climax forests. He based this assumption on the fact that a European congener (*N. germanicus*) of similar size has undergone a decrease in abundance following the destruction of its preferred habitat, primary forest. However, as indicated by the historical distribution of the American burying beetle across much of the eastern half of North America, *N. americanus* has frequented many types of habitats (Schweitzer & Master, 1987). Based on an analysis considering habitats within two relatively large areas, Lomolino *et al.* (1995) showed that, when feeding, *N. americanus* is a habitat generalist at Camp Gruber Training Site (20 000 ha) in Oklahoma and at Fort Chaffee Military Reservation (29 000 ha) in Arkansas. The habitats at the two military installations, which are 85 km apart, range from open grasslands to old fields, and to bottomland forests and oak–hickory forests.

In a study of the Block Island population, Schweitzer and Master (1987) concluded that vegetation and soil may not be directly limiting for *N. americanus* (but see Lomolino *et al.* (1995) for data on association between soil characteristics and beetle numbers at Fort Chaffee). Vegetation and soil type, even if not affecting the beetle directly, could influence the potential food resource base and the types of competitors for the carrion (US Fish and Wildlife Service, 1991). Our purpose was to determine whether there is an association across sites of the numbers of *N. americanus* at Fort Chaffee, and the abundance of small birds and mammals, which are potential food sources.

Nomenclature follows the *Flora of the Great Plains* (Great Plains Flora Association, 1986) for plants, *Arkansas Mammals* (Sealander & Heidt, 1990) for mammals, and the *AOU Check-list* (American Ornithologists' Union, 1983) for birds.

METHODS

Study site

Beetles, birds and mammals were censused at 52 sites located throughout Fort Chaffee Military Reservation in northwestern Arkansas. At its widest points, Fort Chaffee is 31 km from east to west and 13 km from north to south, covering 29 000 ha. Most of Fort Chaffee is in the Arkansas River valley, but the southeastern corner of the reservation extends to the Ouchita Mountains. The installation is located near the northern boundary of the subtropical humid climate zone (Trewartha, 1968). The temperatures range from below freezing an average of 81 days/year to above 32°C an average of 72 days/year, with June, July and August being the hottest months. The average precipitation per year is 107 cm, with the heaviest rainfall occurring in May and June (Cox *et al.*, 1975).

Fort Chaffee has a variety of habitats (Johnson *et al.*, 1990), including old fields, which comprise of abandoned farmland or other areas that have been cleared of vegetation and allowed to revegetate. This habitat is highly variable in both species composition and vegetation structure depending on factors such as soil nutrient status, crops grown before abandonment and fire history. Seven other terrestrial habitats (based on the system devised by Küchler, 1964) are represented on the installation (Johnson *et al.*, 1990): (1) bluestem prairie dominated by big bluestem *Andropogon gerardii* and little bluestem *Schizachyrium scoparium*; (2) cedar glade dominated by red cedar *Juniperus virginiana*; (3) cross timbers dominated by post-oak *Quercus stellata*, blackjack oak *Q. marilandica*, red cedar or some combination of the three; (4) elm–ash forest or more appropriately bottomland forest that often is dominated by trees not including elm *Ulmus* or ash *Fraxinus*; (5) oak–hickory forest dominated by oaks (other than post-oak and blackjack oak) and hickories *Carya*; (6) oak–pine forest, which often resembles cross timbers with the addition of pines; and (7) oak–hickory–pine forest, a forest similar to the oak–hickory type, but having one or more pine species as important constituents. Vegetation forms a continuum on Fort Chaffee, each of the habitats grading in to others (Johnson *et al.*, 1990). Much of the area is subject to periodic burning.

All the habitats were represented in the 52 sites used for sampling. Sites included open grasslands, grassy areas with considerable shrub development, woodlands with little underbrush, and woodlands with a definite shrub layer (Lomolino *et al.*, 1995). There was no substantial inter-year variation in vegetation for given sites over the years covered in our analyses.

The soil types on Fort Chaffee vary considerably. Sites sampled ranged from about 15 to 75% sand, 3 to 35% clay and 20 to 65% silt (Lomolino *et al.*, 1995).

Census methods

Beetles were trapped 16–25 June, 24 July–6 August and 26 August–5 September in 1992 and 24 July–2 August in 1993 using pitfall traps as outlined in Creighton *et al.*

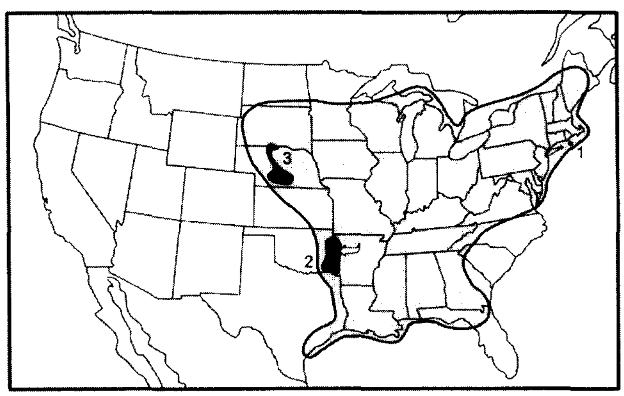

Fig. 1. Historic (shaded) and current (black) range of *N. americanus* (modified from Lomolino *et al.*, 1995; Ratcliffe, 1996). Current range includes: (1) Block Island, Rhode Island; (2) eastern Oklahoma and western Arkansas; and (3) central Nebraska and southern South Dakota. Arrow indicates location of Fort Chaffee.

(1993*a*). At each site, eight traps were placed at 20 m intervals along a transect line. Each pitfall trap consisted of two 0·7 liter plastic cups stacked together and inserted into the ground so that the cup rims were flush with the surface. The bait, 15–20 g of aged chicken, was placed in the bottom third of a trimmed, 0·2 liter polystyrene cup and suspended with a wire over the two plastic cups. A hemispheric plastic dome (25 cm in diameter with substantial openings cut in three places along the bottom edge) was placed over each trap to shield it from rain. The traps were set in the evening before 17:00 h DST and checked before 10:00 h each morning for 3 days. Data on beetles are given in numbers captured per trap-night (i.e. a trap-night equals one trap set for one night).

A modified point-count transect technique was used to census birds (Blondel *et al.*, 1981) during three periods: 14–25 May 1989; 5–14 June 1990; and 24 May–2 June 1991. Birds were observed for 20 min in the morning at each site in 1989 and for 20 min in both the morning and afternoon in 1990 and 1991. The observer (Schnell) walked the length of the transect slowly in 6 min, tabulating all birds perched, flying and vocalizing within 100 m of the transect. He then stood at the 100 m mark of the transect for 8 min and recorded additional birds observed. Finally, he walked back to the beginning of the transect line in 6 min, recording any birds not previously noted.

Techniques as outlined by Tazik *et al.* (1992) were used to trap small mammals during three census periods: 13–25 May 1989; 1–8 June 1990; and 20–25 May 1991. Two rows of 20 'museum special' snap traps (base 7×14 cm) and five rat traps (8·5×17·5 cm) were set, one row offset 15 m on each side of the transect. Snap traps were spaced 7·5 m apart and baited with a mixture of rolled oats and peanut butter. Similarly baited rat traps were spaced evenly along each side of the transect 2·5 m from the museum specials. During a given census, transects were run for two nights, resulting in 100 trap-nights per plot. Traps were set during the late afternoon or evening of the first day, checked early the next morning, reset during the late afternoon or evening of the second day and checked on the following morning. Captures for each site were placed in separate Ziplock bags, labeled and then frozen or stored on ice until they could be identified.

Biomass calculations

Biomass per site of birds was calculated by adding the masses of 0–200 g birds observed per site for each observation period and then dividing by the number of observation periods. Mass values for birds were obtained from Dunning (1993). The mammal biomass per site was calculated by adding the masses of all 0–200 g mammals trapped per site during each trapping period and dividing by the number of trapping periods. Mammal mass values were obtained from adult specimens taken at Fort Chaffee.

Statistical analyses

The number of beetles trapped at each site was plotted against the biomass of 0–200 g birds, mammals and combined birds and mammals, using SigmaPlot for Windows (Tilling *et al.*, 1994). We also plotted beetle numbers against the numbers of 0–200 g individual birds, individual mammals, species of birds and species of mammals. Spearman's rank correlations (r_s) were calculated using SYSTAT for Windows (Wilkinson *et al.*, 1992) to evaluate the relationship between beetle densities and the potential food resource base at each site. Use of a rank correlation reduces the weight of extreme points in the analysis (Sokal & Rohlf, 1995).

Contour maps of numbers of beetles per trap-night, birds per census, and mammals per census were created using a kriging method (Cressie, 1991) in Surfer for Windows (Keckler, 1994). Kriging is a geostatistical gridding technique that uses information on patterns of spatial correlation among sampled locations to estimate interpolated points (Maurer, 1994). A grid is a rectangular region comprised of rows and columns that is georeferenced to a coordinate system. Kriging expresses trends that are suggested in the data so that, for example, high points are connected along a ridge, rather than isolated by bull's-eye-type contours (Keckler, 1994). A variogram model determines the local neighborhood of observations used when interpolating each grid cell, and how the weights are applied to the observations during grid-cell calculations. We used a linear variogram model

$$\gamma(h) = Ch, \qquad (1)$$

where C is the scale for the structured component of the variogram and h is the anisotropically rescaled, relative separation distance. From a grid file of rows and columns of values for the variable of interest, contour lines are mapped at defined levels to delineate groups of similar values.

RESULTS

During a given trapping period, from 0.00 to 0.60 American burying beetles per trap-night were captured on each transect, with a total of 608 beetles being caught during the four trapping periods. On the five bird censuses, 3426 individual 0–200 g birds of 76 species were observed. The most common bird species were the tufted titmouse *Parus bicolor* ($n = 283$), field sparrow *Spizella pusilla* ($n = 260$), blue-gray gnatcatcher *Polioptila caerulea* ($n = 254$) and northern cardinal *Cardinalis cardinalis* ($n = 248$). During mammal trapping in the three years, 416 individual 0–200 g mammals of 16 species were caught. The most common species were the deer mouse *Peromyscus maniculatus* ($n = 202$), white-footed mouse *P. leucopus* ($n = 90$) and fulvous harvest mouse *Reithrodontomys fulvescens* ($n = 41$).

The biomass of 0–200 g birds, mammals and combined birds and mammals per census was compared with the number of beetles per trap-night at each site (Fig. 2). There was no relationship between the number of beetles and the biomass of 0–200 g birds (Fig. 2(a)). In contrast, the number of beetles was significantly correlated with the biomass of 0–200 g mammals (Fig. 2(b)), and the biomass of combined 0–200 g birds and mammals was significantly correlated with the number of beetles (Fig. 2(c)).

The average numbers of bird and mammal species per census at each site were compared separately with the average number of beetles captured (Fig. 3). The number of bird species was not significantly correlated with the number of beetles (Fig. 3(a)), but there was a positive association with the number of mammal species (Fig. 3(b)).

The average numbers of individual birds and mammals per census at each site were separately compared with the number of beetles per trap-night (Fig. 4). There was no significant correlation between the numbers of individual birds and the number of beetles (Fig. 4(a)). However, the numbers of individual mammals were significantly associated to the number of beetles

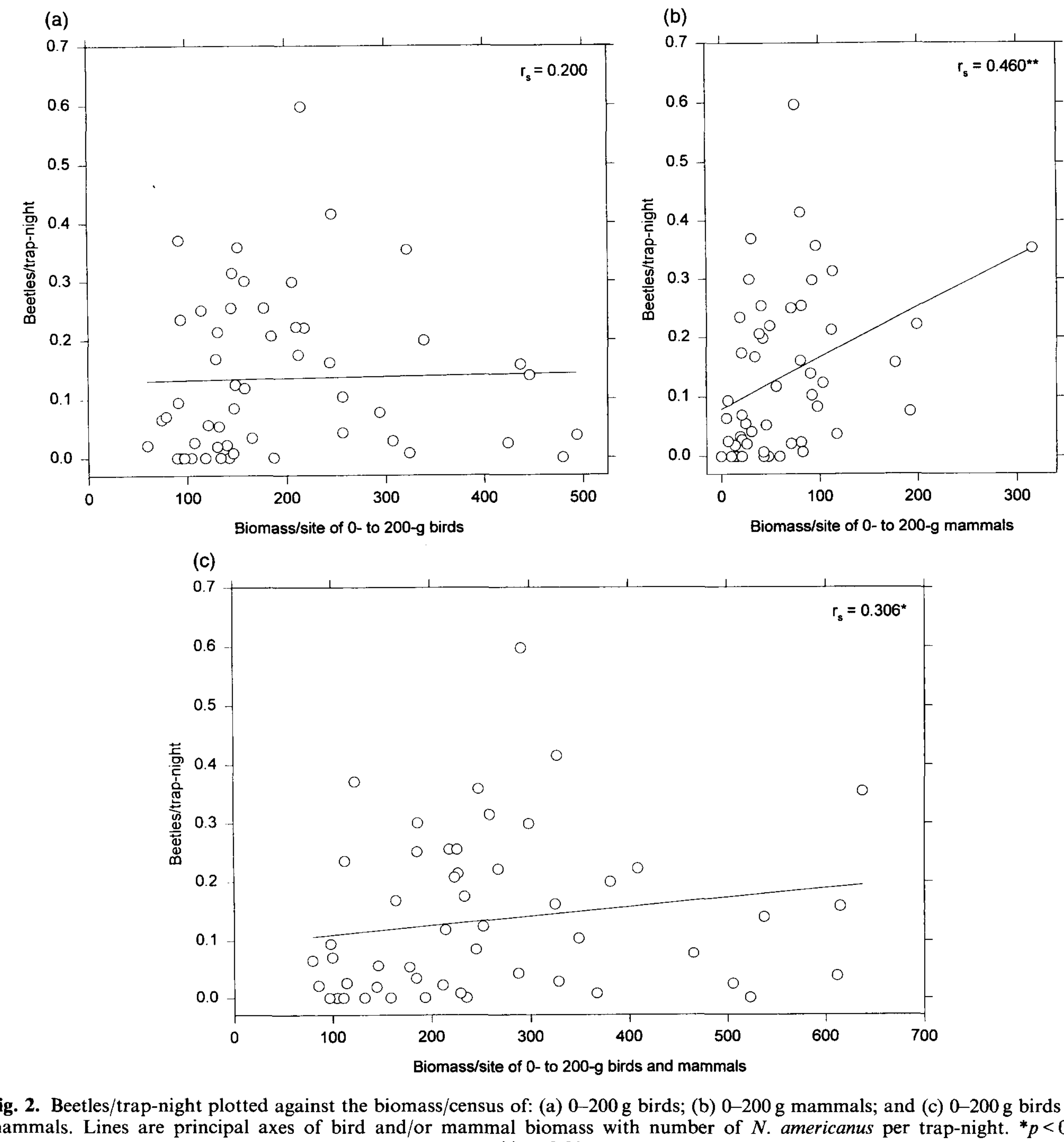

Fig. 2. Beetles/trap-night plotted against the biomass/census of: (a) 0–200 g birds; (b) 0–200 g mammals; and (c) 0–200 g birds and mammals. Lines are principal axes of bird and/or mammal biomass with number of *N. americanus* per trap-night. $^*p < 0.05$; $^{**}p < 0.01$.

(Fig. 4(b)), producing the highest Spearman rank correlation ($r_s = 0{\cdot}466$) found in the study.

While American burying beetles were found throughout Fort Chaffee, they were concentrated in two main areas on the installation (Fig. 5(a)). Not surprisingly, given the correlations reported above, these areas of concentration do not correspond particularly closely with areas having the highest numbers of birds (Fig. 5(b)). However, the geographic pattern of mammal captures (Fig. 5(c)) exhibits notable concordance with that of *N. americanus*. Except for the upper half of the eastern edge of Fort Chaffee (Fig. 5(c)), the areas with relatively high numbers of mammal captures correspond with areas having high beetle numbers (Fig. 5(a)).

DISCUSSION

Overall, the biomass, numbers and species of 0–200 g mammals and the combined biomass of 0–200 g birds and mammals inhabiting the sites at Fort Chaffee are

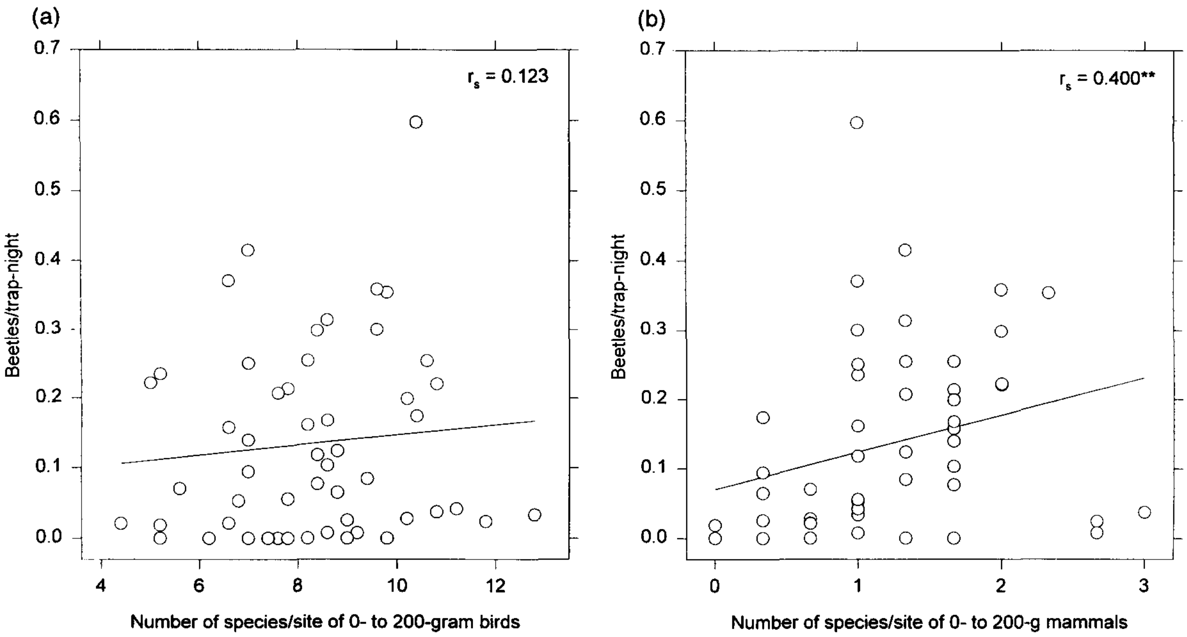

Fig. 3. Beetles/trap-night plotted against the number of species/census of: (a) 0–200 g birds; and (b) 0–200 g mammals. $^{**}p < 0.01$.

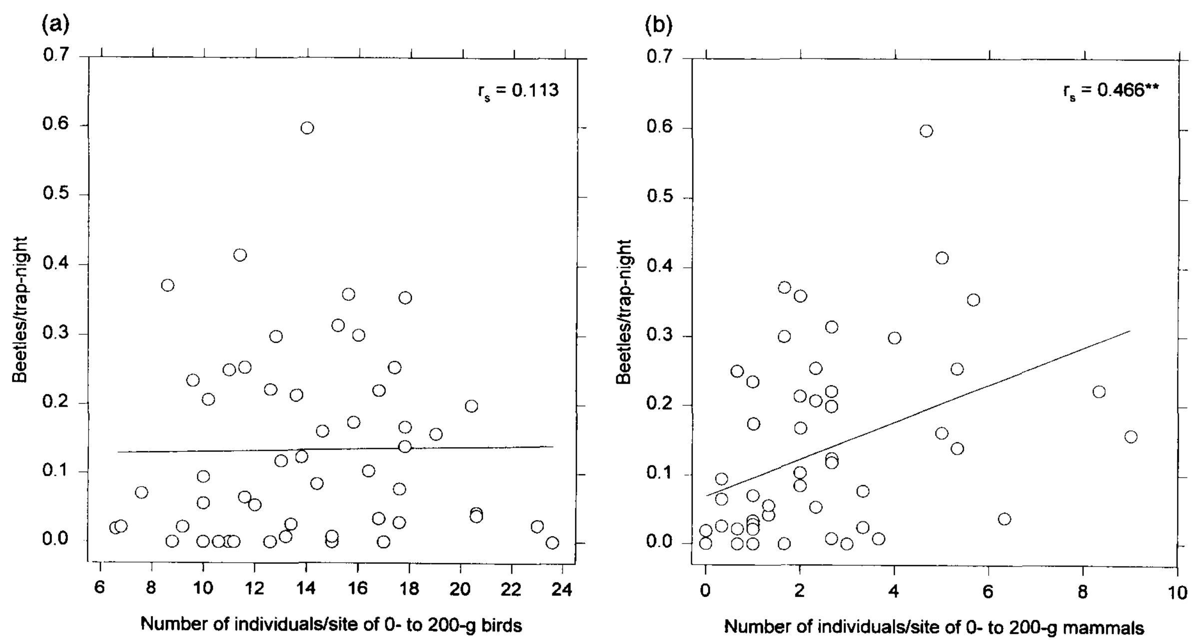

Fig. 4. Beetles/trap-night plotted against the number of individuals/census of: (a) 0–200 g birds; and (b) 0–200 g mammals. $^{**}p < 0.01$.

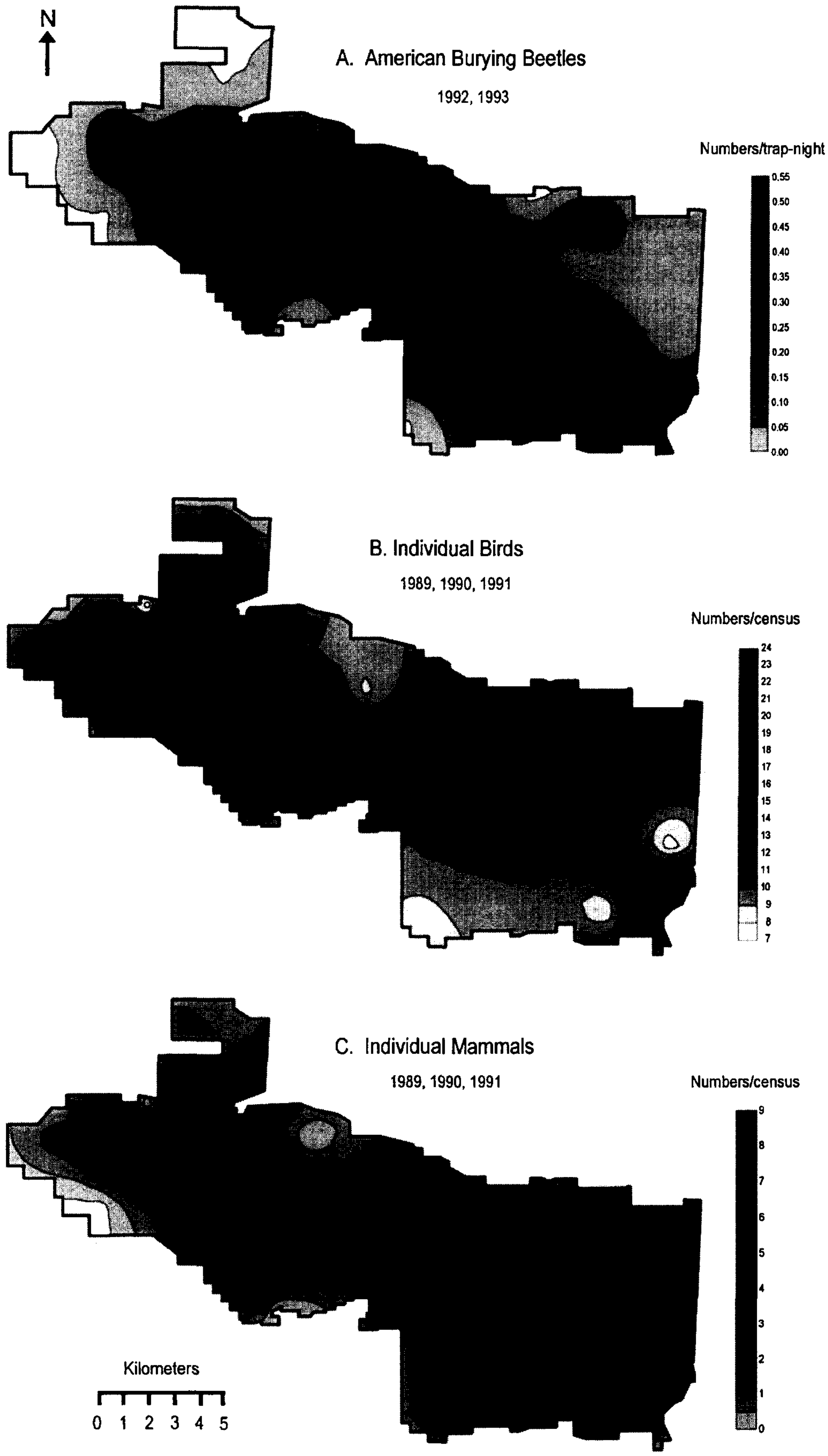

Fig. 5. Contour maps summarizing geographic distributions on Fort Chaffee of numbers of: (a) American burying beetles/trap-night; (b) individual birds/census; and (c) individual mammals/census.

positively associated with the numbers of *N. americanus* found at those sites. There is, however, no relationship between numbers of *N. americanus* and biomass, numbers or species of 0–200 g birds. Birds may be a more ephemeral and/or unpredictable food source because of factors such as seasonal migration and relatively long daily movements, which might explain the lack of correspondence of their numbers with those of *N. americanus*. Possibly the census method used to evaluate birds does not reflect well the actual availability of bird carcasses to the beetles, a proposition that merits further study.

While we found a number of statistically significant associations of *N. americanus* numbers with measures of biomass, numbers and numbers of species of animals that constitute its food base, there was also considerable scatter in the data points (see Figs 2–4). This is not unexpected for several reasons. Firstly, the data for beetles were gathered a year following the three years during which birds and mammals were censused, thus introducing statistical error due to inter-year variation. Secondly, the trapping and census methods used for beetles, small mammals and birds are inexact, producing only general indicators of populations present. Thirdly, the beetles are known to be highly mobile and could, potentially, travel considerable distances before entering our traps. The fact that the statistical associations stand up in spite of these factors indicates to us that the statistical relationship also is one of biological significance. The beetles are frequenting locations with potentially the richest food base.

One suggestion is that the primary cause of decline in *N. americanus* is its dependence on a decreasing food resource base (US Fish and Wildlife Service, 1991). Decreased abundance of optimal-sized carcasses and increased competition for them may be changes concomitant with deforestation of major portions of the eastern United States and with shifts in land use (Lovejoy *et al.*, 1986; Klein, 1989; US Fish and Wildlife Service, 1991), although as presently known the greatest numbers of *N. americanus* in the remaining remnant populations of the west are at Fort Chaffee and Camp Gruber, installations where old-field habitat and not mature forest predominates. Increases in habitat edge due to fragmentation can result in increases in the numbers of scavengers, such as crows, foxes and skunks, that compete with burying beetles for carrion (US Fish and Wildlife Service, 1991).

J. C. Creighton (pers. comm.) noted that *N. americanus* in Oklahoma and Arkansas prefer 80–200 g carcasses for breeding. They also feed on smaller carcasses. Kozol *et al.* (1988) conducted field trials on Block Island (in the eastern United States) which indicated that the species there prefers 80–100 g carcasses for breeding, but readily feeds on smaller carcasses. The use of land for grazing and other agricultural activities typically results in a reduction in numbers of relatively large rodents (Lovejoy *et al.*, 1986), such as hispid cotton rats *Sigmodon hispidus* (100–225 g in our sample from Fort Chaffee), which are of optimal feeding and breeding size for the American burying beetle. Generally, increases in farming and ranching are accompanied by larger numbers of small rodents, such as deer mice, which can be fed on by *N. americanus*, but are probably too small (i.e. only 15–25 g) for them to use successfully when breeding. Within the geographic range of *N. americanus*, an increase of smaller congenerics (e.g. *N. orbicollis*) has been suspected, purportedly due to the increase in optimal-sized food sources for smaller species of burying beetles (US Fish and Wildlife Service, 1991); while the suggested cause is plausible, it remains speculation since there are no historic data on abundance or population trends for other *Nicrophorus* species. In our evaluation of potential food resources, we considered all birds and mammals up to 200 g, thus including small- and medium-sized rodents.

Investigators have focused on trying to define the optimal habitat(s) for the American burying beetle based primarily on gross vegetational characteristics. However, given that we have shown that *N. americanus* frequents sites where small mammals are relatively abundant, it may be more profitable to focus on those areas with higher densities of small- and medium-sized vertebrates and the concomitant carcasses. Clearly, for breeding the carcasses used must be in areas with soil characteristics conducive to burial and successful reproduction. Favorable areas for the American burying beetle occur in more than one habitat (as defined by vegetation structure) provided that carrion is available and, for breeding, soils are suitable for brood rearing.

ACKNOWLEDGEMENTS

The authors would like to thank Anthony J. Stancampiano, Janet K. Braun, Brian R. Chapman and assistants for their work trapping mammals. Ana E. Hiott, Thomas W. Haner and David L. Certain, as well as other field-crew members, assisted in trapping beetles. Michael J. Amaral, J. Curtis Creighton, Ana E. Hiott, Mark V. Lomolino, Darrell W. Pogue, Chris Raithel, Caryn C. Vaughn and two anonymous reviewers provided useful suggestions concerning the manuscript and analyses of data. This research was supported by funds from Fort Chaffee and the US Army Construction Engineering Laboratories, Champaign, IL. We thank Jerry C. Sturdy at Fort Chaffee for assisting in numerous ways during our investigations.

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