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Resource availability and population dynamics of *Nicrophorus investigator*, an obligate carrion breeder

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Abstract. 1. Food resources for rearing young may influence insect populations. This is particularly true for insects that breed obligately on rare, ephemeral resources such as dung, fungi, or carrion.

2. Beetles in the genus *Nicrophorus* bury small vertebrate carcasses for rearing their young. Studies reviewed by Scott (1998) have found a positive relationship between carcass mass and total brood size. It is likely that access to carcasses suitable for breeding, and not food or mates, limits reproduction in both male and female *Nicrophorus*. Thus, small mammal densities could determine *Nicrophorus* population sizes.

3. The work reported here examined the relationship between *Nicrophorus investigator* (Coleoptera: Silphidae) population size and small mammal abundance at two sites over a 4-year period.

4. *Nicrophorus investigator* buried and reared young on all the native small rodent species trapped at two sites in south-western Colorado, U.S.A. (*Peromyscus maniculatus*, *Microtus montanus*, *Zapus princeps*, *Tamias minimus*, *Thomomys talpoides*). They preferred to bury and reproduce on rodent carcasses weighing between 16 and 48 g; rodents of this size represented 82% of captures.

5. Population sizes of *N. investigator* and small rodents were estimated simultaneously using mark-recapture censuses over a 4-year period. Considering only rodents within the size range used by *N. investigator*, the estimated small mammal biomass per hectare in one year and the beetle population size in the following year were correlated significantly.

Key words. *Nicrophorus*, population dynamics, reproductive ecology, resource availability, small mammal abundance.

Introduction

Insect populations are known to vary spatially and temporally in response to changes in climatic factors, vegetation, and the presence of parasites and predators. For insects whose reproduction depends on discrete and ephemeral resources such as dung, fungi, and carrion, however, the limiting factor may be the availability of resources for rearing young. For example, Hanski and Cambefort (1991) reviewed a variety of studies linking dung beetle population sizes with dung quality and quantity. Breitmeyer and Markow (1998) found that population size of *Drosophila* was greatest for species that utilised the longest-lasting cactus necroses. Randall (1982) found that between-year variation in larval food supply was an important factor determining fluctuations in moth populations. The positive association between resource abundance and local insect population densities may be particularly pronounced among the carrion beetles (Holloway & Schnell, 1997), where carcasses, not mates or food, limit reproductive opportunities (Scott, 1998). Thus, studies of carrion beetles are potential models to address the relationship between spatial and temporal variations in resource availability and population biology.

Burying beetles in the genus *Nicrophorus* (Silphidae) require carcasses of small vertebrates for rearing offspring (Milne & Milne, 1976; Wilson & Fudge, 1984; Trumbo, 1990b, 1991; Scott, 1998). The unique behaviours involved in

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carcass selection, burial, biparental care of larvae, and reproductive decisions of *Nicrophorus* have been studied extensively (Wilson & Fudge, 1984; Kozol *et al*., 1988; Scott & Traniello, 1990; Robertson, 1992; Sikes, 1996; Scott, 1998) but often in captive experiments and with either laboratory mice and rats or other domestic animals as the offered carcasses (but see Smith & Heese, 1995). Little is known about the availability of carrion in nature or the choices and reproductive decisions made by *Nicrophorus* under field conditions on naturally occurring carrion of small vertebrates. An understanding of the factors that influence population dynamics of *Nicrophorus* is particularly important in light of the current efforts to protect populations of the endangered (in the U.S.A.) American burying beetle *Nicrophorus americanus* (Kozol *et al*., 1988; Lomolino *et al*., 1995; Lomolino & Creighton, 1996; Holloway & Schnell, 1997) and the rare European *N. germanicus*.

Nicrophorus investigator is one of several species of burying beetle native to the montane regions of western North America (Peck & Kaulbars, 1987; Smith & Heese, 1995), though its range also includes northern regions of Japan and Europe. In Colorado, this species depends on small mammal carcasses for reproduction and prefers open meadow over spruce or aspen forest habitats (Smith & Heese, 1995). It has not been observed to rear young on birds, though adults do feed on bird carcasses (R. Smith, pers. obs.). *Nicrophorus investigator* co-occurs with the locally much rarer *N. defodiens*. As in other *Nicrophorus* (Wilson & Fudge, 1984; Kozol *et al*., 1988; Scott & Traniello, 1990; Robertson, 1992; Sikes, 1996; Scott, 1998), *Nicrophorus investigator* brood size is associated positively with carcass mass, over a specific size range of carcasses (16–48 g; Smith & Heese, 1995; this study). *Nicrophorus investigator* appears to be univoltine. Larvae develop during the first summer and overwinter as pre-pupae. The following summer they pupate, eclose, and adult beetles reproduce (Scott, 1998; R. Smith, pers. obs.).

Nicrophorus investigator depends on small rodents for reproduction. In addition, there is a positive relationship between carcass mass and brood size. Thus, local abundance of *N. investigator* may be determined by local small mammal densities, particularly by rodents whose body size is within the range utilised by *N. investigator*. If *N. investigator* prefers to reproduce on carcasses of particular mammal species, or if certain species fall outside the size range utilised by *N. investigator*, *Nicrophorus* population dynamics may also be expected to vary with spatial or temporal changes in small mammal species composition.

The purpose of the work reported here was to test whether *N. investigator* population densities are correlated with the abundance of their reproductive resource. Carcass quality was assessed by identifying the relative reproductive success of *N. investigator* utilising five small native mammal species of varying body size under field and outdoor enclosure conditions. Simultaneous mark-recapture censuses of small mammals and beetles were then conducted in order to estimate population sizes. Finally, the covariation of beetle densities with quality and abundance of reproductive resources was assessed.

Materials and methods

Study sites

The study was conducted in the vicinity of the Rocky Mountain Biological Laboratory, located in the Upper East River Valley, Colorado, U.S.A. (39°N, 107°W). Typically, snow-melt occurs on 23 May (B. Barr, Rocky Mountain Biological Laboratory, pers. comm.), ground temperatures reach 12–15 °C on 15 June, and *Nicrophorus* adults emerge in late June (Smith & Heese, 1995). The two study sites were: (1) Kettle Ponds: an open, gently-sloping (10°), low-elevation (2866 m) meadow located 2.5 km south of the Rocky Mountain Biological Laboratory in Gunnison National Forest, 200–500 m east of the East River. Vegetation consists of dominant grasses *Festuca thurberi*, *Agropyron trachycaulum*, *Bromus polyanthus*, *Bromopsis inermis*, and the forb *Lupinus argenteus*. The habitat is characteristic of the fescue community type described by Langenheim (1962); (2) Bellview Mountain: an open, slightly-steeper (20°), high-elevation (3170 m) meadow located 8 km north of the Rocky Mountain Biological Laboratory in Gunnison National Forest, 200–500 m east of the East River. Vegetation is an upland herb community (Langenheim, 1962) dominated by *Senecio crassulus*, *Ligusticum porteri*, *Lupinus parviflorus*, and *Chamerion danielsii*. The soil is considerably more rocky and less stable than at the Kettle Ponds site, as a result of talus accumulation and movement of sediment and debris (Langenheim, 1962).

Beetle carcass choice

Preference by *N. investigator* for specific sizes or species of small mammals was determined by offering beetles an assortment of carcasses first in a field situation (1993–1996) then in a field enclosure (1997–1999). Carcasses were obtained from trapping in cabins at the Rocky Mountain Biological Laboratory and from cat-kills brought in by a cat owner from a nearby town. Carcasses ranged in size from 8.5 to 107 g and included deer mice *Peromyscus maniculatus*, montane voles *Microtus montanus*, jumping mice *Zapus princeps*, least chipmunks *Tamias minimus*, and pocket gophers *Thomomys talpoides*. Following the methods of Smith and Heese (1995), 117 small mammal carcasses were placed 30–50 m apart in open meadows near the Rocky Mountain Biological Laboratory. Carcasses were checked daily and the presence or absence of beetles and whether or not the carcass was buried were noted. Monitoring continued until the carcass was either lost to scavengers, buried, or no longer suitable for burial (≈ 5 days).

Captive reproduction experiments at the two sites were carried out to determine the effect of carcass size and species on reproduction. The breeding container consisted of a metal can (18 cm deep, 15 cm diameter) pierced to allow drainage, filled with soil. Cans were buried 14 cm into the ground, leaving a 4-cm lip exposed, to which a metal screen cover was attached using a large rubber band. The cans were protected from rain by leaning a sheet of plastic stapled to a wooden

1.5 × 1.5 m frame over the cans (12 cans per frame). The rain cover was placed at an angle from the base of the north side of the cans and limited sunlight and air movement over the cans only slightly. A recently wild-caught male and female *N. investigator* were enclosed in a can with a single carcass of a rodent species found in the mammal census (*P. maniculatus*, *M. montanus*, *Z. princeps*, *T. minimus*, or *T. talpoides*). One hundred and sixteen carcasses of the above species were used, ranging in size from 18 to 50 g. After 2 weeks, the cans were inspected to determine whether the beetles raised a brood successfully.

Beetle censuses

In 1995, one trap line at each site was established with 10 traps spaced 20 m apart. Traps consisted of metal cans (18 cm deep, 15 cm diameter), pierced to allow drainage, half-filled with soil, and covered with a wire-mesh lid fashioned into a funnel shape and held on with a large rubber band. Each trap was suspended ≈40 cm in the air by wiring it to a wooden stake (this reduced vertebrate scavengers and potential injury to livestock from buried traps). Traps were baited with a fresh chicken drumstick 2 days before the beginning of the census. Each census lasted 5 days and was repeated every other week for 8 weeks. The two sites were censused simultaneously.

On each of the 5 census days, the number of beetles per trap and the species of *Nicrophorus* (*N. investigator* or *N. defodiens*) captured were recorded. Each beetle was sexed, the length of its elytron was measured using digital calipers (Digimatic Model CD-6″B, Mitutoyo, Kanagawa, Japan), and the beetle was marked with 1-mm triangular or square cuts on the end or side of its elytron (Goldwasser *et al*., 1993). Unique combinations of markings indicated census period and site. Each beetle was handled and released at the site of capture. The specific mark was noted on recapture.

Rodent community analysis

Small mammal trapping grids were established at each site. In 1997, 100 aluminium, medium-sized (23 × 8 × 8.5 cm) Sherman live traps were spaced 10 m apart in a 10 × 10 grid. In 1998 and 1999, the grids were reduced in size to 7 × 7, giving a total of 49 traps. The location of the 1998 and 1999 grids overlapped one corner of the 1997 grids. Traps were baited with a mix of peanut butter, rolled oats, millet, and sunflower seeds, and a piece of polyfill bedding material was added to each trap for warmth. Traps were opened at 19.30 hours and checked between 05.45 and 09.00 hours the following day. From late June until early August, traps were set for 2–4 nights each week, alternating weeks between sites as weather permitted; traps were not set during heavy rain or below-freezing nights. In 1997, traps were set for seven nights at Kettle Ponds and six nights at Bellview Mountain. In 1998, traps were set for 12 nights at Kettle Ponds and 10 nights at Bellview; in 1999 for 11 nights at Kettle Ponds and 5 nights at Bellview.

The sex, age, and weight of each mammal trapped were recorded. Each animal's abdominal fur was dyed using permanent hair dye (Miss Clairol 51D Black Velvet, Clairol Inc., Stamford, Connecticut, mixed with equal parts of hydrogen peroxide developer) applied using a toothbrush and spray bottle. After the dye was applied, the animal was released at the site of capture. Recaptured animals were noted during subsequent censuses. For the dominant species, population estimates were calculated using the Schnabel mark-recapture technique (Sutherland, 1996). For the rarer species, the Minimum Known Alive was determined. Biomass per hectare was calculated by multiplying these densities by average rodent mass determined separately at each site.

In addition, an estimate of rodent biomass was obtained in 1996 from data collected in collaboration with the Rocky Mountain Biological Laboratory Field Mammalogy class (S. A. Smith, pers. comm.). Students established 10 × 10 trapping grids at the two elevation sites and recorded mass, sex, and species of all rodents caught. The grids at each site were within 100 m of the grids used in 1997–1999. Total rodent biomass was estimated at each site by summing the multiple of average body mass and Peterson–Lincoln Index estimate of population size across all species.

Results

Beetle carcass choice

The proportion of carcasses located by beetles that was buried successfully is shown in Fig. 1 as a function of carcass size class. Note that beetles very rarely buried carcasses < 16 g and seldom buried those > 48 g. The success rate of reproduction (proportion of carcasses with broods) of *N. investigator* in the outdoor enclosures on each of the five species of rodent (all weighing 18–50 g) at the low and high elevation sites is shown

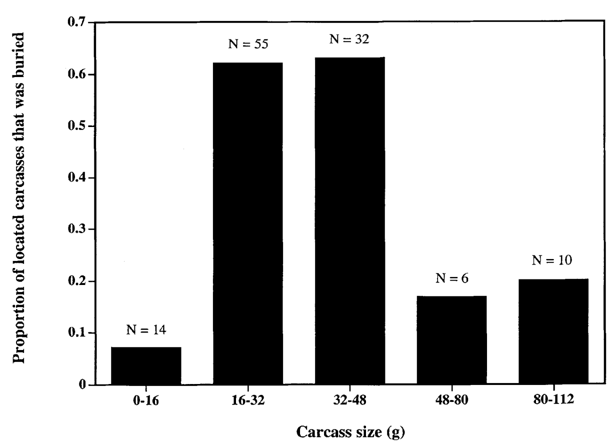

Fig. 1. The relationship between carcass size class and the proportion of located carcasses that was buried. *Nicrophorus investigator* bury a greater proportion of carcasses within the 16–48 g size classes. N refers to the number of carcasses located by *N. investigator* within each size class.

in Table 1. It was found that *N. investigator* could reproduce successfully (70–100% of the time) on all five species captured in the mammal censuses. There were no differences between sites.

Beetle census

The total number of individuals of *N. investigator* captured over each season was significantly greater at the lower elevation site than at the higher elevation site (1995–1999; Wilcoxon paired signed-rank test, $Z = -2.023$, $P < 0.05$). The estimated population sizes of *N. investigator* (mark-recapture, Schnabel method) at the Kettle Ponds site were at least three times larger than at the Bellview site in 1996–1999 (Fig. 2). In 1996 and 1997, no *N. defodiens* were captured at the Bellview site; in 1998, six adults were captured and in 1999 four were captured. At the Kettle Ponds site, 51 *N. defodiens* were captured in 1996, 61 in 1997, 112 in 1998, and 80 in 1999. These represent < 5% of total *Nicrophorus* captures.

Table 1. *Nicrophorus investigator* rears broods successfully on all five species of native small rodent. Data are shown as the proportion of all offered carcasses (N) with broods. Carcasses weighed 18 to 50 g. Only two species had non-zero cells necessary to test for significance (*G*-test of independence).

	Proportion with brood (N)			
Rodent species	Kettle Ponds	Bellview	*G*	P
Peromyscus maniculatus	0.87 (30)	0.94 (36)	1.20	> 0.05 NS
Microtus montanus	0.80 (10)	0.70 (10)	0.27	> 0.05 NS
Zapus princeps	1.00 (3)	1.00 (3)	–	–
Thomomys talpoides	0.75 (5)	1.00 (2)	–	–
Tamias minimus	1.00 (6)	1.00 (2)	–	–

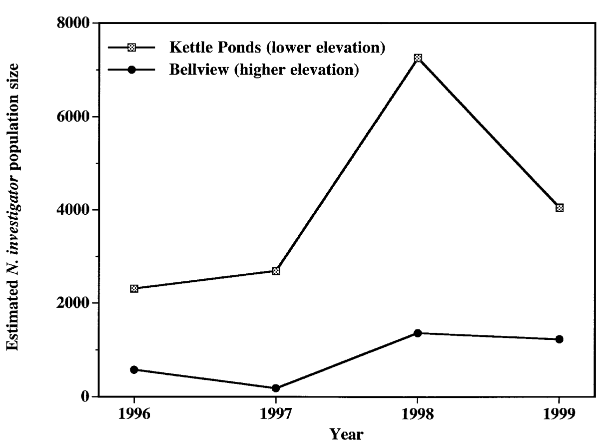

Fig. 2. A comparison over 4 years of population sizes of *N. investigator* at two sites. *Nicrophorus investigator* are significantly more abundant at the lower elevation site (Kettle Ponds) than at the higher elevation site (Bellview).

Mammal community analysis

The mammal census results indicate that the species of small rodent present did not vary with elevation. *Microtus montanus*, *Peromyscus maniculatus*, *Tamias minimus*, *Thomomys talpoides*, and *Zapus princeps* were captured or their presence was noted at both sites in all years. The most abundant species at the low elevation site were *M. montanus* and *P. maniculatus*, whereas at the high elevation site *Z. princeps* and *P. maniculatus* were dominant.

Schnabel population estimates for the more common species were calculated for the 1997–1999 data. Species-specific and total abundance varied with elevation (Fig. 3). *Peromyscus* was similarly abundant across sites and years; *Microtus* was more abundant in 2 years at the Kettle Ponds site, and *Zapus* was more abundant at the Bellview site in all years. Total estimated number per hectare was greater at the Kettle Ponds site than at the Bellview site in 2 out of 3 years (it was lower in 1999 when *Microtus* populations crashed).

Species-specific and total rodent biomass at each site were calculated by multiplying Schnabel population estimates or Minimum Known Alive counts (for rare species) by average rodent body mass (calculated separately for each site, based on trapping data). In 1997 and 1998, total rodent biomass was higher at the lower elevation site than at the higher elevation site, while in 1999 it was lower due to the absence of *Microtus*.

The relative frequency of captured rodents falling into five different biomass categories (1997–1999) is shown in Fig. 4. The proportion of rodents falling into the size-classes of 16–48 g ranged across years from 60 to 88% at the Kettle Ponds site and 81 to 83% at the Bellview site. Combining years indicates that at both sites 82% of all rodents fall within the 16–48 g range.

Correlating rodent biomass with beetle abundance

Two regression analyses were used to determine the relationship between rodent biomass and beetle abundance. The first analysis (Fig. 5a) regressed current year rodent biomass with current estimated beetle population size using data from 4 years at both sites. No significant relationship was found ($n = 8$, $F = 0.272$, $P = \text{NS}$, $r^2 = \text{NS}$). The second analysis (Fig. 5b) regressed the previous year's rodent biomass with current year estimated beetle population size. A significant positive relationship was found with a high correlation coefficient ($n = 6$, $F = 19.623$, $P < 0.05$, $r^2 = 0.831$).

In addition, an ANCOVA was used to examine the possible effects of combining data from two sites in the regression analysis. In the ANCOVA, site was the factor (block), mammal biomass the covariate, and beetle population size the dependent variable. The ANCOVA for biomass and beetle population size in the same year was not significant (site effect d.f. = 1, $F = 1.73$, $P = \text{NS}$; biomass effect, d.f. = 1, $F = 0.010$,

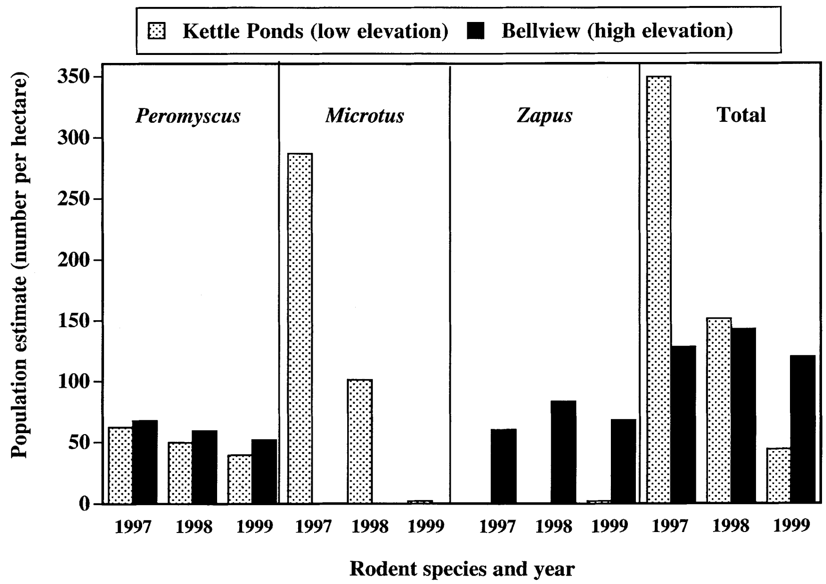

Fig. 3. Estimated population sizes of rodent species over a 3-year period at two sites. Populations vary yearly at the Kettle Ponds and Bellview sites. Only the estimates for the two dominant species at each site and their totals are shown but all five rodent species occur at each site.

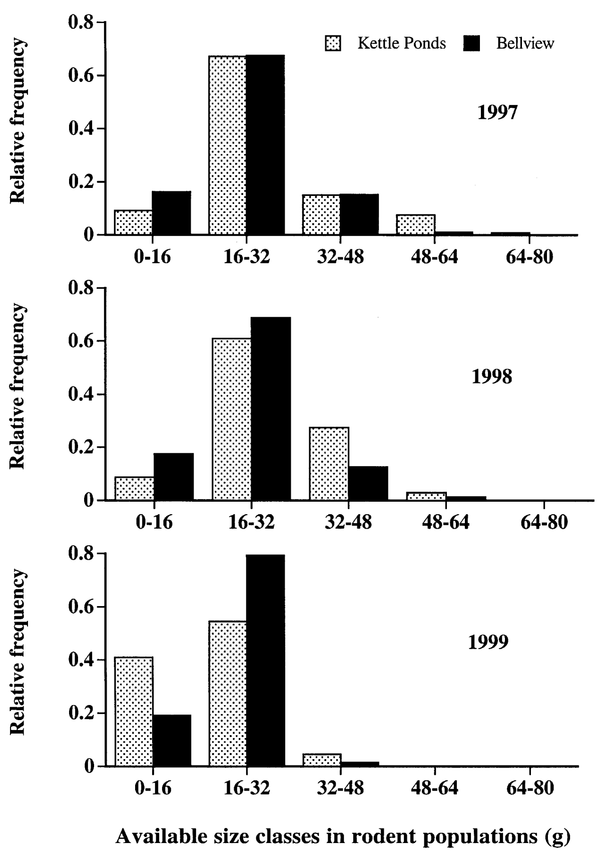

Fig. 4. The relative frequency of each rodent size class compared between sites, for 3 consecutive years. A high proportion (82%) of available rodents falls within the size classes known to be utilised by *Nicrophorus investigator* for rearing young.

P=NS); however the ANCOVA for biomass and beetle population size in the following year yielded a marginally significant effect of site (d.f=1, F=18.95, P=0.05) and a significant effect of biomass (d.f.=1, F=82.33, P<0.05). There was no significant interaction (d.f.=1, F=3.34, P=NS).

Discussion

Nicrophorus investigator is abundant in montane meadows and is capable of rearing young on carcasses of all the small rodent species found in these habitats (*Microtus montanus*, *Peromyscus maniculatus*, *Tamias minimus*, *Thomomys talpoides*, and *Zapus princeps*). Carcass size is an important determinant of use by *N. investigator*; few successful broods were raised on carcasses <16 g or >64 g. This selectivity is not, however, likely to limit *N. investigator* populations strongly because 82% of rodents captured in the surveys were within this size range. The smallest rodent, *P. maniculatus*, reaches 16 g at the late juvenile stage; *Zapus*, *Microtus*, *Tamias*, and *Thomomys* generally achieve 16 g before weaning. Of the five species, only *Tamias* and *Thomomys* are commonly >50 g, and these two species were relatively rare in the censuses. It appears that *N. investigator* does not specialise on any particular rodent species, and thus its population is probably influenced by overall rodent density, not necessarily by the availability of a particular species.

It was found that small mammal densities tended to decrease with increased elevation, consistent with patterns found at other locations (Armstrong *et al.*, 1973; Taylor *et al.*, 1985). Elevation may affect small mammal populations through a combination of resource availability, climatic stress, predation risk, and competitive interactions. In general, arthropods also

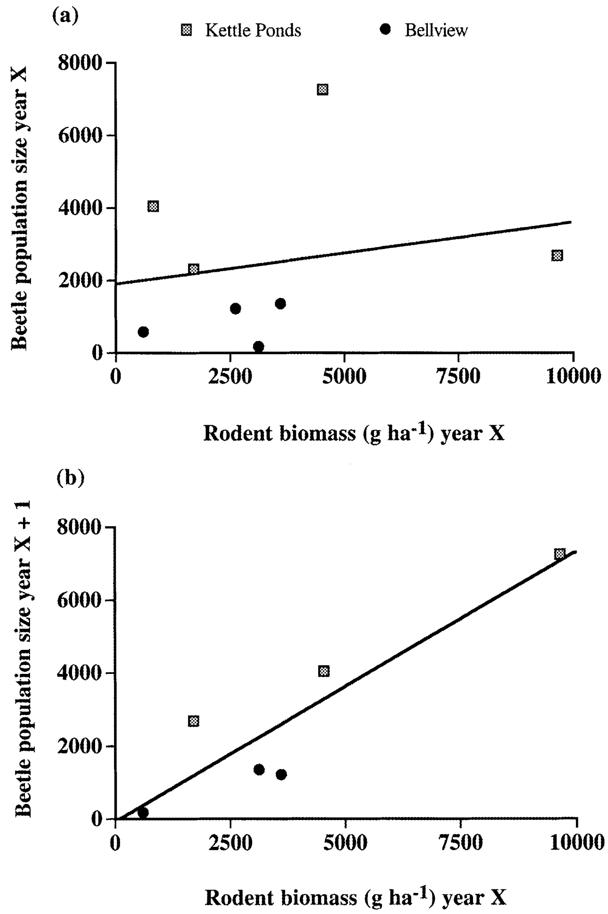

Fig. 5. The relationship between rodent biomass and beetle population size. (a) There is no association between rodent biomass (g ha^{-1}) and *Nicrophorus* population size in the same year ($y = 0.17x + 1900.79$, $r^2 = 0.043$). (b) When current *N. investigator* populations are compared with the previous year's rodent biomass, there is a significant positive relationship ($y = 0.74x - 71.48$, $r^2 = 0.831$).

experience a loss of species diversity and abundance with elevation (Janzen *et al.*, 1976; Kearns, 1992; Martin-Piera & Lobo, 1993; Coxwell & Bock, 1995; Sparks *et al.*, 1995), probably due to similar ecological factors. For *Nicrophorus*, an important factor is availability of suitable carcass resources.

Measures of total biomass probably underestimated available biomass for two reasons. First, there was some difficulty trapping *Tamias* and *Thomomys*, *Tamias* because it is primarily diurnal and *Thomomys* because it is not very active above ground. Second, because some species were rare, Minimum Known Alive numbers were substituted for Schnabel population estimates. It is assumed that these biases are similar at the two sites, thus the primary comparison of relative biomass at each site is still valid. In addition, these two species are both larger and therefore less likely to be used for reproduction by *N. investigator*.

In both 1997 and 1998, the sites with higher rodent biomass also had greater beetle abundance. Holloway and Schnell (1997) also found a significant, if somewhat weak, relationship between rodent biomass and current year *Nicrophorus americanus* captures, however they combined rodent biomass data over a number of years and could not distinguish between rodents used for food and those used for rearing young. The results shown here indicate that most of the available small rodent biomass is useable, i.e. within the range of body sizes accepted by *N. investigator* for reproduction. The relationship between resource availability and adult beetle population size is poor when comparing rodent and beetle data for the same year; however, there is a strong positive relationship when comparing current adult beetle population size with the *previous* year's rodent biomass. This is best explained with reference to the beetle life cycle. In *N. investigator*, there is a 1-year lag between resource availability and adult population size because one year's rodent carcass leads to the following year's adult *Nicrophorus*.

Univoltine species with long overwintering periods and nonoverlapping generations are well suited to studies of the relationship between breeding resource and population size. The study site and system described here are particularly amenable for study because only one species of *Nicrophorus* is abundant and it is possible to census the breeding resource. The results also indicate that combining data from two sites is not particularly problematic, though it is clear that a longer term study would be required to account for the variation among sites. Additional data on the time-lag effect collected from other *Nicrophorus* populations would be profitable. Ideally, rodent density would be used to predict the abundance of adult beetles the following year. This would be particularly beneficial for studies of rare or endangered populations, for example the American burying beetle *N. americanus* (Kozol *et al.*, 1988; Lomolino *et al.*, 1995; Lomolino & Creighton, 1996; Holloway & Schnell, 1997) or the European *N. germanicus*.

In 1997, the high rodent abundance and biomass measures at the Kettle Ponds site were driven primarily by very large numbers of *Microtus montanus*; in 1999, they were low due to the nearly complete absence of *Microtus*. Many microtine rodents are well known to have cyclical fluctuations in population density, with *boom and bust* type population dynamics, whereas other rodent species are less likely to fluctuate as greatly. Population dynamics in this study fit this pattern, with *Peromyscus* and *Zapus* fluctuating little from year to year, and *Microtus* populations at the Kettle Ponds site fluctuating greatly (populations were three times larger in 1997 than in 1998, and only one individual was captured in 1999). Overall, *Microtus* is much more abundant at the Kettle Ponds site than at the Bellview site, so there is the potential for *Nicrophorus* populations to fluctuate much more at the Kettle Ponds than at the Bellview site if they track rodent abundance. The *N. investigator* census data (Fig. 2) support this hypothesis, though population data from more sites with and without fluctuating populations of *Microtus* would be necessary to confirm it.

Despite the correlation between small mammal and beetle populations, there are still many unknowns. In particular, this study assumes that rodent mortality rates are equivalent at different sites. There is also no good measure of the proportion of rodent deaths that lead to useable carcasses. For example, a rodent may be consumed immediately by a predator, be eaten by a vertebrate scavenger, die deep in its burrow, or be consumed by other carrion eaters such as flies, ants, or even other carrion beetles (Johnson, 1975; McKinnery, 1978; Scott *et al*., 1987; Trumbo, 1990a; Trumbo & Fiore, 1994; Smith & Heese, 1995) and thus not be available to *Nicrophorus*. The entire carrion-utilising community must be studied in greater detail to determine the flow of energy through the different species in the food web.

It is possible to attack the problem from the other direction, i.e. from the adult beetle population. For example, if the estimated population of *Nicrophorus* at the Kettle Ponds site in 1997 ($N = 3000$) is taken, drawn from an area of 300 hectares (based on a dispersal distance of 1 km), the average brood size is determined ($N = 10$; R. Smith, unpublished), and over-winter mortality is estimated (30%, R. Smith, unpublished), it can be calculated that a minimum of 429 rodents must have been available to produce the beetles captured. Assuming that these rodents died over the same 300 ha over which the beetles were found, this equates to just over 1.43 dead rodents per hectare. This is not an unreasonable number, given that average densities of small rodents were estimated at 50–100 per hectare. Thus, only 1–2% of the available rodents would support the observed populations of *Nicrophorus*.

There has been little speculation on the causes of death of small rodents that would leave them available to *Nicrophorus*, but death may result from respiratory diseases, parasites, exposure, predators, or vehicle injuries. There is anecdotal evidence of beetles locating carcasses at caches made by foxes and weasels, however the extent of this behavior is unknown. The great difficulty of determining or even estimating causes of small mammal mortality, and specifically mortality leading to accessible carcasses, limits a full understanding of burying beetle population dynamics.

A number of studies has described relative abundances of *Nicrophorus* in various habitats (Anderson, 1981; Beninger & Peck, 1992; Creighton *et al*., 1993; Sikes, 1996). Holloway and Schnell (1997) concluded, and this study concurs, that it is more profitable to focus on variations in small vertebrate availability across habitats than on specific habitat types. Soil types and microclimatic effects cannot, however, be ignored as important features influencing reproductive success in specific habitats such as bogs, forests, and deserts. One should also caution against using census data from baited traps as measures of habitat value, as earlier studies (Smith & Heese, 1995) found that *N. investigator* can be captured at carcasses and in baited traps in a wider variety of habitats than those in which it can reproduce successfully.

Although rodent abundance and species composition are likely to influence *Nicrophorus* abundance, competition may also play a role in some communities (Anderson, 1981; Wilson *et al*., 1984; Trumbo, 1990a; Beninger & Peck, 1992). At the Kettle Ponds and Bellview study sites, it is fortunate that only two species of *Nicrophorus* occur, and one, *N. defodiens*, is captured at very low density (R. Smith and S. Richmond, in prep.). Thus, resource partitioning is unlikely to explain the observed pattern of abundance between sites. In fact, abundance of *N. investigator* is lowest at the site in which *N. defodiens* occurs only incidentally. Vertebrate scavengers, ants, and flies may also reduce the availability of carcass resources to *Nicrophorus*, though in field studies they bury nearly 70% of suitable carcasses (Fig. 1; R. Smith, unpublished).

The results of this study indicate that *N. investigator* can utilise the full range of available native small rodents for reproduction, and that local variations in *Nicrophorus* population abundance correlate with small rodent populations, with a 1-year time lag. To understand *Nicrophorus* population dynamics fully, further studies of temporal and spatial variations in breeding carcass availability, microclimate, and biotic interactions among members of the carrion-utilising community are warranted.

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