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Reproductive Success, Phenology and Biogeography of Burying Beetles (Silphidae, Nicrophorus)

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ABSTRACT.—Burying beetles locate and bury small vertebrate carcasses which they form into brood balls for their young. The ability of burying beetles to outcompete vertebrate scavengers and other carrion-feeding invertebrates for carcasses was investigated by placing dead mice on the forest floor in the North Carolina piedmont. From May to September (1984–1985), beetles discovered only about 25% of carcasses on the 1st night. During midsummer of 1984, less than one-half of the carcasses that beetles managed to bury produced broods. Although three species of burying beetles (*Nicrophorus orbicollis* Say, *N. tomentosus* Weber and *N. pustulatus* Herschel) were caught in pitfall traps baited with a large quantity of carrion, only the first two were active on mouse carcasses. Compared with earlier studies in northern habitats of North America, burying beetles are less abundant, less diverse and not as successful in southeastern woodlands. Temperature-dependent competition is hypothesized to be an important determinant of burying beetle success.

INTRODUCTION

Burying beetles (Silphidae, *Nicrophorus* Fabricius) have a number of adaptations which allow them to compete for small carcasses in a diverse carrion-feeding community that includes congeners, other insects and vertebrate scavengers. Fabre (1919) investigated burying behavior which sometimes permits beetles to pre-empt carcasses before competitors become well-established and the carcass is depleted. Pukowski (1933) detailed how a male-female pair contributes to the rapid development of larvae by modifying the carcass and regurgitating liquified carrion. Springett (1968) and Wilson and Knollenberg (1987) demonstrated that phoretic mites (*Poecilochirus* Vitzthum) of burying beetles destroy carrion fly eggs which have been oviposited on the carcass prior to the arrival of beetles. Although burying beetles recently have been the subject of diverse studies in behavioral ecology (Wilson *et al.*, 1984; Scott and Traniello, 1987; Bartlett, 1988; Müller and Eggert, 1989; Trumbo, 1990; and references therein), large-scale studies of the ecology and life history of burying beetles in North America have been concentrated in northern habitats (Leech, 1934; Milne and Milne, 1944, 1976; Schubeck, 1969; Schubeck *et al.*, 1981; Anderson, 1982; Schubeck and Schleppnik, 1984; Wilson and Fudge, 1984; Scott *et al.*, 1987).

The purpose of this study was to examine burying beetle ecology in southeastern woodlands of North America. Information on abundance, phenology, sex ratio, sexual dimor-

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phism, species diversity and reproductive success was collected by using pitfall traps, rearing broods in the laboratory, and studying beetle activity on single mouse carcasses in the field. The methods of the study, in particular the use of carcasses randomly placed on grid points, was modeled after Wilson *et al.* (1984) so that geographical differences could be compared directly.

MATERIALS AND METHODS

Single mouse carcasses.—The study was conducted in two oak-hickory woodlands of mixed composition in the North Carolina piedmont: Mason Farm Biological Reserve (MFBR), Orange County, and Duke Forest (DF), Durham County. Two grids were established at MFBR (#1, 325 m × 200 m and #2, 275 m × 175 m) and one in DF (150 m × 225 m) to determine the ability of burying beetles to discover and exploit mouse carcasses as a breeding resource.

Mice (25–40 g) were killed with CO_2, frozen until needed and thawed to room temperature prior to being used in experiments. Carcasses were placed randomly at grid points between 10 A.M. and 12 noon at a maximum density of one undiscovered mouse carcass/8000 m^2 (a maximum of eight for MFBR #1, six for MFBR #2 and four for DF). A 1-m length of dental floss was tied to the hindleg of the mouse to help locate the carcass after burial. Carcasses were checked each morning and classified as discovered by burying beetles, discovered by vertebrate scavengers (removed from the site) or undiscovered. Carcasses that were discovered were replaced the following morning with new mice placed randomly at new grid points. During 1984 and 1985, a total of 263 carcasses were placed on the three grids. The initial study was run from 6 June to 22 August in 1984. Because it became clear that burying beetles in North Carolina are reproductively active in spring and autumn, carcasses were placed in the field from 10 May to 28 May and from 2 October to 27 October in 1985.

Mice discovered by burying beetles in May, June and October were exhumed the next morning and the species, number, sex and size (length from the tip of the mandibles to the edge of the elytra) of adult beetles were recorded. During July and August, when it was expected that beetles would have the most difficulty rearing a brood because of competition with blowflies (Wardle, 1930; Kneidel, 1984a), carcasses were exhumed 10 days after discovery. At this time the species of adult beetles and the presence or absence of larvae were noted. Because burying beetle activity varied little among the three grids, results were combined for analysis.

A different methodology was used to study reproductive success on small carcasses in the Sandhills Gamelands, 5 km S of Aberdeen, North Carolina [an open-canopy long-leaf pine (*Pinus palustris* Miller) forest with sandy soil]. Ten mouse carcasses were placed at randomly selected points between 10 A.M. and 12 noon on 25 July, 2, 9 and 26 August and 4 September on a 400 m × 200 m grid. Mice were examined 7 days after each date and the presence of beetles and the condition of the carcasses were recorded.

Pitfall trapping.—From April to November, 1983 and 1984, pitfall traps were maintained in MFBR, DF and W. B. Umstead State Park, Wake County (WBU). During 12 trapping periods (12–26 days each), traps were baited with 150–250 g of carrion (*Rattus rattus*) and covered with rain shields. The traps were located at least 0.5 km from experimental grids. In 1983, only the species and number of adult burying beetles were recorded. Species, number, sex, size and whether or not the beetle was injured (severance of legs or antennae) were recorded in 1984.

From 2 July to 21 July, 1984, four pitfall traps were maintained in an open field at MFBR and baited with 150–250 g of carrion (*Rattus rattus*). In addition, five pitfall traps baited with 150–250 g of carrion were maintained from 22 June to 9 July, 1986, at The

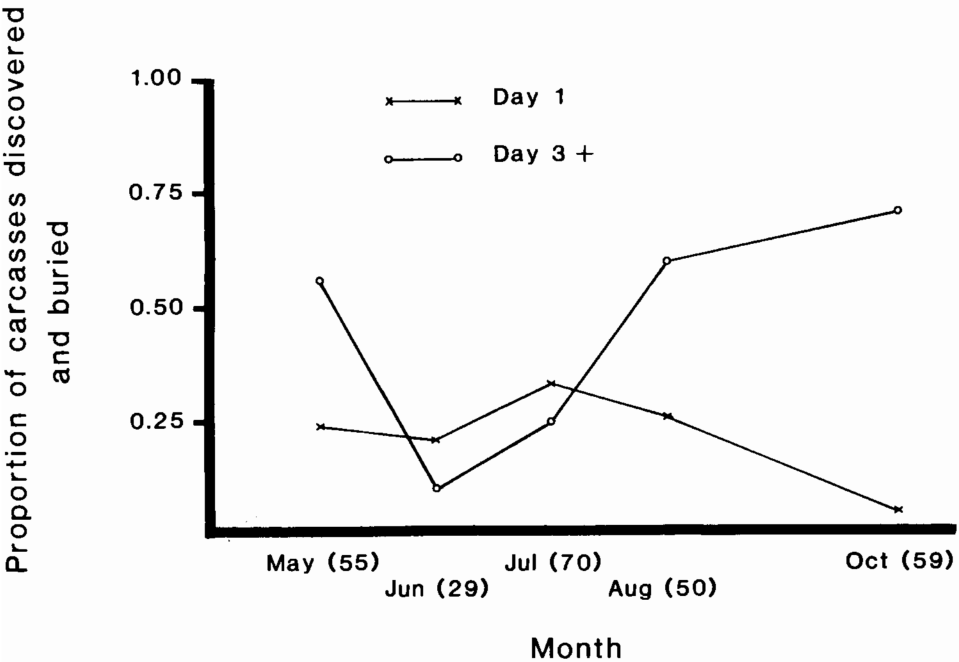

FIG. 1.—Seasonal pattern of the proportion of carcasses that were discovered and buried by burying beetles on Day 1 and the proportion of carcasses that were still available on Day 3 that were eventually buried by beetles. The original numbers of carcasses placed on the grids are shown in parentheses following the month

University of Michigan Biological Station (Douglas Lake) in birch-beech-aspen secondary woodlands. Species, number, sex, size and whether or not the adult beetles were injured were recorded.

Laboratory rearing experiments.—Thirty-eight pairs of *Nicrophorus orbicollis* Say were placed in plastic containers filled with soil and were provided with mouse carcasses (20–40 g). After larvae dispersed from the carcass they were transferred to containers with fresh soil and their sex was determined upon emergence as adults.

RESULTS

Single mouse carcasses.—At the two North Carolina piedmont sites (total of three grids), the proportion of carcasses that were discovered and buried by burying beetles on Day 1 remained between 20% and 32% from May–August (Fig. 1). *Nicrophorus orbicollis* was the only species of burying beetle that came to single mice in woodland habitats during this period. Even though both *N. orbicollis* and *N. tomentosus* Weber were active in October, the proportion of carcasses that were found and buried within 24 h fell with the onset of cooler weather ($\chi^2 = 21.59$, df = 1, $P < 0.001$). *Nicrophorus tomentosus* was the predominant species on small carcasses at this time (20/24 discoveries).

The opposite seasonal trend was observed for carcasses that remained available on Day 3 (not discovered by beetles or vertebrate scavengers within 48 h). During the two warmest months (June and July), carcasses exposed to invertebrate competitors for 2 full days were less likely to be buried by beetles compared to the beginning or end of the breeding season ($\chi^2 = 42.56$, df = 1, $P < 0.001$; Fig. 1).

TABLE 1.—The proportion of available mouse carcasses (n) discovered and displaced by burying beetles and vertebrates on Day 1, Day 2 and Day 3+. Carcasses that were never displaced from the site eventually were consumed by other insects

	n	Beetles	Vertebrate scavengers	Not displaced
Day 1	263	0.22	0.11	0.67
Day 2	176	0.26	0.22	0.52
Day 3+	92	0.51	0.18	0.31

For the entire study, only 33% of carcasses were discovered by either burying beetles or vertebrate scavengers within 24 h (Table 1). The percentage of available carcasses discovered on Day 2 increased to 48%, perhaps reflecting the greater attractiveness of carrion exposed for a longer period but not badly decomposed. Insects other than burying beetles also were active on carcasses. Within 24 h, ants were active on over 95%, and carrion flies had oviposited large numbers of eggs on the majority of carcasses.

During July and August, burying beetles (*Nicrophorus orbicollis*) discovered and buried 76 of the 120 carcasses available. After 10 days, 32% of these 76 carcasses had been scavenged by vertebrates, 26% were abandoned and 42% produced broods.

In the Sandhills region of North Carolina, burying beetles did not bury or reproduce on any carcasses during late summer. Of 50 carcasses, 29 were completely reduced to hair and bone on the spot where they were placed, and 21 were removed by vertebrate scavengers. No beetles were found around single mouse carcasses.

Pitfall trapping.—*Nicrophorus orbicollis* was the most frequently caught burying beetle in pitfall traps at MFBR, DF and WBU in 1983 and 1984 (Fig. 2). At all three sites, *N. tomentosus* was caught more frequently than *N. orbicollis* only during the months of October and November. Relative to *N. orbicollis,* a greater proportion of *N. tomentosus* was trapped in open fields than in woodlands in July 1984 at MFBR ($\chi^2 = 30.05$, df = 1, $P < 0.001$). Preliminary attempts to monitor activity on small carrion in open fields at MFBR during midsummer were abandoned because burying beetles did not displace or bury a single mouse carcass (n = 15).

In 1984, females of *Nicrophorus orbicollis* were caught more frequently than males in pitfall traps ($P < 0.05$, binomial test; Table 2). I obtained a similar result when trapping *N. orbicollis* at The University of Michigan Biological Station (sex ratio = 0.71, n = 427,

TABLE 2.—Number of beetles caught in pitfall traps in 1983 and number, sex ratio and body length of beetles trapped in 1984. N.o., N.p. and N.t. refer to *Nicrophorus orbicollis, N. pustulatus* and *N. tomentosus*, respectively

	Species		
	N.o.	N.p.	N.t.
Number trapped:			
1983	578	45	110
1984	383	27	104
Sex ratio (male : female)	0.80	1.08	1.21
Mean (±SD) body length of males (mm)	19.9	17.3	16.7
	(2.4)	(2.1)	(1.6)
Mean (±SD) body length of females (mm)	19.7	18.2	16.2
	(2.0)	(1.8)	(1.3)

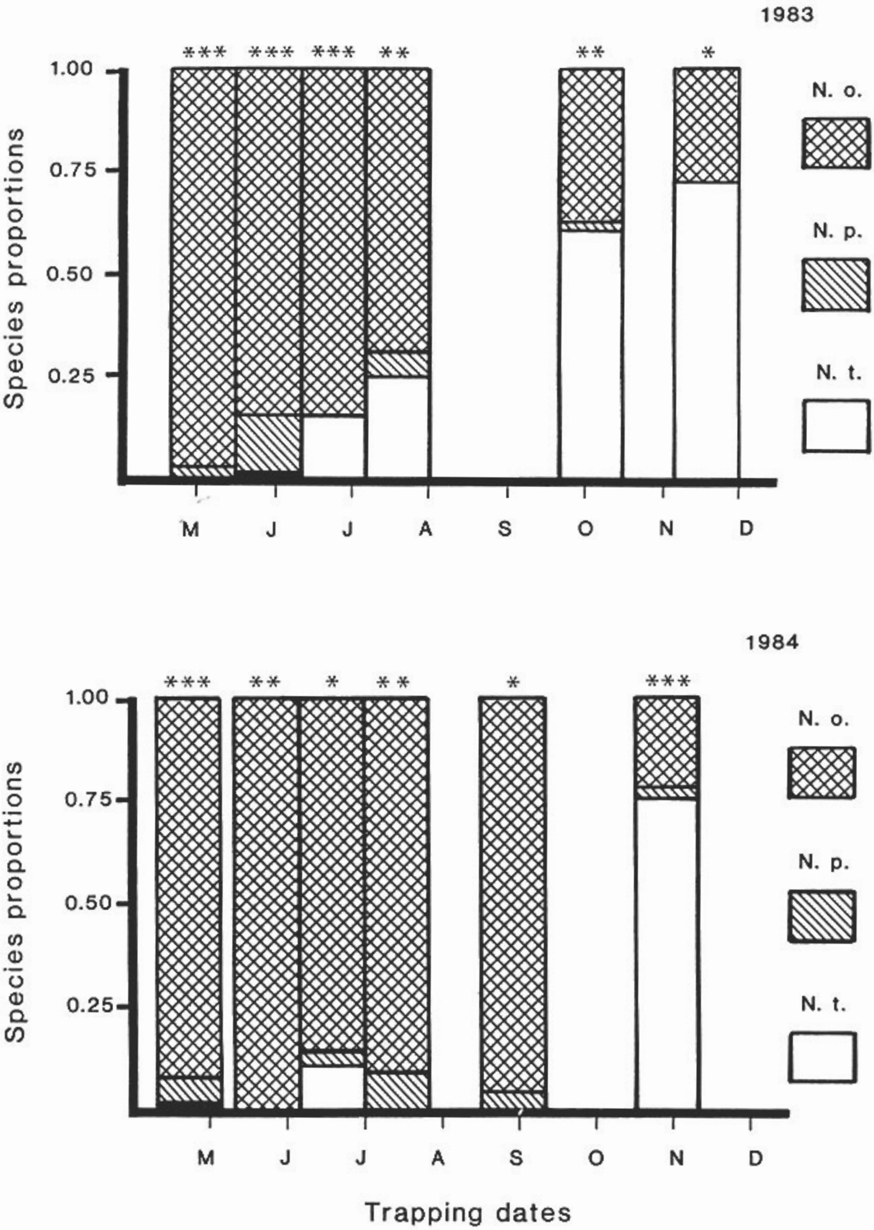

FIG. 2.—The proportion of *Nicrophorus* caught in pitfall traps placed in woodlands during 1983 and 1984 that were *N. orbicollis, N. pustulatus* or *N. tomentosus*. Mid-points of each bar graph approximate the mid-point of the trapping period. Tick marks for dates represent the first of the month. Sample sizes were as follows: 30–50 (*), 51–100 (**) and 101+ (***)

TABLE 3.—Mean (±SD) adult length of injured and uninjured individuals for four species of burying beetles collected in pitfall traps

	Site[a]	n	Percent injured	Length of injured adults (mm)	Length of uninjured adults (mm)	P[b]
N. defodiens	UMBS	277	19.9	13.1(1.3)	13.5 (1.1)	<0.05
N. tomentosus	MFBR	104	4.8	15.2 (1.6)	16.6 (1.5)	<0.05
N. sayi	UMBS	282	29.4	19.9 (2.5)	19.8 (2.3)	>0.20
N. orbicollis	MFBR	175	12.0	18.9 (1.5)	20.0 (2.1)	<0.05
N. orbicollis	UMBS	338	18.9	19.8 (1.9)	20.2 (2.0)	=0.11

[a] UMBS = University of Michigan Biological Station, 1986; MFBR = Mason Farm Biological Reserve, 1984

[b] Mann-Whitney U tests, comparison of body length of injured and uninjured beetles

$P < 0.001$, binomial test). There was no evidence of a skew in the sex ratio at emergence while rearing *N. orbicollis* in the laboratory (177 males/196 females in 38 broods, $P > 0.20$, binomial test). The sex ratio of *N. tomentosus* and *N. pustulatus* caught in pitfall traps in North Carolina did not differ significantly from 1:1 (Table 2; $P > 0.20$).

There were no significant differences between the sexes in body length (Mann-Whitney U tests, all $P > 0.05$; Table 2) or in the percentage of beetles injured (2×2 contingency test, all $P > 0.05$; Table 3) for all species sampled. In three of four species examined, there was evidence that injured individuals were smaller in size than noninjured individuals (Table 3; populations of *Nicrophorus sayi, N. defodiens* and *N. orbicollis* at UMBS were included in the analysis). Body length of both males and females of *N. orbicollis* collected in North Carolina in 1984 did not differ when individuals collected in pitfall traps were compared to those found on single mice ($P > 0.20$, Mann-Whitney U test).

DISCUSSION

From its emergence in April until early September, *Nicrophorus orbicollis* is clearly the dominant burying beetle on small carcasses in piedmont woodlands of North Carolina. Comparison of activity at pitfall traps and at single mouse carcasses reveals that although *N. tomentosus* is active by mid-June in traps, it was not found on small carcasses until September. Wilson *et al.* (1984) made a similar observation in Michigan and suggested that *N. tomentosus* emerges in summer but does not reproduce immediately because of competition with its larger competitors. Because of the longer active season of *N. orbicollis* in North Carolina woodlands, *N. tomentosus* perhaps postpones the onset of reproduction until mid-September while in Michigan it can begin breeding in early August.

Nicrophorus pustulatus Herschel were never found on single mouse carcasses, as was also noted by Wilson and Fudge (1984). *Nicrophorus pustulatus* readily breeds on large carcasses (>100 g) in the laboratory and probably specializes on this resource in the field.

Besides burying beetles, carrion flies and ants constituted the majority of insect competitors for carrion that were active during the summer in piedmont woodlands of North Carolina. Wardle (1930) demonstrated the extreme sensitivity of calliphorid egg and larval development to temperature and humidity. Increased carrion fly activity and faster growth at higher temperatures have also been reported in the field (Payne, 1965; Nabaglo, 1973). Rapid development of carrion fly larvae presents considerable problems for nocturnal burying beetles such as *Nicrophorus orbicollis* since carrion flies often discover a fresh carcass within

TABLE 4.—Comparison of burying beetle richness, abundance, activity and reproductive success in North Carolina piedmont (NCP), Kellogg Biological Station (KBS) and The University of Michigan Biological Station (UMBS). Data from KBS and UMBS are derived from Wilson and Fudge (1984) and Anderson and Peck (1985)

	Study site		
	NCP	KBS	UMBS
Number of species	4	6	7
Number of carcasses placed in study	263	330	778
Proportion of unscavenged carcasses found by beetles on:			
Day 1	0.24	0.68	0.91[a]
Day 2	0.33	0.61	0.87[a]
Mean number of adults on the carcass the morning after discovery (*N. orbicollis*)	1.60	2.04	2.75[b]
Proportion of discovered carcasses that produced a brood (*N. orbicollis*)	0.42	0.89	0.89[c]

[a] $P < 0.01$, 2×3 contingency test
[b] $P < 0.01$, Mann-Whitney U test
[c] $P < 0.001$, 2×2 contingency test

an hour and might have a considerable headstart in exploiting the resource (Nabaglo, 1973; Putnam, 1983). At warmer temperatures, carrion flies and ants can render a carcass unsuitable for burying beetles before beetles discover the resource. The present study and previous reports (Milne and Milne, 1944; Putnam, 1978; Easton, 1979) note that burying beetles sometimes abandon carcasses that are heavily exploited by other invertebrates. This occurs even though beetles carry mutualistic phoretic mites (*Poecilochirus* Vitzthum) which roam over the surface of the carcass and destroy carrion fly eggs. These mites are much less effective if carrion fly eggs have hatched prior to the arrival of the beetles on the carcass (Springett, 1968; Wilson, 1983; Wilson and Knollenberg, 1987), a situation that occurs more readily at warmer temperatures. Carrion flies were very important in the decomposition of small vertebrate carcasses in North Carolina (Kneidel, 1983, 1984a, b) but appear to be less important in northern Michigan (Wilson *et al.*, 1984).

In this study, many carcasses exposed for 2 full days were never buried by burying beetles during the warmest months. It could not be determined if beetles failed to discover these carcasses or if carcasses were located and rejected as breeding resources because of heavy exploitation by ants and carrion flies. The ease with which beetles discovered old carcasses in pitfall traps, however, suggests that the second possibility is more likely.

Ants add substantial complexity to carrion-feeding communities because they consume both carrion and dipteran larvae (Fuller, 1934; McKinnery, 1978). Burying beetles apparently experience a decline in reproductive success because of competition with ants in Florida (Scott *et al.*, 1987) and are absent in some tropical habitats where ants are dominant members of the carrion-feeding community (Cornaby, 1974; Janzen, 1983).

The Sandhills habitat in North Carolina was not conducive to burying beetle reproduction in late summer. The open canopy forest might increase surface temperature and speed decomposition, favoring exploitative competitors such as carrion flies and ants which tend to be the first to arrive on carcasses placed in the field during daylight. Burying beetles are certainly present in this habitat; I have trapped beetles in early March and as late as mid-

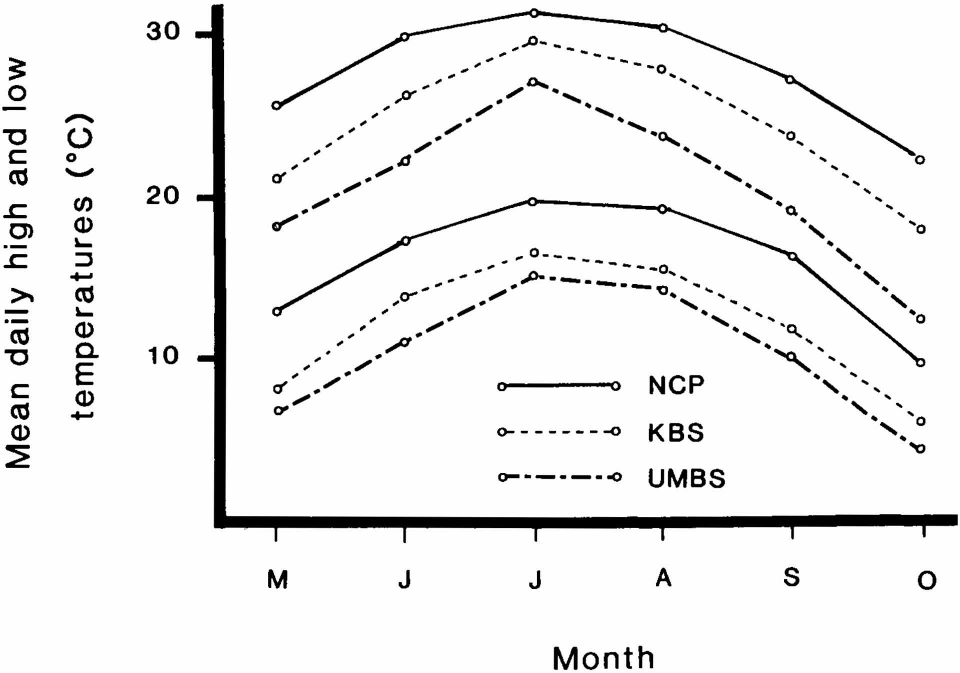

FIG. 3.—Mean daily high and low temperatures for the months of May through October for three habitats. NCP temperatures were from Raleigh-Durham Airport, 1971–1986; KBS temperatures were from Gull Lake Biological Station, 1971–1986; and UMBS temperatures were supplied by B. Vande Kopple, 1981–1987

December. Because carcasses were not even moved from placement sites, I concluded that burying beetles did not attempt to reproduce in this locale in late summer.

One aim of this study was to examine phenology and reproductive success of burying beetles in southeastern woodlands of North America and to compare these findings with previous studies in northern habitats, especially with those of Wilson and Fudge (1984) (Table 4). On both Days 1 and 2, burying beetles discover and bury a greater proportion of available carcasses in Michigan than in North Carolina (Table 4). Also, more adults were found near the carcass on the morning of discovery in northern locales. All three means are minimal estimates of the number of adults on a carcass since some individuals undoubtedly discover the carcass and subsequently leave before the investigator arrives.

Beetles in Michigan also produced broods more successfully after they located and buried a carcass (Table 4). This measure of success is not directly comparable among studies since Wilson and Fudge (1984) collected data over an entire breeding season while the present study only measured brood success on carcasses discovered in July and August. Nevertheless, Wilson and Fudge (1984) did not indicate extreme fluctuations in the ability to rear a brood, so it is clear that at least in midsummer, burying beetles in the southeast experience more reproductive failures. Beetles might have more difficulty in North Carolina because the later average time of discovery and warmer temperatures lead to more advanced decomposition of the carcass before nest-building is completed and oviposition by beetles begins.

Mean daily high and low temperatures for the months May through October are 3–8 C higher in the North Carolina piedmont than in Michigan (Fig. 3). The geographical trends noted suggest that burying beetles are more successful in cooler habitats.

The greater success of burying beetles in northern habitats also is reflected by greater species diversity (Table 4). Northern locales support both habitat specialist and habitat generalist species while the Southeast supports only generalists (Anderson, 1982). Perhaps the lower reproductive success of beetles in the Southeast has prevented specialists from maintaining viable populations. As further evidence of the importance of temperature, the two primarily northern species found in North Carolina (*Nicrophorus defodien* Mannerheim and *N. sayi* Laporte) occur only in the mountains at higher elevations (Lumpkin, 1971; pers. collections).

Geographic distributions of *Nicrophorus* on a larger scale also reveal a consistent pattern. Burying beetles were not collected in carrion studies in tropical lowlands of Panama (Arnett, 1946), Costa Rica (Cornaby, 1974), El Salvador (Howden and Peck, 1972), Brazil (Young, 1978; Penny and Arias, 1982) or Borneo (Hanski, 1983). Ants, carrion flies and scarabs were all mentioned as important carrion competitors in these areas. Burying beetles were found at higher elevations in the tropics in Panama (Arnett, 1946), Mexico (Halffter *et al.*, 1983), El Salvador (Howden and Peck, 1972) and Borneo (Hanski, 1983). An extensive examination of collections by Peck and Anderson (1985) also suggests larger populations of *Nicrophorus* in montane rather than lowland habitats in the tropics. In addition, burying beetles appear to be more abundant at higher rather than lower elevations in the American Southwest (McKinnery, 1978).

Although temperature is likely to be important in distributions of burying beetles, historical factors also must play a role. *Nicrophorus* is thought to have originated in temperate Eurasia (Peck and Anderson, 1985). It is a small group of ca. 85 species, all of which use small carcasses in a similar way (with the exception of *N. pustulatus*), and is the sole genus in the Silphidae to have posthatching parental care. The scarabs, on the other hand, are a morphologically and behaviorally diverse group of beetles, largely found in the tropics, which successfully pre-empt small carcasses from exploitative competitors in tropical lowlands (Halffter and Matthews, 1966; Hanski, 1987). Studies of competition between scarabs and burying beetles need to be done where both groups actively exploit small carcasses.

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