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Species packing and temperature dependent competition among burying beetles (Silphidae, *Nicrophorus*)

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ABSTRACT. 1. Burying beetles are carrion feeders that specialize on small carcasses. We investigated interactions among congeners at two sites in Michigan, U.S.A., that differ in both number and relative proportion of species.

2. Intra- and interspecific competition for carcasses is intense. The majority of carcasses are found within 24 h of their placement.

3. Competition between *N.orbicollis* and *N.defodiens* is temperature dependent. *N.orbicollis* can displace *N.defodiens* on single carcasses, but requires warm temperatures to find the carcasses. Cool weather therefore serves as a refuge for *N.defodiens*.

4. The southern edge of *N.defodien's* geographical range is probably determined by competition with *N.orbicollis*.

5. *N.sayi* and *N.tomentosus* are spring and autumn breeders respectively, and rarely interact with each other or the other two species. Nevertheless, interspecific competition is the most likely evolutionary force leading to seasonal segregation.

Key words. Burying beetle, *Nicrophorus*, Silphidae, competition, species packing, geographical distributions, temperature.

Introduction

Interspecific competition is one of ecology's most venerable topics, but its prevalence in nature remains controversial (Connell, 1983; Schoener, 1983; Wiens, 1977). Most authors agree that competition will be important for species whose densities are limited primarily by the availability of resources. The disagreement seems to centre on the extent to which species are limited by resources, as opposed to predators, climate, or other forms of disturbance.

This paper reports on mechanisms of coexistence in burying beetles (Silphidae, *Nicrophorus*). These are carrion feeders that specialize on small carcasses, such as dead rodents, which they bury in the ground to raise their brood upon. A single carcass is often found by several beetles, but it is eventually monopolized by a single pair. As we will show, burying beetles are sufficiently numerous at our study sites for most carcasses to be discovered soon after they are made available. It is therefore reasonable to expect competition to operate among these insects. The specific mechanisms that allow coexistence of *Nicrophorus* species within a single habitat involve both seasonality and temperature. Finally, the same mechanisms that explain coexistence within a single habitat can be extended to explain aspects of geographical distributions.

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Methods

The study was conducted from 1980 to 1983 at two localities in Michigan, U.S.A. The University of Michigan Biological Station (UMBS) in Pellston (lat. 45° 34′), and Michigan State University's Kellogg Biological Station (KBS) in Hickory Corner (lat. 42°34′), 315 km south of UMBS.

Pitfall trapping. Beetles were collected in hanging pitfall traps consisting of a 1 × 1 m wooden platform with a 15 cm diameter hole cut in the centre, which lead into a tin can held under the platform by an elastic band. A roof over the hole protected the can from rain. With carrion placed in the cans, these traps were suspended from trees a few feet above the ground. Beetles attracted to the bait landed on the platform and entered the cans as they would if the cans had been buried flush with the surface of the ground. The hanging traps were used because they protected the bait from marauding vertebrates, and because they were easier to set up, check, and take down. Pilot experiments demonstrated that they captured the same proportions of *Nicrophorus* species as traps buried in the ground (Wilson, unpublished). For bait we used approximately 50 g of smelt (*Osmerus mordax* Mitchill) that had been allowed to rot in the sun for 2 days prior to use. The traps were used to investigate habitat affinities, phenology and diurnal activity. At UMBS, eight sites representing a diversity of habitats were sampled during three time periods, from early July to late August 1979. A similar trapping regime took place at KBS from 1 June to 15 September 1980. Diurnal activity patterns were monitored at UMBS by visiting pitfall traps at 17, 19, 21, 23 and 07 hours from 5 to 21 July 1979. The results were extended on 26 June 1981 by continuously patrolling a transect of eight traps spaced 100 m apart for a single night. Pitfall trapping also accompanied the grid and transect studies described below.

Grid study. At KBS in 1980 and UMBS in 1981, flags were placed in deciduous forest at 20 m intervals to form large grids. Dead mice (*Mus musculus* L.) were placed on random points of the grid, at a density of one mouse/8000 m^2 (five mice on a 5 × 20 grid at KBS; ten mice on a 10 × 20 grid at UMBS). The mice were checked daily for discovery by burying beetles or vertebrates. For every mouse discovered, another was randomly placed on the grid. Half of the mice discovered by burying beetles were inspected (and removed) immediately; the other half were collected after 10 days, when the broods were nearing their prepupal stage. In this fashion, the fate of 330 mice at KBS and 802 at UMBS was followed. Detailed methods for this study and results for intraspecific interactions are presented in a companion paper (Wilson & Fudge, 1984). In terms of interspecific interactions, the grid studies provided information on the rate that mice were discovered by burying beetles, and which species were successful at reproducing upon them.

Transect studies. The 1980–81 data generated questions whose answers required a larger sample of mice placed out on a single night. Therefore, 1982 and 1983 experiments at UMBS consisted of twenty to thirty mice spaced 20 m apart in single transects. The mice were placed in the morning and collected the following morning. In nine cases we also inspected the mice with minimal disturbance during the evening. In eight cases two size classes of mice (15–20 g and 35–40 g) were placed in alternating sequence. Finally, on 15 June 1983, sixty pairs of marked *Nicrophorus defodiens* were placed on mice in the field, using methods described in Wilson (1983). The mice were protected from discovery from free-flying burying beetles for a single night, and then inspected later to determine the proportion of mice retained by beetles that initially buried them.

Weather data and geographical distribution. Temperature data were obtained from biological station records. Geographical distributions were obtained from our own pitfall trapping, and from unpublished data kindly provided by R. S. Anderson, S. B. Peck and J. Haarstad.

The results are presented for UMBS and KBS separately.

UMBS Results

Habitat associations. Table 1 lists the five *Nicrophorus* species found at UMBS, their body weights and relative proportions,

TABLE 1. Five species of *Nicrophorus*, dry weights, and relative proportion found at the University of Michigan Biological Station (UMBS) and the Kellogg Biological Station (KBS).

Species	Abbreviation in other tables and figures	Dry wt (g)	Relative proportions	
			UMBS	KBS
N.defodiens Mannerheim	N.d.	0.044	0.28	0
N.tomentosus Weber	N.t.	0.072	0.29	0.19
N.pustulatus Herschel	N.p.	0.086	0.01	0.01
N.orbicollis Say	N.o.	0.099	0.31	0.78
N.sayi LaPorte	N.s.	0.099	0.11	0.02

TABLE 2. Relative proportion of *Nicrophorus* species found in eight habitats that vary in moisture, understory and forest type. Sampling periods were 3–6 July, 27 July–3 August and 17–23 August 1979. (Species – names as Table 1.)

Site	Moisture	Understory	Habitat	N.o.	N.t.	N.d.	N.s.	N.p.	Total
1	Moderate	Open	Beech/maple	0.53	0.28	0.11	0.07	0.01	237
2	Moderate	Moderate	Beech/maple/pine	0.35	0.29	0.23	0.12	0.01	280
3	Wet	Closed	Beech/maple	0.38	0.15	0.41	0.05	0.01	240
4	Wet	Closed	Cedar/hemlock	0.18	0.21	0.53	0.08	0.01	170
5	Moderate	Open	White pine	0.18	0.20	0.32	0.31	0.01	358
6	Moderate	Moderate	Aspen	0.17	0.40	0.37	0.06	0.01	615
7	Dry	Open	Meadow	0.41	0.52	0.02	0.03	0.02	117
8	Dry	Open	Meadow	0.39	0.44	0	0.14	0.03	36
Grand total				0.31	0.29	0.28	0.11	0.0	2053

averaged over all habitats and all time periods. A sixth species, *N.vespilloides*, can also be collected in nearby bogs and marshes (Anderson, 1982; Wilson, unpublished data). It is a true habitat specialist and will not be considered further. *N.pustulatus* was rare in pitfall traps and never came to mice. Its breeding biology is under investigation and will not be considered further here.

Table 2 shows the relative proportions of the five species for eight habitats. All species were collected in all habitats sampled, although their relative proportions differed. The most striking pattern is the scarcity of *N.defodiens* from meadow habitats (sites 7 and 8). Other differences are more difficult to interpret, and in no case can a species be identified with a given habitat, as can *N.vespilloides*. Given the inherent variability of pitfall traps as a sampling device, the overall picture is one of coexistence within each habitat.

Diurnal activity. Fig. 1A presents the results of the 1979 study, and shows that three of the four species differ significantly in their daily activity. *N.tomentosus* is well known to be a day flier, and in fact mimics a bumble bee in flight. The sharp crepuscular peak of *N.defodiens* has not previously been recognized. To confirm it, a transect of eight pitfall traps was patrolled continuously for a single night on 26 June 1981 (prior to the emergence of *N.tomentosus*), and the beetles removed as they arrived. The results are shown in Fig. 1B, and demonstrate that there is almost no overlap between the flight periods of *N.defodiens* and the two nocturnal species.

The differences shown in Fig. 1 are undoubtedly important, but they are also somewhat misleading. The problem is that after a carcass is found it must be dragged to a suitable place and buried. This process takes about 24 h, during which the carcass may be discovered by species that fly at other times of the day. As we shall show, the matter is not as simple as *N.tomentosus* getting the day's supply of carcasses, *N.defodiens* the evening's supply, and the other two species the night's supply.

Carcass size. Within a range of 15–40 g, carcass size has no effect on the species of *Nicrophorus* that discovers it ($\chi_1^2 = 0.17$, n.s.).

Interactions within a single habitat. Competition requires limiting resources. In

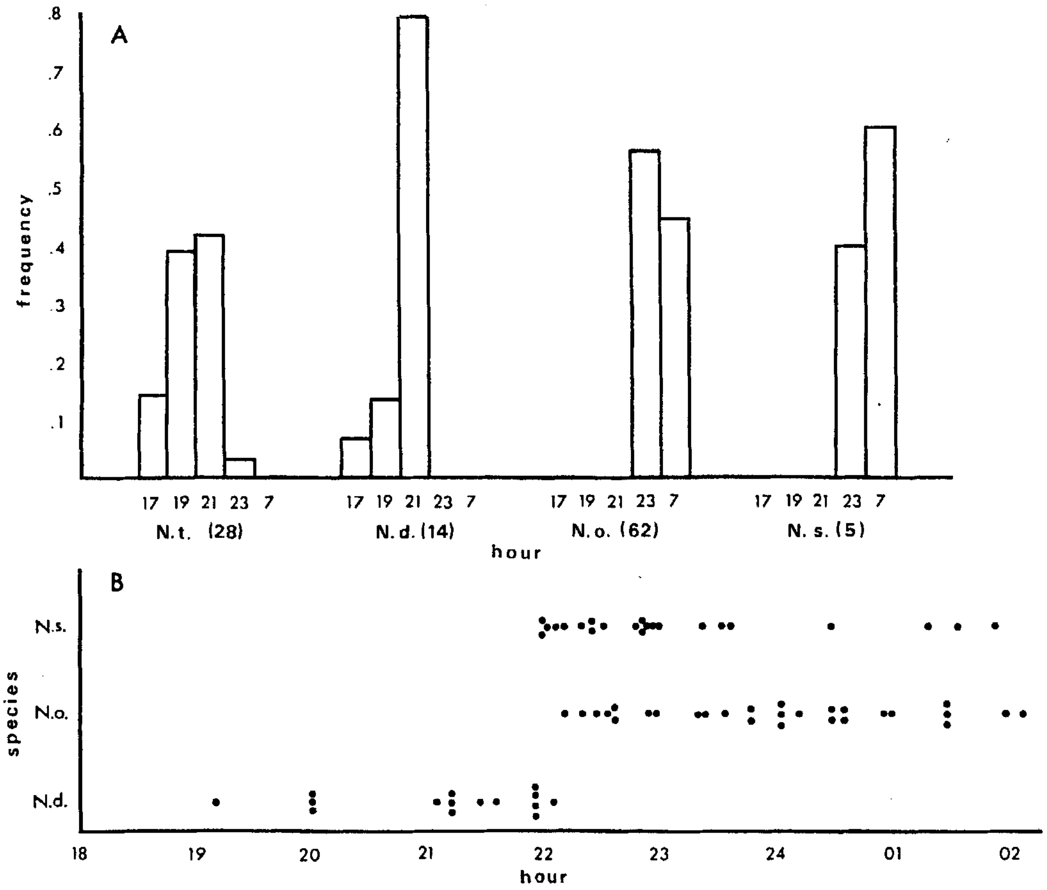

FIG. 1. Diurnal activity of burying beetles. Fig. 1A gives the proportions of beetles captured at 17, 19, 21, 23 and 07 hours from 5 to 21 July 1979. Species abbreviations are as in Table 1, and total number of beetles captured are in parentheses. Fig. 1B shows the number of beetles captured at a transect of eight pitfall traps patrolled continuously for a single night on 26 June 1981. Each point represents a capture.

the UMBS grid study, 94% of the mice were discovered within 24 h, and 95% of the discoverers were burying beetles ($N = 802$ mice). The beetles are therefore very abundant relative to their resource.

Fig. 2(a–c) displays the results of the UMBS grid study. Fig. 2(a) shows the species composition arriving at pitfall traps on five sampling dates. *N.tomentosus* is known to overwinter in the prepupal stage, and does not emerge until July (Anderson, 1982). The other species were present throughout the sampling period.

It is important to recognize that although burying beetles reproduce exclusively on small carcasses, adults also search out large carcasses to feed themselves. The presence of beetles in pitfall traps does not signify that they are reproductively active; they may be newly emerged with immature ovaries, or in reproductive diapause. Indeed, reproductively active beetles may actually ignore the powerful odour of pitfall traps, and confine their search to small carcasses that can be buried (Wilson & Knollenberg, 1984). Pitfall traps are therefore highly biased sampling devices that may underrepresent the breeding portion of the community.

Fig. 2(b) shows the species composition of beetles collected on mice the morning after discovery. Data were combined into 5-day intervals to calculate proportions. A pronounced seasonal pattern emerges, that only partially resembles the pitfall trap data.

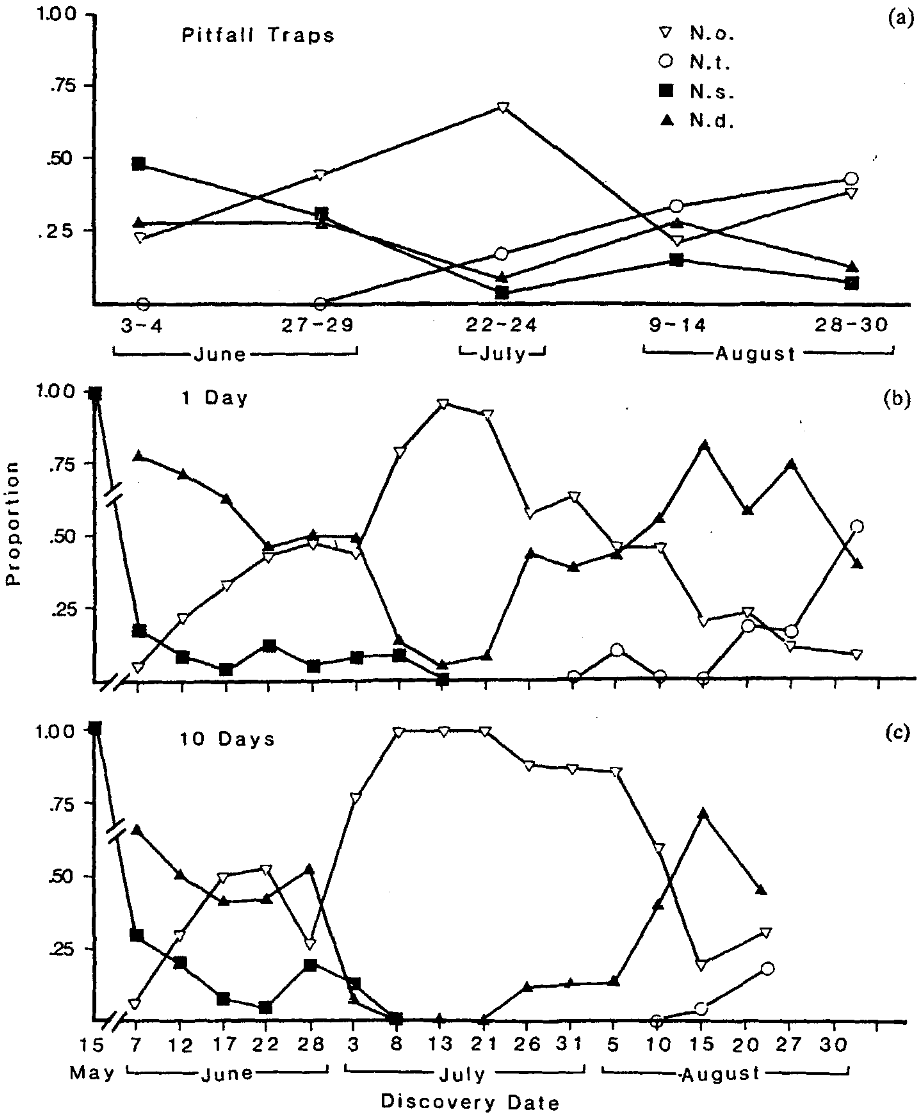

FIG. 2. UMBS 1981 grid study. Fig. 2(a) is the proportion of species captured in baited pitfall traps. Fig. 2(b) is the proportion of species found on mice the morning after discovery. Fig. 2(c) is the proportion of species found on mice 10 days after discovery. See text for further details.

N.sayi is a spring breeder. During an early sampling trip on 15 May, it discovered 100% of the mice ($N = 25$). By the time continuous sampling began on 1 June, *N.sayi* were rarely found on mice, in spite of their continuing presence in pitfall traps. These adults are in reproductive diapause, and will not raise a brood even when provided a mouse in the laboratory or field (unpublished data). *N.tomentosus* is an autumn breeder, and does not successfully obtain mice until several weeks after it appears in pitfall traps (see also Wilson & Knollenberg, 1984). *N.orbicollis* occupies mice during the central portion of the summer, and *N.defodiens*, the smallest species, has a bimodal distribution that appears to fit the spaces between the other three.

Fig. 2(c) shows the species composition of beetles collected with their maturing broods

10 days after discovery. The patterns resemble Fig. 2(b), except that *N.orbicollis* occupies a broader portion of the season, seemingly at the expense of *N.defodiens.*

Competition for single carcasses. Two or more species of *Nicrophorus* were collected on 18% of the mice inspected on the morning after discovery ($N = 358$ mice). Interspecific contests over single mice are therefore fairly common. When beetles are placed on mice in the laboratory, larger individuals drive smaller individuals away, of both the same and different species (Pukowski, 1933; Easton, 1979; J. Haarstad & D. S. Wilson, unpublished data). In the field, the same result can be inferred from the spatial arrangement of beetles around the mice, as shown in Table 3. In almost every case the larger species was next to the mouse, while the smaller species was a short distance away in the leaf litter (peripherally located species are not included in Fig. 2(b); see Wilson & Fudge (1984) for a similar analysis of intraspecific competition). Also notice that the majority of two-species interactions are between *N.orbicollis* and *N.defodiens*, as one would expect from the phenological distributions (Fig. 2b).

Table 3 demonstrates that even though *N.defodiens* has a 'head start' in searching for mice (Fig. 1), those same mice are often rediscovered and appropriated by *N.orbicollis* a few hours later. In addition, *N.defodiens* appears prone to losing its mice throughout the 10-day period of brood development. The x-axis of Fig. 2 represents discovery date; i.e.

TABLE 3. Spatial position of beetles on mice found by two or more species. Central refers to the immediate vicinity of the mouse; peripheral refers to a short distance away in the leaf litter.

	Peripheral			
Central	N.o.	N.t.	N.d.	N.s.
N.o.	—	6	43	3
N.t.	0	—	4	0
N.d.	3	1	—	0
N.s.	4	0	3	—

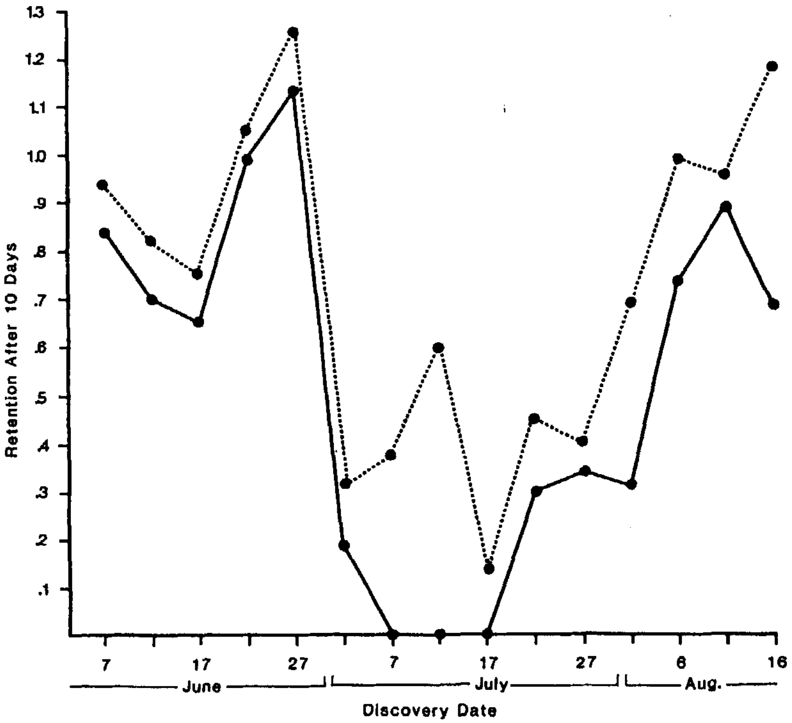

FIG. 3. The ability of *N.defodiens* to retain mice for the 10 days of brood development, relative to the ability of the other species, obtained by dividing the proportion retained on day 10 by the proportion retained on day 1. The solid line does not consider failed broods. The dashed line assumes that *N.defodiens* is more highly represented among the failed broods by a factor of 4.

for any point on the *x*-axis, the mice in Figs. 2(b) and 2(c) were discovered on the same days, so any differences between these two graphs are caused by events during the 10-day interval that separated their collection. The fact that *N.defodiens* is less well represented in Fig. 2(c) signifies that it has a higher failure rate during this period than the other species. This could happen in two ways: (1) The higher failure rate could be caused by outside factors. Of the mice left for 10 days, 13% were robbed by vertebrates, 3% were taken over by fly larvae, and 6% failed for unknown reasons. It is possible that *N.defodiens* is overrepresented in these categories. (2) The higher failure rate could be caused by discovery and takeover by larger burying beetle species. In other words, even if *N.defodiens* remains in possession of the carcass the morning after discovery, it still may not be safe from interspecific competition.

These two factors are explored in more detail in Fig. 3. The ability of *N.defodiens* to keep its mouse for 10 days after discovery, relative to the ability of the other species, can be estimated by dividing the proportion retained on day 10 (Fig. 2c) by the proportion retained on the morning after discovery (Fig. 2b), as shown by the solid line. A value less than one indicates that *N.defodiens* loses a greater proportion of mice than the other species. Notice the striking seasonal trend; *N.defodiens* has a reasonable chance of retaining its mice during the early and late summer, but is almost certain to lose its mice during the midsummer. The broken line is a revised estimate which assumes that *N. defodiens* is more highly represented among the failed broods by a factor of 4. This does not substantially alter the shape of the curve, which remains low during mid summer. Even if all failed broods are attributed to *N.defodiens*, the midsummer gap remains. Thus, *N.defodien*'s inability to raise broods is substantially due to takeovers by other burying beetle species.

The effect of temperature. Our study demonstrates that *N.defodiens* loses in interspecific competition over single mice. Why then can it exist at all, and what accounts for its bimodal distribution? Two possibilities can be discarded immediately: (1) The bimodal distribution does not represent two generations. Wilson & Knollenberg (1984) dissected the ovaries of *N.defodiens* throughout the season and found no evidence for a second generation. Anderson (1982) drew the same conclusion based on the presence of teneral individuals. (2) The bimodal distribution does not represent a single cohort that all successfully find mice during the early summer, spend the middle summer below ground tending their broods, and then successfully find mice for a second brood during the late summer. Because brood development requires only 10–12 days for *N.defodiens*, the duration of the midsummer gap is too long to be explained in this way. Neither can this hypothesis explain why those few *defodiens* that do find mice in midsummer have such a poor chance of keeping them (Fig. 3).

A third possibility involves the effect of temperature on beetle searching ability. Assume that *N.orbicollis* requires a certain minimum temperature to fly, or that ability to detect a carcass is directly proportional to temperature. On warm nights, *N.orbicollis* would find the majority of mice, excluding *N.defodiens*. Cold nights, however, could constitute a 'time refuge' for *N.defodiens* to breed. *N.defodiens* might successfully find mice when *N.orbicollis* cannot because of lower temperature tolerances, or perhaps because it flies during a warmer part of the day. Since cold nights are more frequent in early and late summer, this would account for the bimodal distribution of *N.defodiens* reproductive success.

This hypothesis was tested on the grid study data using an all possible subsets regression analysis (BMDP P-series), relating the proportion of mice found by *N.orbicollis* and on a given day to the temperature at 18, 20, 22, 24 and 02 hours (Table 4, line 1). A significant positive relationship was found; the most predictive temperatures occur at 20 and 22 hours, which are not significantly different from each other. Recall that 22 hours is the start of the *N.orbicollis* activity period.

Physiologically, the ability of *N.defodiens* to find mice presumably is also enhanced by high temperatures. Interference competition by *N.orbicollis*, however, actually causes the proportion of mice found by *N.defodiens* to correlate negatively with temperature (Table 4, line 2).

TABLE 4. All possible subset regression analysis for 1981 and 1982 UMBS data, relating the proportion of mice found by beetles to temperature at 18, 20, 22, 24 and 02 hours. *P* indicates the level of significance. The regression equation indicates the best fit according to BMDP criteria. See text for explanation; t_{20} is temperature at 20 hours etc.

	r^2	*P*	Regression
(1) 1981 *N.orbicollis*	0.28	0.0001	$(0.032)t_{20}-1.82$
(2) 1981 *N.defodiens*	0.19	0.0001	$(-0.027)t_{22}+2.17$
(3) 1982 *N.orbicollis*, all data points	0.57	0.001	$(0.028)t_{20}-1.68$
(4) 1982 *N.orbicollis*, four data points removed	0.74	0.0001	$(0.014)t_{18}+(0.017)t_{24}-1.71$
(5) 1982 *N.defodiens*, all data points	0.39	0.004	$(0.084)t_{22}-(0.091)t_{24}+0.40$

The results of the UMBS grid study can be summarized as follows. (1) *N.sayi* and *N.tomentosus* are spring and autumn breeders respectively, and seldom interact with the other species on mice. (2) In spite of differences in diurnal activity, mice found by *N.defodiens* are often rediscovered a few hours later by *N.orbicollis*. (3) Mice retained by *N.defodiens* for an entire night may still be rediscovered during brood development. (4) Discovery of mice by *N.orbicollis* is positively correlated with temperature. This imposes a negative correlation between temperature and rate of discovery by *N.defodiens*.

Transect study. Although the grid study results were encouraging, they were deficient in at least three respects. First, the grid study was not well suited for exploring the effect of temperature, because at most only five mice were available per day to calculate proportions. With such a small daily sample, even a strong relationship with temperature would yield low r^2 values. More mice needed to be placed on a single night. Second, the figure of 18% almost certainly underestimates the proportion of mice found by two or more species of burying beetles, because losers in competition can easily fly away or crawl outside the radius around the mouse that was inspected the following morning. Mice should be inspected during *N.defodien*'s active period in the evening, and then again the following morning. Third, *N.defodien*'s tendency to lose mice during brood development was only inferred by comparing Fig. 2(b) with 2(c). *N.defodiens* should be placed on mice in the field, protected from rediscovery during the first night, and the followed during brood development.

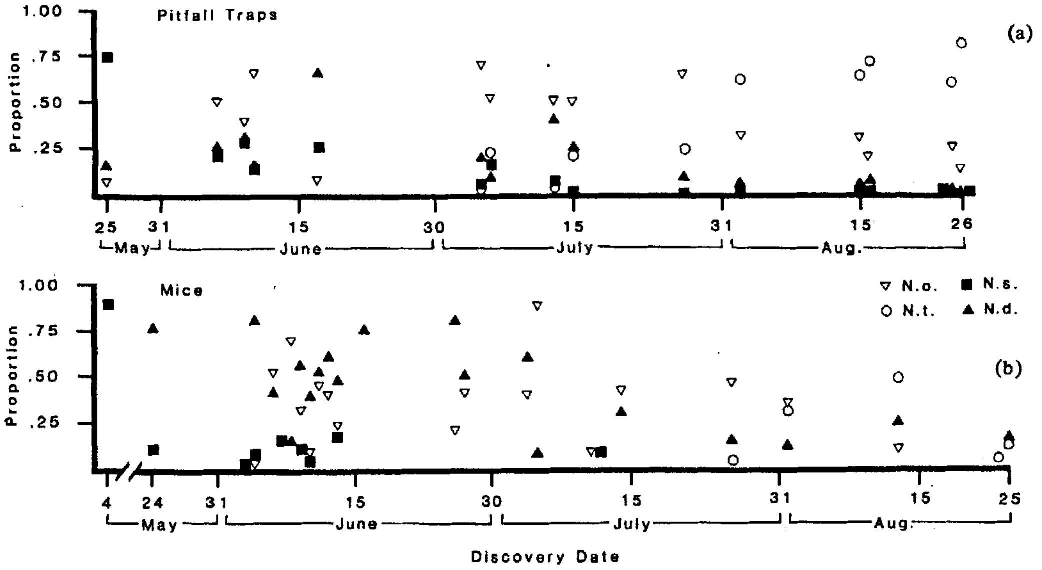

FIG. 4. UMBS 1982 transect study. Fig. 4(a) is the proportion of species captured in baited pitfall traps. Fig. 4(b) is the proportion of species found on mice the morning after discovery.

The transect study was designed to correct these deficiencies. The results are displayed along with matching pitfall trap data in Figs. 4(a) and 4(b). These are analogous to Figs. 2(a) and 2(b) for 1981, except that each point represents a single day, rather than an aggregate of 5 days. The points are not connected in Fig. 4 because they vary so widely over short time periods. Clearly, something is happening on a daily basis that alters the relative ability of *N.orbicollis* and *N.defodiens* to find and secure mice.

Three important differences distinguish 1982 from 1981. First, a higher proportion of mice remained undiscovered after 24 h (35% of 789 mice). Second, the breeding success of *N.defodiens* was not bimodal. In 1982 this species successfully obtained mice even in midsummer. Third, the average temperature was lower and the variance in temperature was higher, resulting in many cold nights, some of which fell during midsummer.

Analysis of the 1982 data required a series of steps, which are displayed in lines 3–5 of Table 4. First, using the entire data set, the proportion of mice discovered by *N.orbicollis* was related to temperature at 18, 20, 22, 24 and 02 hours, as for 1981. A strong positive relationship exists, with 57% of the variance accounted for (Table 4, line 3). The most predictive times are 20 and 22 hours, as for 1981, and neither the slopes nor the intercepts are significantly different for the two years. Thus, although Figs. 2(b) and 4(b) look very different, they both seem to follow the same relationship with temperature.

Next, four data points were removed from the analysis, based on biological considerations independent of temperature. These were the first sampling date, before *N.orbicollis* emerged, and the last three sampling dates, after most *N.orbicollis* had entered reproductive diapause in preparation for winter. The decision to remove these points was made before analysis began, and their omission increased the amount of variance accounted for to 74%. Furthermore, two temperatures in combination provide the best fit to the data. *N.orbicollis* finds the highest proportion of mice during nights that are warm at 18 hours, and remain warm at 24 hours (Table 4, line 4); in other words, nights that are warm throughout the entire flight period of *N.orbicollis*.

The situation is very different for *N.defodiens*, for whom two opposing forces are at work. If the temperature is too low, then *N.defodiens* cannot find mice, and if the temperature is too high, then *N.defodiens* loses the mice to *N.orbicollis*. In 1981, high temperatures caused the latter force to predominate, creating a negative correlation with temperature. Both forces predominate in 1982. Thus, two temperatures in combination best fit the data, but the later temperature has a negative effect (Table 4, line 5). In other words, *N.defodiens* obtains the most mice during nights that are warm at 22 hours, but cold at 24 hours. Several other pairs of temperature provide an equally good fit (e.g. 20 and 24 hours, 18 and 02 hours). The importance of steeply declining temperatures for *N.defodiens* can best be attributed to competition by *N.orbicollis*.

Mice were inspected both evening and morning on nine days in 1982 and 1983. From this data we can directly calculate the proportion of mice known to be found by *N.defodiens* in the evening, that are appropriated by *N.orbicollis* or *N.sayi* by the following morning. As shown in Fig. 5A, the proportion of rediscoveries is usually higher than 18%, and is strongly related to temperature ($r^2 = 0.77$). The slope and intercept are virtually identical to those in steps 1 and 3 of Table 3; in other words, for any given temperature, *N.orbicollis* appears as likely to find a mouse previously discovered by *N. defodiens*, as it is to find mice in general.

Finally, on 15 June 1983 we placed sixty pairs of *N.defodiens* on mice in the field, protected them from discovery by free-flying burying beetles on the first night, and then retrieved the mice 10 days later. Thirty-two of the mice were occupied by *N.orbicollis*, three by *N.sayi*, and only thirteen by *N.defodiens*. The others were discovered by vertebrates or abandoned.

There can be no doubt that without the refuge of cool temperature, *N.defodiens* is highly vulnerable to competition from larger *Nicrophorus* species.

KBS Results and Geographical Distributions

Because competition among burying beetles is temperature dependent, one might expect the

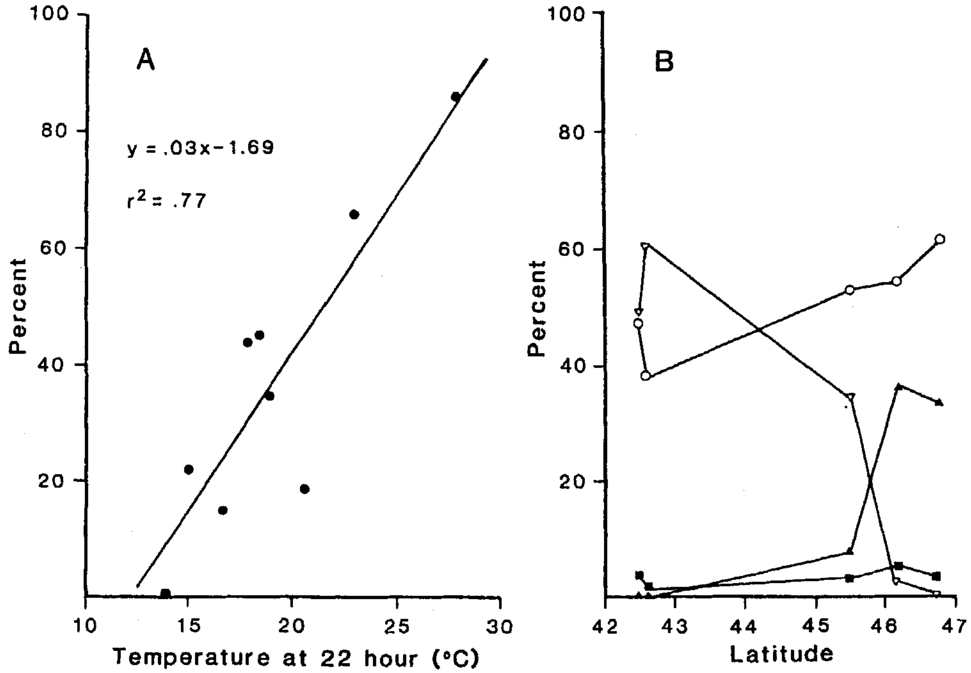

FIG. 5. (A) The proportion of mice known to be discovered by *N.defodiens* that subsequently were discovered by *N.orbicollis* or *N.sayi* (*y*-axis), related to temperature at 22 hours (*x*-axis). (B) The relative proportions of *N.orbicollis* (▽), *N.tomentosus* (○), *N.sayi* (■) and *N.defodiens* (▲) in pitfall traps as a function of latitude.

relative proportion of species to vary with latitude. In particular, *N.orbicollis* should increase in warmer regions, at the expense of *N.defodiens* and possibly also *N.tomentosus* and *N.sayi*. This expectation is supported by the KBS data, our own sampling throughout the stage of Michigan, and the published literature.

Daily temperature at KBS from June to September 1981 and 1982 averages approximately 3°C higher than at UMBS. As shown in Table 1, *N.orbicollis* constitutes 78% of all beetles captured in pitfall traps, followed by *N.tomentosus* and *N.sayi*. *N.sayi* would probably be better represented if trapping commenced in early spring, when it is reproductively active. *N.defodiens* has never been collected at KBS. These relative proportions hold for all habitats sampled.

Fig. 5B shows the results of a collecting trip throughout Michigan during 1–8 August 1983. The relative abundance of *N.defodiens* and *N.tomentosus* is strongly related to latitude. These results are consistent with the published literature (Anderson, 1982), museum specimens (Anderson, 1981) and also the unpublished data of S. B. Peck, who conducted a transect from New York to Florida during May–August 1981. *N.defodiens* was found at only four of ten sampling stations; these were the two most northern stations (Binghamton, New York and Hazelton, Pa.) and the two highest altitude stations (Jeffress Park, N.C., 1066 m and Balsam Mt, N.C., 1340 m). These results support the hypothesis that *N.defodiens* requires cool temperatures to coexist with competitively dominant species, and that competition is an important determinant of geographical distributions for this genus.

Fig. 6 displays the results of the KBS grid study. *N.orbicollis* is the only species breeding until late August. As at UMBS, *N.tomentosus* is an autumn breeder; however, even though *N.tomentosus* emerges earlier at KBS (the first individuals appeared in pitfall traps in late June), they do not appear on mice until 2–3 weeks later than at UMBS.

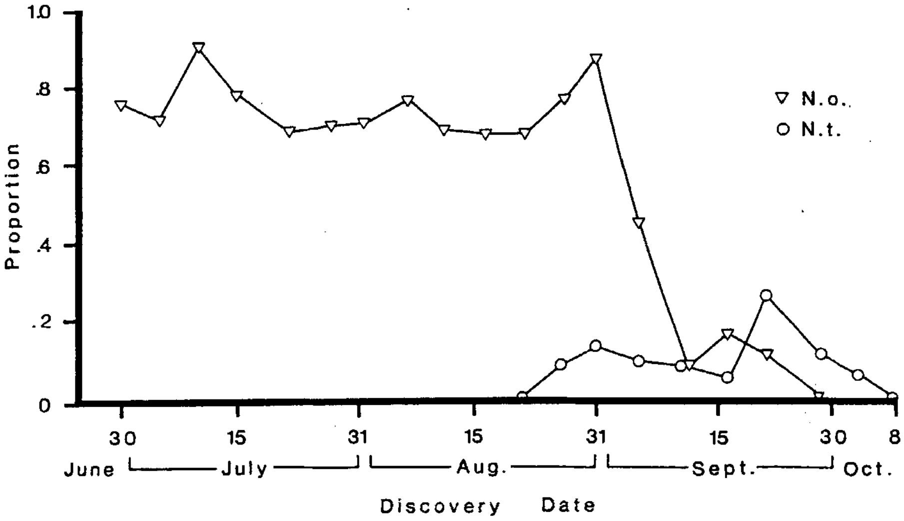

FIG. 6. KBS 1980 grid study, showing the proportion of species found on mice the morning after discovery.

Discussion

Competition is sometimes said to be less common among invertebrates than vertebrates, because the former are more vulnerable to predation and other forms of disturbance (e.g. Connell, 1983). This rule has so many exceptions (e.g. Lawton & Hassell, 1981) that perhaps it should be dropped altogether. It is more useful to focus on the factors that influence competition, rather than weak correlations between these factors and large taxonomic groups. For burying beetles, the resource is discrete and easily monopolized. Predation is important (otherwise *N.tomentosus* would not mimic a bumblebee), but population densities remain sufficiently large that most carcasses are found by several individual beetles, often of different species. Given this ecological situation, it is not surprising that the number of coexisting *Nicrophorus* species and their relative proportions are influenced by competition.

Several authors have stressed the importance of temperature in competition among poikilotherms. Heinrich & Bartholomew (1979) showed that body temperature was more important than body size in determining the outcome of dung beetle fights (*Scarabaeus laevistriatus*). Schoener (1974) showed that terrestrial poikilotherms often partition food by being active at different times of the day. In our study, temperature has no effect on the outcome of fights between *N.orbicollis* and *N.defodiens* (or fights among conspecifics; Wilson & Fudge 1984), and diurnal differences promote coexistence only when they allow *N.defodiens* to forage on days when *N.orbicollis* cannot.

Our study has focused mostly on the interaction between *N.orbicollis* and *N.defodiens*. Is competition also responsible for the seasonal segregation of *N.sayi, N.orbicollis* and *N.tomentosus*? Connell (1980) has justly criticized the literature on competition for assuming that present-day differences in habitat or phenology are caused by a past history of competition. Nevertheless, some speculation is warranted, if only to guide future research.

N.sayi and *N.orbicollis* are the same size, and both overwinter as adults, yet *N.sayi* emerges several weeks before *N.orbicollis*, and adults enter reproductive diapause by early June. It seems unlikely that this diapause is a response to temperature by itself, because the adults continue to fly, and soil temperatures are moderate throughout the year. Indeed, we have successfully raised *N.sayi* broods during May in the laboratory, at temperatures that are higher than midsummer soil temperatures (unpublished data). On the other hand, even slight differences in temperature optima could bestow competitive superiority on *N.sayi* in the spring and on *N.orbicollis* in the summer. We can think of no other reason why *N.sayi* should forgo three months of reproduction.

Both *N.orbicollis* and *N.defodiens* appear to enter reproductive diapause in late summer, before temperatures become too cold to find mice (unpublished data). This presumably is an adaptation to season length, since only broods that have enough time to reach the adult stage successfully overwinter. By contrast, *N.tomentosus* overwinters in the prepupal stage, and thus always has a 2 or 3 week 'refuge' during the autumn when mice will be uncontested by *N.orbicollis*. We therefore predict that *N.tomentosus* can never entirely be excluded by *N.orbicollis*, as can *N.defodiens*. The onset of reproduction for *N.tomentosus*, however, is another matter. We have demonstrated that *N.tomentosus* at UMBS search for mice as soon as their ovaries mature, while at KBS the same species first enters reproductive diapause (unpublished data). This would explain why *N.tomentosus* at KBS emerge earlier, but do not obtain mice until later than at UMBS. Competition with *N.orbicollis* is a likely factor in the evolution of reproductive diapause in *N.tomentosus*.

Some of these questions may best be answered by studying the same species at different localities. Our own study hints that KBS and UMBS differ not only in the relative proportions of burying beetle species, but also in adaptations possessed by the species (e.g. diapause in *N.tomentosus*; for other possible examples of local adaptation see Wilson, 1982; Wilson & Fudge, 1984). In other words, natural selection may have 'fine-tuned' the burying beetles to their competitive environment within each locality. If so, then this would be the best sort of evidence that on an evolutionary level, competition is an important determinant of burying beetle community structure.

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