

The Ecology of a Predaceous Troglobitic Beetle, *Neaphaenops tellkampfi* (Coleoptera: Carabidae, Trechinae)

I. Seasonality of Food Input and Early Life History Stages

by

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INTRODUCTION

Although many authors have emphasized the constancy of the cave environment, Barr and Kuehne (1971) describe seasonal fluctuations which suggest corresponding adaptations in the fauna. We have examined the adaptations in the life history of *Neaphaenops tellkampfi* (Coleoptera: Carabidae, Trechinae) to seasonal food input. *Neaphaenops* is the largest and most abundant of several species of carabid beetles of the tribe Trechini which inhabit the caves of central and western Kentucky. As a result, *Neaphaenops* is an important component of the terrestrial cave community.

The studies reported here were carried out in the extensive cave systems of Mammoth Cave National Park, Ky. In this area, *Neaphaenops* is by far the most abundant trechine in most of the caves in which it occurs and reaches its highest local densities in areas of uncompacted sands and silts. In these substrates, *Neaphaenops* has been reported to prey on the eggs and nymphs of the common cave cricket *Hadenoeus subterraneus* (Orthoptera: Gryllacridoidea, Rhaphidophoridae communities (Barr and Kuehne, 1971).

Obvious evolutionary convergence has occurred between *Neaphaenops* and two other species of carabid cricket egg predators, *Darlingtonia kentuckensis* a trechine in the caves of eastern Kentucky (Marsh 1969) and *Rhadine subterranea*, a member of the tribe Agonini which occurs in a Texas cave system (Mitchell, 1971 a, b, c). *Darlingtonia*, like *Neaphaenops*, feeds on the eggs of *Hadenoeus*; while *Rhadine* feeds on the eggs of two species of camel cricket, *Ceuthophilus cunicularis* and *C.*

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secretus (Orthoptera: Gryllacridoidea, Rhabdophoridae). Convergence seems to have occurred in body size, searching behavior, and substrate preference. *Neapphaenops* size ranges between 6.5-7.5 mm (Barr, 1966) and *Darlingtonia* between 5.7-7.2 mm (Marsh, 1969), whereas the other species of troglotic trechines with which they co-occur are significantly smaller, with a size range of 3.3-6.0 mm (Marsh, 1969; and Barr, 1966). Although *Rhadine* are usually larger than *Neapphaenops* and *Darlingtonia*, the size range of *R. subterranea*, 7.3-8.9 mm (Barr, 1960), is fairly close to that of the two trechines. All three species reach their highest densities on uncompacted substrates. Kane and Poulson (1973) have demonstrated that *Neapphaenops* will choose loose sand over mud, rock, or detritus substrates in the field. In such loose substrates with sufficient moisture, cricket eggs are especially abundant [cf. Mitchell (1971 a, b, c) for *Ceuthophilus* and our data for *Hadenocercus*].

There also seems to be a convergence between *Neapphaenops* and *Darlingtonia* with regard to life history pattern and seasonality. An hypothesis for the apparent lack of convergence in seasonality between these two species and *Rhadine* is also offered.

PROCEDURE

Two areas were selected for this study. The first was located at the end of Marion Avenue in Mammoth Cave and the second at the end of Edwards Avenue in Great Onyx Cave. Both caves are located in Mammoth Cave National Park, Kentucky. Each study area consisted of a relatively homogeneous expanse of uncompacted substrate with bits of rock and large populations of *Neapphaenops tellkampffii*.

Data on all life history stages were collected by systematic visual census in both study areas. In Marion Avenue this has been done at irregular times during the periods 1969-72 and on a regular basis during 1973; however, all seasons of the year are represented. In Edwards Avenue data were collected on an irregular basis from April 1972-October 1972 and on a regular monthly basis from October 1972-December 1973.

Sclerotization of adults occurs slowly in *Neapphaenops*. Field studies indicate that newly emerged adults can be recognized for approximately 2-2.5 months as lightly colored teneralis. These unsclerotized individuals were recorded separately from fully sclerotized adults during the visual census.

In Marion Avenue, census data on density of adults were obtained by counting all beetles within the fixed 300m² area from a network of paths. Since teneral beetles are less visible than fully sclerotized beetles, the census method underestimates teneralis located more than a few feet from the paths. However, the bias is consistent, and the pattern is thus accurate. There are very few rocks, and these were not disturbed. During each census period, beetles were sexed to follow changes in sex ratio.

Density estimates in Edwards Avenue were made by setting out ten 1m² quadrats using a random number table. All the beetles in these quadrats were scored for

sex and as either teneral or sclerotized adults. An additional collection of generally at least one hundred adults was made from the same area. These were also scored for sex and degree of sclerotization. Generally twenty-five to thirty-five fully sclerotized females from this collection were preserved in FAA (50 parts 95% EtOH; 10 parts formaldehyde, 2 parts acetic acid; 40 parts H₂O Knudsen (1972) and returned to the laboratory where they were examined for mature eggs; the rest were released. In addition to a census of the entire open area, all rocks were examined and carefully replaced in a search for larvae, pupae, and further teneral adults. On two dates, April 1972 and July 1972, last instar larvae and pupae were returned to the laboratory and reared in an attempt to determine the duration of these life history stages.

Observations of feeding and copulations were also recorded for both of these areas. Despite many hours of field study the number of these observations during the study period are few. As a result we are adding additional observations from other areas and/or dates in the hope of inferring some pattern. Any feeding observations that might have resulted from human disturbance (e.g. stepping on a beetle) are not included.

Hadenocetus egg input uncorrected for predation was monitored monthly in Edwards Avenue. Four plots 0.5m² in area were sampled during each census using a Standard Sieve of 4.0 mesh/cm mesh size. All *Hadenocetus* eggs were counted and removed.

RESULTS

A. Observations of copulation

Table I lists all available observations of *Neaphaenops* in copula by area and date. Differences in timing between areas may obscure a pattern, but there is no seasonal pattern evident from our 24 observations of copulation. Copulations apparently are clumped in both time and space, and do not merely reflect the distribution of field work time.

B. Egg production

Dissection of several hundred female *Neaphaenops* indicated the maximum size of an egg in the ovary to be 0.8mm in length. Since this is the same value as that reported by Marsh (1969) for *Darlingtonia*, we utilized his criterion of considering all eggs 0.75 times the maximum or larger (i.e. 0.6-0.8mm) as mature eggs. Dissection of teneral females at all times of year showed no mature eggs and indicated that the ovaries of these recently hatched beetles were small. Fully sclerotized adults collected simultaneously carried many mature eggs and/or had well developed ovaries. We felt, therefore, that the female reproductive system was not functional in tenerals and collection of such individuals was discontinued. The data shown in Figures 1 and 2 are based on fully sclerotized adults only.

The pattern of egg production in terms of per cent females with eggs (Fig. 1) is a fall low followed by a rise to a value of approximately 50% by early winter. This

value remains fairly constant until the following fall when a decrease is again noted. Figure 2 represents the ratio of eggs per female in each monthly collection. The seasonal trend in these data closely parallels that of per cent of females fecund until mid-summer 1973 when a peak of over 6 eggs per female was reached (compare Figs. 1 & 2). The summer peak in egg production is synchronous with a pulse of first instar *Hadenococcus* nymphs (Fig. 4). The fall decrease in *Hadenococcus* eggs and nymphs coupled with the large number of newly recruited and sexually immature *Neaphaenops* adults may account for the fall drop in female fecundity. The fall

Table 1. *Neaphaenops* Copulations.

	Date	Location	
29	January 1973	Radio Room	Mammoth
21	January 1973	Marion Avenue	Mammoth
	February 1967	Malott Avenue	Flint
13	February 1970	Natural Bridge	Mammoth
29	March 1972	Radio Room	Mammoth
29	March 1972	Marion Avenue	Mammoth
28	March 1972	Pohl Avenue	Flint
12	March 1974	Edwards Avenue	Great Onyx
6	April 1963	Marion Avenue	Mammoth
	April 1967	Malott Avenue	Flint
28	April 1974	Marion Avenue, end	Mammoth
29	June 1968	Wretched River	Flint
15	June 1973	Marion Avenue	Mammoth
12	July 1968	Marion Avenue	Mammoth
13	July 1968	Marion Avenue	Mammoth
14	July 1973	Marion Avenue, end	Mammoth
	September 1973	Hansons Cave	Sinkhole Plain
6	September 1974	Sophys Avenue	Mammoth
6	September 1974	Sophys Avenue	Mammoth
11	September 1974	Edwards Avenue, end	Great Onyx
19	October 1974	Edwards Avenue, end	Great Onyx
18	November 1974	Marion Avenue, end	Mammoth
28	December 1968	Gertas Grotto	Mammoth

Observations of *Neaphaenops* in copula, all available, data. Although differences in timing between areas may obscure a pattern, the present data for any single locale or substrate type do not show any seasonality. The copulations apparently are clumped in both time and space.

decrease in egg production in 1973 was much less than that observed in 1972. This may be due to the fact that the October and November 1972 samples were 50-60% smaller than all subsequent samples and therefore a sampling error was incurred, or to the fact that *Hadenoeus* egg input was greater in the fall of 1973 than in the fall of 1972 (Fig. 4).

C. Early life history stages

Two qualitatively different *Neaphaenops* larvae were regularly observed in the field. The first was active and had a size range of 6.0-8.0mm in length. It was often observed on the surface of the sand or under rocks. The second type was very quiescent and was always found in a small cell it apparently excavated under a rock. This larva had a size range of 6.5-9.0mm in length. Since all pupae were observed in similar cells, and because of the overlap in size of the larvae, we conclude that all these larvae represent the last instar and quiescence in a cell is a result of preparation for pupation.

The seasonal pattern in the juvenile life history stages (Fig. 3) is one of appearance of last instar larvae in late winter and early spring. We have looked for earlier instars at all times of the year but find very few of them. The last instar larvae that we regularly find appear to become quiescent and pupate within a month. Appear-

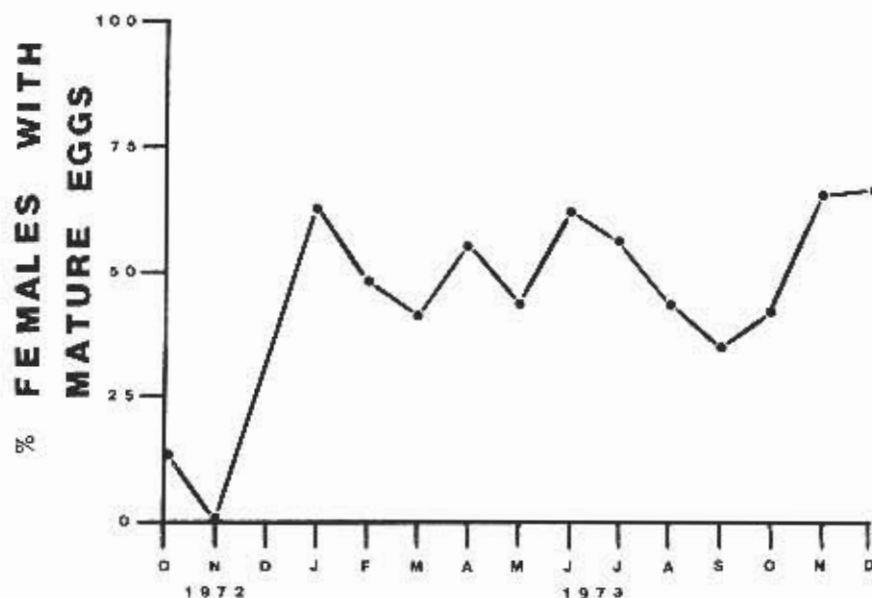


Fig. 1. The monthly percentage of female *Neaphaenops* containing at least one mature egg. Data obtained by dissection of preserved specimens collected in Edwards Avenue, Great Onyx Cave from October 1972-December 1973. The percentage remains fairly constant at approximately 50% for most of the year but shows a brief drop in the fall.

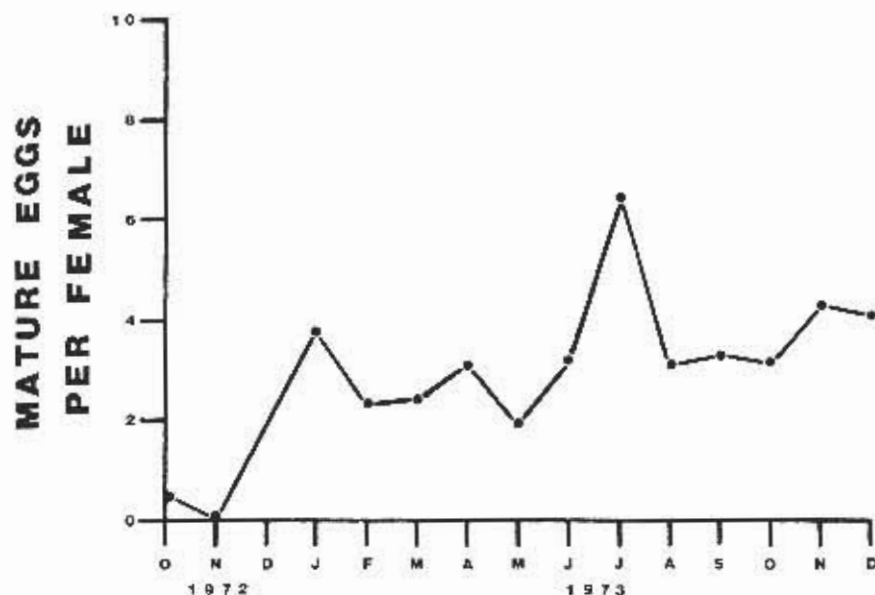


Fig. 2. The mean number of mature eggs per female *Neaphaenops* as determined by dissection of monthly collections of female beetles from Edwards Avenue, Great Onyx Cave from October 1972-December 1973. The July peak in fecundity coincides with the peak time of emergence of 1st instar *Ildenoecus* nymphs.

ance of large numbers of teneral begins in June and reaches a mid-summer peak after which it declines during the autumn and reaches a winter low. On two dates, (March 29 and 31, 1972) a census was carried out in Marion Avenue, resulting in the observation of 3 active larvae, 3 quiescent larvae in cells, and 1 pupa. The observed distribution of life history stages closely parallels the April 1, 1972 census in Great Onyx Cave (Fig. 3).

A small number of earlier instar larvae were observed in the latter half of 1974 in Edwards Avenue. These included one 4mm larvae in July, which included two 3mm and one 4mm larvae in August, one 2mm, one 3mm and two 5-6mm larvae in September, and one 5mm larva in October. Of these nine larvae, seven were caught in pitfall traps being employed in a different study. This may suggest that the visual census technique we normally employed for larval census was not adequate for observing early larval stages. It is interesting to note that this late summer-fall appearance of early instars is consistent with the mid-summer peak in *Neaphaenops* egg production and late winter-early spring appearance of late larvae and pupae.

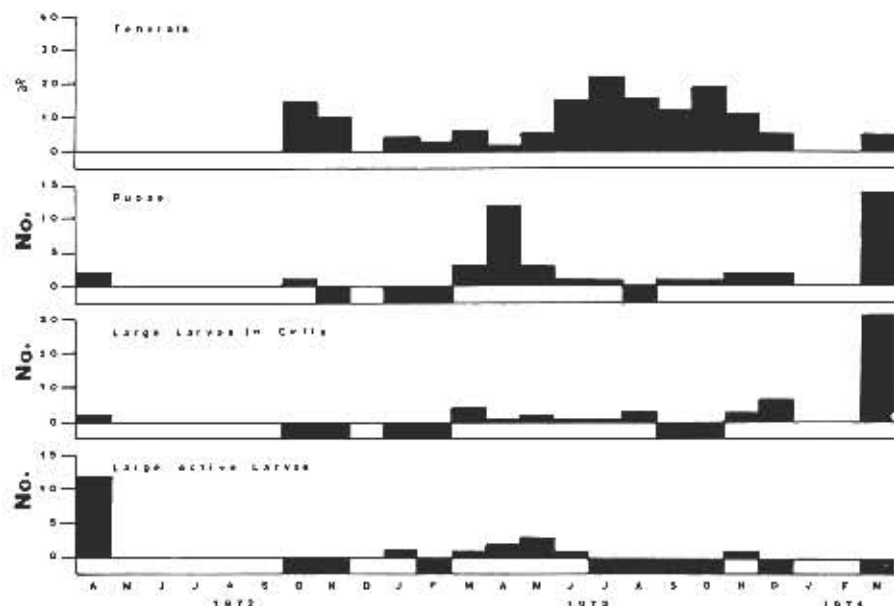


Fig. 3. The seasonal pattern of appearance of last instar larvae, pupae and teneral adult *Neaphaenops* in Edwards Avenue, Great Onyx Cave from April 1972-March 1974. In all three years, larvae and pupae peak in early spring. The 2 to 3 month lag between pupal and teneral appearance is consistent with laboratory estimates of length of pupal stage. (Note that zero values are listed only for those months in which census was conducted and no individuals were found. No values are given for months in which field census was not conducted.)

Four of the large larvae collected in 1972 pupated within a few days of collection and hatched in the laboratory at 15°C in 7 to 8 weeks. The pupae collected at the same time hatched after 6-8 weeks. From this evidence we conclude the pupal stage to be of 7-8 weeks duration which closely approximates the time found by Marsh (1969) for the pupal stage of *Darlingtonia* at the same cave temperature. Studies of teneralis isolated in the lab and in the field indicate the full sclerotization process to be of approximately 2-2 1/2 months duration.

D. Seasonal pattern of Hadenoeus oviposition

Hadenoeus oviposition shows a highly pulsed, seasonal pattern (Fig. 4). Egg density uncorrected for predation remained below 20 eggs/m² in the census plots for most of the year and reached a low point in early fall. A rapid rise was noted in the March sample with a peak density of 77 eggs/m² observed in April. This input had fallen sharply by May and the June sample again showed a density of less than 20 eggs/m² which persisted until December. Data for March 1974 indicated a repetition of the spring pulse observed in 1973.

Hadenoeus eggs of known age were incubated at cave temperature in the laboratory and hatched within 80-90 days. As a result we expected a pulse of first instar nymphs to appear in the June-July time period. Field census verified this expectation (Fig. 4).

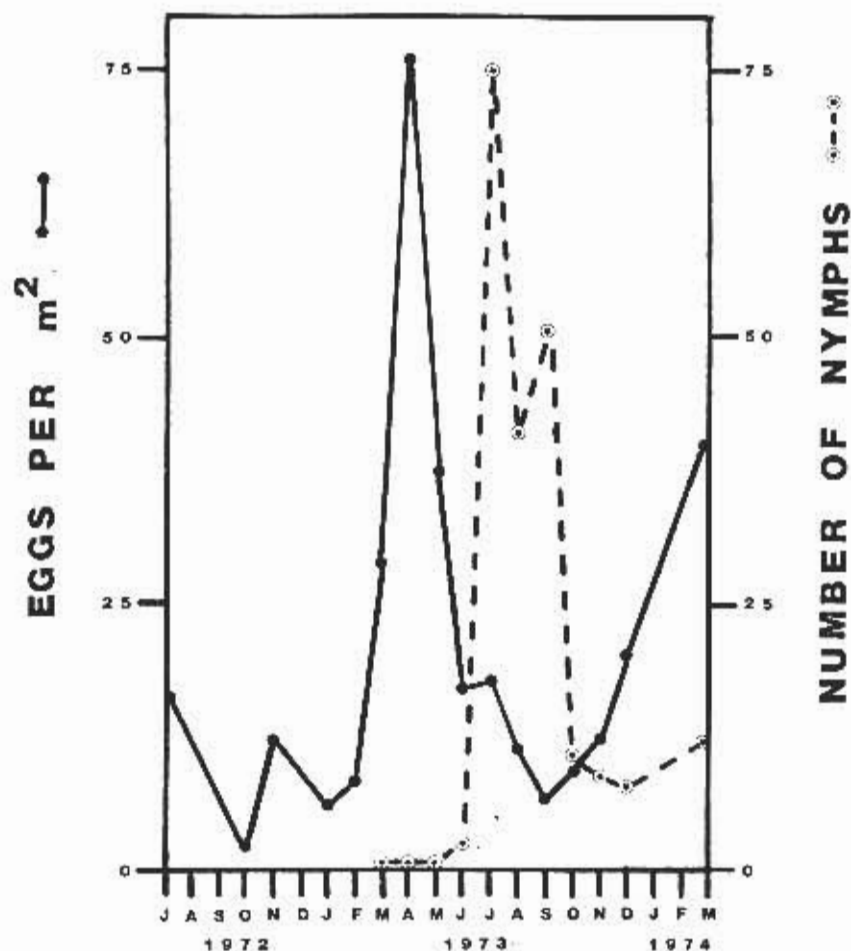


Fig. 4. Seasonal abundance of *Hadenoeus* eggs and first instar nymphs in Edwards Avenue, Great Onyx Cave from July 1972. Both are highly pulsed with eggs peaking in early spring. The three month lag between egg and nymph peaks is consistent with laboratory estimates of hatching time for *Hadenoeus* eggs.

DISCUSSION OF RESULTS

A. Copulations

We do not have enough data for any single locale or substrate type to determine whether copulation is seasonal. However, the 24 observations listed in Table 1 show a clumping in both time and space which cannot be explained as a clumping in field work time. Areas such as the Radio Room, Marion Avenue, and Sophys Avenue are quite similar habitats and appear to show synchrony both in recruitment and copulation.

B. Egg Production

Egg production in *Neaphaenops* closely parallels that observed by Marsh (1969) for *Darlingtonia* with both having 0.7-0.8mm mature eggs and a mean clutch size of 3.2 eggs. Data are not available for *Rhadine*.

The seasonal pattern in *Neaphaenops* seems different from the multi-peaked egg production pattern Marsh describes for *Darlingtonia*. With the exception of a 1-2 month period in the fall of 1972, female *Neaphaenops* were always found to carry 2-6 mature eggs. We believe this brief period of low fecundity is the result of (1) high mortality in the old females which have completed oviposition; (2) the fact that few newly recruited sclerotized adults have developed mature ovaries; (3) low food supply due to the fall 1972 nadir in cricket oviposition (Fig. 4). In 1973 the cricket egg input did not decline as sharply (Fig. 4), and we see only an early fall decrease in percent females with eggs (Fig. 1).

One definite peak in the graph of eggs/female (Fig. 2) occurred during the study period. The July peak coincides with the peak in appearance of first instar *Hadenocercus* nymphs 3 months after the peak of egg input (Fig. 4). Although the evidence of a causal relationship is not conclusive, it is certainly compelling since cricket eggs and nymphs could provide the protein and lipid rich food source often required by insects (Englemann, 1970) for egg production.

C. Larvae and Pupae

We suggest that the pulse of last instar larvae and pupae found in March 1974 (Fig. 3) reflects the July 1973 pulse in beetle egg production. If we are correct, this would indicate a larval period of 6 to 7 months plus a known 2 month period from pupation to eclosion and a additional 2 to 3 week period before the adult emerges from the cell after eclosion (Marsh, 1969). The nine observations of early instar larvae seen from August-October 1974 give some additional support to this proposed life history time table. This gives an expected 3 month lag from pupation to teneral appearance which is what we observe (Fig. 3). We believe the few scattered records of larvae, pupae, and teneralis censused at other times of the year, are the results of the lower but consistent egg production during the non-peak months. The greater spread in teneral occurrence is due to the fact that teneralis can be recognized for 2-3 months.

We reject the possibility that females are holding mature eggs and all oviposition synchronously as we find an increasing percentage of non-ovigerous females with

corpora lutea as the season progresses. Corpora lutea indicate that oviposition has occurred. However, essentially nothing is known of the feeding habits of the larvae, and so we cannot rule out the possibility that some event related to food supply may synchronize the development of larvae hatched at different times.

In dealing with the seasonal pattern of *Neaphaenops* life history, we have taken care, when possible, to consider both sites and years on an individual basis rather than lumping data from either or both considerations. The reason for this is that slight differences in timing between years, such as earlier or later *Hadenoeus* oviposition, or between sites within a year may cause a blurring of seasonal pattern when data are lumped or averaged. This obscures the otherwise obvious seasonal pattern in each area in any given year.