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

II. Adult Seasonality, Feeding and Recruitment.

by

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INTRODUCTION

This is the second of two papers dealing with the ecology of *Neaphaenops*. The procedure and a general introduction will be found in the first paper.

RESULTS

A. Adult Recruitment

Recruitment of teneral adults in both Marion Avenue and Edwards Avenue shows a marked seasonality (Figure 7). Teneral adults emerge chiefly in late spring through early fall, although there is some emergence throughout the year.

B. Adult Seasonality

Census data for all adult *Neaphaenops* from the Marion Avenue and Edwards Avenue study areas are presented in Figures 5 and 6, respectively. Both areas show a summer through early fall population maximum coincident with the recruitment of teneral adults into the population, and a decrease through the rest of the year.

Sex ratio data for both areas are presented in Table 3. Although the sex ratio for tenerals is 1:1 (N>400), the sex ratio for fully sclerotized adults on sandy areas changes seasonally to a female majority (up to 2:1) just prior to the recruitment of sclerotized tenerals.

C. Adult Feeding

The 46 feeding observations recorded for *Neaphaenops* to date are listed in Table 2. Of these, the *ne plus ultra* is a female in copula feeding on a *Hadenoecus* nymph. The two observations of *Neaphaenops* feeding on non cave-limited organisms were both made near entrances.

About one third of the predated first instar *Hadenoecus* nymphs appeared to have been captured during emergence since they seemed to still be partially bound by the vitelline membrane. We have also observed laboratory hatched nymphs unable to free themselves completely from the membrane.

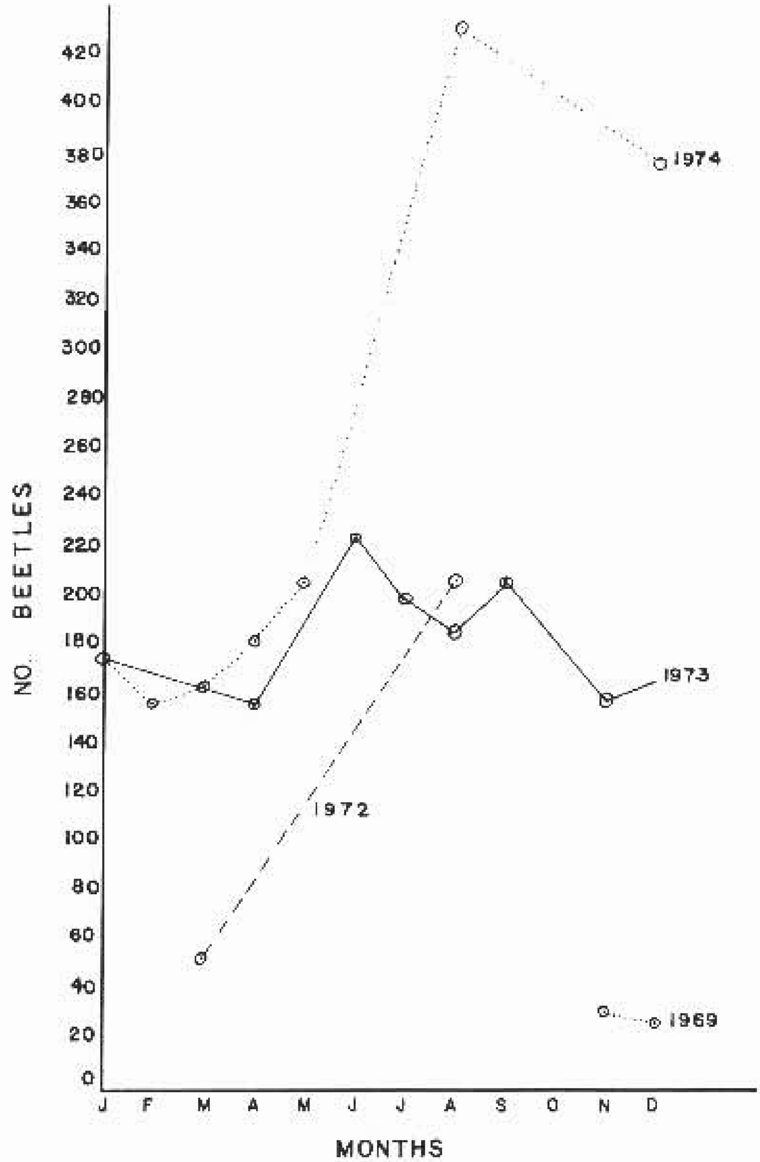

Fig. 5. Adult *Neaphaenops* population censuses in Marion Ave., Mammoth Cave. Despite great year to year differences in population census, there is a summer-fall peak every year coincident with maximal recruitment of adults.

DISCUSSION

A. Adult Recruitment

The seasonal pattern of adult recruitment in sandy areas seems well established. Adult longevity, however, remains enigmatic. Since marking methods for *Neaphaenops* longevity and abundance are notoriously unreliable, it would be desirable to estimate longevity from the recruitment rate data. However, we have found teneral feeding decreases sclerotization time, and there is difficulty in deciding whether to count nearly sclerotized beetles as tenerals. Finally, the estimation of longevity is confounded by year to year differences in recruitment and survival as well as emigration and immigration. It seems safest to estimate adult longevity as somewhat in excess of one year although it may possibly be more nearly two.

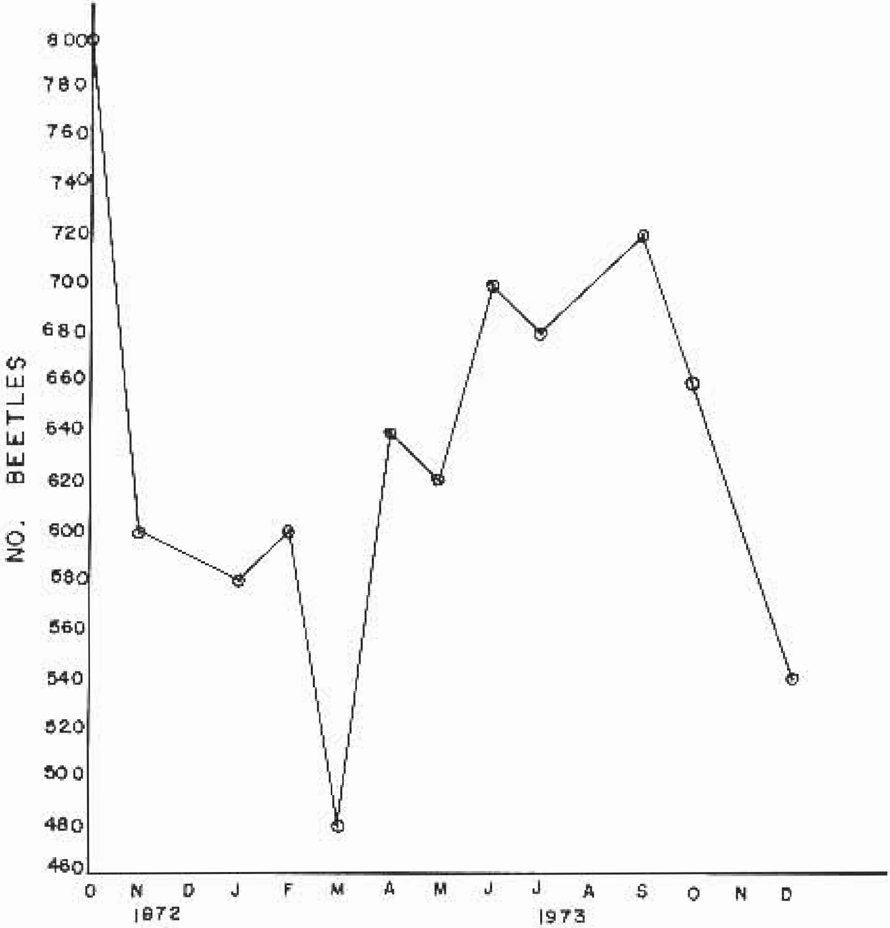

Fig. 6. Adult *Neaphaenops* population censuses in Edwards Ave., Great Onyx Cave. The pattern is like that seen in Marion Ave. (Fig. 5).

Table 2. Feeding by Adult *Neaphaenops.*

	Food Item			
Month	*Hadenoecus*		*Neaphaenops*	Other
	eggs	nymphs	all stages	
Unknown				1
January	1			
February	1	2	1	
March	7	3		
April	2	2	1	
May		2		
June	6	1		
July	3		1	1*
August	1	4	1	1,1*
September				
October				
November		1+		2*
December				
Totals	21	15	4	6

Notes: * = troglobite, + = second or higher instar nymph.

B. Adult Seasonality

The adult census data shows a population maximum during maximum recruitment followed by a steady decline. This pattern is a result of seasonal recruitment, overlapping generations and an adult lifespan of between one and two years. Survivorship data from marking studies of fully sclerotized beetles at the beginning of maximum recruitment are consistent with the adult longevity estimate (Norton, unpublished).

Although the annual pattern of female predominance on sandy areas just prior to recruitment seems well established, the meaning remains obscure. Females have higher survivorship than males in the laboratory, but the situation is complicated by habitat selection. Females tend to occur on sandy floors where eggs are the predominant prey while males tend to occur on the ceiling and walls where first instar nymphs are the prey (Norton, unpublished).

This system has the coincidental advantages of: a) providing a mechanism for the systematic partition of the food niche, b) keeping most females on the appropriate substrate for copulation and oviposition, and c) allowing prey eggs to be converted to predator eggs with minimal intervening metabolism.

C. Adult Feeding

Field experiments (Norton and Kane, unpublished) indicate *Neaphaenops* eats over 90% of the *Hadenoecus* eggs laid in loose silt. However, relatively few feeding observations are available; partially because feeding tends to be rapid and cryptic for *Neaphaenops* as well as *Darlingtonea*, for which Marsh (1969) reports a short, spectacular struggle between two beetles for a single food item. Several similar struggles have been observed for *Neaphaenops*, and serve to emphasize the scarcity of food.

Since about one third of the first instar nymphs appear to have been taken during emergence, and active first instar nymphs are able to persist in three dimensional confinement with *Neaphaenops* until ecdysis (Norton, unpublished); the majority of the healthy first instar nymphs in the diet of *Neaphaenops* were probably either in eclosion or ecdysis. Healthy nymphs are possibly captured in situations where they are unable to escape by jumping.

Table 3. Sex ratio for fully sclerotized *Neaphaenops*. Starred dates had a significantly greater number of females than males; the sex ratio does not differ significantly from 1:1 on other dates. Sample sizes range from 50-250.

	LOCALITY					
	Marion Avenue			Edwards Avenue		
Month	1968	1973	1974	1972	1973	1974
January		**	ns		ns	
February			**		ns	
March	**		**		ns	ns
April		*	**		ns	
May			**		ns	ns
June		ns			ns	
July	**	ns			**	ns
August	ns	ns			**	
September		ns			*	
October				**	ns	
November	ns	ns		ns	ns	
December	ns	ns	ns		ns	

ns = not significant, * = $p < .05$, ** = $p < .025$

These data suggest the observed female majorities are the result of differential survival, but that recruitment of newly scleritized adults returns the sex ratio to equality. Differences in the onset of significant female majorities probably reflect differences in prey availibility.

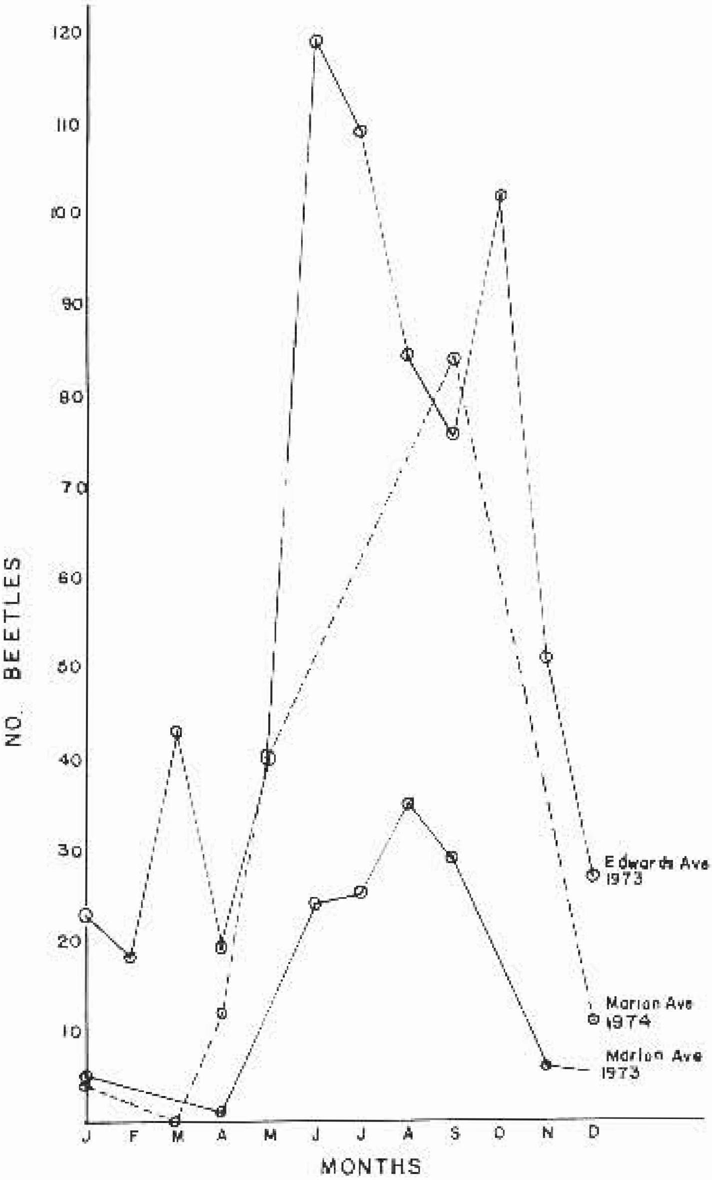

Fig. 7. Teneral *Neaphaenops* census data from Mammoth Cave (Marion Ave.) and Great Onyx Cave (Edwards Ave). The marked seasonal recruitment in summer is consistent between years and localities.

The feeding observations reported here show that while about 80% of the diet of *Neaphaenops* may be exclusively eggs and first instar nymphs of *Hadenoecus*, its diet can be diverse. Laboratory observations by Christiansen (1971) have shown Neaphaenops readily feeds on several species of collembola. Laboratory observations (Kane and Norton, unpublished) also show *Neaphaenops* is able to catch confined first instar nymphs, flies, and other microarthropods.

The observations suggest that *Neaphaenops* is an opportunistic predator which may be able to maintain its populations at higher densities by seasonally switching its diet from *Hadenoecus* eggs to nymphs as well as to microarthropods and other food items, and by cannibalizing nearly all its own life stages.

The two observations of *Neaphaenops* feeding on non cave-limited fauna suggest the diet of *Neaphaenops* may be somewhat expanded in small caves since as abundance of different items would be available near entrances due to the increase in guano, detritus, and accidental species.

D. General

The life history pattern described for *Neaphaenops* seems to represent an adaptation to a seasonal food supply. We expect other troglobitic cricket egg predators with similar food input patterns to exhibit similar life history patterns, while those with significantly different food input patterns should have different life history patterns. *Rhadine subterranea* and *Darlingtonea kentuckensis* are both troglobites predacious on cave cricket eggs and show convergence with *Neaphaenops* in body size, food preference, and habitat selection.

Since *Darlingtonea* also utilizes the eggs and nymphs of *Hadenoecus* it has a seasonal food input pattern very similar to that of *Neaphaenops*. Marsh (1969) has shown that appearance of larval, pupal, and teneral *Darlingtonea* is seasonal and parallel to *Neaphaenops*. While there appears to be some discrepancy in the pattern of egg production between the two species, the two life histories seem essentially identical. Further supportive evidence is that *Darlingtonea*, like *Neaphaenops*, shows some habitat niche breadth (Marsh, 1969). Both beetles reach maximum abundance on uncompacted substrates, but are still found in significant numbers on other substrates. *Darlingtonea* and *Neaphaenops* appear to show the expected parallels in life history pattern.

The seasonal pattern of food availability for *Rhadine* (Mitchell, 1971a-c) is different than that for *Neaphaenops*. The two species of camel cricket, *Ceuthophilus cunicularis* and *C. secretus*, whose eggs are eaten by *Rhadine*, are summer and winter species respectively. We infer that cricket eggs are fairly evenly distributed throughout the year. The fact that Mitchell observed *Rhadine* feeding only on eggs in the field, and could not get *Rhadine* to feed on either cricket nymphs or collembola in the laboratory, strongly supports this inference.

Data are not available on egg production, larve, or pupae for *Rhadine*. However, Mitchell indicates teneral frequency was approximately even throughout the year. This situation is strikingly different from that observed for *Neaphaenops* and *Darlingtonea* and presumably reflects the lack of seasonal fluctuation in food availability to *Rhadine*.

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SUMMARY

In deep cave areas with loose substrate and sufficient moisture, the life history of *Neaphaenops tellkampfii* (Coleoptera: Carabidae, Trechinae) is synchronized with the seasonal pattern of its primary food sources, the eggs and first instar nymphs of the cave cricket *Hadenoecus subterraneus* (Orthoptera : Gryllacridoidea, Rhaphidophoridae). *Neaphaenops* reproduction coincides with an order of magnitude increase in *Hadenoecus* egg input in the spring. Our 46 observations of predation by *Neaphaenops* suggest some switching to other cave animals as cricket egg and first instar nymph densities decrease during the summer.

Neaphaenops life history in areas of *Hadenoecus* egg input is as follows: (1) female *Neaphaenops* reach maximum fecundity at the time of the maximum density of first instar *Hadenoecus* nymphs; (2) early instar *Neaphaenops* larvae appear in late summer and fall; (3) last instar *Neaphaenops* larve appear in early spring and pupation occurs shortly thereafter; (4) lightly colored teneral adults emerge two to three months later, a time consistent with laboratory estimates of the length of the pupal stage. Seasonal changes in sex ratio due to differential mortality appear to be consistent with this seasonal pattern.

A comparison of *Neaphaenops* with two other species of carabid cricket egg predators suggests the importance of seasonal food abundance in determining life history seasonality. *Darlingtonea kentuckensis* has a food resource pattern which appears identical to that of Neaphaenops, and the life history seasonality is also parallel. *Rhadine subterranea*, however, seems to have a much more equitable food input throughout the year, and appears to have an aseasonal life history.

RESUME

Dans les régions profondes des grottes où le substrat est meuble et l'humidité suffisante, le cycle biologique du Coléoptère troglobie *Neaphaenops tellkampfii (Coleoptera : Carabidae, Trechinae)* est synchrone du caractère saisonnier des principales sources de nourriture que constituent les oeufs et les premières nymphes

du grillon cavernicole *Hadenoecus subterraneus (Orthoptera : Gryllacridoidea, Rhaphidophoridae)*. La reproduction de *Neaphaenops* coïncide avec l'abondance du nombre des oeufs déposés par *Hadenoecus* au printemps. Nos 46 observations sur la prédation chez les *Neaphaenops*, suggèrent que, à mesure que la densité d'oeufs de Grillon diminue au cours de l'été, ils s'attaquent alors aux nymphes de Grillon ou à d'autres cavernicoles.

Le cycle biologique de *Neaphaenops* dans les territoires de ponte de *Hadenoecus* se présente de la façon suivante: (1) la femelle de *Neaphaenops* présente une fécondité maximale au moment de la plus forte densité des jeunes nymphes de *Hadenoecus*; (2) les premières éclosions larvaires de *Neaphaenops* se produisent à la fin de l'été et en automne; (3) l'apparition des larves de dernier stade a lieu au début du printemps et elle est rapidement suivie de la pupaison; (4) de jeunes adultes faiblement colorés apparaissent deux à trois mois plus tard, laps de temps conforme aux évaluations faites en laboratoire de la durée du stade pupe. Les variations saisonnières de la sex-ratio, dues à une mortalité différentielle, semblent être la conséquence de ce régime saisionnier.

La comparaison de *Neaphaenops* avec deux autres espèces de Coléoptères cavernicoles prédateurs d'oeufs de Grillon, suggère l'importance de l'abondance de la nourriture saisonnière dans la détermination du rythme saisonnier du cycle biologique. *Darlingtonea kentuckensis* a le même régime alimentaire que *Neaphaenops* et son cycle biologique saisionnier est identique. Par contre *Rhadine subterranea*

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