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Author(s): William J. Resetarits, Jr.

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Ecology of Cave Use by the Frog, *Rana palustris*

WILLIAM J. RESETARITS, JR.¹

Department of Biology, Saint Louis University, St. Louis, Missouri 63103

ABSTRACT: A troglaxene population of the pickerel frog, *Rana palustris*, was studied at Ralph's Ford Bluff Shelter (RFBS), a cave on the northern edge of the Ozark Plateau in central Missouri. Males were present beginning in July with females first observed in September. Overall numbers began to increase in September with maximum numbers present from late November through early March. Wintering population numbered in the hundreds. Movement of frogs within the cave corresponded to changes in surface and cave temperatures. Frogs became inactive at cave temperatures below 6 C and concentrated in large numbers in a physically and thermally sheltered hibernaculum near the center of the cave. Entry and emergence from hibernation in the cave corresponded with the seasonal reversals of temperature gradient between the cave interior and the surface. Emergence date varied by 6 weeks over 4 years of study. Winter mortality was skewed towards juveniles and concentrated in the latter half of winter (January-March). Feeding was suspended from mid-November through early-March. *Rana palustris* is an important component of cave ecosystems in the Ozarks. The origin and importance of cave utilization in the species is probably related to historical factors, and dependent upon physiological pre-adaptations and certain ecological advantages of troglaxene habits.

INTRODUCTION

Rana palustris (LeConte) occupies a broad geographic range encompassing much of eastern North America (Schaaf and Smith, 1970, 1971). Its typical habitat varies geographically, ranging from "black water" swamps in the Carolinas (Hardy, 1964) to cool clear springs and caves in the limestone karst areas of Arkansas, Missouri, Illinois, Kentucky, Tennessee, Mississippi and Alabama (Schaaf and Smith, 1970). The pervasiveness of this latter association prompted Schaaf and Smith (1970) to suggest that caves and cold springs may be a necessary component of *R. palustris* habitat in this region.

Cave-associated populations of *Rana palustris* are perplexing in terms of the distribution, taxonomy and ecology of the species (Schaaf and Smith, 1970). Many North American species of the genus *Rana* have been observed in caves, including *R. catesbeiana* (Barr, 1953; Holman, 1958; Lee, 1969; Pingleton *et al.*, 1975; this study), *R. clamitans* (Myers, 1958; this study), *R. sylvatica* (Barr, 1953), *R. pipiens* complex (Rand, 1950; Blair, 1951; Holman, 1958; Myers, 1958), *R. sphenoccephala* (this study) and *R. palustris* (Smith, 1948; Barr, 1953; Brown and Boschung, 1954; Brode, 1958; Myers, 1958; Schaaf and Smith, 1970; Black, 1971; Knight, 1972; Brown, 1984; this study). With the exception of *R. palustris*, these instances appear to be sporadic, unrelated events. The cave habits of *R. palustris* are unique among North American Anura, and may be unique among temperate zone Anura.

Rana palustris has been classified as troglaxene (Black, 1971) based on its persistent association with caves. Troglaxenes are species which occur in caves but are incapable of completing their life cycles there (Barr, 1963, 1968). Cave use, even at the troglaxene level, is especially interesting in an order containing no troglobitic or troglaphilic species (Vandel, 1965) and raises questions regarding the origin and adaptive nature of cave use in troglaxenes.

The major objectives of this study were to document the extent and nature of cave use in a troglaxene population of *Rana palustris* and to explore the possible role of caves in the distribution and ecology of the species.

¹Present address: Department of Zoology, Duke University, Durham, North Carolina 27706.

STUDY SITE

The site chosen was Ralph's Ford Bluff Shelter (RFBS), located in southeastern Boone Co., Missouri, on Cedar Creek, at an elevation of approximately 200 m. RFBS (Fig. 1) consists of approximately 213 m of main passageway, beginning in a bluff-face entrance 2 m above the normal level of Cedar Creek and ending in a collapsed chamber (sinkhole) in wooded pasture ~ 18 m above the creek. A single side passage branches off the central portion of the cave and is traversible for ~ 50 m. The floor of this passage is higher than the main passage, consists of hard-packed clay, and is usually dry. No surface entrance to this passage is known.

The main passage contains a small intermittent stream with moderately deep (30-60 cm), permanent pools connected by short shallow runs. Flow is maintained in all but the driest conditions and is fed by direct surface discharge into the sinkhole entrance (during wet periods), and subterranean flow entering at several points along the cave stream. Flow varies from a trickle during prolonged droughts, to flash floods which fill the main passage to the ceiling.

The main passageway was divided into six zones for the purposes of this study (Fig. 1). Zones 1 and 6 correspond roughly to the lower and upper twilight zones, respectively; 2 through 5 divide the interior into approximately equal sections (Fig. 1). The most significant microhabitat within the cave with respect to *Rana palustris* is the pool in the center of Zone 4 (hereafter referred to as the pool) (Fig. 1A.). The pool is slab and gravel bottomed, and approximately 1 m x 4 m and 40-50 cm at its greatest depth. The hibernaculum is a partially submerged, physically and thermally sheltered area off the NW edge of the pool. It consists of a shallow, 5-15 cm high, shelf-like cave, approximately 60 cm across at the entrance and of unknown depth. In midwinter the hibernaculum site contains almost the entire overwintering population of *R. palustris* at RFBS. Water in the hibernaculum remains approximately 1.5-2.0 C warmer than the pool proper during midwinter as a result of the depth of the passage into the rock and the direct influx of groundwater.

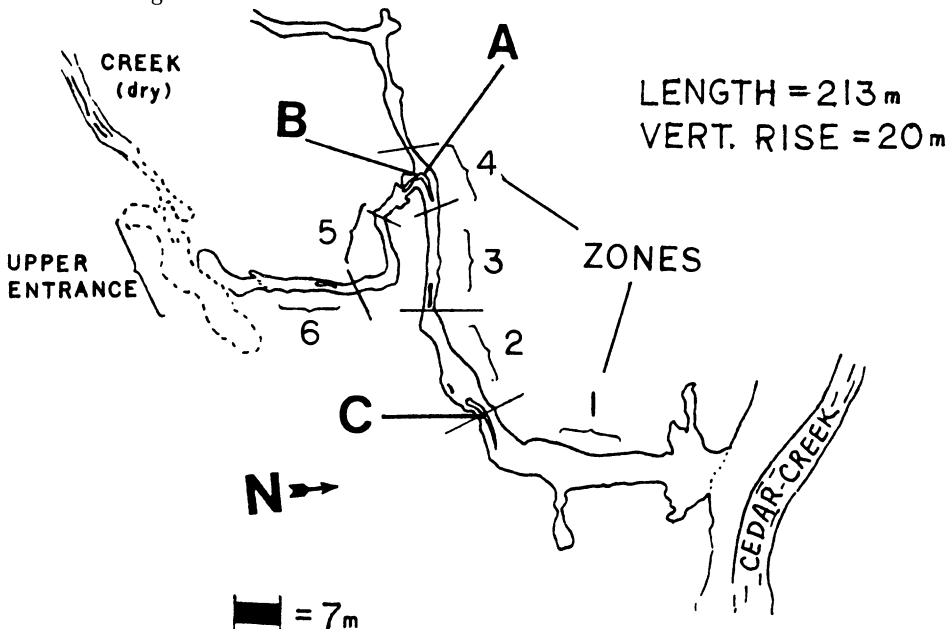


Fig. 1. — Map of RFBS showing cave zones and significant features. (A) indicates location of the pool, (B) the hibernaculum and (C) the DP (divider pool) temperature station

Ozark caves typically maintain a uniform temperature throughout the year, approximated by the local mean annual surface temperature. RFBS temperatures vary markedly from expected and closely parallel changes in external ambient temperature (Fig. 2). Lowest temperatures measured at the pool were 0 C air and 5.2 C water and the highest were 18.9 C air and 13.2 C water. Air temperature extremes were measured using a Taylor Max-Min thermometer placed over the pool on a rock ledge. Water temperature extremes were recorded during cave visits using a Schultheis Quick-Read thermometer. Water in RFBS froze to beyond Zone 1 during the winter of 1980-1981, the furthest extent of ice observed. Water 10 m from the upper entrance was not frozen at this time.

MATERIALS AND METHODS

The study site (RFBS) was visited on an irregular basis from August 1979 through March 1982. The entire main passage was surveyed on most cave visits. Location and estimated numbers of frogs were recorded. Air and water temperature data were taken at six stations using Schultheis Quick-Read and Taylor Max-Min thermometers. Supplemental visits to the cave continued through April 1984.

A mark-recapture study was completed in the winter of 1979-1980. Frogs were captured by hand, freeze-branded with a number on the venter (Daugherty, 1976), and released at the point of capture. Nine frogs marked and kept in the laboratory showed no evidence of deterioration of the brands over several months. Frog #36, marked on 1 January 1980, carried the clearly legible brand when collected and preserved on 14 February 1981.

Population estimates were made using the Schumacher method (Schumacher and Eschmeyer, 1943). This method was chosen for its usefulness in providing a single reliable population estimate from a series of mark-recapture episodes.

Seventy-five *Rana palustris* (33 females and 42 males) were collected from RFBS during the study. All but three were taken after completion of mark-recapture. Specimens were preserved in 10% formalin within 24 hr, weighed to the nearest 0.01 g and measured (snout-vent length (SVL)) to the nearest millimeter. Stomachs were removed and contents weighed and placed in individual vials. Coelomic fat was removed and wet mass determined for all specimens. Sex was confirmed by dissection.

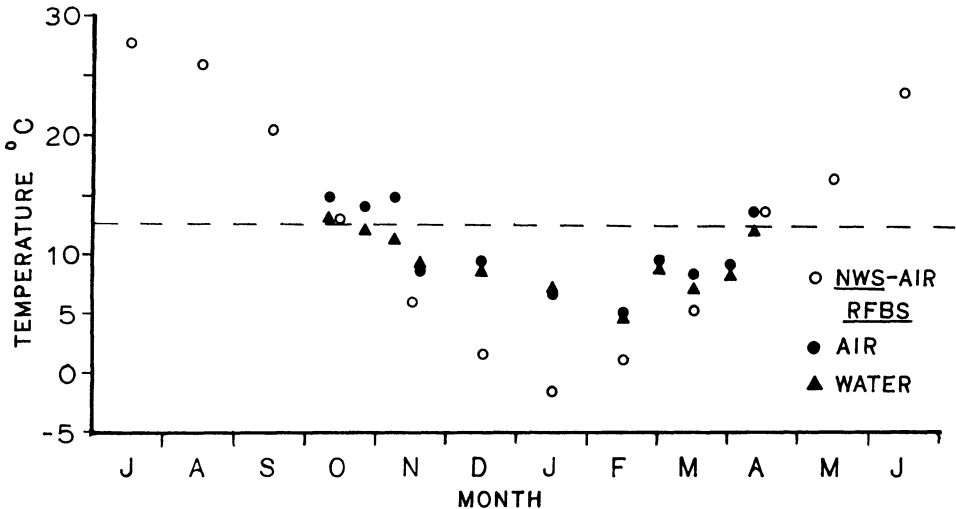


Fig. 2.—Mean monthly temperatures recorded at the National Weather Service Station, 5 km E of RFBS (open circles), RFBS air temperatures (closed circles) and RFBS water temperatures (solid triangles). All data are for 1979-1981. Dotted line represents the predicted cave temperature [= mean annual surface temperature (NWS)] for RFBS

RESULTS

ECOLOGY OF CAVE USE

Population Size and Demography.—The estimated overwintering population of *Rana palustris* at RFBS (adults only) was 365 (95% CI, 252 to 661). This estimate should be considered conservative because of the possibility of small undetected hibernacula within the cave. Number of juveniles was not estimated by mark-recapture because of the difficulty of marking small individuals with the branding equipment available. Juveniles comprised 11% (10 of 93) of a population sample taken on 30 March-1 April 1984. This estimate may be low due to the difficulty of detecting small individuals and the differential effects of winter mortality (*see below*).

The study population used RFBS from July through March, with large variation in numbers present (Fig. 3). Highest number (*see above*) occurred in November-February, and lowest (10-20) during July-August. No frogs were found from mid-April-June. Numbers increased beginning in September with a maximum reached by early November (Fig. 3). Populations remained at this level until initiation of emergence in March or early April.

Males and females differed in temporal use of RFBS; males appeared in July whereas females were not observed until September (Fig. 4). No sexual differences in time of emergence were observed.

Seasonal variation in microhabitat use was also observed. From September through March, frogs were usually found in or near water on the cave floor; in July and August frogs (males) used small solution pockets, and cracks and crevices in the cave walls. These sites usually held no water and were in relatively dry sections of the cave walls. Both males and females were occasionally found in similar places at other times of the year, so that seasonal, rather than sexual, factors appear to be responsible for this variation.

Distribution within the cave paralleled changes in cave temperature and external ambient temperature (*see Figs. 2, 3, 5*). With decreasing air and water temperatures, frogs moved toward the pool and, as temperature decreased in the pool proper, frogs concentrated in dense aggregations in the hibernaculum (Fig. 1B).

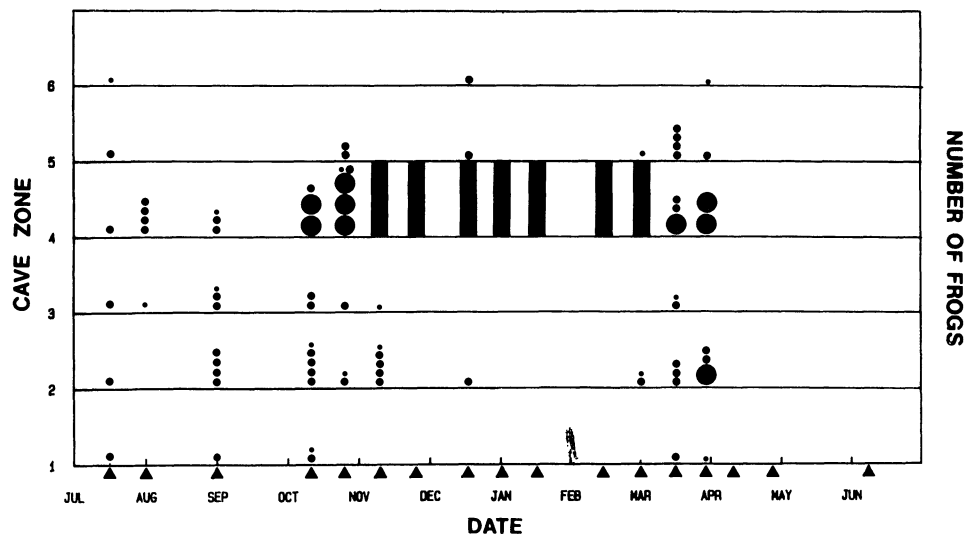


Fig. 3.—Number and distribution of *Rana palustris* in RFBS: August 1979—March 1981. Small circles represent 1 frog; medium circles, 2 frogs; large circles, 10 frogs; bars, >100 frogs. Triangles indicate observation dates

From late November through early March few frogs were present in the pool, their presence there being limited to periods of warmer cave temperatures. Increasing temperatures in March corresponded with movement of *Rana palustris*, first from the hibernaculum to the pool and then into the lower portions of the cave, prior to emergence. Initiation of emergence from the cave corresponded with reversal of the thermal gradient between the pool and the lower portions of the cave in 1981 (temperature data not available for other years) (Fig. 5). The earliest date at which emergence from RFBS was complete was 1 March in 1982. *Rana palustris* were abundant in RFBS past mid-March in 1980 and 1981, and large numbers were present well into the 1st week of April 1984, a 5 to 6-week difference in emergence dates over 4 years of observations. Weather was unseasonably warm in February and March of 1982, and unseasonably cold in late February, March and the beginning of April 1984, indicating that weather

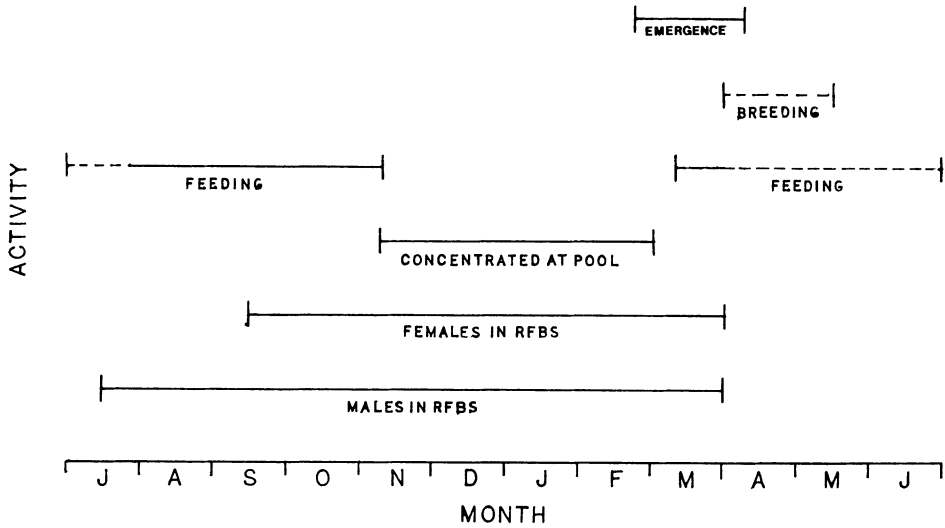


Fig. 4. — Summary of *Rana palustris* activity at RFBS

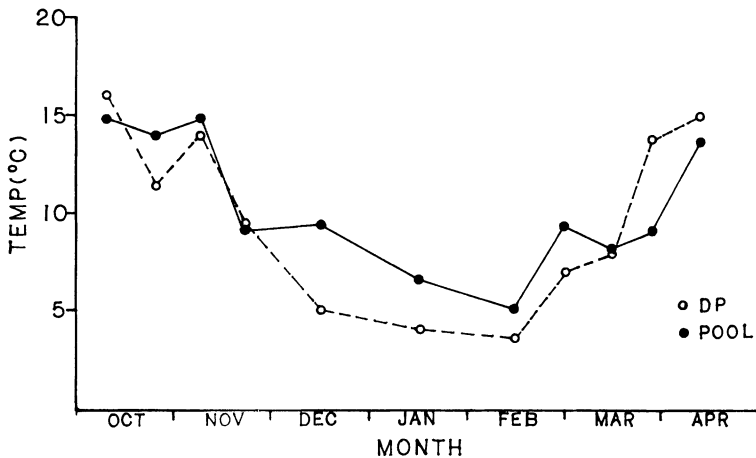


Fig. 5. — Temperature at pool and DP stations showing seasonal reversals of thermal gradient

conditions greatly affect the date of emergence from RFBS and that 1980 and 1981 dates may best approximate average emergence dates from RFBS.

Winter activity.—After *Rana palustris* concentrated at the pool in November, little movement within the cave occurred (Fig. 3). At temperatures (air and water) above approximately 7 C, frogs were found in the pool and around its edge, especially near the hibernaculum entrance, and remained active and capable of fairly rapid movements. At temperatures below 6 C few frogs were found outside the hibernaculum and little activity occurred. None was found out of water at low temperatures. Frogs found outside the hibernaculum under such conditions usually concealed themselves among rocks on the pool floor and moved very slowly when disturbed. Most were quite emaciated, especially the juveniles. The presence of these individuals in the pool did not result from lack of space in the hibernaculum.

Winter mortality.—Levels of overwintering mortality in this population can only be inferred as no direct determination was made. Thirty-six corpses were observed during the study, suggesting low overall winter mortality. Juveniles comprised 11% of a sample taken on 30 March-1 April 1984, but comprised 84% of the 25 corpses in which size class was noted. Mortality increased dramatically in the latter half of winter (Fig. 6), especially among juveniles. Throughout the study it was juveniles that appeared most affected by overwintering stress, the majority appearing emaciated by midwinter. Mortality among adults was more evenly distributed, suggesting factors other than winter stress may have been acting.

Feeding activity.—Most frogs examined during the study (58/75 = 77%) contained no food in the stomach, and the few that did provided little identifiable material. Feeding was seasonal in the RFBS population (Fig. 7). The latest incidence of feeding occurred in early November, the earliest in early March, indicating that no feeding occurred during the winter.

DISCUSSION

Wintering population at RFBS.—RFBS contains a large overwintering population of *Rana palustris*, numbering in the hundreds, with fewer present much of the remainder of the year. The literature contains no information on the size of cave-associated populations of *R. palustris*. Sweet (1960) reported a hibernating aggregation of 71 from an “ar-

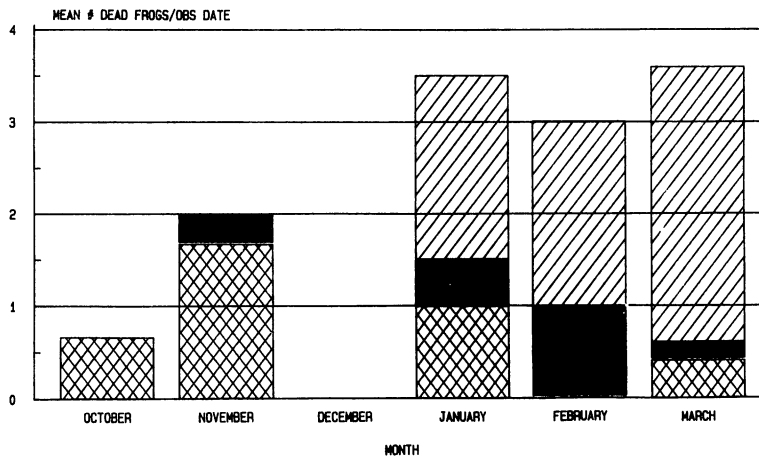


Fig. 6.—Overwintering mortality in *Rana palustris* at RFBS. Bars represent observed mortality corrected for number of cave visits. Bar divisions indicate abundance of juveniles (//), adults (solid) and undetermined (XX) individuals in samples. Data are pooled from the winters of 1979-1980 and 1980-1981

tificial" cave. Gardner (pers. comm.) observed 65 and 92 in two Missouri caves in January and March, numbers similar to the maximum observed in a single day (outside the hibernaculum) at RFBS (60 +), suggesting that the large number present at RFBS may not be unusual.

Breeding season and potential breeding sites.—Potential breeding sites near RFBS include numerous farm ponds ranging in size from a few square meters to more than a hectare, small woodland ponds and pools, Cedar Creek and its tributaries, the intermittent creek that feeds RFBS and the cave stream itself. No evidence exists for the use of caves as breeding sites. Brown (1984) reported oviposition by a single female in an Indiana cave but provided insufficient detail.

Rana palustris in Missouri use a variety of breeding sites, including woodland pools and ponds, stream overflow pools and farm ponds, usually in late March or April (pers. observ.). Emergence from the cave occurs in March or early April and both males and females appear reproductively "ready." The state of energy reserves may affect breeding date, as both males and females at RFBS show total reduction of coelomic fat stores by spring so that feeding and replenishment of reserves may be necessary before breeding. Brenner (1969) demonstrated a period of fat deposition prior to the onset of breeding activity in *Rana clamitans* and *Acris crepitans*, followed by increased energy use and decrease in fat reserves during breeding.

Cave use.—*Rana palustris* were observed at RFBS from July through March. Most published observations fall within this period, with additional observations in June in Tennessee (Barr, 1953), Missouri (Smith, 1948) and Mississippi (Knight, 1972), and May in Missouri (Myers, 1958). Brode (1958) provides evidence that cave use may occur year-round in Mississippi. Gardner (pers. comm.), in a biological survey of Missouri caves, observed *Rana palustris* in all months.

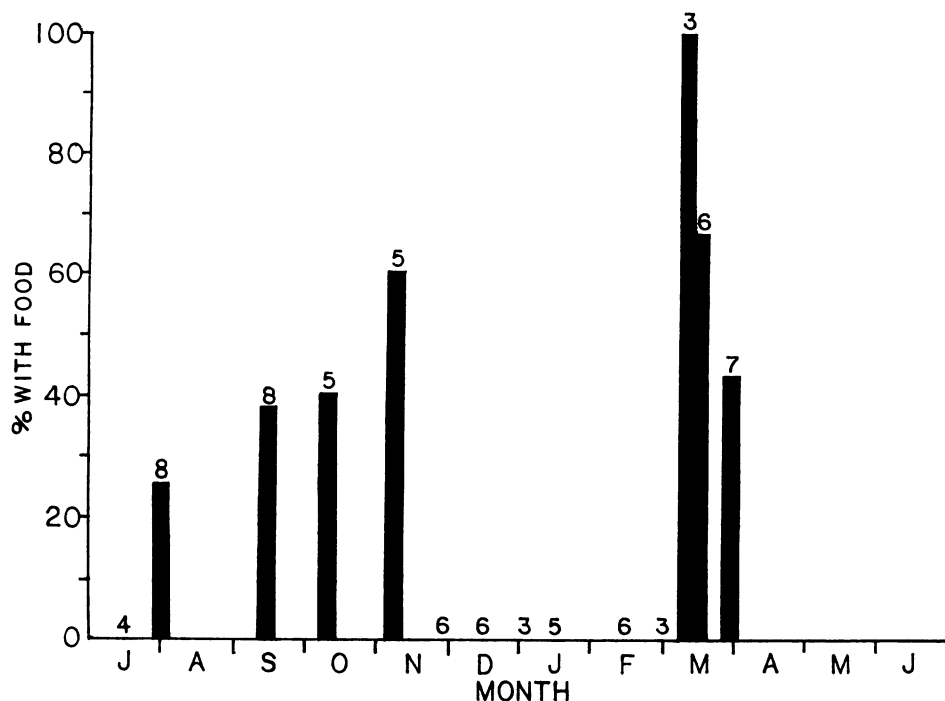


Fig. 7.—Seasonal change in percentage of *Rana palustris* actively feeding, as indicated by stomach contents. Numbers above bars indicate sample size

Males were observed at RFBS 2 months earlier than females. This may suggest differences in the ecology of the sexes, reflecting differences in behavior or physiological requirements at this time of year. Individual time of arrival at RFBS also varies. A critical consideration may be the completion of oogenesis and spermatogenesis and the accumulation of sufficient energy reserves for overwintering. This may partly explain the early arrival of some males; males which may have met their energy needs "early" and seek the safe shelter and lower temperatures of the cave. Adult females may need a longer period of activity to meet increased energy needs for growth and clutch development. Juveniles may similarly require a longer active season for growth.

Distribution of *Rana palustris* within RFBS follows changes in external and cave temperatures. Frogs move toward the more thermally stable central portion of the cave with decreasing temperatures, eventually entering the thermally buffered hibernaculum (Zone 4). Movement within the cave appears similar to that described by Sexton and Hunt (1980) for two species of snake in a cave hibernaculum. The snakes responded to reversal of the thermal gradient between the front and rear of the cave, and movements into and emergence from hibernation were related to these seasonal (autumn-winter, winter-spring) reversals (Sexton and Hunt, 1980). Hibernation at RFBS involves two distinct gradients: an air and water temperature gradient influencing movements into and out of the cave and within the cave passage, and a water temperature gradient influencing movement between the pool and the hibernaculum. Emergence from the cave is closely linked to the spring thermal gradient reversal, whereas autumn movements are less synchronous, perhaps owing to factors such as distance traveled and energy requirements. Seasonal gradient reversals may be important for other species of anurans as well, both those that hibernate in terrestrial or subterranean sites and those that use aquatic sites.

Though *Rana palustris* are most abundant in caves in winter, and cave use appears to center on the cave as a hibernaculum, it is notable that they may be active in considerable numbers deep within caves at almost any time of year (J.E. Gardner, pers. comm.; pers. observ.). This is not an isolated phenomenon and can be observed in caves throughout the Ozark Plateau. These observations, perhaps even more than the data on the RFBS population, speak to the prevalence and intensity of the troglodyte habits of *R. palustris* in this region.

Temperature and cave use.—The stable environment of caves is buffered against summer heat, winter cold and desiccation. Brattstrom (1967) and Brattstrom and Lawrence (1962) investigated the rate of thermal acclimation and critical thermal maximum (CTM) in several species of *Rana*, including *R. palustris*; of 10 species of Nearctic and Neotropical ranids, including four species with which *R. palustris* occurs sympatrically (*R. pipiens*, *R. sylvatica*, *R. clamitans* and *R. catesbeiana*), *R. palustris* has the least capacity for thermal acclimation and the lowest CTM (Brattstrom, 1967). It also has the slowest rate of thermal acclimation (Brattstrom and Lawrence, 1962; Brattstrom, 1967). These data suggest that the cave may be important as a refugium against both temperature extremes and rapid fluctuations in temperature. In overall acclimation ability and CTM, *R. palustris* most closely resembles *R. sylvatica*, clearly the most northerly, cold-adapted species tested. No data on critical thermal minimum or temperature preferences are available for *R. palustris*.

Several studies demonstrated significant differences in desiccation tolerance among species of *Rana*, including such closely related species as *R. pipiens* and *R. blairi* (Thorson and Svihla, 1943; Thorson, 1955; Schmid, 1965; Gillis, 1979). Though no data are available on *R. palustris*, the wide range of desiccation tolerances within *Rana*, and correlation of these differences with habitat preference, suggest water conservation as a potentially important factor in the cave habits of *R. palustris*.

A potential advantage of using a cave hibernaculum rather than a pond or stream is that the medium for hibernation in the latter may preclude detection of brief, unseasonal periods of favorable weather. Cave-hibernating frogs may extend their active sea-

son by detecting and using these favorable periods during the "transition" periods between the active season and hibernation. This increased responsiveness to environmental change in cave hibernation vs. hibernation in a stream or pond may be important. Caves such as RFBS (weakly buffered caves) fluctuate with external environmental conditions, especially temperature and rainfall, and frogs may be able to more closely monitor external conditions than if they are buried in the mud of a stream or pond. Even more typical, environmentally stable (strongly buffered) caves are less thoroughly buffered than aquatic hibernation sites against short-term fluctuations in external conditions; clues to these changes penetrate more easily. This reflects what may be the less "committed" nature of cave hibernation: an animal need not leave the safety of the cave to assess external conditions, and perhaps, take advantage of unseasonable surface conditions. It seems likely that the feeding incidents in November and March result from such a situation. The advantages of a potential increase in feeding season and, therefore, available energy, have important implications for survival, growth and reproduction. Increase in energy, whether gained through expanded opportunities for surface feeding, limited cave feeding or both, may alone provide the ecological impetus for cave use.

The impact of Rana palustris on cave ecology. — The role of *R. palustris* in the ecology of caves is unclear. In RFBS, and in other *R. palustris* caves which do not support large numbers of bats, the species may have the greatest total biomass of any species present in winter (excluding also such large mammals as raccoon, bobcat, bear, etc.). Though empirical evidence is lacking, observations suggest that at RFBS *R. palustris* not only has the greatest biomass of any species, but may approach the combined total for all other species during the winter. This massive influx (by cave standards) of biomass must, almost by definition, have a significant impact on the cave ecosystem. Actual deposition of organic materials resulting from excretion and death, both of which occur in RFBS, provides significant energy input to the cave ecosystem. Cave feeding by *R. palustris*, though still problematical, may also be significant in terms of the total productivity, energy availability, energy flow and species composition of the cave.

Caves and Rana palustris ecology. — The strong association of *R. palustris* with caves and karst features over a large portion of its range suggests an important role for caves in the distribution and ecology of the species in these areas (Schaaf and Smith, 1970). We have presented suggestions regarding possible advantages of cave use but we are quite far from identifying any requirements that caves fulfill in the ecology of *R. palustris* and any constraints on distribution that may be imposed by these requirements. The actual ecological or evolutionary advantages of cave use remain obscure. A final consideration is that clues to the ecological or evolutionary advantage may lie not in the species' present, but in the species' past.

Pleistocene glaciations and cave use. — Trogllobites arise by the isolation of populations of troglomorphic species in caves and the extinction of intervening surface populations as a result of climatic change (Barr, 1968; Vandel, 1965). This process was especially prevalent during the Pleistocene, when caves in the temperate zone served as refugia for the ancestors of many troglomorphic organisms during both Glacial and Interglacial periods (Barr, 1968; Poulson and White, 1969; Vandel, 1965). The cave habits of certain troglomorphic animals may have arisen in an analogous way, by the isolation of populations in association with cave/spring systems during Glacial and Interglacial periods. Species in the Interior Highlands, which lay at the edge of maximum glacial advance, would have been faced with two options: to retreat and advance in response to Glacial movements, or to use what refugia were available within this zone of major climatic fluctuation. The refugia in this region which were buffered against both temperature and aridity extremes were the numerous cave/spring systems.

For *Rana palustris* the facultative use of cave and karst areas as seasonal and long-term refugia, while maintaining opportunistic breeding habits, would ensure survival over a wide range of climatic conditions and preserve the mechanism for rapid dispersal

and colonization during favorable periods. Recurrent use of such refugia (as a result of the periodicity of glaciation events) would isolate both local populations and regional metapopulations, with resulting genetic and ecological divergence. This is precisely the situation suggested by Schaaf and Smith's data on geographic variation in the species: specimens from karst areas were highly variable and unassignable to geographic race (Schaaf and Smith, 1970). Study of local and regional genetic variation in *Rana palustris* populations would shed considerable light on the problem.

The hypothesis that best fits the available data is that cave use in *Rana palustris* originated as a result of the isolation of populations in association with cave/spring systems during the climatic fluctuations accompanying Pleistocene glaciations. This behavioral adaptation was facilitated by "preadaptive" physiological characters and the proximate ecological advantages of cave use itself, and is maintained as a function of these factors and the periodicity of glaciation events.

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