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ASPECTS OF THE LIFE HISTORY AND ECOLOGY OF THE GREEN SALAMANDER, *ANEIDES AENEUS*, IN KENTUCKY

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ABSTRACT

The annual cycle of the green salamander, *Aneides aeneus*, in southeastern Kentucky is presented and compared to populations from other localities. The four main periods of the cycle were studied with emphasis on the breeding period, which extended from late April to early November. Pairing and mating occurred primarily in the spring and fall. Most egg clutches were deposited from 1 to 16 July and brooded by an attending female over a period averaging 73.1 days (range = 67–82 days, n = 21). Most of the young hatched during 16 to 30 September. Females remained with hatchlings an average of 23.5 days (range = 3–5 weeks, n = 17). The dispersal and aggregation period, during which the visible population reached its highest numbers, extended from early November to mid–December. The hibernation period, a time when *A. aeneus* were rarely observed, extended from mid–December to early March. The posthibernation aggregation and dispersal period, during which the visible population increased as they dispersed from hibernating crevices, extended from mid–March to late April. The salamanders were most active on humid nights, although some diurnal activity was observed on overcast days and in shaded areas under rock ledges. The activity of *A. aeneus* was confined primarily to sandstone cliffs.

INTRODUCTION

Gordon (1952) provided considerable information about the life history and ecology of the green salamander, *Aneides aeneus*, based on observations of populations in North Carolina and Georgia. Woods (1968) did a similar study on a population in northeastern Mississippi. Snyder (1971) conducted an extensive study on brooding behavior of females in this species. Cupp (1971, 1980) reported on courtship and mating behavior and possible territoriality in *A. aeneus*. Recently, Juterbock (1989) reported on some restricted populations in southern Ohio.

This species typically occurs in rock crevices of sandstone cliffs and rock outcrops along the Appalachian Mountains in the eastern United States. Some individuals have been found under the bark of fallen trees and stumps (Pope 1928, Barbour 1971) and in limestone crevices, as reported in southern Ohio (Walker and Goodpaster 1941). They are well–adapted for the rock cliff habitat, with a flattened body, long, square–tipped toes, and a muscular tail that aids in climbing. Their cryptic coloration allows them to blend in very well with the lichen–covered rock cliffs.

When closely examined, *A. aeneus* exhibits a distinct sexual dimorphism. Males have enlarged jaw muscles and elongated maxillary and premaxillary teeth that penetrate the upper lip. Females have somewhat enlarged jaw muscles and spinelike maxillary and premaxillary teeth that are usually less well–developed than in males (Wake 1963, Gordon 1967). Males have a mental hedonic gland which is used during courtship (Cupp 1971). This gland is often yellowish–orange and easily observed in most males.

Most intensive studies (Gordon 1952, Snyder 1971) on *A. aeneus* have centered on populations in the Blue Ridge Mountains, leaving much to be done in other parts of the range. In addition, no long–term studies exist in which populations have been monitored over a period of several years. And only limited observations have been reported on courtship and mating, territoriality, and reproduction. Thus, in 1976 I initiated a long–term study on selected populations of *A. aeneus* in southeastern Kentucky. This paper, based on parts of that study, reviews the annual cycle of this species, and reports on some observations of their activity patterns.

METHODS

This study was conducted at localities in Whitley and McCreary counties in Kentucky, where populations of *A. aeneus* occur in sandstone cliffs and outcrops. Systematic searches for individuals were made during each visit to the study area. Animals caught and removed from the rock crevices were categorized by sex and breeding condition, and then returned to their original crevices. The presence of egg clutches with attending females was noted. Searches were conducted in most months of the year, but primarily March through November as these salamanders are more easily found during this time. One to four visits per month were made during the years 1977–1988, except no visits were made during 1980.

The annual cycle of *A. aeneus* was divided into four main periods (Table 1) as described by Gordon (1952). Sexes were distinguished by the

Table 1. The annual cycle of the green salamander (*Aneides aeneus*) from southeastern Kentucky compared with data from two other localities.

Period	Highlands, NC (Gordon 1952)	Tishomingo Co, MS (Woods 1968)	SE Kentucky (this study)
Breeding	late May–late Sept.	late March–Nov.	late April–early Nov.
Pairing and mating	late May–early June	late May–June	late March–early Nov.
Egg deposition	June	15–20 July	25 June–25 July
Egg hatching	early Sept.	7–20 Oct.	14 Sept.–6 Oct.
Brooding of hatchlings	4 weeks	—	3–5 weeks
Prehibernation dispersal and aggregation	late Sept.–Nov.	Oct.–Nov.	late Oct.–mid Dec.
Hibernation	Nov.–April	Dec.–March	mid Dec.–mid March
Posthibernation aggregation and dispersal	late April–late May	late March–early April	mid March–late April

presence (in males) or absence (in females) of a mental gland (Cupp 1971), and females were noted as being gravid or nongravid. Two indicators of the mating period were noted. These included the presence of male–female pairs within crevices and females with a sperm plug in the cloacal vent.

To ascertain the egg development period (and brooding time of females), individual egg clutches were monitored from the time of deposition to hatching during 1985–1990. Also noted was the amount of time females remained with the young after hatching.

Observations were made on activity patterns of *A. aeneus* during nocturnal and diurnal searches. Also, extensive searches were conducted in habitats other than rock outcrops (e.g., under tree bark and assorted ground cover—rocks, logs, etc.).

RESULTS AND DISCUSSION

Annual Cycle

The annual cycle of *A. aeneus* was divided into four main periods (Gordon 1952) primarily to provide an organizational framework for study. Thus, one might expect some overlap of activity characteristic of adjacent periods within any one annual cycle. Also, annual cycles may vary from year to year due to seasonal fluctuations of temperature, rainfall, food supply, and perhaps other factors. In this study, comparisons were made between Kentucky populations and those populations studied by Gordon (1952) and Woods (1968) as listed in Table 1.

Breeding Period. The breeding period was by far the longest of the main periods of the annual cycle. It was subdivided into four phases: pairing and mating, egg deposition, egg hatching, and brooding. The breeding period appeared to extend from late April to early November when pairing and mating occurred, primarily in spring and fall and perhaps to a limited degree in the summer. Male–female pairs were found from 31 March to 5 November, with most of these observed in May and October (Figure 1). Several pairs were also found in June and early November. If the amount of search time (man–hours) required to locate pairs is considered, the April and November data would increase to about twice that in Figure 1. Sperm plugs were found in the cloacal vents of females in April, May, and June. Snyder (1971) reported finding a gravid female with a sperm plug in September. I observed mating in the field in June and October (Cupp 1971).

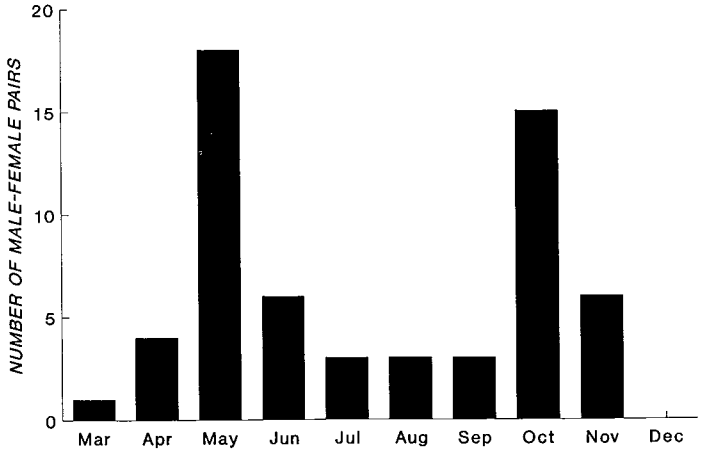

Figure 1. Number of male-female pairs of *Aneides aeneus* noted by month over the 11-year study period.

During the egg–deposition phase, females laid clutches of 14–20 eggs in individual rock crevices. This usually occurred during the period 25 June to 25 July, with most clutches being deposited from 1 to 16 July. Females remained with their eggs for an average of 73.1 days (range = 67–82, n = 21). When compared to the findings of others (Table 1), this mean seems rather low and the range surprisingly high. Development of Kentucky *A. aeneus* was about two weeks faster than that reported for the Highlands, North Carolina population, which required 86.8 days (range = 84–91, n = 5) (Gordon 1952). This may be explained by the higher altitude of the Highlands population. However, the northeastern Mississippi population required 82 days (n = 1) or longer (Table 1) for development (Woods 1968), even though the climate there is warmer than the Kentucky locality. The egg deposition time was about the same for the two localities, but the egg hatching time was at least nine days earlier in Kentucky.

I observed one instance of egg deposition in which a gravid female, before laying any eggs, was first located on her back (in egg–laying position) in a narrow, flat crevice at 2000 hours on 1 July 1977 (Figure 2a).

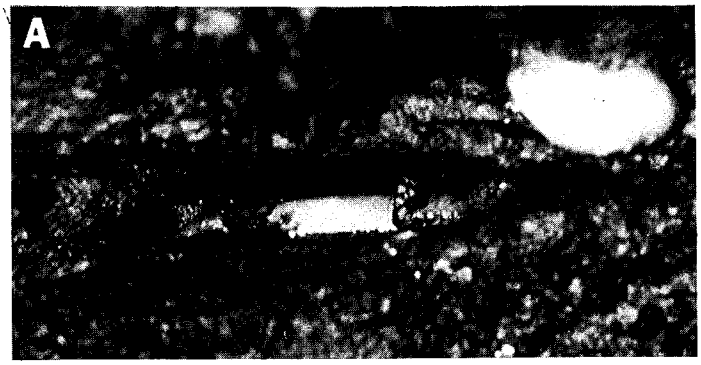

Figure 2. (a) Female Aneides aeneus in egg-laying position at 2000 hours on 1 July.

By 1000 hours on 2 July, 12 eggs had been attached to the ceiling of the crevice. The entire process was similar to that described by Gordon (1952). The female was observed to attach individual eggs directly to the ceiling by raising the cloacal vent upward until the emerging egg was in contact with the ceiling (Figure 2b). Adhesive secretions released by the female were used to attach the eggs to the ceiling of the rock crevice. She

Figure 2 (b) By 1000 hours on 2 July, the female had deposited 12 eggs and is shown here raising the cloacal vent upward and attaching an egg to the crevice ceiling.

shifted her body about at intervals during the process and was observed using her hind legs to cluster the eggs. Complete egg deposition has been reported to take 23–31 hours (Gordon 1952).

The brooding behavior of females benefits the eggs in various ways, including: maintaining water balance of eggs, protection from small predators, providing a possible antifungal effect, and removal by consumption of eggs that have died within the clutch (Gordon 1952, Snyder 1971).

Hatching of eggs occurred during the period 14 September to 6 October, with most of the young emerging during the period 16 to 30 September. Brooding of young occurred from the time of hatching to the time when the female left the crevice between mid–October and early November, a 3–5 week period ($\bar{X}$ = 23.5 days, n = 17). The behavior of females and hatchlings during this time was similar to that described by Gordon (1952).

Prehibernation Dispersal and Aggregation Period. This period extended from late October through the first half of December. During this time, the visible population of *A. aeneus* reached its highest numbers in this and Gordon's (1952) study. This, I found, was because many adults appeared that were not seen during the summer. By this time, females had usually left the hatchlings in the brooding crevices. Small groups of hatchlings remained in the breeding crevices for some time, while some had dispersed to other crevices. Young, dispersing *A. aeneus* hatchlings and juveniles were occasionally found in areas where adults were usually not found (e.g., in interfaces between rock cliffs and tree limbs, on more moist rock faces and crevices, and on one occasion, in a crevice of a wooden handrail on a forest service trail).

Hibernation. This period extended from mid–December to early March when animals were scarce at the surface. I observed a few animals during this period when the weather was mild, but then only in areas where the crevices extended deep into the cliff. This is similar to the observations of Gordon (1952).

Posthibernation Aggregation and Dispersal Period. This period extended from mid–March to late April and overlapped somewhat with the breeding period. During this time, the visible population of salamanders increased as individuals emerged from hibernation crevices and dispersed into adjacent areas. First, the salamanders apparently moved near the cliff surface to crevice hibernacula favorable for shelter and feeding. Then, some individuals may have migrated to outlying rock outcrops (perhaps 100 m distant), while others occupied crevices not far from the hibernacula. I did not observe aggregations of salamanders as described by Gordon (1952). A number of males with well–developed mental glands were observed, whereas very few gravid females were seen during this period. Many young first– and second–year animals were observed as well. Larger, older males appeared somewhat later (late April to early June) and often occupied crevices used in previous years.

Males are territorial and aggressively defend their crevices against other intruding males (Cupp 1980). Within a few days or weeks, gravid females apparently select males that occupy favorable crevices and pair with them. Females will either remain in those crevices to lay and brood eggs, or move to other favorable crevices to lay their eggs. My observations and those of Gordon (1952) suggest that individual females apparently often select the same brooding crevices that they used in previous years.

During this period and the early part of the breeding period, many *A. aeneus* apparently migrate to outlying rock outcrops from hibernation crevices or hibernacula (Gordon 1952). Williams and Gordon (1961) collected two dead green salamanders from a road adjacent to some rock ledges in Whitley County, Kentucky on 17 April 1960. They suggested that the salamanders were migrating from hibernation crevices during the posthibernation dispersal period. In Oconee County, South Carolina, six green salamanders were observed crossing a highway on the evening of 8 May 1973 (Edmund D. Brodie, Jr., pers. comm.). In Whitley County, Kentucky, I observed a single *A. aeneus* crossing a highway near my study area on the evening of 19 June 1976. Similar movements to hibernacula probably occur during the fall dispersal and aggregation period.

Diel Activity

Green salamanders were primarily active on humid nights when they emerged from their crevices to crawl about on the rock surface, foraging for prey. On less humid evenings, they remained in their crevices but often extended their heads from the opening. During the day they typically remained in the crevices, often with their heads facing the crevice opening. Some movement apparently occurs within crevices, including the taking of prey organisms that enter the crevices during the day. In a study of the food habits of *A. aeneus* Lee and Norden (1973) believed that the salamanders were actively foraging at the time of collection (1530–1800 hours), based on the condition of the prey organisms that were removed from their stomachs. *A. aeneus* readily accepted prey items I offered them in the laboratory during the day or night.

Some diurnal activity has been documented outside the crevices, especially on cloudy, humid days (Gordon 1952, Brandon and Huheey 1975). I reported courtship and mating behavior of *A. aeneus* at noon on 17 October, an overcast day (Cupp 1971). Since then, I have observed several *A. aeneus* individuals moving in shaded areas under rock ledges of cliffs (16 July 1987, 18 April 1981), on top of a large outcrop (27 July 1978), and on the vertical surfaces of cliffs (at least twice) during the day. In several instances, individuals were found with their heads and upper bodies leaning out of crevices on overcast days, apparently looking for prey. Thus, diurnal activity in green salamanders is not unusual, and their cryptic coloration would aid them in avoiding predation during this time (Brandon and Huheey 1975).

In my study area, I have observed *A. aeneus* only on sandstone cliffs and outcrops, with the exception of two individuals found on different nights on the same tree trunk about 1.5 m from the base. This tree was associated with adjacent rocks from which the salamander presumably came. Many other trees (standing and fallen) were searched for *A. aeneus* both day and night, but none were found. Also, many hours during all seasons were spend turning rocks and debris on the forest floor adjacent to the cliffs with the same result. This suggests that foraging activity must occur on the rock surfaces, on cliff ledges, or within crevices. Prey known to be consumed by *A. aeneus* have been found in rock cliffs (Woods 1968, Lee and Norden 1973).

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