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Longevity and Abandonment of Burrows Used by the Red Hills Salamander (*Phaeognathus hubrichti*)

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The Red Hills salamander, *Phaeognathus hubrichti*, is a fossorial species endemic to the Red Hills region of Alabama between the Alabama and Conecuh Rivers (Schwaner and Mount, 1970). These salamanders prefer steep mesic slopes composed of sandy soil and siltstone shaded by a hardwood overstory where they build extensive burrow systems (French and Mount, 1978; Dodd, 1991). Burrows typically follow root tracings or are created from existing burrows of invertebrates, small mammals, or conspecifics (Brandon, 1965). Salamanders can be observed in the hours after dusk when they forage for snails, arthropods, and other invertebrates in and around entrances of their burrows (Brandon, 1965). *Phaeognathus hubrichti* was designated a threatened species by the U.S. Fish and Wildlife Service in 1976 due to direct habitat loss and habitat degradation caused by forestry practices (French and Mount, 1978).

Little is known about the life history of *P. hubrichti* because most activities are believed to take place within a burrow (Jordan, 1975). This close association between a salamander and its burrow suggests that burrow longevity may play an important role in the activities of this species. Closure of burrows may result in above-ground movement of salamanders to a new burrow or below-ground burrowing to create a new burrow entrance.

Burrows of *P. hubrichti* are positioned on steep hillsides and several factors could affect the amount of time a burrow remains open. Erosion results in a concentration of burrows in the middle section of a slope at disturbed sites, whereas at undisturbed sites burrows are usually located in the upper portion of the slope (Dodd, 1991). Predators (e.g., armadillos, *Dasy-*

APPENDIX

All lizards from which chromosomes were examined are individually catalogued in the collection of the Laboratorio de Citogenética, Facultad de Ciencias, Universidad de Chile. Catalogue numbers are in pa-

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TABLE 1. Summary of censuses of *Phaeognathus hubrichti* burrows. Closed is number of burrows closed since the previous census. New is number of new burrows recorded. New burrows were not recorded on some dates (2 May 1996 and 15 Oct. 1996) and closed burrows could not be recorded on the first sampling date (4 Nov. 1995), so these data were not available (NA). Occupied is the number of burrows observed with salamanders inside. Total number of burrows includes occupied (SAL) and empty (OP) active burrows.

Date	Closed	New	Occupied	Total burrows
4 Nov. 1995	NA	25	25	25
2 May 1996	9	NA	9	16
15 Oct. 1996	5	NA	4	11
29 Oct. 1996	0	9	13	20
19 Nov. 1996	1	3	12	22
2 Feb. 1997	6	3	8	19
8 Feb. 1997	3	2	3	18
9 Mar. 1997	2	5	9	21
13 Apr. 1997	2	3	6	22
26 Apr. 1997	2	10	14	30
4 May 1997	8	1	6	23

pus novemcinctus; feral pigs, *Sus scrofa*; and small mammals such as shrews) could destroy burrows by digging the salamanders out (Dodds, 1991). Finally, rocks, fallen trees, and vegetation such as moss could increase the length of time a burrow remains intact by sheltering it from erosion and stabilizing the soil. The objective of this study was to determine burrow longevity at a relatively undisturbed site. Here we present baseline data on *P. hubrichti* burrow dynamics and evaluate factors associated with burrow longevity.

This study was conducted at Haines Island Park, an Army Corps of Engineers property in Monroe County, Alabama. The study site was approximately 18 m long and 4 m wide on a steep hillside below a rock bluff and shaded by a hardwood overstory. On 4 November 1995, 25 burrows in which we observed *P. hubrichti* were marked with metal tags and colored flags. During subsequent censuses over the next year and a half, burrows were classified as either: (1) occupied; those where a salamander was observed (SAL), (2) open; those where no salamander was observed, but recent use was evident (burrow entrance smooth and oval in shape; width greater than height) (OP), and (3) closed; those where no active burrow was present (CLO). New burrows were identified by observing unmarked holes with a salamander inside and were marked with a numbered metal tag and colored flag near the burrow entrance. We revisited the site 10 times from May 1996 to May 1997 and status was recorded for all marked burrows. Data were taken from dusk until approximately 2200 h on sampling dates.

To estimate the length of time a burrow remained open, transition matrices were constructed by determining the probability of a burrow changing from one category to another between sampling dates (Caswell, 1989; Guyer and Hermann, 1997). The first sampling date (4 November 1995) was not used in the analysis

TABLE 2. Transition matrix constructed for burrow use patterns of *Phaeognathus hubrichti*. Categories are: salamander observed within burrow (SAL), burrow open, but with no salamander (OP) and burrow closed (CLO). The data represent the mean of nine individual matrices where each number represents the probability of a burrow in one category changing to another category over a period of time; t is date of first census, c is intercensus interval (mean c = 42 d, SD = 50 d).

		Status on day t + c		
		SAL	OP	CLO
Status on day t	SAL	0.35	0.47	0.18
	OP	0.15	0.69	0.16
	CLO	0.0	0.0	1.0

because only burrows in the SAL condition were recorded. This resulted in nine matrices from intercensus intervals from 2 May 1996 to 4 May 1997. An overall matrix representing the average of each category within the matrix was constructed. From this matrix using mean values, a survivorship curve for the burrows was constructed using the categories SAL and OP. This curve was used to predict the longevity of 1000 hypothetical burrows over time. Burrow half-life, the time at which half of the 1000 hypothetical burrows were estimated to become closed, was determined. In addition, we used a burrow abandonment curve to examine the relationship between the number of salamanders remaining inside their burrows and the number of days elapsed between censuses. This curve was constructed from the transition matrix using only the category SAL. Because data on burrow occupancy of *P. hubrichti* is limited and to simplify our analysis, we assumed that each salamander occupied only one burrow, and that each burrow was occupied by only one salamander. There is some evidence that more than one salamander may occupy a burrow system, but each salamander is assumed to use a separate burrow entrance (Jordan, 1975).

The total number of active burrows (SAL and OP) present each trip fluctuated among censuses (range 11–30, \bar{x} = 20.6, SD = 4.9), but no consistent trend over time was observed (Table 1). Number of new burrows and burrows closed since the last census also fluctuated among censuses but displayed no consistent trend over time (Table 1). The mean of nine matrices (calculated from censuses starting 2 May 1996) resulted in an overall matrix with a mean intercensus interval of 42 d (SD = 50 d) (Table 2). The minimum burrow half-life was determined to be 150 d (Fig. 1). From the abandonment curve we estimated that half of the salamanders abandoned their burrows within 30 d (Fig. 1).

Approximately 50% of the original burrows remained open at our study site after about six months, while only four burrows (6.7% of total burrows) remained open for the duration of the study (18 mo). The total number of active burrows at our site conforms to a dynamic equilibrium with the number of recently filled burrows offset by a similar number of newly opened ones. Closure of burrows was probably not due to natural salamander mortality, as *P. hubrichti*

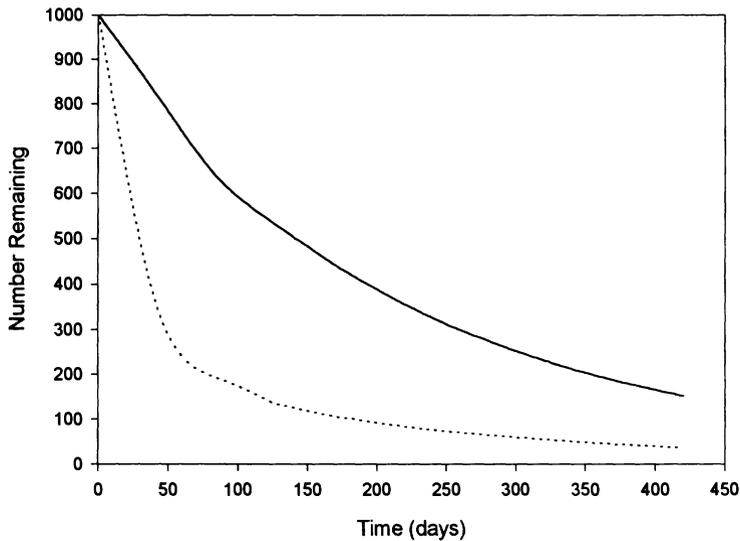


FIG. 1. Longevity and abandonment of 1000 hypothetical *Phaeognathus hubrichti* burrows. Solid line is number of burrows remaining open over time, dashed line is number of burrows retaining salamanders. This graph assumes that each salamander occupies only one burrow at a time.

can live at least 11 yr (Parham et al., 1996). We also know that at least two adult-sized animals marked with PIT tags at this site in November 1995 were still present in April 1997.

From these observations we conclude that *P. hubrichti* must respond to their dynamic habitat. Our study site is relatively undisturbed by forestry operations but the siltstone that composes the slope appears to be eroding rapidly, especially after heavy rainfall. The bluff above the study site has crumbled in the recent past to create a sediment pile below the region where the burrows are located. These apparently natural disturbances result in a habitat where burrows are unlikely to remain open for extended periods of time. We suspect that in order to maintain burrows for several months, salamanders must continually repair damage. Our data suggest that half of *P. hubrichti* present at this site abandon their burrows approximately 120 d before the structure itself is filled in. However, it seems unlikely that in this dynamic habitat a burrow would remain open for almost four months after abandonment, so our measurement of burrow abandonment may be less robust than that of burrow longevity. Because this data does not involve telemetered animals, it is possible that some salamanders were present but not active at the burrow entrance during subsequent censuses.

Nevertheless, we infer that some salamanders must abandon their burrows and create new ones. Many burrows became closed over the duration of the study, yet burrow numbers did not decrease consistently over time. This pattern indicates that *P. hubrichti* either move above-ground or burrow out to the surface following burrow closure to create a new entrance. Little is known of the burrowing abilities of the Red Hills salamander, but it is possible that burrows are constructed from the inside out. *Phaeognathus hubrichti* possesses morphological features (e.g., elongate body form and reduced limbs) characteristic of organisms

specialized for burrowing (Highton, 1961). While terrestrial activity in this species is considered rare, at least three salamanders have been observed moving outside of a burrow on the substrate, indicating that *P. hubrichti* may move aboveground to new burrows. One such occurrence at our study site was on 15 October 1996, when a salamander was seen exiting a burrow tail first, then continuing to crawl upslope and eventually disappearing into a hole that did not have the characteristic shape of a *P. hubrichti* burrow (C. Guyer, pers. obs.). Also, the type specimen of this species was collected from the surface under leaf litter (Highton, 1961) and another specimen was found crawling on the leaf litter in the type locality by Valentine (1963).

Burrow dynamics could have implications for determining the extent of area needed to maintain a population of Red Hills salamanders and the ability of a population to respond to habitat modification. Timber companies "mark out" area containing Red Hills salamanders and do not harvest these portions (Dodd, 1991). To control erosion and provide shade, Dodd (1991) suggested that a "buffer zone" of trees also be left standing above and below the slopes containing salamanders. However, portions of the slope adjacent to populations of Red Hills salamanders also need to be preserved in order to ensure that salamanders searching for new burrows encounter suitable habitat.

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The Modulation of Movement as a Behavioral Adaptation to Extreme Environments in the Newt *Triturus alpestris cyreni*

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The most frequent element of the sexual display of the Alpine newt (*Triturus alpestris*) is the fan. During this act the male is in front of the female. The tail is flexed close to the body and beats rapidly, producing a steady stream of water. This stream transports pheromones from the male's cloaca to the female's snout (Halliday, 1977; Malacarne and Giacoma, 1986). The female detects them through her olfactory epithelium,

irrigated by frequent pumping of her buccal floor (Joly, 1979). Pheromones signal to the female the identity of her sexual partner and probably contribute to raise her sexual motivation, as suggested for *T. vulgaris* by Teyssedre and Halliday (1986). In addition to chemical stimulation, the fan display provides vibrational and visual stimuli. Quantitatively it is the most important display: 34% of the total acts exhibited by *T. a. cyreni* males were fanning bouts (Denoël, 1996).

Among *Triturus* species, the tail beats at different frequencies during the fanning movement. For example, mean values reported are 12 Hz for *T. helveticus*, 6 Hz for *T. vulgaris*, and *T. montandoni* (Halliday, 1977; Wambreuse and Bels, 1984; Pecio and Rafinski, 1985). In the Alpine newt, however, tail beat frequencies can be variable and different authors have reported values varying from 3–4 Hz (Halliday, 1977) to 6.63 Hz (Andreone, 1990). Variation has also been reported among subspecies: 6.63 Hz in *T. a. alpestris* and 5.59 Hz in *T. a. apuanus* (Andreone, 1990). Quantitative and qualitative differences in the newts' behaviour may act as isolating barriers and some of them are phylogenetically informative, supplementing data obtained by molecular techniques (Arntzen and Sparreboom, 1989; Halliday and Arano, 1991).

Temperature is known to affect performance in amphibians (Rome et al., 1992). Measures of locomotor performance such as swimming and running in salamanders (Else and Bennett, 1987), swimming in frogs (John-Adler et al., 1989), hopping in toads (Londos and Brooks, 1988) and jumping in frogs (Whitehead et al., 1989), are depressed at low temperatures. Acoustic signals in anurans (Vasara et al., 1991; Sullivan and Malmos, 1994) and digestion in newts (Jiang and Claussen, 1993; Schabetsberger, 1994) are also strongly dependent on temperature. To my knowledge, however, nothing is known about the influence of the temperature on the courtship behavior of newts and salamanders.

The aim of this study was to determine if the tail-beat frequencies of male Alpine newts vary with water temperature and thus evaluate whether taxonomic conclusions are justified on the basis of differences in tail-beat frequencies (previous studies on the Alpine newts' courtship were conducted at varying temperatures).

Sixty two adult Alpine newts were collected early in their reproductive period in the Cantabrian mountains of Northern Spain. To aid identification of individuals, all newts were toe-clipped using a code similar to that of Twitty (1966). Males and females were kept separate in ten aquaria. My experiment consisted of placing one male and one female together in an aquarium and videotaping all sexual interactions. Two sets of trials were conducted: the first at the temperature of 6–8 C and the second at 13–17 C. Before observing behavior at a low temperature, newts were kept for 5 to 10 d at a temperature of 6.5 C. All male newts tested at 6–8 C were also tested at 13–17 C (N = 8). I also staged trials only at the high temperature for some males to obtain additional data. Courtship was recorded with a Sony-Hi8 video camera at 25 frames per sec. Frame by frame analysis allowed me to determine tail-beat frequencies during fanning (I considered only those bouts of at least 3 sec duration). I recorded 83 encounters and analyzed the behavior