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Reviewed work(s :
Source: *Copeia*, Vol. 1979, No. 1 Feb. 20, 1979), pp. 92-95
Published by: American Society of Ichthyologists and Herpetologists (ASIH)
Stable URL: http://www.jstor.org/stable/1443733
Accessed: 27/09/2012 16:23

Copeia, 1979(1), pp. 92-95

Diel Activity Rhythms in the Hellbender, *Cryptobranchus alleganiensis* (Caudata: Cryptobranchidae)

TERESA A. NOESKE AND MAX A. NICKERSON

Activity rhythms of the hellbender *Cryptobranchus alleganiensis* were similar prior to and during the breeding season. The activity rhythms were biphasic under photoperiodic regimes or in constant light, but were monophasic in constant dark.

DAILY rhythms of locomotor activity have been found in many animals including salamanders (Ralph, 1957; Bennett and Stanley, 1960; Adler, 1969). We were interested in determining the activity rhythms in hellbenders, *Cryptobranchus alleganiensis,* to aid in the interpretation of field observations and proposed laboratory work. Field observations indicate that *C. alleganiensis* is primarily nocturnal (for references see: Nickerson and Mays, 1973). However, there have been reports of diurnal activity at certain times of year, particularly during the breeding season (Smith, 1907; Bishop, 1941). Therefore, we determined the activity rhythm in the laboratory at two times of year, prior to and during the breeding season.

MATERIALS AND METHODS

Each *C. alleganiensis* was placed in an 80 l aquarium containing 20 l of aerated tap water. Room temperature was maintained at 20 ± 2 C. Partitions separated the aquaria and prevented visual contact between animals. Routine tank maintenance (i.e., siphoning, water replacement) was done at unscheduled times of day. Hellbender locomotor activity was detected by a plexiglass treadle on the bottom of each aquarium. When an animal moved to one side of the aquarium, its weight forced that side of the treadle downward, making or breaking a microswitch contact. The microswitches were connected to an Esterline-Angus event recorder. The animals were not fed for the duration of the experiment.

Ten hellbenders were captured from the North Fork of White River, Ozark County, Missouri. These animals were acclimated to LD 15:9 (light onset at 0530 h CST) starting in mid-July for 2 weeks prior to testing. This light-dark regime approximates the natural photoperiod of southern Missouri in July. Light was provided by daylight fluorescent bulbs (300 lux). Activity was recorded on this lighting regime for 1 week. The light regimen was then switched to constant light (LL) and activity was recorded for 3 days.

Another group of 11 hellbenders was tested in late October and early November. Hellbenders were captured from the N. Fork of White R., Ozark Co., and the Niangua River, Texas County, Missouri, during the breeding season, early September to mid November (Nickerson and Mays, 1973). The experimental apparatus was identical to that used in the summer. These hellbenders were acclimated for 2 weeks to LD 13:11 (light onset at 0500 h CST). This light-dark regime approximates the natural photoperiod of southern Missouri in October. The activity was recorded for 1 week starting October 20, then the light cycle was inverted (DL 11:13). After activity on this regime was recorded for 1 week, the hellbenders were placed in constant darkness (DD) for 3 days and activity was recorded. All animals were between 280 and 380 mm TL.

The hellbenders were not killed in order to determine their sex. Previous capture experiments in Niangua and North Fork rivers, Missouri, revealed a male to female ratio of 1.3:1 and 1:1, respectively, during mid-summer (Nickerson and Mays, 1973). Estimates of the male to female ratio are even higher (2:1 to 3:1) at other times of year (Smith, 1912). Therefore, we assume the hellbenders used were of mixed sexes and included the more territorial males.

Activity per hour was computed and expressed as a percent of the total activity each

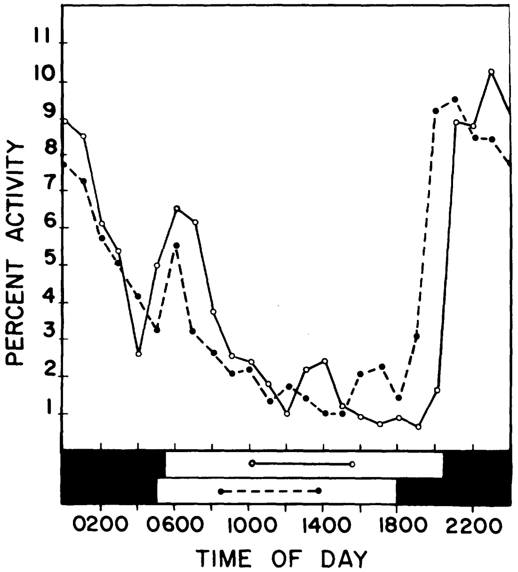

Fig. 1. Percent daily activity per hour of hellbenders in fall (———) and summer (– – –). Horizontal bars represent photoperiods LD 13:11 (fall) and LD 15:9 (summer).

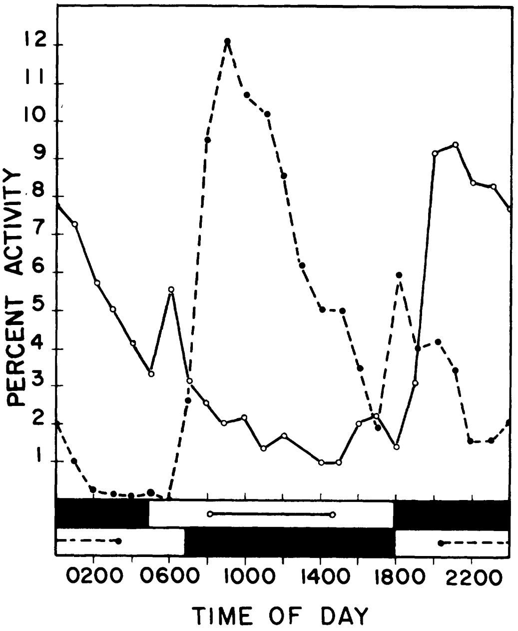

Fig. 2. Percent daily activity per hour of hellbenders held in LD 13:11 (——) and in the inverted photoperiod DL 11:13 (– – –). Horizontal bars represent the photoperiod.

day (e.g. 0800 data point encompasses data from 0800–0859). Mean period length was calculated by the conventional method:

$$t = \frac{(t_2 - t_1) + (t_3 - t_2) + \cdots (t_n - t_{n-1})}{n - 1}$$

where t is the mean period and t_1, t_2, t_3 and t_n refer to the time of initiation of activity (Gourley, 1972). A one-way analysis of variance (Snedecor and Cochran, 1967) was performed on data from each lighting regime.

RESULTS

C. alleganiensis exhibited daily activity rhythms ($P < 0.01$) when tested under LD schedules (Summer—LD 15:9; Fall—LD 13:11, Fig. 1). The percent activity was high during the dark phase of the photoperiod and low during most of the light period, indicating that hellbenders are primarily nocturnal. The activity rhythms were biphasic; an increase in activity was observed after both light onset and offset. Maximum daily activity occurred 2–2½ h after dark onset and a smaller peak of locomotor activity occurred immediately after light onset. The activity rhythm was resynchronized with the light-dark cycle 48 h after the photoperiodic regime was inverted (Fig. 2), demonstrating that the rhythm can be entrained by the photoperiod. Also, it appears that the hellbender locomotor rhythm is endogenous (Aschoff, 1960) because it persisted under conditions of constant light and constant dark for more than 48 h (Fig. 3). The calculated mean period length was 22.32 h (range 20.6–24.5) for animals held in DD during the fall, and 23.50 h (range 19.0–25.7) in LL during the summer.

The form of the activity rhythms varied depending on the light regime. The activity patterns were biphasic under LD regimes and in LL. However, the activity pattern was monophasic in DD (Fig. 3). Also, the phase angle between the activity rhythm and the subjective time of day was different under LL and DD. In DD, the activity peaked 2 h after subjective dark onset whereas in LL, the activity peaked at subjective light onset with a smaller peak 1 h after dark onset.

DISCUSSION

The activity rhythms of *C. alleganiensis* from experiments conducted before and during the

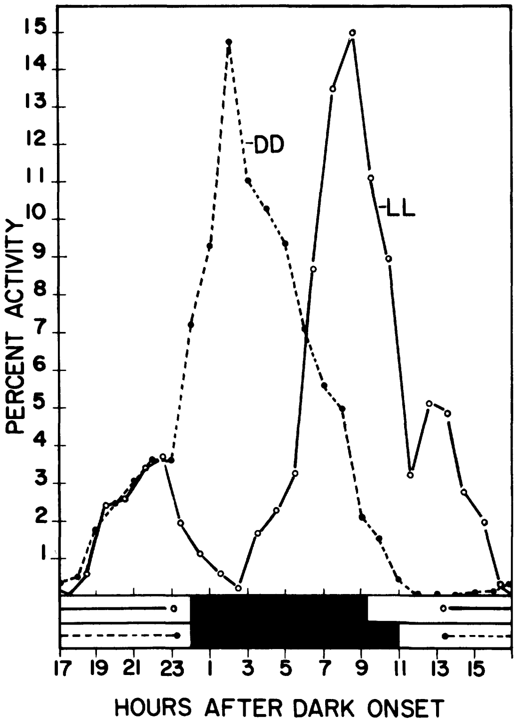

Fig. 3. Percent daily per hour of hellbenders in constant light (———) and constant dark (– – –). Horizontal bars represent subjective photoperiods.

breeding season were almost identical (Fig. 1). At both seasons, activity was lowest at midday. Thus, the increased diurnal activity reported from field observations during the breeding season or at midday (Nickerson and Mays, 1973) may result from other environmental variables such as rainfall, light intensity and temperature change which have been shown to affect activity rhythms (Aschoff, 1954).

Normal LD cycles usually entrain circadian rhythms to periods of exactly 24 h. However, a circadian rhythm of a "free-running" animal under conditions of constant light (LL) or constant dark (DD) and constant temperature can be greater or less than 24 h. According to the "Circadian rule," the length of a free-running period for diurnally active animals is shorter in LL than it is in DD; the period length of nocturnally active animals is shorter in DD than in LL (Aschoff, 1960). The period for the primarily nocturnal hellbenders (Fig. 1) was less in DD (22.32 h) than in LL (23.50 h). Thus, it appears that the activity rhythm of hellbenders follows the circadian rule. The mean period lengths of the hellbender activity rhythms are within those values (22–28 h) usually obtained for free-running rhythms of other animals (Bünning, 1973).

Constant conditions may affect not only the period length of activity cycles, but also the form of the rhythm. The hellbender activity rhythms were biphasic under photoperiodic regimes (Fig. 1) or in constant light, but monophasic in constant dark (Fig. 3). A partial explanation for these results may be that the phase of the rhythm is determined by different aspects of the photoperiod (i.e., light onset and dark onset). There is often a good correlation between the acrophase of the activity rhythm and either dawn or twilight (DeCoursey, 1959) or both (Aschoff, 1960, 1967). In our study, hellbenders had two peaks of activity—a large peak after dark onset, and a smaller one after light onset. In constant light, the larger activity peak occurred at subjective light onset; in constant dark the peak occurred after subjective dark onset. However, this correlation does not explain why two peaks of activity occurred in constant light, whereas only one peak occurred in constant dark (Fig. 3).

An alternate explanation of our results is that some aspect of the photoperiod (i.e., the onset of dark) sets the nocturnal peak of activity. In addition, dark onset may set a light sensitive phase. If light is present at this time, it phases a peak of activity. Thus, on either a LD regime or LL, two activity peaks are present; in DD only the nocturnal peak of activity is present. Such a physiological mechanism might have adaptive value. Hellbenders in nature are nocturnally active and remain concealed under rocks in the daytime (Bishop, 1941). Presumably the exposed animals would be vulnerable during the daylight hours when they are normally inactive. Thus, it would be to the advantage of an animal that finds its shelter insufficient (a lighted position) to become active and seek a more suitable shelter. Our laboratory experiment provided no shelter in the aquaria, thus light onset was followed by increased activity as the animals attempted to find refuge.

Field work and the results of this study (Fig. 1) indicate that hellbenders are not strictly nocturnal. However, further field work is necessary to demonstrate whether there is an early morning peak of activity or whether the early morning activity noted in our study was a response to conditions which are not normally encountered in nature.

ACKNOWLEDGMENTS

The authors thank Richard E. Spieler for suggesting this study. Albert H. Meier, Louisiana State University, and Charles Weise, University of Wisconsin-Milwaukee, allowed us the use of their Esterline-Angus recorders. The All-Glass Aquarium Co. of Milwaukee kindly donated the aquaria. Albert H. Meier, Richard E. Spieler and Albert J. Fivizzani reviewed the manuscript. Jon Shapiro aided in animal maintenance. Some of the funding for this study was provided by Friends of the Museum, Milwaukee and Max Allen's Zoological Gardens, Eldon, Missouri.

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Copeia, 1979(1), pp. 95–110

Genetic Relationships of the Eastern Large *Plethodon* of the Ouachita Mountains

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An electrophoretic study of 23 genetic loci in 20 samples of *Plethodon ouachitae* and *P. caddoensis*, species endemic to the Ouachita Mountains of Arkansas and Oklahoma, indicates that there is a third member of the group, as genetically different from the two named species as they are from each other. It is described as a new species, *Plethodon fourchensis*. The three species are also differentiated by color pattern characters and by size. Genetic variation at four localities in a narrow hybrid zone between *P. ouachitae* and *P. fourchensis* is analyzed. A comparison of the genetic relationships of the three endemic Ouachita Mountain species with sympatric *P. glutinosus* from nine localities and with *P. yonahlossee* from two localities in the southern Appalachian Mountains indicates that they are more closely related to *P. glutinosus* than they are to *P. yonahlossee*. No genetic evidence of hybridization between *P. ouachitae* and *P. glutinosus* is found.

PLETHODON *ouachitae* Dunn and Heinze and *P. caddoensis* Pope and Pope are species of eastern large woodland salamanders endemic to the Ouachita Mountains of Arkansas and Oklahoma. Blair and Lindsay (1965) present a summary of a study on geographic variation of the group but have not as yet published their data or analysis. They conclude that