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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

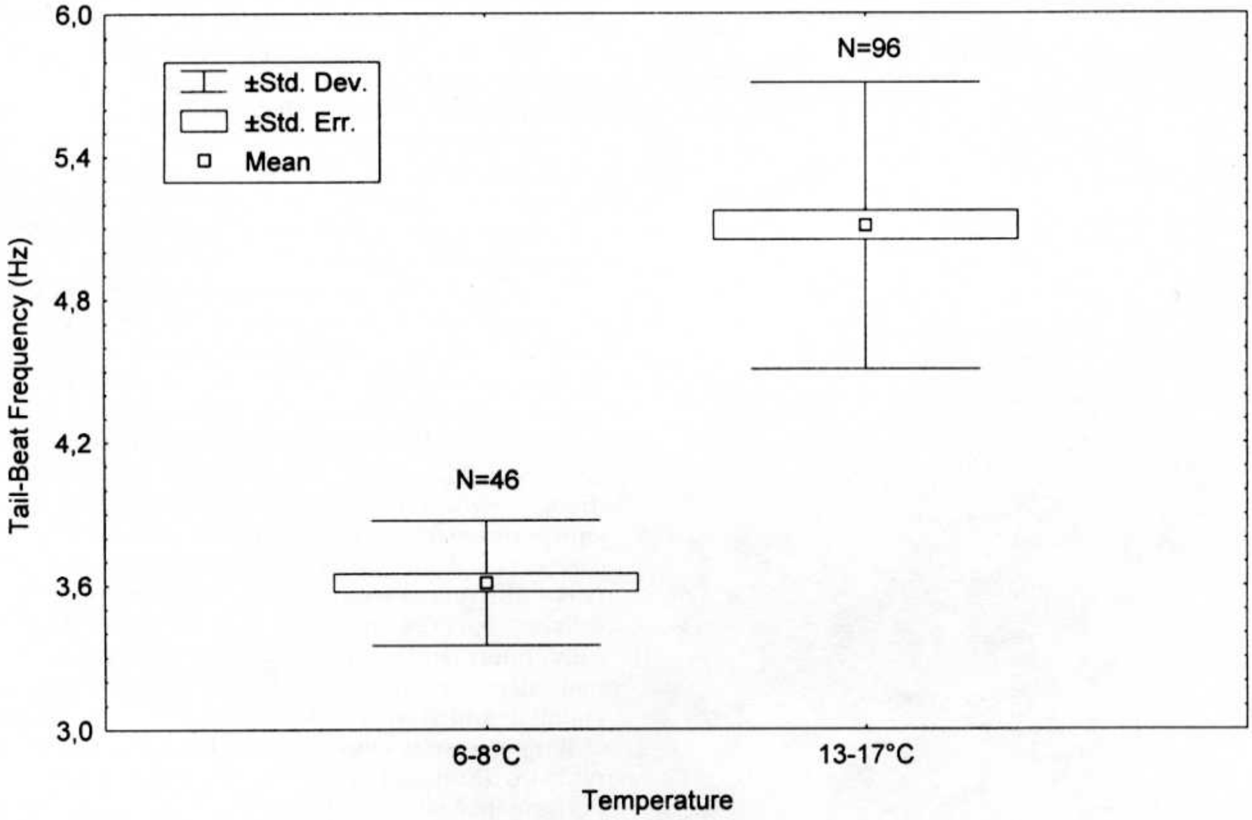

FIG. 1. Tail-beat frequencies during the fanning movement at two temperature ratings in *Triturus alpestris cyreni*: Differences are significant (Mann-Whitney U = 33, $P < 0.0001$).

of 25 males. I also observed several encounters (N = 13) on the field to validate my laboratory observations. Statistical tests were made using Statistica (Statsoft, 1996).

My laboratory results reveal obvious differences in tail beat frequencies between the two sets of trials. The frequency range was 3.33–6.66 Hz (mean ± SE = 5.11 ± 0.06 Hz, N = 96) with a temperature ranging between 13 and 17 C, whereas at low temperatures, 6–8 C, beat frequencies varied between 3.00 and 4.00 Hz (mean ± SE = 3.61 ± 0.04 Hz, N = 46) (Fig. 1). Differences were highly significant (Mann-Whitney U = 33, $P < 0.0001$). The mean tail beat frequencies of the eight males tested at both temperatures are also significantly different (Fig. 2, Wilcoxon Matched Pairs Test Z = 2.521, $P = 0.012$). My field observations confirm these laboratory data. In a pond at 1850 m elevation, all observed newts exhibited low tail beat frequencies during fanning (3–4 Hz). The water temperature was 7 C and during the night and the morning the surface water froze. Sexual displays were observed only in the early morning.

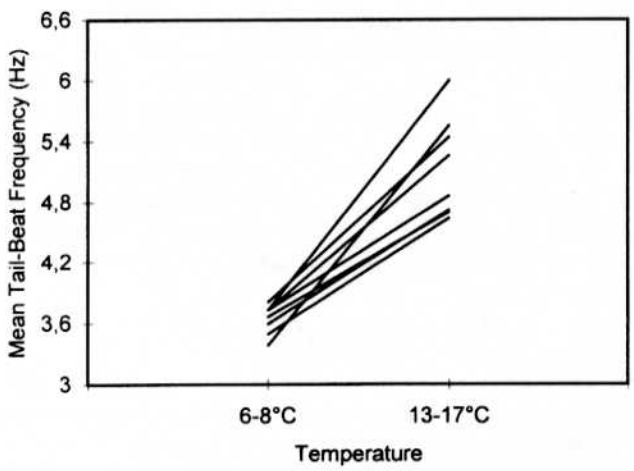

FIG. 2. Mean tail-beat frequencies during the fanning movement at two temperature ratings for each of the 8 Iberian Alpine newt males tested. Differences are significant (Wilcoxon Matched Pairs Test Z = 2.521, $P = 0.012$).

My data indicate that the tail beat frequency of the fanning movement varies with temperature in the Alpine newt, with slower beats at low temperatures. The disparate observations of different authors may thus be explained by variation in water temperature during observations. From a subspecific level, particularly in *T. alpestris*, taxonomic conclusions based on fanning may not be justified. Thus observations of *T. a. alpestris* and *T. a. cyreni* do not show differences in the same temperature range (Denoël, 1996) and differences between *T. a. alpestris* and *T. a. apuanus* (Andreone, 1990) are small. Moreover, females can react positively to low as well as high frequencies of fanning : this character may not act as an isolating mechanism in the Alpine newt, at least between 3.00 and 6.66 Hz.

Muscle contractibility is known to be affected by temperature, but animals can also recruit more muscle fibers when temperature is low and in this way produce the same performance as at high temperature (Rome et al., 1990, 1992). However low temperature decreases the male Alpine newt's sexual performance, i.e., the tail beat frequency which is a sexual signal. So, at a low temperature, the tail beat frequency is not increased or cannot be increased to compensate the effects of cold. Nevertheless, as the female can respond positively to the displaying male in this condition, reproduction is possible early in the season and this can be considered as an adaptation to unpredictable and extreme environments, like high altitude lakes and temporary ponds. It is surely beneficial to mate as early as possible in these habitats and thus display in low temperatures. Indeed, at a high altitude, time available for larval growth is short; also, in temporary ponds, dessication may occur before larvae metamorphose. Thus male newts are forced to exhibit sexual activity at low temperatures. Eddy and McDonald (1978) showed that, for sexually active *T. cristatus*, cutaneous respiration is insufficient to meet the male's O_2 need and must be supplemented by pulmonary respiration. However, my field observations and those of J. Kauffmann (T. Halliday, pers. comm.) suggest that, at low temperatures, newts do not need to breathe from the water surface, perhaps because of the lower demands placed by production of a low tail-beat frequency. Moreover the use of the lungs is not necessarily possible; a sheet of ice frequently covers the water surface.

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