



Behavioural adaptations of *Rana temporaria* to cold climates



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ABSTRACT

Environmental conditions at the edge of a species' ecological optimum can exert great ecological or evolutionary pressure at local populations. For ectotherms like amphibians temperature is one of the most important abiotic factors of their environment as it influences directly their metabolism and sets limits to their distribution. Amphibians have evolved three ways to cope with sub-zero temperatures: freeze tolerance, freeze protection, freeze avoidance. The aim of this study was to assess which strategy common frogs at mid and high elevation use to survive and thrive in cold climates. In particular we (1) tested for the presence of physiological freeze protection, (2) evaluated autumnal activity and overwintering behaviour with respect to freeze avoidance and (3) assessed the importance of different high-elevation microhabitats for behavioural thermoregulation. Common frogs did not exhibit any signs of freeze protection when experiencing temperatures around 0 °C. Instead they retreated to open water for protection and overwintering. High elevation common frogs remained active for around the same period of time than their conspecifics at lower elevation. Our results suggest that at mid and high elevation common frogs use freeze avoidance alone to survive temperatures below 0 °C. The availability of warm microhabitats, such as rock or pasture, provides high elevation frogs with the opportunity of behavioural thermoregulation and thus allows them to remain active at temperatures at which common frogs at lower elevation cease activity.

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1. Introduction

Environmental conditions at the edge of a species' ecological optimum can exert great ecological or evolutionary pressure at local population level. In this case adaptive or plastic responses to stressor at individual level facilitate the survival of populations (Hangartner et al., 2012; Dallinger and Höckner, 2013). Exploring the mechanisms that allow a species to persist in challenging environments is crucial for understanding how species deal with ecological and evolutionary pressure, especially in the light of global climate change. For ectotherms ambient temperature is one of the most important physical aspects of their environment. It affects directly physiological processes such as metabolism, growth, development and reproduction, muscle contraction, oxygen transport, and digestion (Carey and Alexander, 2003; Laugen et al., 2003a) and thus influences timing of hibernation and reproduction (e.g. Terhivuo, 1988; Beebe, 1994; Reading, 1998, 2003; Tryjanowski et al., 2003; Carroll et al., 2009) and global species richness patterns (Buckley and Jetz, 2007). Shorter

growing seasons impose time constraints on growth and development (Laugen et al., 2003b; Muir et al., 2014a), sub-zero temperatures during winter pose the risk of freezing and set geographical limits to the distribution of species. Only two amphibian species, the North American wood frog (*Lithobates [Rana] sylvaticus*) and the European common frog (*Rana temporaria*) are able to inhabit regions north of the Arctic Circle. Both species exhibit a wide geographic distribution: *L. sylvaticus* occurs from Alaska to Labrador, south to New Jersey, northern Georgia and northern Idaho (Chubbs and Phillips, 1998). *R. temporaria* is found from north of the Arctic Circle in Scandinavia to northern Spain, and in mountainous regions up to an elevation of 2600 m (Gasc et al., 1997). In both species populations are subject to a variety of climatic conditions, which substantially modify their annual activity cycle. For example, at the southern edge of their distribution, common frogs do not hibernate and breeding is initiated at the beginning of winter (Bea et al., 1986). In lowland populations in Switzerland and France common frogs can be found breeding as early as February (e.g. Ryser, 1989; Augert and Joly, 1993). With increasing latitude or altitude breeding starts later (e.g. Elmberg, 1990; Elmberg and Lundberg, 1991) and can occur as late as May in northern or high alpine populations.

In general, there are three ways amphibians can cope with temperatures below zero (Pinder et al., 1992): (1) tolerate freezing

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of extra-cellular body fluids (freeze tolerance) (Storey and Storey, 1984); (2) production of cryoprotectants to prevent cells from freezing (freeze protection) (Storey and Storey, 1988) and (3) choosing hibernation sites where temperatures do not drop below zero (freeze avoidance) (Boutilier et al., 2000; Sinsch and Leskovaar, 2011). The behavioural and physiological adaptations of *L. sylvaticus* to sub-zero temperatures are well studied. Wood frogs cease activity when temperatures drop below 4.4 °C (Bellis, 1962). Their ability to tolerate extra-cellular freezing and to prevent intra-cellular freezing by using glucose as cryoprotectant (e.g. Storey and Storey, 1984, 1988; Layne and Lee, 1987; Costanzo et al., 1992), allows for terrestrial hibernation underneath leaf litter and snow, where temperatures drop as low as -7 °C (Schmid, 1982; MacArthur and Dandy, 1982). In contrast, our understanding of how *R. temporaria* deals with low temperatures is less clear. So far studies in high elevation or northern populations have focused on summer microhabitat use and diel activity (Vences et al., 2000), age structure (Ryser, 1996; Patrelle et al., 2012), breeding behavior (Elmberg, 1990; Elmberg and Lundberg, 1991) and larval development (e.g. Aebli, 1966; Angelier and Angelier, 1968; Brand and Grossenbacher, 1979; Laugen et al., 2003a; Muir et al., 2014a). With respect to the hibernation ecology of *R. temporaria*, the occurrence of both, aquatic and terrestrial hibernation has been reported (Viitanen, 1965; Koskela and Pasanen, 1974; Hagström, 1982; Elmberg, 1990; Pasanen and Sorjonen, 1994). Voituron et al. (2009) found 100% mortality in adult common frogs after eight hours of complete freezing of body fluids. Pasanen and Karhapää (1997) observed that adult *R. temporaria* survived 24 h exposure to sub-zero temperatures, but died within three days after exposure. Muir et al. (2014a) found that 82% of *R. temporaria* larvae from low-elevation sites survived short periods of freezing. From high elevation sites, only 32% survived. However, data on physiological and behavioural responses to low temperatures of wild adult common frogs are lacking. This gap of knowledge in the general biology of *R. temporaria* limits our ability to link local responses to phenotypes and thus assess the impact of environmental change on this species. Therefore the objectives of the present study were to compare mid- and high-elevation adult common frogs in terms of their physiological and behavioural adaptations to cold climates. In particular we (1) tested for the presence of physiological freeze protection, (2) evaluated autumnal activity and overwintering behaviour with respect to freeze avoidance and (3) assessed the importance of different high-elevation microhabitats for behavioural thermoregulation.

2. Material and methods

2.1. Study areas

The study was conducted in two common frog populations at different elevations. The high elevation population is located in an alpine basin in the Fotsch Valley in the northern Stubai Alps, Austria (11°12'53"E, 47°08'59"N) at an elevation of 2300 m. A detailed description of this site is found in Ludwig et al. (2013). Based on annual egg mass counts during the breeding periods between 2011 and 2014 population size is estimated to be around 700 adults. Reproductive activity usually starts in mid to late May. The subalpine population is located in a small wetland area in the northeast of the city of Innsbruck, Austria (11°24'58"E, 47°17'11"N) at an elevation of 650 m. Several small ponds are surrounded by marsh area and mixed forest. Based on egg mass counts in spring 2013 and 2014 the population size is estimated to be around 200 adults. Breeding usually starts in mid-March.

2.2. Experiments to test for freeze protection

In 2013 17 adult common (16 males, 1 female) frogs were caught in breeding ponds at the beginning of spawning at the subalpine site and their blood glucose levels measured. At the alpine site 23 adults (21 males, 2 females) were caught on snow or ice-slush right after emergence from overwintering and tested for elevated blood glucose levels. Blood was drawn into a heparinized capillary tube from the *Vena angularis* as described by Nöller (1958) and transferred to a blood glucose meter (Accu-Chek Performa Nano, Roche Diagnostics GmbH, Germany, measuring range: 10–600 mg/dl; measuring precision according to EN ISO 15197:2003 standard: 95% of the individual glucose results shall fall within ± 15 mg/dL of the results of the manufacturer's measurement procedure at glucose concentrations of < 75 mg/dL). Sampling was done in situ and did not last longer than 1 min. In addition we recorded air and water temperature using a digital thermometer (RS Digital Thermometer AH-50A Typ K, RS Components, Austria; measuring range: -50 °C to 200 °C; measurement precision: 0.1 °C; measuring error: ± 1.5 °C). To test for seasonal changes, we repeated blood glucose measurements in the alpine population in June ($N=29$, 19 males, 29 females) and late August ($N=19$, all males). These individuals were all caught in ponds. Blood glucose levels were compared using One-Way ANOVA. Significance level was set to $\alpha=0.05$.

2.3. Experiments to test for freeze avoidance

Over a period of three years (2011–2013) a total of 46 adult *R. temporaria* (mass > 40 g; 31 males, 15 females) in both populations were marked with radio transmitters (BD-2H, 3.4 g and BD-2TH, 2.9 g, Holohil Systems Ltd., Canada) to monitor their movements. In 2011 transmitters were attached externally. The method of external attachment is described in Ludwig et al. (2013). In 2012 and 2013 transmitters were implanted into the body cavity. For surgery, frogs caught in the field were brought back to the lab and anaesthetized by submersion in a buffered solution of MS-222 (4 mg/L), through a small incision transmitters were implanted into the body cavity. The incision was closed using absorbable sutures (Novosyn HS 15, Braun, Spain) and frogs were rinsed under fresh water until fully recovered. After surgery frogs were kept in a tempered climate chamber (18 °C, L:D=13:11) for three days to facilitate wound healing and then released at the site of capture. Marked frogs were located at least once a week. At each relocation we recorded the frog's position using GPS (Garmin, eTrex). In addition, we measured the line-of-sight distance each individual had moved between two observations. An animal moving more than 5 m between relocations was classified as active. When an individual remained sedentary for two or more consecutive relocations we assumed it had reached its hibernation site. At each site one data logger (TG-4100 Tinytag Aquatic 2, Gemini Data Loggers Ltd., UK) was placed on the ground and one in the stream to record air and water temperature during fall, winter and spring. Every year data loggers were placed in the same spots on the ground and in streams. Data loggers recording air temperature were placed directly on the ground shaded by a rock (alpine site) or shrubs (subalpine site). Temperatures were recorded in 2 h intervals from the beginning of September until the end of March in the subalpine population and the end of June in the alpine population.

We used the telemetry data to calculate the autumnal activity period for each marked frog, defined as the number of days from September 16 (by this date all frogs had been released back into the field) until it reached its hibernation site. For each year in each population we calculated daily average, minimum and maximum temperature between September 16 and December 10. As activity patterns and hibernation behaviour in the alpine population were

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