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Effect of chronic low body temperature on feeding and gut passage in a plethodontid salamander

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ABSTRACT

Although feeding in some plethodontid salamander species, such as Dusky Salamanders (*Desmognathus*, family Plethodontidae), occurs at short-term (acute) low temperature below 5 °C, it is unknown whether feeding, digestion, and gut passage continue to occur during periods of long-term (chronic) low temperature. We performed a controlled laboratory experiment to examine the effect of several chronic low environmental temperatures on both feeding and gut passage in semiaquatic Spotted Dusky Salamanders (*D. conanti*). We quantified salamander feeding and defecation for different experimental groups maintained for many weeks at a constant temperature of 4, 7, 10, or 13 °C. Although feeding frequency, number of prey items consumed per feeding, and defecation frequency were significantly less for individuals at 4 °C than for individuals at 10 or 13 °C, salamanders continued to feed, defecate, and maintain body mass for 12 weeks at 4 °C. The ratio of the number of fecal pellets produced to the number of prey items consumed each week by individuals did not significantly decrease at 4 °C, which indicates gut passage was sustained at this temperature. Because both time between feeding and time between defecation were similarly affected by prolonged low temperature, the significant decrease in feeding frequency at 4 °C may depend, in part, on a decrease in digestive function and an extended time for gut passage at low temperature. We conclude that most individuals of *D. conanti* can feed, digest, and maintain body mass for several months at constant low temperature down to 4 °C. Our results support a growing body of data that indicate some plethodontid salamanders may acquire energy at environmental temperatures only a few degrees above freezing.

1. Introduction

Variation in body temperature (T_b) often has a significant effect on the behavior, physiology, and ecology of ectothermic animals. For instance, low temperature can diminish the acquisition of energy by individuals via effects on movement, foraging behavior, prey capture, digestion, absorption, and gut-passage time (Angilletta, 2001; Beaupre et al., 1993; Greenwald, 1974; Stevenson et al., 1985; Van Damme et al., 1991; Waldschmidt et al., 1986; Zimmerman and Tracy, 1989). Consequently, insects and reptiles often use temporal and spatial thermal heterogeneity in their environments to optimize T_b and enhance energy acquisition (e.g., Avery et al., 1982; Ayers and Shine, 1997; Harrison and Fewell, 1995). Likewise, some amphibians behaviorally regulate T_b in moist environments where temperature varies sufficiently among microhabitats (Balogová and Gvoždík, 2015; Camp et al., 2013; Feder and Pough, 1975; Hutchison and Spriestersbach, 1986; Marek and Gvoždík, 2012; Sievert and Andreadis, 2002); however, regulation of T_b is not possible for individuals in many populations because either their environments do not have adequate thermal diversity (e.g., Piasečná et al., 2015) or moisture restrictions prohibit individuals from selecting more thermally favorable microhabitats (Feder, 1982, 1983; Spotila, 1972). Thus, because T_b often varies greatly with season and elevation for amphibians such as salamanders (Feder and Lynch, 1982), an ability to diminish the effect of low temperature on energy acquisition could provide a selective advantage for individuals. This may be why individuals of some salamander species can feed at temperatures only a few degrees above freezing (Deban and Richardson, 2011; Keen, 1979; Marvin et al., 2016).

Individuals of some salamander species have abilities which may allow them to forage, avoid predators, capture prey, and assimilate energy at low T_b. Although physiological rates can be significantly reduced at low temperatures [e.g., $Q_{10} > 2$ for metabolism (White et al., 2006), $Q_{10} > 3$ for regeneration (Marvin and Lewis, 2013), a relatively low thermal sensitivity for locomotion, and some ability for thermal acclimation of locomotor performance, may allow individuals of some

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species to remain active at low environmental temperatures (Else and Bennett, 1987; Jiang and Claussen, 1992; Marvin, 2003a, 2003b). While the performance of muscles involved in tongue movement is diminished at low temperature, energy stored in elastic tissue maintains quick tongue projection for prey capture at T_b below 5 °C in some species (Anderson et al., 2014; Deban and Richardson, 2011). Individuals of some species can capture prey with high efficiency during short-term (acute) T_b below 5 °C (Marvin et al., 2016). Whereas digestion and energy-assimilation efficiency may be greatly reduced at low temperatures in many ectotherms such as reptiles and insects (Ayers and Shine, 1997; Harlow et al., 1976; Harrison and Fewell, 1995; Kingsolver and Woods, 1997; Kukal and Dawson, 1989), assimilation efficiency is often greater at lower temperature and can be 90% at T_b of 10 °C for some salamanders (Bobka et al., 1981; Jaeger, 1980). However, if digestive processes and gut passage rates for salamanders are much more thermally sensitive than locomotion and prey capture, then continued feeding during extended periods of very low T_b (e.g., below 5 °C during winter) might be harmful or lethal if putrefaction processes prevailed (Podhajský and Gvoždík, 2016). Consequently, data on feeding, digestive ability, and gut passage during long-term (chronic) low T_b are needed to determine whether individuals of some salamander species can continue to feed and maintain digestion during prolonged periods of very low environmental temperatures.

The low-temperature limit for feeding by some plethodontid salamanders (i.e., of the family Plethodontidae) in the genus *Desmognathus* has been inferred from variation in activity and gut contents of individuals in the field at different seasons and temperatures (Ashton, 1975; Keen, 1979; Shealy, 1975). Ashton (1975) reported that individuals of the semiaquatic species *D. fuscus* move into subterranean, winter retreats when stream temperatures drop below 7 °C, but because retreats remain between 1 and 6 °C when stream temperatures drop to 0–4 °C, he proposed that individuals may continue to feed in their retreats throughout the winter. However, while individuals of several *Desmognathus* species feed at acute $T_b \leq 5$ °C (Ashton, 1975; Keen, 1979; Marvin et al., 2016), possible changes in feeding, digestion, and energy acquisition for individuals during chronic $T_b \leq 15$ °C are unknown (Fitzpatrick, 1973).

We performed a controlled laboratory experiment to assess long-term thermal effects on feeding and gut passage in semiaquatic Spotted Dusky Salamanders (*D. conanti*), which inhabit seeps and streams of the south-central United States (Bonnett, 2002; Rossman, 1958; Titus and Larson, 1996). Like individuals of other *Desmognathus* species, individuals of *D. conanti* are ambush, generalist predators that primarily eat small, semiaquatic and terrestrial invertebrate animals (Petranka, 1998). We quantified feeding and defecation by individuals in different experimental groups that were maintained at constant low environmental temperature (4, 7, 10, or 13 °C) for many weeks to determine (1) whether individuals continue to feed and defecate at chronic low temperature down to 4 °C, and if so, (2) how chronic low temperature affects feeding frequency per week, number of prey items consumed per feeding, defecation frequency per week, and the ratio of the number of fecal pellets produced to the number of prey items consumed by individuals, and (3) whether feeding frequency and defecation frequency are similarly affected by chronic low temperature. Such data could help to determine whether individuals of *Desmognathus* continue to feed, maintain digestion and gut passage, and consequently acquire energy during extended periods of very low environmental temperatures which they may experience during winter.

2. Materials and methods

2.1. Experimental groups and body size

Individuals ($n = 62$) of *Desmognathus conanti* (from “Group B” lineage; Bonnett, 2002) were collected during April of 2016 from Colbert County in northwestern Alabama (34°47.63′N, 087°37.85′W). After completion of experiments, animals were released at the collection locality. Body length (i.e., standard length measured from tip of snout to the posterior angle of the vent), body mass, and tail length were measured for each individual. Based on body size at sexual maturity in closely related species [i.e., about 35–40 mm in body length (Jones, 1986; Juterbock, 1978)], most individuals were likely sexually mature. Salamander sex was inferred from sexual dimorphism in body size, head width, and size of premaxillary teeth for *Desmognathus* species (Bakkegard and Rhea, 2012; Bruce, 1993; Juterbock, 1978). Sixty of the individuals were initially placed in size-matched groups of four (i.e., tetrads) based on similarity in sexual maturity, sex, and body length. Then each individual from a size-matched tetrad was randomly assigned to one of four experimental groups (i.e., 4, 7, 10, or 13 °C group). The remaining two individuals were randomly assigned to two of the four experimental groups.

2.2. Acclimation, housing, and fasting

After collection, all salamanders were initially acclimated to a constant temperature of 16 °C and a constant photoperiod of LD 12:12 h for five weeks in environmental chambers. Light inside environmental chambers was provided by three 25-W fluorescent bulbs (Philips F25T8/TL741). The purpose of the initial acclimation for all individuals was to allow their gut contents from the field to pass prior to the feeding experiment, and thus animals were not fed during this initial acclimation period. Each experimental group was then acclimated in a different environmental chamber at one of the four constant experimental temperatures (4, 7, 10, or 13 °C) and constant photoperiod (LD 12:12 h) without feeding for three weeks prior to the experiment. The purpose of the second acclimation period was to allow physiological adjustment by individuals to their experimental temperature prior to the feeding experiment. Thus, our experimental design allowed us to quantify the effect of prolonged low environmental temperature, but no other factors such as variation in photoperiod, on feeding and gut passage. During the acclimation periods and the feeding experiment, salamanders were housed individually in 14 (l) × 14 (w) × 4.5 (h) cm translucent plastic food-storage containers. To maintain humidity inside each housing container, we lined the bottom with two flattened layers of moist filter paper. The housing containers allowed sufficient air exchange to supply oxygen for salamander respiration, but yet minimized water loss to prevent salamander dehydration and reduce the effect of evaporative cooling on salamander T_b. Thus, because evaporation rate was very low, we inferred that salamander T_b was equivalent or very similar to the experimental temperature. To ensure that prey items were always visible to the salamander during the feeding experiment, we did not allow sufficient space under or between the layers of filter paper for either the salamander or the prey to hide.

2.3. Feeding and gut passage experiment

The feeding experiment began at the same time (in the first week of July) for all experimental groups. Once each week (at same time of day on same day of the week) during the experiment, two live prey items (i.e., juvenile Dubia roaches, *Blaptica dubia*) were placed into the housing container of each salamander for all experimental groups. To minimize the possible effect of prey size on salamander feeding, the body size of each roach corresponded to the body size of each salamander. Body length of each roach (range 6–11 mm) was approximately 16 to 18% of the salamander's body length (range 37–63 mm). At the same time each day for six days after feeding, we recorded the number of prey items (live and/or dead) and fecal pellets present in the housing container of each salamander. Based on counts for fecal pellets and the number of prey items present in each housing container at the end of the week, we determined both the number of prey items consumed and the number of fecal pellets deposited by each individual each week. At the end of each week, we removed fecal pellets and any