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Effect of acute low body temperature on predatory behavior and prey-capture efficiency in a plethodontid salamander

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HIGHLIGHTS

- Foraging by ectotherms is influenced by thermal effects on predator and prey.
- Thermal effect on salamander predator, independent of prey, is not known.
- Feeding behavior of cold salamanders was quantified in lab with warm prey.
- Many individuals (50%) exhibited predatory behavior at 3 °C.
- Individuals captured prey with high efficiency at 3 °C.

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ABSTRACT

The low-temperature limit for feeding in some salamander species (*Desmognathus*, Plethodontidae) has been inferred from field studies of seasonal variation in salamander activity and gut contents, which could not determine whether feeding is more dependent on environmental conditions influencing salamander foraging behavior or prey availability and movement. We performed two controlled laboratory experiments to examine the effect of short-term (acute) low body temperature on predatory behavior and prey-capture efficiency in a semiaquatic plethodontid salamander (*Desmognathus conanti*). In the first experiment, we quantified variation in the feeding responses of cold salamanders (at 1, 3, 5 and 7 °C) to a video recording of a walking, warm (15 °C) cricket to determine the lower thermal limit for predatory behavior, independent of any temperature effect on movement of prey. Experimental-group salamanders exhibited vigorous feeding responses at 5 and 7 °C, large variation in feeding responses both among and within individuals (over time) at 3 °C, and little to no feeding response at 1 °C. Feeding responses at both 1 and 3 °C were significantly less than at each higher temperature, whereas responses of control-group individuals at 15 °C did not vary over time. In the second experiment, we quantified feeding by cold salamanders (at 3, 5, 7 and 11 °C) on live, warm crickets to examine thermal effects on prey-capture ability. The mean feeding response to live crickets was significantly less at 3 °C than at higher temperatures; however, 50% of salamanders captured and ingested prey with high efficiency at this temperature. We conclude that many individuals stalk and capture prey at very low temperatures (down to 3 °C). Our results support a growing body of data that indicate many plethodontid salamanders feed at temperatures only a few degrees above freezing.

1. Introduction

Physiology and behavior of ectothermic animals can be profoundly affected by variation in environmental temperature. For example, the acquisition of energy in many species is strongly influenced by changes in body temperature (T_b). Thermal effects on movement, foraging behavior, prey capture, digestion, and absorption can alter food consumption and energy-assimilation rates. Consequently, the relationship between T_b and performance for such physiological and behavioral processes has been investigated in a variety of species (e.g., [3,7,22,52,54,55]). Individuals of some species can diminish thermal effects on energy acquisition by altering behavior and/or physiology to maintain T_b within a range that is narrower than that of the environment. For example, many insects and reptiles utilize spatial and temporal heterogeneity in the thermal environment to optimize T_b and enhance foraging success and food-assimilation efficiency (e.g., [6,7,22,24,25]).

Some amphibians behaviorally regulate T_b in adequately moist environments where temperature varies sufficiently among microhabitats [9,13,20,26,36,49]. However, regulation of T_b is not possible in many populations or species because the environment does not have sufficient thermal diversity to allow thermoregulation [42] or moisture restrictions prevent individuals from choosing among thermally-diverse microhabitats [17,18,50]. Under these conditions, individual T_b often

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closely follows changes in environmental temperature, is negatively correlated with elevation, and experiences predictable seasonal variation [19]. Thus, the ability to minimize the effect of low temperature on energy acquisition would provide a selective advantage for individuals. This may partly explain why (1) the lower thermal limit for feeding is much less in many amphibians than in other ectothermic vertebrates and (2) the low-temperature limits for feeding in plethodontid salamanders (family Plethodontidae) in temperate zone environments are similar to those of some invertebrate animals in polar environments (Table 1).

Various adaptations may allow plethodontid salamanders to have a relatively low thermal limit for feeding. Whereas some physiological rates are greatly diminished at low temperatures (e.g., $Q_{10} > 2$ for metabolism [57], $Q_{10} > 3$ for regeneration [39]), a relatively low thermal sensitivity for locomotor ability, and some capacity for thermal acclimation of locomotor performance, may allow individuals of some species to maintain activity at low environmental temperatures [16,37,38]. Although low temperature reduces performance of muscles involved in tongue movement, the quick release of energy stored in elastic tissue allows ballistic tongue projection for prey capture below 5 °C in some plethodontid salamanders [2,15]. While foraging success and food-assimilation efficiency for many ectothermic animals (e.g., insects, lizards, and snakes) are directly related to T_b [7,25,34], assimilation efficiency in some species of plethodontid salamanders is inversely related to temperature and can be ≥90% at $T_b \leq 10$ °C [10,27]. However, it is not known whether the ability to maintain energy acquisition at very low temperatures is prevalent among salamander populations or species that inhabit diverse thermal environments (e.g., at different elevations or latitudes) or those that exhibit disparity in temperature preference in the same environment [13,49].

Variation in activity and gut contents for individuals in the field at different seasons and temperatures has been used to infer the low-temperature limit for feeding in some species of desmognathan plethodontid salamanders (i.e., Dusky Salamanders, genus *Desmognathus*) [4,29,47]. Dusky Salamanders are ambush, generalist predators that primarily eat a variety of small, semiaquatic and terrestrial invertebrate animals [41]. Based on our observations, a typical predatory behavior pattern consists of visual orientation (by turning the head) toward moving prey, very slow locomotion toward the prey (i.e., stalking of the prey) until it is within capture distance (approximately 1–4 cm), and then capture of the prey with the tongue and jaws. Often during stalking, the salamander lunges (i.e., jumps [45]) toward the prey immediately before capture to quickly traverse the remaining distance.

In the field, the effect of low temperature on Dusky Salamander foraging could be attributable to a combination of thermal effects on predator walking and jumping performance, predator tongue and jaw kinematics, prey activity, prey locomotor performance, and prey availability (including possible variation in types and densities of various prey species among seasons). The low-temperature limit for feeding could also be influenced by both short-term (acute) and long-term thermal effects (i.e., via seasonal acclimatization in the field) on physiology and behavior of predator and prey. Because field studies could not determine whether salamander feeding is more dependent on thermal conditions influencing foraging behavior or prey availability and movement, we examined the effect of low T_b on salamander feeding behavior under controlled laboratory conditions.

We performed two experiments with several low temperatures to assess acute thermal effects on predatory behavior and prey-capture ability in Spotted Dusky Salamanders (*Desmognathus conanti*), which inhabit seeps and streams of the south-central United States [11,44,53]. Prior to experiments, we established that the predatory behavior exhibited by salamanders to either a live, walking cricket or a video recording of a walking cricket was the same. In the first experiment, we quantified the feeding responses by cold salamanders to a video recording of a walking, warm cricket to determine the (1) effect of acute low temperature on predatory behavior (independent of any thermal effect on prey movement), (2) low-temperature limit for feeding behavior, (3) degree of variability among individuals for feeding behavior near the low-temperature limit, and (4) temporal variability for feeding responses by individuals near the low-temperature limit. In the second experiment, we quantified the feeding responses by cold salamanders to live, warm crickets and observed prey capture to determine whether (1) salamanders can capture prey near the low-temperature limit for feeding behavior, (2) prey-capture efficiency decreases near the low-temperature limit, and (3) prey-capture time increases near the low-temperature limit. We also used these data to evaluate whether the low-temperature limit for feeding in this species is similar to that proposed for other salamander species (e.g., species of *Desmognathus* with geographic distributions that extend to higher latitudes).

Table 1
Examples of low-temperature limits for feeding in ectothermic animals.

Taxonomic group	Common name	Scientific name	Limit (°C)	Reference
Echinodermata	Antarctic Starfish	*Odontaster validus*	<0	[40]
Mollusca	Common Oyster Drill	*Urosalpinx cinerea*	6	[23]
Crustacea	Daphnia	*Daphnia rosea*	<5	[32]
Insecta	Two-striped Grasshopper	*Melanoplus bivittatus*	11	[25]
	Arctic Woolly-bear Caterpillar	*Gynaephora groenlandica*	<5	[34]
	Tobacco Hornworm Caterpillar	*Manduca sexta*	14	[31]
Osteichthyes	Lionfish	*Pterois volitans/miles*	16	[30]
	Channel Catfish	*Ictalurus punctatus*	12	[43]
	Brook Charr (juvenile)	*Salvelinus fontinalis*	<17	[35]
	Three-spot Seahorse (juvenile)	*Hippocampus trimaculatus*	19	[48]
Amphibia	American Toad	*Bufo americanus*	5	[51]
	Southern Toad	*Bufo terrestris*	<11	[14]
	Green Frog (tadpole)	*Rana clamitans*	<20	[56]
	Red-backed Salamander	*Plethodon cinereus*	<5	[27]
	Spotted Dusky Salamander	*Desmognathus conanti*	3	Present study
	Northern Dusky Salamander	*Desmognathus fuscus*	<6	[4]
	Mountain Dusky Salamander	*Desmognathus ochrophaeus*	<5	[21,29]
	Three-lined Salamander	*Eurycea guttolineata*	<5	[2]
	Mount Lyell Salamander	*Hydromantes platycephalus*	2	[15]
Reptilia	Diamond Python	*Morelia spilota*	10	[7]
	Gopher Snake	*Pituophis catenifer affinis*	<18	[22]
	Chuckwalla Lizard	*Dipsosaurus dorsalis*	28	[24]
	Common Lizard	*Lacerta vivipara*	10	[5]
	Veiled Chameleon	*Chamaeleo calyptratus*	15	[1]