

Cold-Blooded Snipers: Thermal Independence of Ballistic Tongue Projection in the Salamander *Hydromantes platycephalus*



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ABSTRACT

Plethodontid salamanders of the genus *Hydromantes* capture prey using the most extreme tongue projection among salamanders, and can shoot the tongue a distance of 80% of body length in less than 20 msec. The tongue skeleton is projected from the body via an elastic-recoil mechanism that decouples muscle contraction from tongue projection, amplifying muscle power tenfold. We tested the hypothesis that the elastic-recoil mechanism also endows tongue projection with low thermal dependence by examining the kinematics and dynamics of tongue projection in *Hydromantes platycephalus* over a range of body temperatures (2–24°C). We found that *H. platycephalus* maintained tongue-projection performance over the tested temperature range and that tongue projection showed thermal independence (Q_{10} values of 0.94–1.04) of all performance parameters including projection distance, average velocity, and peak instantaneous values of velocity, acceleration, and power. Nonelastic, muscle-powered tongue retraction, in contrast, responded to temperature changes significantly differently than elastic tongue projection; performance parameters of retraction displayed thermal dependence typical of muscle-powered movement (Q_{10} values of 1.63–4.97). These results reveal that the elastic-recoil mechanism liberates tongue projection from the effects of temperature on muscle contractile rates. We suggest that relative thermal independence is a general characteristic of elastic-recoil mechanisms and may promote the evolution of these mechanisms in ectothermic animals. *J. Exp. Zool.* 315:618–630, 2011. © 2011 Wiley Periodicals, Inc.

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The plethodontid salamander taxon *Hydromantes* is characterized by extreme tongue projection. *Hydromantes* can project the tongue the greatest distance of any amphibian relative to body length using a mechanism in which its tongue skeleton is launched ballistically from its body by the rapid recoil of elastic tissues (Deban et al., '97, 2007). Similar to shooting a bow and arrow, the mechanism of projection separates muscle contraction from launch of the projectile. One notable advantage of this elastic mechanism is a high rate of kinetic energy release (i.e., mechanical power) that is beyond the capabilities of direct muscle contraction. Here we examine another advantage—thermal independence of tongue projection. We reason that because the recoil mechanism decouples active muscle contraction from tongue movement, the level of performance of the movement

should be freed from the limitations that low temperatures place on muscle contractile rates.

Dynamic properties of muscle contraction, such as time to peak tension, peak velocity, and peak power, show strong effects of temperature, decreasing by at least half with each 10°C drop (i.e., $Q_{10} \geq 2$) (Bennett, '85). This phenomenon of thermal sensitivity of muscle contractile rates is well established based

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on studies of a diversity of muscles from a variety of animals, including both ectotherms and endotherms (Putnam and Bennett, '82; Bennett, '84; Bennett and John-Alder, '84; Hirano and Rome, '84; Renaud and Stevens, '84; Bennett, '85; Else and Bennett, '87; John-Alder et al., '89; Faulkner et al., '90; Barnes and Ingalls, '91; Rome and Swank, '92; Rome et al., '92a,b; Asmussen et al., '94; Sobol and Nasledov, '94; Altringham and Block, '97; Choi et al., '98; Donley et al., 2007; Herrel et al., 2007). In contrast to dynamic properties, static properties of muscle contraction, such as peak tetanic tension and twitch tension, are either weakly thermally dependent or thermally independent, with Q_{10} (i.e., R_{10}) values near 1.0 and sometimes lower (Hill, '51; Bennett, '84).

Dynamic behavior such as locomotion is accordingly slowed at low muscle temperatures by virtue of its reliance on contractile rate properties of muscle, as has been demonstrated in many taxa. Lizard sprinting speed and frog jumping distance, for example, are reduced at low body temperatures, with temperature coefficients (Q_{10}) of 1.6–1.8 (Huey and Stevenson, '79; Bennett, '84; Hirano and Rome, '84; Bennett, '90; Herrel et al., 2007). Numerous studies document strong temperature dependence of locomotor speed or frequency of cyclical movements, including studies of frog swimming, frog jumping, frog calling, and salamander, lizard and fish locomotion, among others (Marsh and Bennett, '85; van Berkum, '86; Else and Bennett, '87; Huey and Bennett, '87; John-Alder et al., '88,'89; Rome and Bennett, '90; Bauwens et al., '95; McLister et al., '95; Lutz and Rome, '96; Altringham and Block, '97; Peplowski and Marsh, '97; Navas et al., '99; Marvin, 2003a,b). In contrast to dynamic movements, behaviors that rely on static muscle properties show low thermal dependence: for example, peak bite force in lizards is thermally independent across a wide temperature range (Herrel et al., 2007).

The effect of low temperature on muscle dynamics such as time to peak tension is expected to slow the rate of loading of elastic structures like those in the tongue apparatus of *Hydromantes*. However, temperature may not change the amount of energy that is stored in elastic structures, because peak isometric tension is thermally independent. Once loaded, the elastic tissues are expected to recoil at the same rate regardless of temperature, because the elastic modulus of elastic tissues in animals—collagen, resilin, and other animal protein rubbers—show either very low thermal dependence (Q_{10} of 1.03–1.11) or complete thermal independence ($Q_{10} \sim 1$) (Rigby et al., '59; Alexander, '66; Denny and Miller, 2006).

A clear prediction from the thermal behavior of muscle and elastic tissues is that elastically powered movements will show low thermal dependence or thermal independence. This prediction has been borne out in studies of tongue projection in chameleons (Anderson and Deban, 2010) and toads (Deban and Lappin, 2011) and jumping in leafhoppers and snow fleas (Burrows and Sutton, 2008; Burrows, 2011). Low Q_{10} values of 1.0–1.3 have been found for these ballistic movements that make use of elastic recoil.

In plethodontid salamanders with ballistic tongue projection—including the genera *Eurycea*, *Bolitoglossa* and *Hydromantes*—activation of cylindrical projector muscles (the paired subarcualis rectus) stretches collagenous elastic tissues within the muscles, and subsequent recoil of these elastic tissues launches the tongue (Deban et al., 2007). The tongue projector muscle surrounds an elongated, tapered hyobranchial skeletal element (the epibranchial cartilage), which extends from the buccal region and passes over the shoulder to lie beneath the skin of the trunk (Fig. 1). Each epibranchial connects medially to paired ceratobranchials, which in turn articulate with the medial, unpaired basibranchial that supports the sticky tongue pad (Wake and Deban, 2000; Deban and Dicke, 2004). This entire tongue skeleton is launched from the body during tongue projection, and the epibranchials evacuate the projector muscles. In *Hydromantes*, the tongue reaches the prey under its own momentum, a distance of up to 80% of body length, in less than 20 msec (Deban et al., '97, 2007). Tongue retraction is much slower than projection and is accomplished by contraction of the lengthy retractor muscles (the paired rectus cervicis profundus), which originate on the pelvis and insert into the tongue pad.

The structure and activity of the subarcualis rectus muscles are appropriate for an elastically powered projection mechanism. Collagen fibers which can act as springs lie in series with the contractile muscle fibers and are in position to transmit muscle forces to the tapered epibranchial cartilage or to be stretched by these forces when the epibranchial is held in place before tongue launch (Deban et al., 2007). The electrical activity of

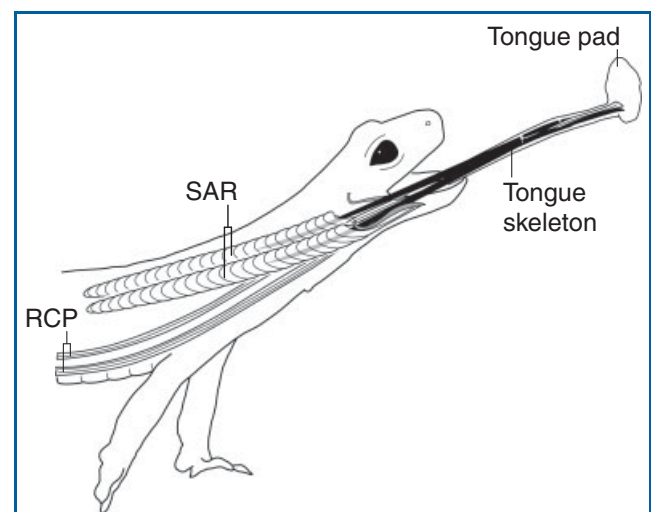


Figure 1. Illustration of the anatomy of the tongue apparatus in *Hydromantes* as it would be configured in mid-projection with the epibranchial tips within the projector muscles (SAR). Retractor muscles (RCP) originate on the pelvis and insert in the tongue pad. Figure modified from Deban and Dicke ('99).

the subarcualis muscles is largely separated in time from the subsequent tongue movement, beginning 80–180 msec before the tongue leaves the mouth and ending at the time the tongue begins its projection in *Hydromantes* (Deban and Dicke, 2004). This period of muscle activity before tongue movement indicates that collagen fibers are stretched and store strain energy. These collagen fibers then recoil against the epibranchial, launching it from the muscle. The temporal separation of muscle fiber activity and elastic recoil of collagen fibers make this system ideal for testing our thermal independence hypothesis. We predict complete thermal independence of projection in *Hydromantes* based on this temporal separation, and on the fact that no additional muscles are involved in powering tongue projection (Lombard and Wake, '77).

We examined tongue projection and retraction in *Hydromantes platycephalus* at a range of body temperatures (2–24°C). Examining the thermal dependence of the kinematics and dynamics of these two phases of feeding allows us to evaluate the hypothesis that elastic recoil liberates movements from the effects of temperature. We expect that elastically powered tongue projection will show thermal independence ($Q_{10} \sim 1$), and in contrast, nonelastic, muscle-powered tongue retraction will show thermal dependence typical of muscle-powered movements ($Q_{10} > 1.5$). *H. platycephalus* was chosen not only for the feeding mechanism it shares with its congeners but also because this species occurs at high elevation and naturally experiences low temperatures—as low as -2°C active body temperature (Brattstrom, '63). Examination of the thermal dependence or independence of its feeding movements is therefore particularly appropriate.

MATERIALS AND METHODS

Three adult *Hydromantes platycephalus* (Camp 1916) of 56, 60, and 64 mm snout–vent length, 2.9, 3.1, and 3.4 g body mass were collected from wild populations in California. They were housed individually in plastic boxes with a substrate of moist paper towels at 12–15°C and maintained on a diet of soldier fly larvae and crickets. All procedures in this study were approved by the appropriate institutional animal use committee.

Feeding Experiments

Salamanders were imaged in lateral or dorsal perspective at 3–6 kHz frame rate and 1/12,000 sec shutter speed with a Fastcam 1024 PCI camera (Photron USA Inc., San Diego, CA) as they captured soldier fly larvae and crickets (approximately 7–9 mm in body length). Illumination was provided by a fiber optic microscope light. Salamanders were permitted to approach the prey and choose their distance to the prey at the start of tongue projection. Image sequences of 102 feedings were obtained from three *Hydromantes platycephalus*. A subset of 63 feedings was deemed suitable for kinematic and dynamic analyses based on image quality, perspective (i.e., axis of the extended tongue

within approximately 15° of the focal plane of the camera), and the visibility of anatomical landmarks. A centimeter scale was imaged in the same plane as the salamander to calibrate distances.

Feeding trials were conducted within an environmental chamber (Environmental Growth Chambers, Chagrin Falls, OH) across a range of ambient temperatures (2–26°C), which were selected based on field recordings of temperature at sites of collection of *Hydromantes platycephalus* (Brattstrom, '63) and because this range overlaps with the range used in thermal preference experiments of this species and extends well above and below its preferred temperature of 13–14°C (Brattstrom, '63). Immediately after each feeding, the temperature of the salamander was measured using an infrared thermometer (Sixth Sense LT300, Williston, VT; $\pm 1^{\circ}\text{C}$ accuracy). Salamander body temperatures ranged from 2 to 24°C.

Kinematic and Dynamic Analyses

Tongue movements were first examined qualitatively in the digital image sequences. Three phases of movement were identified that were used in the subsequent quantitative analysis. The first phase was *tongue projection*, in which the tongue was extended from the mouth in a single, rapid, smooth movement. This was followed by *elastic tongue retraction*, in which the tongue retracted rapidly a portion of its extended length, apparently under elastic recoil of the tongue retractor muscles and associated connective tissue. Elastic tongue retraction was followed by the slower *nonelastic tongue retraction*, in which the tongue was retracted the remaining distance into the mouth under active muscle contraction. The transition from elastic to nonelastic tongue retraction was marked by a conspicuous and abrupt drop in retraction velocity and often a brief pause in retraction (a pause which is visible in the 12°C feeding in Fig. 2).

The timing and amplitude of tongue movements were next quantified from the image sequences. The x , y coordinates of the tongue tip and the tip of the snout or lower jaw were recorded from the image sequences using NIH ImageJ software running on an Apple iMac computer. Four events were identified in the image sequences and their times measured relative to the start of ballistic tongue projection at time zero: (1) maximum tongue reach, the time at which the tongue pad was the greatest distance from the snout or jaw; (2) the start of elastic tongue retraction, the time of the start of movement of the tongue toward the salamander; (3) the start of nonelastic tongue retraction (i.e., muscle-powered) retraction; (4) the end of tongue retraction, when the tongue pad entered the mouth completely. Two durations were calculated from these events: *Projection duration* is equivalent to time 1, and *retraction duration* was calculated as time 4 minus time 2. Performance parameters that were calculated from these events and their corresponding position data included durations, distances, and average velocities of tongue projection and tongue retraction. Prey distance was

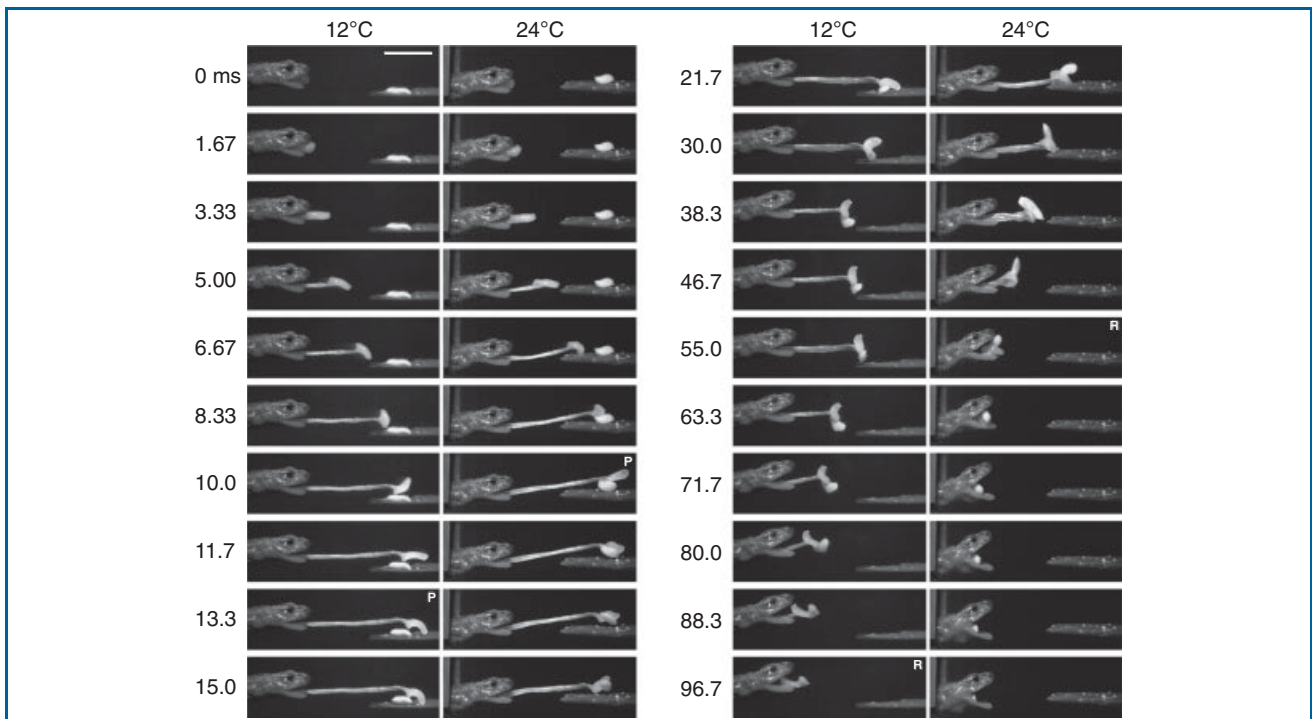


Figure 2. Image sequences of one individual of *Hydromantes platycephalus* feeding at 12 and 24°C showing little difference in the duration of elastically powered tongue projection (P indicates peak projection) yet pronounced differences in the duration of nonelastic, muscle-powered tongue retraction (ending at frames marked R). Sequences progress downward beginning at the top of the left column and continue at the top of the right column, and begin at the start of tongue projection at time 0. The time step is 1.67 msec in the left column and 18.3 msec in the right column. Note the brief pause in tongue retraction in the 12°C feeding (between 38.3 and 55.0 msec), which demarcates elastic and nonelastic retraction. For a movie of these feeding sequences, refer to the supplemental materials.

measured as the distance at the start of tongue projection between the tips of the salamander's jaws to the nearest point on the body of the prey.

The dynamics of tongue movements were calculated (using published methods; Deban et al., 2007) by smoothing the distance data with the P spline package in R statistical software (www.r-project.org). First and second derivatives of the quintic spline function were computed to produce instantaneous velocity and acceleration at an interpolated rate of 10 kHz. Instantaneous mass-specific power was calculated as the product of acceleration and velocity. The power required to produce the observed kinematics was calculated by multiplying instantaneous mass-specific power by the ratio of tongue mass to combined mass of the subarcualis rectus muscles (i.e., projector muscles) (1.04 for *Hydromantes platycephalus*; (Deban et al., 2007)). Performance parameters obtained from these calculations included the maximum values of instantaneous velocity, acceleration, and power of both tongue projection and nonelastic tongue retraction, as well as average velocity, duration, and tongue projection distance.

Statistical Analyses

All kinematic and dynamic performance parameters were \log_{10} transformed before statistical analysis, because biological rate variables typically have an exponential relationship with temperature. Analysis of covariance (ANCOVA) was used to examine the effects of temperature, individual, and tongue projection distance on the performance parameters. Temperature was included as a continuous variable to examine how elastically powered tongue projection and nonelastic tongue retraction were affected by changes in salamander body temperature. The analysis included an individual effect (as a random effect) to account for differences in body size and other random individual differences. Tongue projection distance was included as a covariate because it has been found in *Hydromantes* to be correlated with muscle activation parameters (Deban and Dicke, '99) and because it was expected to affect movement kinematics and dynamics; specifically, greater tongue projection distance was expected to be coupled with greater duration and velocity of tongue movements. Projection distance was dropped from the model when not significant to increase statistical power. Two

interactions were examined (temperature \times projection distance and individual \times temperature); however, no significant effects were found so these were dropped from the model. To account for multiple tests, a Bonferroni correction adjusted α to 0.0038 for 13 variables.

Temperature coefficients (Q_{10}) were calculated for each performance parameter across the entire temperature range (2–24°C) from the partial regression coefficients (PRC) of the temperature effect in the ANCOVA. Temperature coefficients were computed in this way because the ANCOVA model includes the effects of individual salamander and tongue projection distance (when significant), which may influence the relationship between temperature and the performance parameters. The Q_{10} value for each parameter was calculated as the base-10 antilogarithm of the PRC of the temperature effect multiplied by 10: $Q_{10} = 10^{(10 \times \text{PRC})}$ (Deban and Lappin, 2011). Temperature coefficients of duration parameters are reported as $1/Q_{10}$ to express them as rates. Because parameters were log10 transformed, significant temperature effects in the ANCOVA indicated that the Q_{10} value of a given parameter was significantly different from 1.0 (i.e., the null hypothesis of no temperature effect).

A second ANCOVA was used to examine the effects of temperature, individual, projection distance, feeding phase (i.e., tongue projection vs. nonelastic retraction) and two-way interactions on four performance parameters—average velocity, maximum velocity, maximum acceleration, and maximum power. Phase was included as a fixed effect to test whether tongue projection was significantly different than tongue retraction. The temperature \times phase interaction term in the model

allowed us to test whether temperature affected projection and nonelastic retraction differently. A Bonferroni correction adjusted α to 0.0125 for four variables to account for multiple tests. All statistical analyses were performed on an Apple iMac computer using JMP software (SAS Institute, Cary, NC).

RESULTS

Hydromantes platycephalus captured prey by ballistic tongue projection after approaching the prey slowly and fixating on it visually. During tongue projection and retraction, the body was held stationary with no forward lunging (Fig. 2). During tongue projection, the gape was sufficient to allow passage of the tongue pad. Upon tongue retraction, the gape increased while the snout was raised to allow passage of the tongue pad and adherent prey, which were delivered to the rear of the buccal cavity and clear of the jaws. Rapid mouth closing immediately followed.

Tongue Kinematics and Dynamics

Salamanders captured prey at 0.005–0.039 m from the tip of the snout, and achieved tongue projection distances of 0.012–0.042 m (Table 1). Tongue projection was rapid, taking 0.007–0.020 sec from the start of tongue acceleration to full projection. Tongue retraction often began with a brief period of rapid movement, presumably powered by elastic recoil. This fast retraction phase was followed by a brief dip in retraction velocity or a pause in retraction, followed in turn by steady, muscle-powered retraction (i.e., nonelastic retraction) that returned the tongue pad to the mouth. Tongue retraction was slower than projection, requiring 0.031–0.227 sec from

Table 1. Minimum and maximum values of kinematic and dynamic variables of prey capture in three *Hydromantes platycephalus*.

	Minimum	Maximum	Feedings
Body temperature (°C)	2	24	63 (12, 20, 31)
Prey distance (m)	0.005	0.039	63 (12, 20, 31)
Projection distance (m)	0.012	0.042	63 (12, 20, 31)
Projection duration (sec)	0.007	0.020	62 (11, 20, 31)
Average projection velocity (m sec ⁻¹)	1.47	3.32	62 (11, 20, 31)
Maximum projection velocity (m sec ⁻¹)	2.10	4.94	63 (12, 20, 31)
Maximum projection acceleration (m sec ⁻²)	413	1750	63 (12, 20, 31)
Maximum projection tongue power (W kg ⁻¹)	686	4800	63 (12, 20, 31)
Maximum projection muscle power (W kg ⁻¹)	713	4992	63 (12, 20, 31)
Retraction duration (sec)	0.031	0.227	62 (11, 20, 31)
Average retraction velocity (m sec ⁻¹)	0.09	0.63	62 (11, 20, 31)
Average nonelastic retraction velocity (m sec ⁻¹)	0.13	0.74	62 (11, 20, 31)
Max. nonelastic retraction velocity (m sec ⁻¹)	0.18	0.91	63 (12, 20, 31)
Max. nonelastic retraction acceleration (m sec ⁻²)	0.22	74.5	63 (12, 20, 31)
Max. nonelastic retraction power (W kg ⁻¹)	0.15	35.8	63 (12, 20, 31)

Total number of feedings and feedings per individual (in parentheses) are shown.

the start of retraction to the time the tongue pad completely entered the mouth.

Salamanders projected the tongue at an average velocity of 1.47–3.32 msec⁻¹ and a maximum instantaneous velocity of 2.10–4.94 msec⁻¹ (Table 1). Tongue-projection duration, average velocity, and peak velocity were significantly higher in projections of greater distance ($P < 0.0001$). The tongue was projected at a maximum instantaneous acceleration of 413–1,750 msec⁻² and a maximum instantaneous power of 686–4,800 W kg⁻¹, requiring a maximum instantaneous muscle-mass specific power of 713–4,992 W kg⁻¹.

Salamanders retracted the tongue more slowly, at an average velocity of 0.09–0.63 msec⁻¹. The nonelastic phase of tongue retraction had an average velocity of 0.13–0.74 msec⁻¹, a maximum instantaneous velocity of 0.18–0.91 msec⁻¹, a maximum instantaneous acceleration of 0.22–74.5 msec⁻², and a maximum instantaneous power of 0.15–35.8 W kg⁻¹. Average velocity of tongue retraction was positively correlated with projection distance ($P < 0.0001$).

Effects of Temperature on Tongue Movements

Hydromantes platycephalus projected the tongue ballistically at all body temperatures (2–24°C). The distance at which the salamanders initiated prey capture showed no significant effect of temperature ($Q_{10} = 0.93$, $P = 0.068$). Temperature had no significant effect on tongue-projection kinematics or dynamics as

revealed by the ANCOVA (Table 2; Fig. 3), resulting in Q_{10} values of 0.94–1.04 for all parameters. The tongue was projected a range of distances at all temperatures (projection distance $Q_{10} = 0.94$, $P = 0.2527$) with similar peak velocity ($Q_{10} = 0.99$, $P = 0.167$) and peak power ($Q_{10} = 1.03$, $P = 0.797$).

Tongue retraction, in contrast to projection, was strongly affected by body temperature, slowing at lower temperatures. The ANCOVA revealed that all kinematic and dynamic parameters were significantly affected by temperature (Table 2), reflected in Q_{10} values of 1.63–4.97. Retraction duration increased by approximately fivefold at a body temperature of 2°C as compared with 24°C ($1/Q_{10} = 1.82$, $P < 0.0001$) and retraction velocity showed a commensurate decline (Fig. 4). The effect of temperature was strong for both average tongue retraction velocity including the initial elastic phase ($Q_{10} = 1.78$, $P < 0.0001$) and average nonelastic retraction velocity ($Q_{10} = 1.71$, $P < 0.0001$) (Fig. 5).

Temperature had a significantly different effect on the two phases of feeding—tongue projection and tongue retraction—as revealed by the ANCOVA that included feeding phase as an effect. Average velocity, maximum velocity, maximum acceleration, and maximum power all showed a significant temperature × phase effect ($P < 0.0001$; Table 3). These variables were also significantly affected by feeding phase ($P < 0.0001$) independently of temperature, indicating that tongue retraction had significantly lower values than tongue projection.

Table 2. Results of ANCOVA examining effects of individual, temperature, and projection distance on kinematic and dynamic variables of tongue movements in three *Hydromantes platycephalus*.

	Individual		Temperature		Projection distance		DF	Temp. slope	Q_{10}	1/ Q_{10}
	F-ratio	P-value	F-ratio	P-value	F-ratio	P-value				
Prey distance	3.691	0.0311	3.461	0.0680	116.409	<0.0001	4,57	-0.0033	0.93	1.08
Projection distance	11.833	<0.0001	1.334	0.2527	-	-	3,59	-0.0025	0.94	1.06
Projection duration	3.441	0.039	0.003	0.954	20.345	<0.0001	4,57	0.0001	1.00	1.00
Average projection velocity	1.020	0.367	0.106	0.747	60.012	<0.0001	4,57	-0.0004	1.00	1.00
Maximum projection velocity	2.356	0.104	1.961	0.167	34.677	<0.0001	4,58	0.0018	0.99	1.01
Maximum projection acceleration	0.985	0.379	0.282	0.598	2.205	0.143	3,59	0.0013	1.04	0.96
Maximum projection power	1.478	0.236	0.067	0.797	6.009	0.017	3,59	0.0011	1.03	0.98
Retraction duration	10.866	<0.0001	178.91	<0.0001	7.836	0.007	3,58	-0.0260	0.55	1.82
Average Retraction Velocity	10.223	0.0002	171.05	<0.0001	30.009	<0.0001	4,57	0.0250	1.78	0.56
Average nonelastic retr. velocity	0.227	0.798	82.298	<0.0001	0.985	0.325	3,58	0.0232	1.71	0.59
Max. nonelastic retr. velocity	0.541	0.585	66.907	<0.0001	4.135	0.047	3,59	0.0212	1.63	0.61
Max. nonelastic retr. acceleration	0.738	0.483	36.104	<0.0001	0.684	0.412	3,59	0.0488	3.08	0.32
Max. nonelastic retr. power	0.513	0.601	66.997	<0.0001	1.339	0.252	3,59	0.0696	4.97	0.20

F-ratios and P-values are shown for individual, temperature, and projection distance, as is the partial regression coefficient for the temperature effect (i.e., Temp. Slope) from the model from which Q_{10} values were calculated. Bold P-values indicate significant effects at the Bonferroni-corrected α (0.0038 for 13 variables). Bold Q_{10} values indicate significant temperature effects. Projection distance was included as a covariate only when it showed a significant effect for that variable. Note the lack of effect of temperature on tongue projection variables, in contrast to the significant effect of temperature on tongue retraction variables.

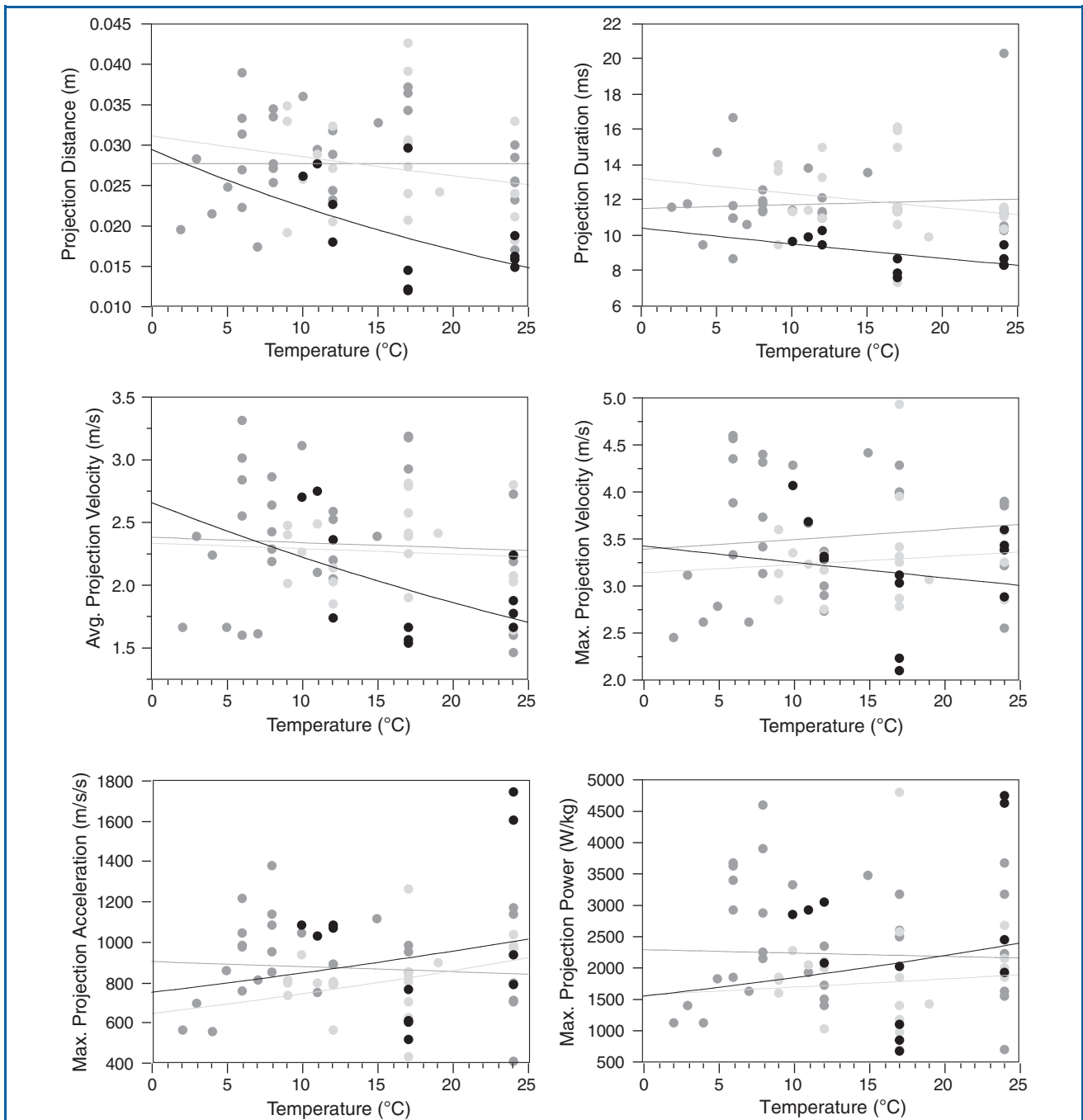


Figure 3. Scatterplots of kinematic and dynamic parameters of tongue projection vs. temperature, showing thermal independence. Individuals are shown in different gray dots and corresponding lines which represent exponential regressions for each individual.

DISCUSSION

Tongue Kinematics and Dynamics

The *Hydromantes platycephalus* examined in this study projected the tongue ballistically up to 4.2 cm from the tip of the snout, as has been previously shown in this and other species of

Hydromantes (Deban et al., '97; Deban and Dicke, 2004; Deban et al., 2007). The range of maximum instantaneous velocities of tongue projection of $2.1\text{--}4.9\text{ msec}^{-1}$ was similar to that previously measured for *Hydromantes* feeding at a much narrower range of temperatures ($1.9\text{--}4.9\text{ msec}^{-1}$ at $22\text{--}24^\circ\text{C}$);

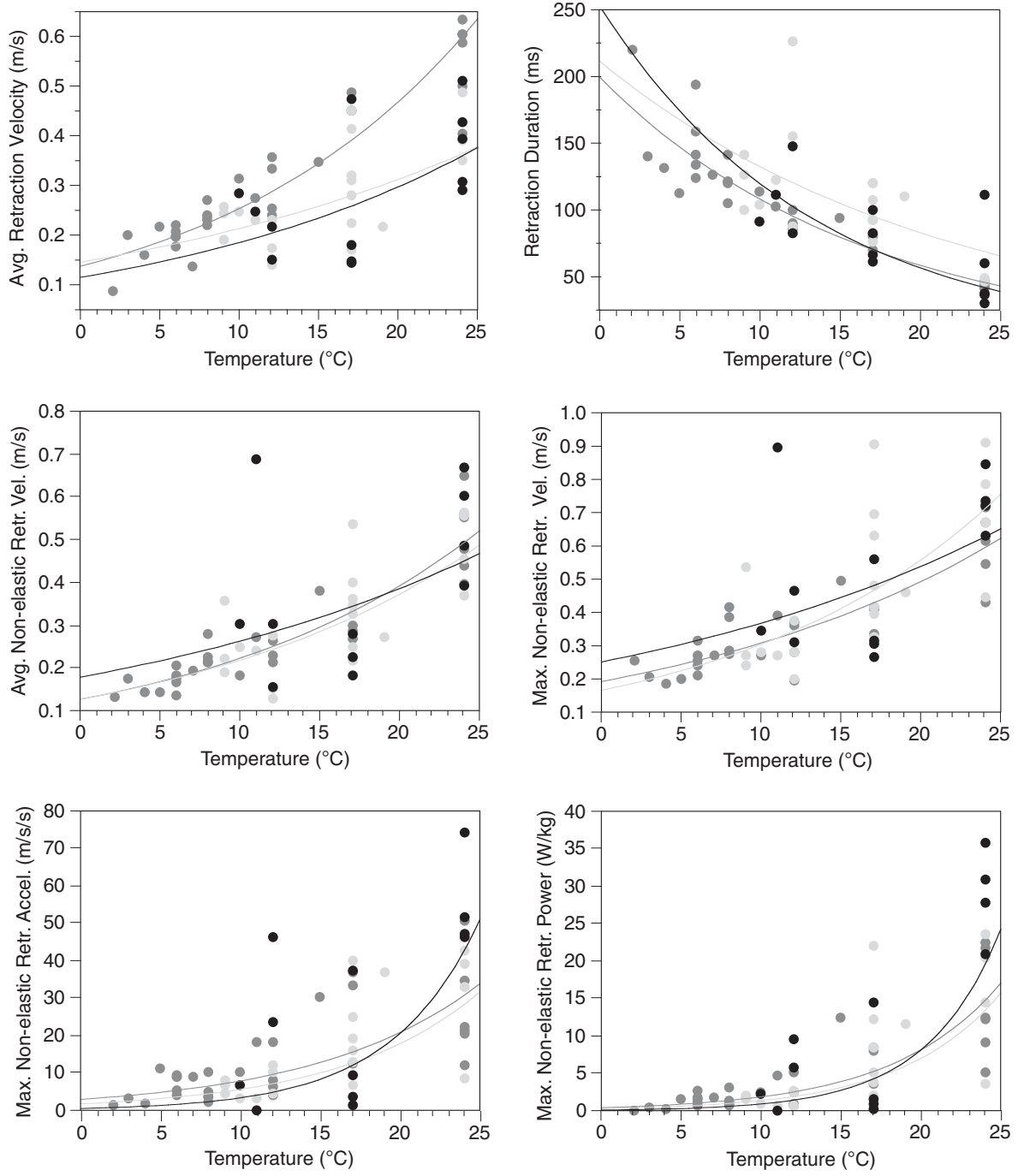


Figure 4. Scatterplots of kinematic and dynamic parameters of tongue retraction vs. temperature, showing strong thermal dependence. Indications as in Figure 3.

similarly, maximum instantaneous power values of $713\text{--}4,992\text{ W kg}^{-1}$ overlapped considerably with published values ($273\text{--}4,305\text{ W kg}^{-1}$; Deban et al., 2007). The minimum power output of tongue projection measured in this study

exceeds the maximum muscle power estimated for amphibians (373 W kg^{-1} at 25°C ; Lutz and Rome, '94), indicating that *Hydromantes* uses an elastic recoil mechanism to enhance power output, also consistent with previous results (Deban et al., 2007).

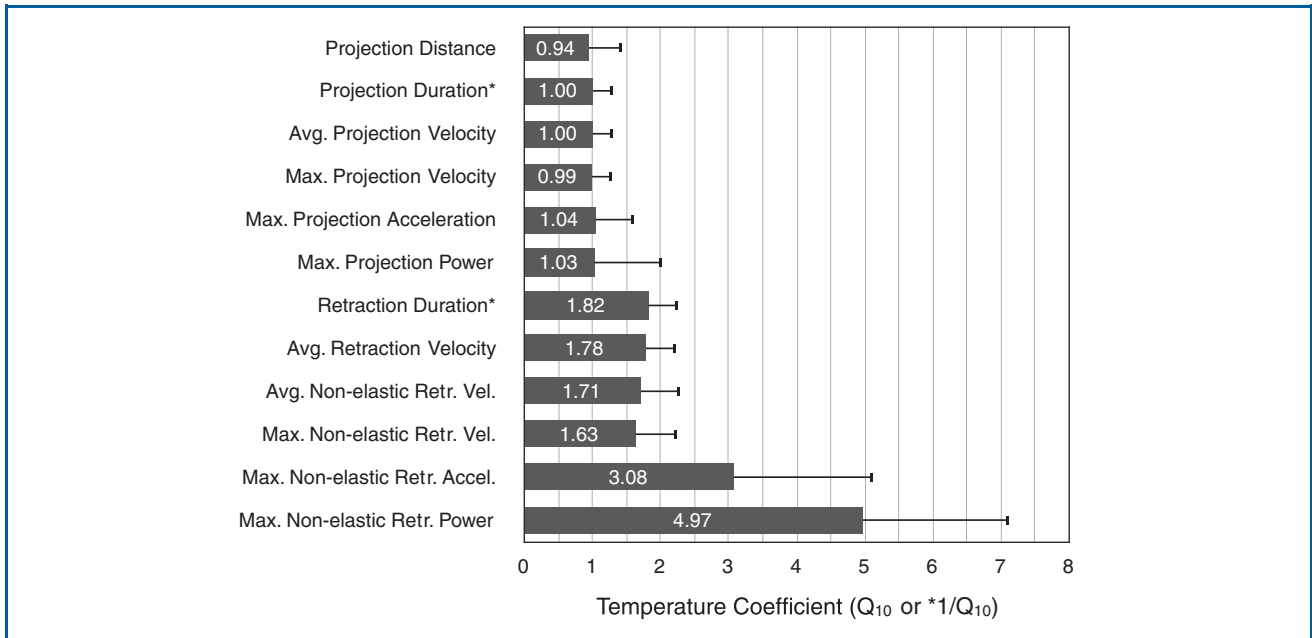


Figure 5. Bar graphs of Q₁₀ values (with standard error bars) of tongue projection and retraction parameters showing difference in thermal responses of the two feeding phases. 1/Q₁₀ is shown for durations. See text for methods used to derive Q₁₀ values.

Table 3. Results of ANCOVA examining effects of individual, temperature, projection distance, and feeding phase (i.e., tongue projection vs. nonelastic retraction) on dynamic variables of tongue movements in three *Hydromantes platycephalus*.

	Individual		Temperature		Projection distance		Phase	
	F-ratio	P-value	F-ratio	P-value	F-ratio	P-value	F-ratio	P-value
Average velocity	6.355	0.0024	77.088	<0.0001	33.421	<0.0001	983.98	<0.0001
Maximum velocity	1.995	0.1406	67.759	<0.0001	19.459	<0.0001	900.90	<0.0001
Maximum acceleration	0.933	0.3961	35.123	<0.0001	1.501	0.2229	418.90	<0.0001
Maximum power	1.305	0.2751	56.327	<0.0001	4.511	0.0357	744.18	<0.0001
		Individual × Proj. distance		Temperature × Phase				
		F-ratio	P-value	F-ratio	P-value	Degrees of freedom		
Average velocity		8.948	0.0002	101.09	<0.0001	8,115		
Maximum velocity		3.046	0.0513	71.337	<0.0001	6,119		
Maximum acceleration		1.633	0.1997	31.367	<0.0001	5,120		
Maximum power		2.603	0.0783	58.335	<0.0001	5,120		

Bold P-values indicate significant effects at the Bonferroni-corrected α (0.0125 for four variables). Projection distance and interaction terms were included in the model only when they showed a significant effect for that variable. Note that the *temperature* × *phase* interaction is a significant effect for all variables, indicating different responses to temperature of elastically powered projection vs. muscle-powered retraction.

Tongue retraction in the *Hydromantes* examined here was considerably slower and less dynamic than projection, and shows evidence of being primarily powered by direct contraction of rectus cervicis profundus muscles. Retraction showed significantly lower values of average velocity, peak velocity, peak acceleration, and peak power than did tongue projection (Tables 1 and 3). The maximum average velocity of the entire

tongue retraction, including the initial phase of apparently elastic retraction, was approximately one-fifth of the maximum average projection velocity. The nonelastic portion of retraction, powered by muscle contraction, had a slightly greater maximum average velocity because it excluded the pause in retraction that often followed the elastic phase, however it was still less than one-fourth of the maximum average velocity of projection

(Fig. 2; Tables 1 and 3). The maximum power observed during the major, nonelastic phase of retraction was 35.8 W kg^{-1} , a value that is well below the maximum estimated mass-specific power of 373 W kg^{-1} for amphibian muscle (Lutz and Rome, '94) and within the capabilities of direct muscle contraction.

Effects of Temperature on Tongue Movements

Tongue-projection performance of *Hydromantes platycephalus* is entirely temperature independent. *Hydromantes* was able to perform ballistic tongue projection at all temperatures ($2\text{--}24^\circ\text{C}$) and showed no deficit at low temperatures in distance of tongue projection, velocity, acceleration, or power output. Tongue-projection kinematics and dynamics (i.e., performance) in *Hydromantes* displayed Q_{10} values of $0.94\text{--}1.04$, and showed no significant effect of temperature in the ANCOVA (Table 2). The performance measures showed a degree of scatter (Fig. 3), with some feedings of low performance at all temperatures; however, high values were also achieved at low temperature. Remarkably, performance was high even at extremely low temperature; one individual achieved a maximum instantaneous power output of $1,130 \text{ W kg}^{-1}$ at 2°C and a maximum instantaneous velocity of 4.6 msec^{-1} at 6°C (Fig. 3).

The dynamics of tongue projection responded differently to temperature than those of tongue retraction, as shown by the significance in the ANCOVA of the "temperature \times phase" effect on average velocity and maximum velocity, acceleration, and power (Table 3). This significant effect reveals that the two phases of tongue movement rely upon mechanisms with different thermal responses. Considered by itself, tongue retraction in *Hydromantes* displayed thermal sensitivity that is typical of muscle-powered movement (Figs. 4, 5). The effect of temperature on tongue retraction velocity was significant even when the initial elastic phase of retraction was included in the calculation of average retraction velocity, likely because the majority of retraction is muscle-powered and subject to thermal effects on muscle contractile velocity. Overall, the Q_{10} values of $1.63\text{--}4.97$ for kinematics and dynamics of tongue retraction were significantly different from 1.00 and encompass Q_{10} values of other muscle-powered movements at cool temperatures such as lizard sprint speed (Herrel et al., 2007) and frog jumping distance (Hirano and Rome, '84) and Q_{10} values of the contractile dynamics of skeletal muscles from diverse taxa (Bennett, '84; Renaud and Stevens, '84; Bennett, '85; Faulkner et al., '90; Asmussen et al., '94; Altringham and Block, '97; Choi et al., '98).

Elastic-Recoil Mechanisms

The observed thermal independence of tongue projection in *Hydromantes platycephalus* is consistent with an elastic-recoil mechanism that circumvents the thermal effects on muscle contractile dynamics and thereby permits high-power movement at low temperature. This mechanism has previously been hypothesized to confer power amplification at moderate

temperatures ($22\text{--}24^\circ\text{C}$) (Deban et al., 2007) by decoupling active muscle contraction from tongue projection. In this model, active contraction of the subarcualis rectus (i.e., projector) muscle fibers before tongue projection stretches in-series collagen fibers within the muscle (and potentially components of the muscle fibers themselves). These elastic elements subsequently recoil rapidly and convert their strain energy into kinetic energy of the projecting tongue skeleton. This temporal decoupling of muscle fiber contraction from movement of the tongue skeleton has the effect of making the active contraction velocity of muscle fibers (i.e., cross-bridge cycling) irrelevant to the velocity of the subsequent movement that is powered by rapid elastic recoil. The slowing of active muscle contraction with low temperature thus has no effect on the dynamics of the subsequent movement.

A "bow and arrow" mechanism such as that operating in *Hydromantes* can confer thermal insensitivity to the movement if two properties have low thermal dependence—the stiffness of the elastic tissues and the tension achieved by the muscle in loading the elastic tissues. Available evidence suggests that these two conditions are met. First, the stiffness and other mechanical properties of elastic tissues (e.g., collagen, resilin and other protein rubbers) have low thermal dependence (Q_{10} of $1.03\text{--}1.11$) (Alexander, '66; Denny and Miller, 2006) or complete thermal independence (Rigby et al., '59). Second, the thermal independence of tetanic tension of skeletal muscles is well established (Hill, '51; Bennett, '84, '85). The projector muscle fibers in *Hydromantes* likely contract with low strain (Deban et al., 2007) and would thus be operating near peak tension. Although the rate of tension development in muscles is strongly affected by temperature (Bennett, '84), *Hydromantes* should be able to achieve similar tension by extending muscle activation further in advance of tongue projection at low temperatures. Modulation in the duration of muscle activity has been observed in the activation of the jaw depressor muscles of the toad *Bufo terrestris* in response to changes in temperature (Deban and Lappin, 2011) and in *Bufo alvarius* in response to changes in prey distance (Lappin et al., 2006). *Hydromantes* has been shown to activate the projector muscle $80\text{--}180 \text{ msec}$ before tongue launch and to modulate activity duration extensively (Deban and Dicke, '99, 2004), indicating that loading of elastic tissues occurs before launch and that the duration of this loading period is modulated.

Low thermal sensitivity of ballistic movement has been documented in the feeding of chameleons and toads, both systems in which elastic-recoil mechanisms are operating. Chameleons project the muscular tongue ballistically from the hyoid skeleton via a combination of contraction of the accelerator muscle and elastic recoil of collagenous sheaths within the lumen of the muscle (de Groot and van Leeuwen, 2004), but retract the tongue by direct contraction of the hyoglossus muscle (Zoond, '33; Gans, '67; Wainwright and Bennett, '92). *Chamaeleo calypttratus* has been shown to project the tongue fully and with high power ($1,892 \text{ W kg}^{-1}$) at 15°C , and

to retain performance over a wide temperature range of 15–35°C, with Q_{10} values of projection dynamics of 1.1–1.3 (Anderson and Deban, 2010). Toads project the tongue via ballistic mouth opening, which is accomplished by elastic recoil of the depressor mandibulae muscles. The tongue is whipped out of the mouth and elongates inertially as the mandible is rapidly depressed, but is withdrawn by direct contraction of the hyoglossus muscle. *Bufo terrestris* has been shown to open its mouth ballistically and project its tongue fully and with high power across a range of temperatures of 11–35°C, with Q_{10} values of projection dynamics of 1.0–1.3 (Deban and Lappin, 2011).

Ecological and Evolutionary Implications

The observation of low thermal dependence of elastically powered tongue projection in *Hydromantes*, *Chamaeleo* and *Bufo*—three independently evolved ballistic systems—suggests that other ballistic systems may show similar thermal insensitivity. Ballistic projection that makes the use of elastic recoil and power amplification has evolved three times in plethodontid salamanders (Deban et al., 2007), and ballistic tongue projection has also evolved multiple times among frogs (Nishikawa, 2000). Among insects, snow fleas have been found to jump with a high performance at 0°C, possibly making use of energy storage in the resilin of their limb articulations (Burrows, 2011). Many other animal movements which make use of elastic-recoil mechanisms to enhance mechanical power output (Roberts and Azizi, 2011) may benefit from thermal independence, including striking in mantis shrimp (Patek et al., 2007; Zack et al., 2009), jaw closure in trap jaw ants (Gronenberg, '96; Patek et al., 2006), jumping in frogs (Roberts and Marsh, 2003) and insects (Bennet-Clark and Lucey, '67; Rothschild et al., '75; Bennet-Clark, '76; Burrows, 2010), and suction feeding in pipefish (Van Wassenbergh et al., 2008).

An elastic-recoil mechanism may be particularly beneficial to *Hydromantes platycephalus*, which lives at elevations of 1,220–3,660 m in the Sierra Nevada mountains of California in talus and crevices and on granite exposures and melting snow banks (Stebbins, '85). Plethodontid salamanders have been found to have a lower minimum voluntary temperatures than other terrestrial salamanders and *Hydromantes platycephalus* has the lowest recorded in a salamander (−2°C) (Brattstrom, '63). This species has been found active at freezing temperatures (i.e., −2°C to 11.5°C) and chose 13–14°C when placed in a thermal gradient of 4–24°C (Brattstrom, '63). Maintaining high performance tongue projection at low body temperatures is thus potentially important for this species. *Hydromantes platycephalus* is a slow-moving, nocturnal predator that relies on ambush or stalking and makes use of its long tongue to capture distant prey without lunging or jumping. The species also possesses noxious skin secretions and engages in a passive “rolling escape” behavior when disturbed (García-París and Deban, '95), rather than the rapid jumping or wriggling responses of many other

amphibian species. Essentially, the only thing *Hydromantes* does quickly is shoot out its tongue. Its reliance on slow locomotor movements, passive escape, and toxicity suggests that its activities may not be unduly impaired by low temperatures.

Another potential benefit of elastic recoil in ectotherms is a reduced need to thermoregulate. Behavioral thermoregulation and other movement through the environment can meet other physiological requirements (e.g., water balance, reproduction, and digestion) once the need to maintain muscles at an optimal temperature is reduced or eliminated. Thermoregulatory behavior has energetic costs as well as costs in exposure to predation (Huey, '74), and in amphibians thermoregulation is restricted to microenvironments that do not cause undue evaporative water loss (Feder, '82, '83a,b). Ectotherms with elastic mechanisms may thus maintain performance in circumstances where thermoregulation would incur costs.

Elastically powered movements often display impressive power output and accelerations that are beyond the capabilities of muscle-powered movement. Indeed, it is often the high performance that attracts the attention of researchers, as in the classic example of flea jumping (Burrows, 2009). However, elastic mechanisms may play an important role in movements of modest performance by endowing them with an expanded thermal breadth. Given that many of the documented elastic power-amplification mechanisms are in ectothermic organisms (Bennet-Clark and Lucey, '67; Rothschild et al., '75; Bennet-Clark, '76; Gronenberg, '96; Roberts and Marsh, 2003; Lappin et al., 2006; Patek et al., 2006; Deban et al., 2007; Van Wassenbergh et al., 2008; Zack et al., 2009; Burrows, 2011), it is conceivable that selection for cold tolerance may favor elastic-recoil mechanisms, which can be subsequently elaborated to produce high performance at a wide range of temperatures.

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