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1 **Title**

2 **Do hypothermic tissue tolerances limit torpor expression?**

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24 **Abstract**

25 1. Arrest temperatures and Q_{10} values for extensor digitorum longus (EDL),
26 soleus, trabecula, and jejunum muscle twitch strength, contraction time, and 0.5
27 relaxation time were calculated for a deep torpor hibernator, white-tailed prairie dog
28 (*Cynomys leucurus*), a shallow torpor hibernator, black-tailed prairie dog (*Cynomys*
29 *ludovicianus*), and a non-hibernator, lab rat (*Rattus norvegicus*) to test the hypothesis that
30 tissue temperature tolerances limit the depth of expressed torpor.

31 2. There were no temperature tolerance differences between the tissues of the two
32 species of hibernators. Both hibernating species had arrest temperatures and Q_{10} values
33 more indicative of cold temperature tolerance than the lab rat in all tissues, with the
34 exception of the soleus muscle.

35 3. These data imply that a limited cold tolerance of contractile tissue does not
36 preclude a shallow torpor hibernator such as the black-tailed prairie dog from expressing
37 deep torpor patterns. Other mechanisms, such as central neural control, are more likely
38 to be important in determining the torpor strategy utilized by hibernating species.

39 **Keywords: hibernation, contractile performance, thermal biology, skeletal muscle,**
40 **smooth muscle, cardiac muscle.**

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47 **1. Introduction**

48 Hibernation allows some small mammals to survive prolonged periods of cold
49 and food scarcity through a marked reduction in metabolic rate with concomitant energy
50 conservation (Nedergaard and Cannon, 1990). Although 7 of the 25 mammalian orders
51 have species that hibernate (Geiser and Ruf, 1995), not all hibernators utilize the same
52 strategies or perhaps do not express genes associated with hibernation to the same extent.
53 Harlow (1995) summarized two different types of torpor strategy in small mammals.
54 One group of hibernators typically express photoperiod driven, circannual onset of winter
55 torpor bouts that are characteristically of regular, long duration and with a low body
56 temperature. For the purposes of this paper, we will refer to these animals as deep torpor
57 hibernators. A second group of hibernators enter sporadic, short duration, mildly
58 hypothermic torpor bouts that can be initiated any time during the winter in association
59 with acute changes in ambient temperature and / or lack of food and shall be referred to
60 as shallow torpor hibernators.

61 Two species that provide a useful model to study these different hibernation
62 strategies are the white-tailed prairie dog (*Cynomys leucurus*) and the black-tailed prairie
63 dog (*C. ludovicianus*). Both of these prairie dog species have evolved from a
64 spermophiline ancestor likely resembling the Gunnison's prairie dog (*C. gunnisonii*),
65 which is a deep hibernator (Pizzimenti, 1975; Rayor et al., 1987). While the white-tailed
66 prairie dog (WTPD) appears to have retained the ancestral expression of deep hibernation
67 as populations expanded into the great basin of North America (Pizzimenti, 1975; Harlow
68 and Menkens, 1986), the black-tailed prairie dog (BTPD) became more of a shallow
69 hibernator that exhibited reduced expression of torpor (Pizzimenti, 1975; Harlow and

70 Menkens, 1986; Lehmer et al., 2003) after populations spread into the Great Plains.
71 WTPDs routinely exhibit rhythmic hypothermic torpor bouts with an average body
72 temperature of 7°C for periods of 5-6 days during their hibernation season (Bakko and
73 Nahorniak, 1986; Harlow and Menkens, 1986). In contrast, BTPDs generally lower their
74 body temperature to 32°C – 27°C with torpor bouts lasting 1 – 2 days and occurring much
75 less frequently than WTPDs (Harlow and Menkens, 1986; Lehmer et al., 2001).
76 However, it has been reported that BTPDs can, on rare occasions, undergo regular bouts
77 of torpor with body temperatures approaching 10°C (Lehmer et al., 2003; Lehmer et al.,
78 2006). Harlow and Menkens (1986) showed in laboratory studies with *ad libitum* food
79 and water, total darkness, and 4°C ambient temperature that WTPDs will initiate these
80 deep torpor bouts in early October, while BTPDs engage in their more shallow and
81 sporadic torpor only when completely deprived of food and water.

82 Several studies have been undertaken to determine if some basic physiological
83 differences exist that explain why the BTPD defends a torpor state with a higher T_b and
84 shorter duration than the closely related WTPD. For example, total body fat content
85 (Harlow, 1997), brown adipose tissue response (Harlow, 1997), polyunsaturated fatty
86 acid profiles (Harlow and Frank, 2001), and renal function (Harlow and Braun, 1995)
87 were not different between the two species. As an alternative, tissue temperature
88 tolerance may influence the expression of deep torpor by these two species. Past studies
89 have consistently shown that hibernators tend to have cardiac tissue (Lyman and Blinks,
90 1959; Lyman, 1964; Jacobs and South, 1973; Burlington and Darvish, 1988), skeletal
91 muscle (South, 1961; Nelson et al., 1977), and smooth muscle (Kamm et al., 1979;
92 Carey, 1990; Wolowyk et al., 1990; Carey, 1992) that are better adapted to survive and

93 perform at the low temperatures associated with hibernation than tissue from non-
94 hibernators. The objective of this study was to investigate the performance of these three
95 muscle types: cardiac (trabecula), skeletal (soleus and extensor digitorum longus), and
96 smooth muscle (jejunum) at low temperatures by a representative non-hibernator (lab
97 rat); deep torpor hibernator (WTPD); and shallow torpor hibernator (BTPD).

98 We hypothesize that there is a gradient of low temperature tolerance and
99 performance of these three muscle types between deep torpor hibernators, shallow torpor
100 hibernators, and non-hibernators. If no such response gradient is observed, tissue
101 tolerance to very cold temperatures may not be a genetically controlled determinant of
102 hibernation ability and it may simply be a result of phenotypic plasticity dictated by other
103 unidentified variables. To answer this question, we measured the arrest temperatures in
104 addition to temperature effects on contraction strength and muscle relaxation time by
105 these three muscle tissues taken from the WTPD, BTPD, and laboratory rat.

106 **2. Methods**

107 Six rats (3 male, 3 female; mean weight = 373.86g, Charles River Albino, 60 days
108 old), six WTPDs (4 male, 2 female; mean weight = 1021.83g), and eight BTPDs (5
109 males, 3 females; mean weight 709.31g) were collected for the study. All experimental
110 protocols were approved by the University of Wyoming IACUC committee.

111 In Vitro Set-up

112 Each animal was anesthetized with ketamine hydrochloride at a dosage of
113 190mg/Kg body mass in late April. After deep anesthesia was obtained, the right and left
114 EDL, soleus, jejunum, and heart trabecula were removed from each animal followed by
115 immediate euthanasia with an overdose of pentobarbitol, Beuthanasia[®]-D Special

116 (Kreeger, 1996). The tissue samples were connected to force transducers and placed into
117 Krebs buffer (NaCl 118.1mM, KCl 3.4mM, KH₂PO₄ 1.2mM, MgSO₄·7H₂O 1.0mM,
118 Dextrose 10.8mM, NaHCO₃ 25.0mM, and CaCl₂ 2.5mM) aerated with a mixture of
119 oxygen and carbon dioxide maintained at a pH of 7.4 at 25°C for the EDL and soleus and
120 37°C for the jejunum and heart trabecula.

121 EDL and soleus tissue preparations were stretched to obtain optimal twitch
122 tension and stimulated every 30 seconds with a 2ms 9V stimulus provided by a CB
123 Sciences CK-100 stimulator. The jejunum was also stretched to obtain optimal
124 contractions, but did not receive external stimulation. The heart trabecula was stretched
125 to obtain optimal twitch tension and stimulated at 0.25Hz using a 10ms 50V stimulus.
126 Using a Haake D1 and Fisher Isotemp 1000 circulating water baths, buffer temperatures
127 were gradually lowered to -2°C for the EDL and soleus and 0°C for the jejunum and heart
128 trabecula. Both tissue arrest temperatures and Q₁₀ data were utilized as indices of
129 temperature sensitivity. Tissue arrest temperatures were recorded when contraction
130 strength dropped below background noise (typically 25mg). Temperature quotient (Q₁₀)
131 values for contraction strength (CS), contraction time (CT), and 0.5 relaxation time
132 (0.5RT) were recorded for each tissue using the equation $Q_{10} = (R_2 / R_1)^{10 / (t_2 - t_1)}$ where
133 R₂ is the rate or measurement at temperature t₂ and R₁ is the rate or measurement at
134 temperature t₁. Using these criteria, Q₁₀ values that deviate from 1.0 indicate tissue that
135 is temperature sensitive, while Q₁₀ values that approximate 1.0 indicate tissues that are
136 temperature insensitive for the given range of temperatures. Q₁₀ values were calculated
137 for the largest temperature range over which all animals could still elicit a viable tissue
138 response. Temperature ranges of 25°C to 10°C for skeletal muscle, 37°C to 20°C for

139 jejunum, and 37°C to 10°C for trabecula were used to compare tissue sensitivity to
140 temperature by these three species. No differences between male and female animals
141 were detected for any of the species, as a result, all male and female data were grouped
142 together.

143 Statistical Analysis

144 Changes in contraction time and 0.5 relaxation time were evaluated using Mann-
145 Whitney rank sum test, while contraction strength for each species was evaluated using a
146 t-test. Arrest temperatures and Q_{10} values were compared using a one-way ANOVA and
147 Tukey post-hoc tests for significant interactions. All statistical analysis was performed
148 using Sigma Stat 3.1 (Systat Software Inc., Point Richmond, CA, USA) with significance
149 accepted at $p < 0.05$.

150 **3. Results**

151 Arrest Temperatures

152 The arrest temperatures for the isolated heart trabecula muscle were significantly
153 lower for both prairie dog species compared to the rat (WTPD $q = 5.597$, $p = 0.003$;
154 BTPD $q = 4.239$, $p = 0.021$) but there were no differences between the two prairie dogs
155 (Figure 1). The jejunum arrest temperatures were also significantly lower for both the
156 WTPD and BTPD compared to the rat but not between each other (WTPD, $q = 4.845$, $p =$
157 0.009 ; BTPD $q = 4.594$, $p = 0.013$; Figure 1). The EDL arrest temperatures for both the
158 WTPDs ($q = 5.067$, $p = 0.006$) and BTPDs ($q = 9.268$, $p < 0.001$, Figure 1) were
159 significantly lower than that of the rat. The EDL arrest temperature was also lower for
160 the BTPDs than the WTPDs ($q = 3.851$, $p = 0.037$, Figure 1). The arrest temperatures for
161 soleus muscles did not differ between the three species (Figure 1).

162 Q₁₀ Values

163 Contraction and 0.5 relaxation times increased for all tissues as temperature
164 decreased (Table 1). There were no differences in EDL or soleus contraction time Q₁₀
165 values between species. However, EDL Q₁₀ values for 0.5 RT were higher in WTPD, but
166 not BTPD, than rats (WTPD q = 5.052, p = 0.006; BTPD q = 3.577, p = 0.054; Table 2),
167 as were the soleus 0.5 RT Q₁₀ values for both prairie dog species compared to the rat
168 (WTPD q = 10.543, p < 0.001; BTPD q = 7.777, p < 0.001, Table 2). There were no
169 differences between species in trabecula and jejunum Q₁₀ values for CT and 0.5RT.
170 There were also no differences in Q₁₀ values between prairie dog species for contraction
171 or 0.5 relaxation times.

172 Strength tended to decrease with temperature for all tissues, the exception being
173 prairie dog trabecula muscle, which increased in contraction strength with decreasing
174 temperature (Figure 2). Both prairie dog species had trabecula contraction strength Q₁₀
175 values that were lower than the rat and less than one, indicating a more robust contraction
176 with low temperatures (WTPD q = 5.508, p = 0.003; BTPD q = 5.226, p = 0.005; Table
177 2). The Q₁₀ value for EDL strength of both prairie dogs was less than the rat (WTPD q =
178 3.611, p = 0.005; BTPD q = 3.943, p = 0.032; Table 2). However, contraction strength
179 Q₁₀ values for the soleus were higher for both species of prairie dogs than the rat (WTPD,
180 q = 3.025, p < 0.05; BTPD q = 2.791, p < 0.05). There were no differences in jejunum
181 contraction strength Q₁₀ values between the species. There were no differences in the Q₁₀
182 values for strength between prairie dog species for any of three muscle tissues
183 investigated.

184 **4. Discussion**

185 There is much interest in identifying which factors may limit an animal's ability
186 to hibernate and what determines whether an animal expresses deep or shallow torpor.
187 However, no studies have examined if there are differential temperature tolerances for
188 muscles which control blood flow, locomotion, and digestion by closely related
189 mammalian species expressing different depths of torpor. The present investigation
190 compares the functional capacity of cardiac, skeletal, and smooth muscle at cold tissue
191 temperatures in a non-hibernator, shallow torpor, and deep torpor hibernator.

192 Cardiac Muscle

193 The ability of the hibernator's cardiovascular system to function at the low
194 temperatures associated with hibernation is a predominant factor limiting non-hibernators
195 from entering deep torpor. The arrest temperature for the rat heart trabecula muscle was
196 considerably higher (6.60°C) than that of both species of prairie dog. However, contrary
197 to our prediction, the deep and shallow torpor prairie dogs had almost identical arrest
198 temperatures (WTPD = 1.58°C and BTPD = 2.76°C) similar to those reported for other
199 deep torpor hibernators such as ground squirrels (Smith and Katzung, 1966; Burlington
200 and Darvish, 1988) and hamsters (South and Jacobs, 1973).

201 A most remarkable observation in this study was that while the rat trabecula had a
202 40% reduction in contraction strength between 37°C and 10°C with a Q_{10} greater than 1.0,
203 both species of prairie dog had a Q_{10} less than 1.0 and exhibited strengths at 10°C that
204 were nearly 150% of euthermic values. The increased strength of the heart at these
205 temperatures may help counteract the effects of increased peripheral vasoconstriction and
206 blood viscosity encountered by hibernators at low temperatures (Zatzman, 1984; Zatzman
207 and Thornhill, 1987), particularly during arousal from deep torpor. Enhanced cardiac

208 performance by the hearts of hibernators at low temperatures is likely a result of
209 increased action potential length (Marshall and Willis, 1962; Jacobs and South, 1973),
210 heightened intracellular ion regulation (Burlington and Darvish, 1988; Wang et al.,
211 2002), and myofilament sensitivity to calcium at low temperatures (Liu et al., 1993), as
212 well as novel expression of genes regulating cardiac metabolism (Andrews et al., 1998).
213 In combination, these aforementioned adaptations could account for the elevated strength
214 of contraction observed for the trabecula muscle from both species of prairie dogs tested
215 at a cold tissue temperature compared to a 40% cold induced drop in performance by rat
216 hearts.

217 Skeletal Muscle

218 Arousing from deep torpor hibernation requires a significant amount of heat
219 generation in the form of shivering and non-shivering thermogenesis. Non-shivering
220 thermogenesis primarily takes place in brown adipose tissue (Hashimoto et al., 2002;
221 Cannon and Nedergaard, 2004), although uncoupling proteins are found in other tissues,
222 such as skeletal muscle (Boyer et al., 1998; Raimbault et al., 2001), and appears to be
223 especially important during the early stages of arousal from torpor (Fons et al., 1997; Ho
224 et al., 2001). However, arousal can take place in the absence of functional BAT in both
225 placental and marsupial hibernators (Lyman and O'Brien, 1986; Geiser and Baudinette,
226 1990). Since skeletal muscle makes up 30-40% of total body mass (Kim et al., 2002),
227 heat generated from this tissue due to uncoupling proteins and / or shivering muscle
228 contractions could offer a significant contribution to elevating the body temperature from
229 a state of torpor during arousal from deep torpor. In addition to thermogenesis, skeletal
230 muscle from deep torpor hibernators may also have adaptations that help maintain ion

231 gradients at low temperatures, such as a decreased K^+ leak and increased Na^+ / K^+ pump
232 activity, thereby preventing excessive K^+ loss to the blood (Willis and Li, 1969; Willis et
233 al., 1971; Willis et al., 1980). Once again, the large size of skeletal muscle makes these
234 adaptations particularly significant. Clearly skeletal muscle in these animals must
235 continue to function without impairment at the low temperatures encountered during deep
236 torpor hibernation.

237 The present study reports lower arrest temperatures and Q_{10} values for strength in
238 both species of prairie dog EDL than in the lab rat EDL, indicating a greater cold
239 tolerance for both species of prairie dog. Overall, the soleus had higher Q_{10} values for
240 strength and higher arrest temperatures than the EDL for all species. This agrees with
241 other studies demonstrating increased temperature sensitivity of predominantly slow
242 oxidative fibers (Johnston and Gleeson, 1984; Ranatunga, 1984; Bottinelli et al., 1996).
243 The soleus was unique in our present study in that arrest temperatures were almost
244 identical for all three species but the Q_{10} values for contraction strength by prairie dogs
245 suggested greater temperature sensitivity for this slow oxidative muscle in prairie dogs.
246 Our results imply that the fast twitch muscles (EDL) are more capable of functioning at
247 low temperatures, even below freezing (Figure 1C), which provide the deep hibernator
248 the capacity to function and arouse from a hypothermic state that renders other muscle
249 tissues inoperable. These observations taken together do not support the hypothesis that a
250 shallow hibernator has less cold tolerant skeletal muscle than a deep hibernator.
251 However, they do suggest that for primarily fast twitch muscle, hibernators have skeletal
252 muscle that is more cold tolerant than non-hibernators.

253 Smooth Muscle

254 Data from this study shows, as hypothesized, that both species of hibernating
255 prairie dogs have lower arrest temperatures for jejunum segments than the rat. Indeed, it
256 has been reported in other studies that the GI tract of hibernators maintain functional
257 enzyme activity (Galluser et al., 1988; Carey and Martin, 1996), epithelial transport
258 (Carey, 1990; Carey, 1992), and perhaps even increase digestive efficiency during torpor
259 (Humphries et al., 2001). We hypothesized that the ability to maintain gut function at
260 relatively low temperatures would be greater for WTPD which enters deeper torpor
261 compared to the BTPD which consumes food throughout the hibernation season but does
262 not enter deep hypothermia. However, we found that the BTPD had similar jejunum
263 arrest temperatures and contractile properties as the deep torpor and anorexic WTPD. It
264 could be that gut function is necessary for both species either in deep or shallow torpor to
265 process ingested food, utilize endogenous proteins that are sloughed from the GI tract of
266 these animals (Carey, 1995), and recycle urea nitrogen during torpor and fasting (Nelson,
267 1973; Riedesel and Steffen, 1980; Harlow, 1987). We believe that, as a result, there is no
268 distinct difference in intestinal smooth muscle function at low temperatures that
269 discriminate between deep and shallow torpor prairie dogs.

270 Summary

271 In both species of prairie dog, heart and EDL have the greatest cold temperature
272 tolerance. Cardiac tissue from both prairie dog species appears to be uniquely adapted to
273 cold temperatures with peak contraction strength occurring at temperatures well below
274 that of the non-hibernator which may help to maintain tissue perfusion in the face of
275 peripheral vasoconstriction and high blood viscosity associated with torpor. Unlike the
276 rat, the anaerobic, fast twitch EDL muscle from both species of hibernators can function

277 below freezing and may act as an emergency heat source to augment BAT nonshivering
278 thermogenesis and prevent the body from falling into the lethal cold range. Results from
279 this study indicate that while muscle tissues of these two hibernators are superior to non-
280 hibernators in many aspects of cold resistance, there does not appear to be any distinctive
281 differences between species utilizing deep or shallow torpor strategies. We believe that
282 while black-tailed prairie dogs have evolved away from a rigid expression of torpor, they
283 have organs which can maintain a functional capacity to operate in deep hibernation,
284 suggesting that the loss of rhythmic bouts of deep hypothermia in their natural history is
285 merely a decrease in the phenotypic expression of this trait and not a loss of its genetic
286 capacity.

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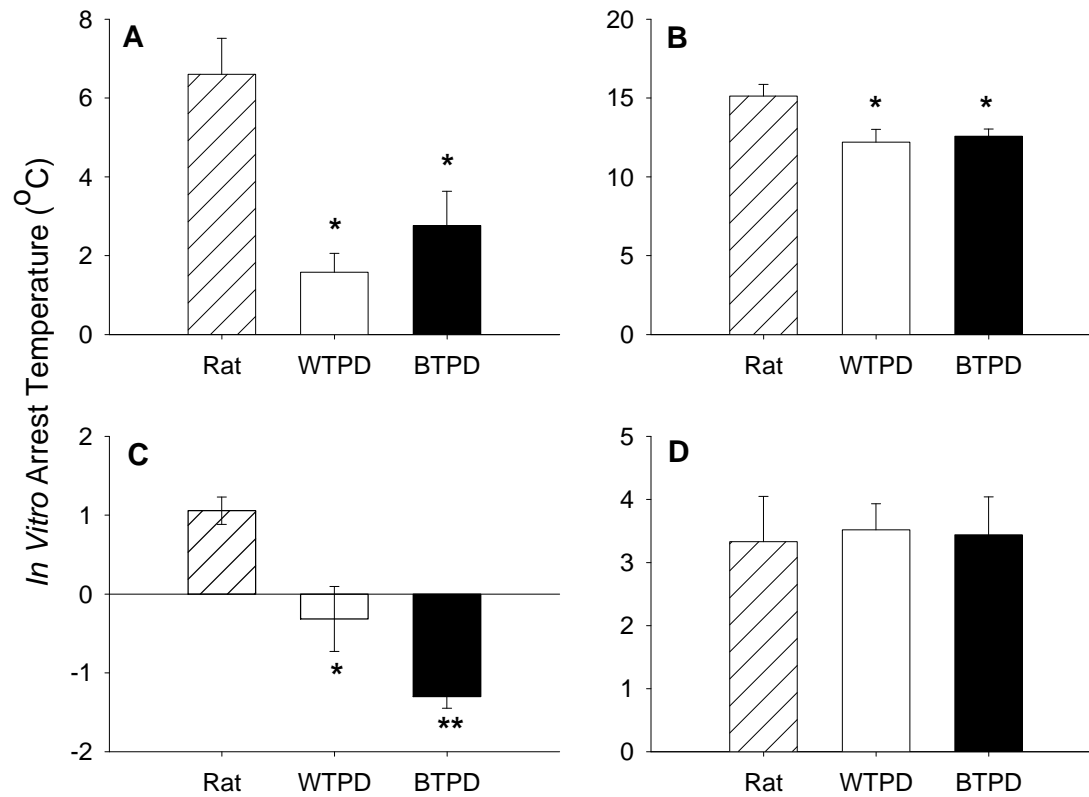
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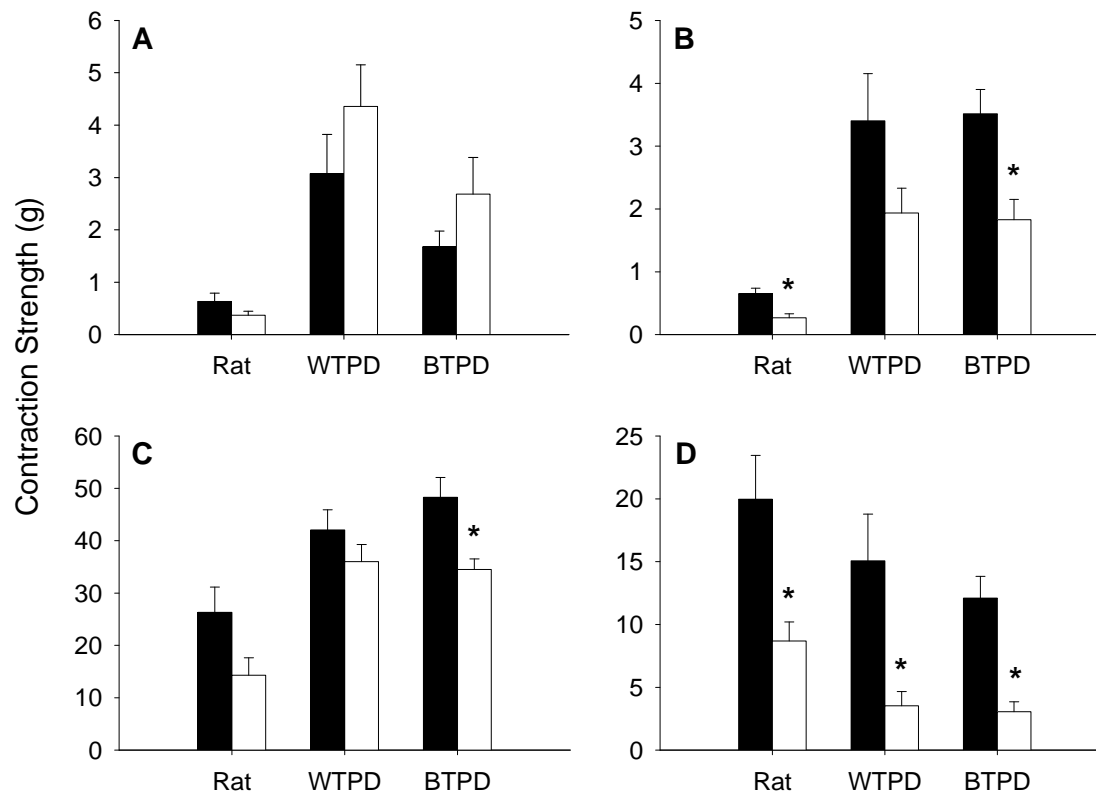
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462 **Figure 1.**
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Figure 2.

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495 **Figure Captions**

496 **Figure 1.** Comparisons of A) trabecula, B) jejunum, C) EDL, and D) soleus arrest
497 temperatures for rat (n = 6), WTPD (n = 6), and BTPD (n = 8). Single asterisk depicts a
498 significant difference in arrest temperature ($p < 0.05$) from rat. Double asterisk depicts a
499 significant difference in arrest temperature ($p < 0.05$) from rat and between prairie dog
500 species. Vertical bars depict \pm SEM.

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502 **Figure 2.** Comparison of (A) trabecula, (B) jejunum, (C) EDL, and (D) soleus
503 contraction strengths for rat (n = 6), WTPD (n = 6), and BTPD (n = 8). Black bars
504 indicate an *in vitro* temperature of 25°C for EDL and soleus, and an *in vitro* temperature
505 of 37°C for trabecula and jejunum. White bars indicate an *in vitro* temperature of 10°C
506 for trabecula, EDL, and soleus and 20°C for jejunum. Single asterisk depicts a significant
507 difference in contraction strength ($p < 0.05$) between the temperature groups. Vertical
508 bars depict \pm SEM.

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540 **Table 1.** Comparison of contraction time (CT) and half relaxation time (0.5RT) for
 541 skeletal muscle, cardiac muscle, and smooth muscle in WTPDs, BTPDs, and Lab Rats

	<u>Rat</u>	<u>WTPD</u>	<u>BTPD</u>
EDL			
CT (sec)			
25°C	0.033 ± 0.001	0.041 ± 0.003	0.046 ± 0.002
10°C	*0.181 ± 0.008	*0.220 ± 0.008	*0.224 ± 0.008
0.5RT (sec)			
25°C	0.021 ± 0.001	0.022 ± 0.002	0.024 ± 0.001
10°C	*0.175 ± 0.010	*0.138 ± 0.008	*0.163 ± 0.007
Soleus			
CT (sec)			
25°C	0.071 ± 0.003	0.129 ± 0.004	0.124 ± 0.004
10°C	*0.506 ± 0.047	*0.848 ± 0.045	*0.841 ± 0.065
0.5RT (sec)			
25°C	0.077 ± 0.004	0.068 ± 0.001	0.073 ± 0.004
10°C	*1.887 ± 0.141	*0.824 ± 0.035	*0.784 ± 0.067
Trabecula			
CT (sec)			
37°C	0.081 ± 0.004	0.120 ± 0.008	0.126 ± 0.005
10°C	*0.716 ± 0.037	*0.907 ± 0.059	*1.052 ± 0.054
0.5RT (sec)			
37°C	0.074 ± 0.018	0.073 ± 0.006	0.078 ± 0.003
10°C	*0.576 ± 0.030	*0.551 ± 0.022	*0.550 ± 0.019
Jejunum			
CT (sec)			
37°C	0.828 ± 0.043	1.655 ± 0.086	1.524 ± 0.050
20°C	*3.538 ± 0.465	*8.273 ± 0.348	*6.871 ± 0.450
0.5RT (sec)			
37°C	0.416 ± 0.027	0.933 ± 0.040	0.895 ± 0.042
20°C	*2.274 ± 0.324	*5.101 ± 0.371	*4.486 ± 0.273

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550 **Table 2.** Comparison of Q_{10} values for skeletal muscle, cardiac muscle, and smooth
 551 muscle twitch strength, contraction time (CT), and half relaxation time (0.5RT) in
 552 WTPDs, BTPDs, and Lab Rats

	<u>Rat</u>	<u>WTPD</u>	<u>BTPD</u>
EDL¹			
Strength	1.589 ± 0.157	*1.110 ± 0.012	*1.250 ± 0.046
CT	0.323 ± 0.007	.324 ± 0.013	0.351 ± 0.012
0.5RT	0.245 ± 0.007	*0.293 ± 0.010	0.277 ± 0.009
Soleus¹			
Strength	1.773 ± 0.113	*3.023 ± 0.291	*3.035 ± 0.386
CT	0.276 ± 0.017	0.286 ± 0.007	0.284 ± 0.010
0.5RT	0.120 ± 0.006	*0.190 ± 0.006	*0.209 ± 0.010
Trabecula²			
Strength	1.211 ± 0.086	*0.855 ± 0.033	*0.895 ± 0.055
CT	0.446 ± 0.009	0.473 ± 0.011	0.457 ± 0.010
0.5RT	0.458 ± 0.040	0.472 ± 0.013	0.484 ± 0.007
Jejunum³			
Strength	1.808 ± 0.195	1.439 ± 0.110	1.637 ± 0.235
CT	0.440 ± 0.034	0.388 ± 0.007	0.417 ± 0.015
0.5RT	0.390 ± 0.039	0.371 ± 0.012	0.390 ± 0.011

553 ¹EDL and soleus Q_{10} values were calculated over a temperature range of 25°C to 10°C.

554 ²Trabecula Q_{10} values were calculated over a temperature range of 37°C to 10°C.

555 ³Jejunum Q_{10} values were calculated over a temperature range of 37°C to 20°C.

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