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FACTORS AFFECTING THE TIMING OF MOVEMENTS TO HIBERNATION SITES BY WESTERN TOADS (*ANAXYRUS BOREAS*)

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ABSTRACT: Toads in northern climates may spend seven months or more in hibernation; therefore, behavioral decisions related to hibernation are important for survival. We examined factors influencing the timing and nature of movements to hibernation sites by western toads (*Anaxyrus boreas*, formerly *Bufo boreas*) at three study areas in north-central Alberta, Canada, with the use of radiotracking. We found that small toads arrived at the general vicinity of their hibernation sites earlier than larger toads. Entry date into hibernation sites was similar for toads of all sizes. Arrival and entry dates were both significantly related to temperature and/or day length. Larger toads moved to hibernation sites later in the year and moved along straighter paths to reach these sites. We propose that larger toads are older individuals that are familiar with their landscape and locations of suitable hibernacula and that they maximize their fitness by remaining at good foraging grounds as late in the year as possible.

Key words: *Anaxyrus boreas*; Hibernation; Movement; Overwintering; Radiotracking; Western toad

INTRODUCTION

In northern localities, toads (family Bufonidae) spend up to seven months in hibernation. Site selection and factors affecting movements to hibernation sites are likely very important for survival. Surprisingly, little research has investigated behavior associated with hibernation compared to breeding, and the factors influencing timing of movements to hibernation sites by toads, and amphibians in general, have been poorly investigated. Changes in temperature are an important cue for reptiles to move into hibernation sites (Nussear et al., 2007; Sexton and Hunt, 1980). Photoperiod is also an important cue for ectotherms, and unlike temperature, which can fluctuate dramatically, photoperiod reliably reflects seasonal changes (Lutterschmidt et al., 2006). Reduced foraging opportunities and precipitation events have also been proposed as cues used by reptiles to induce hibernation (Gregory, 1982).

The western toad (*Anaxyrus boreas*, formerly *Bufo boreas*) is a wide-ranging North American species, occurring from California to southern Alaska (Hammerson et al., 2004). Mullally (1952) reported that western toads in California were very sensitive to light and also temperature; he noted that western toads became active at the same time each evening and if temperatures fell below 3 °C, toads took

shelter. Campbell (1970) noted that western toads in Colorado began to move to their hibernacula in late August and early September and most had entered their hibernacula by October. We suspect that toads generally use temperature and/or photoperiod as cues for the initiation of movement to hibernation sites.

Kelleher and Tester (1969) found that Canadian toads (*A. hemiophrys*) in Minnesota hibernated communally and displayed fidelity to hibernation sites. Adults displayed greater site fidelity or homing ability than juveniles, as 97.1% of adult toads returned to their specific hibernation site compared to only 89.8% of juveniles (Kelleher and Tester, 1969). Breckenridge and Tester (1961) studied Canadian toads at this same area and reported that large adults tended to hibernate earlier, and adult toads entered hibernacula earlier than young of the year; however, they did not investigate what influenced differences in hibernation timing. Contrary to these results, observations from radiotelemetry in Alberta led us to suspect that larger western toads moved to their hibernation sites later in the active season than smaller toads and moved to overwintering sites more directly, along straighter paths. We hypothesized that older (larger) toads are familiar with their landscape and locations of suitable hibernacula and may maximize their fitness by remaining at good foraging grounds as late in the year as

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possible. Western toads are sexually dimorphic (female toads are larger than males), and previous research has found that female western toads travel farther from breeding ponds to reach their summer foraging grounds than males do (Bartelt et al., 2004; Browne, 2010; Bull, 2006; Goates et al., 2007; Muths, 2003); therefore, movement patterns from foraging grounds to hibernation sites may also differ between sexes.

The objectives of the present study were (1) to determine if arrival date at the hibernating site and entry date into the site differ with toad size or sex, (2) to examine our hypothesis that larger (likely older) toads display behavior consistent with greater familiarity with their landscape and remain at their foraging grounds later in the year than smaller (likely younger) toads, and (3) to examine relationships between the timing of toads' arrival at and entry into hibernation sites and temperature and date. Our study is unique because it is the first detailed investigation to examine these questions for any amphibian and was conducted near the northern edge of the global range of Bufonidae.

METHODS

Study Area

Our research took place at three study areas in the north-central region of Alberta, Canada. The park area was located in Elk Island National Park (53.675 N, -112.792 W) in an isolated patch of dry mixed-wood boreal forest in the Aspen Parkland natural region (Alberta Government, 2005). This area was relatively pristine and mostly comprised of upland forest surrounding shallow lakes and marsh habitats. Forests consisted primarily of aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and white spruce (*Picea glauca*), with a hazelnut understory (*Corylus cornuta*). Western toads bred in shallow lakes. Toads used wet shrubland, human-modified grasslands (e.g., roadsides), deciduous forest, and marsh during the foraging period and used meadow, marsh, and deciduous forest for hibernation (listed approximately in order of selection; Browne, 2010; Browne and Paszkowski, 2010).

The pasture area was located adjacent to Elk Island National Park (53.704 N, -112.931 W) and consisted of dry mixed-wood boreal forest that had been converted to agriculture. This area supported cattle grazing, cultivation of crops and hay (e.g., wheat, barley, oats, canola, timothy, alfalfa), and rural housing. It also contained relatively undisturbed woodlots and peat land. Common tree species included trembling aspen, balsam poplar, white spruce, black spruce (*Picea mariana*), paper birch (*Betula papyrifera*), tamarack (*Larix laricina*), and jack pine (*Pinus banksiana*). Western toads bred in naturalized man-made ponds that were originally created during sand extraction; the surrounding land was used for cattle grazing. Toads used human-modified grasslands, crop/hay fields, mowed lawn, emergent vegetation, dry shrubland, wet shrubland, water, deciduous forest, conifer forest, mixed-wood forest, and cattle pasture during the foraging period and used conifer forest, dry shrubland, mixed-wood forest, and deciduous forest for hibernation (Browne, 2010; Browne and Paszkowski, 2010).

The "boreal" area was located north of Lac La Biche (55.052 N, -111.704 W) in the central mixed-wood subregion of the Boreal Forest natural region (Alberta Government, 2005). This region was moderately altered by the forestry and oil/gas industries, and mostly comprised of shrub swamps, fens, upland boreal mixed-wood forest, and forestry cut blocks. Common tree/shrub species included trembling aspen, balsam poplar, white spruce, black spruce, paper birch, tamarack, jack pine, willow (*Salix* sp.), and dwarf birch (*B. nana*). Western toads bred in a small shallow pond that formed next to a gravel road and was directly under a major utility corridor. A small permanent stream fed this pond. Toads used wet shrubland, human-modified grassland, deciduous forest, grass- or shrub-dominated cut blocks, forest that had recently burned, conifer forest, moss-covered peat land, and mixed-wood forest during the foraging period and used conifer forest, wet shrubland, and forest that had recently burned for hibernation (Browne, 2010; Browne and Paszkowski, 2010). More detailed descriptions of habitat types used by western toads during their

annual cycle in all three areas can be found in Browne (2010).

Radiotelemetry

We captured toads during the active season (May–October) in 2004 at the park and pasture areas, 2005 at the boreal area, and 2006 at the pasture area, either while toads were breeding at ponds or opportunistically while we were tracking other individuals. We measured and recorded the snout–urostyle length (SUL to nearest millimeter), mass (to nearest gram), and sex of each toad at the time of capture. Toads captured between May and August were toe-clipped (maximum two toes per toad) for future identification of recaptured toads that had lost their transmitters.

We radiotracked adult toads for one week to five months prior to hibernation to locate their hibernation sites. We followed methods described by Bartelt and Peterson (2000) for attaching radiotransmitters. Holohil BD-2, BD-2T, and PD-2 transmitters, weighing 1.0–2.3 g (minimum battery life 28 days to three months) were attached with the use of a waist belt made of soft surgical-grade polyethylene tubing (outside diameter = 0.965 mm; VWR International, CA-63018-667) and a large-size fly-line eyelet (size 9; the Fishin' Hole, Edmonton, Alberta, Canada). All transmitters/belts were less than 10% of body mass and most were less than 5%; Bartelt and Peterson (2000) examined the influence of transmitters/belts that weighed up to 5% of body mass for western toads and showed that behavior was not significantly affected. We located toads two–four times/week.

Over three years, we radiotracked 116 western toads and were able to follow 49 to hibernation sites. Toads moved up to 2239 m (straight-line distance) from their initial capture point. We considered a toad to be in its hibernation site if it remained underground in the same site for over one week in September or October, or if it was found underground with other toads (communal hibernacula). Toads were often active within their hibernation sites and would move up to 7 m through tunnels underground if we disturbed a site by digging. On only four occasions did we observe a toad above ground after it had entered its eventual hibernation site. We

concluded that all individuals were in their hibernation sites by 14 October in 2004; a heavy snow fell on 15 October 2004 that lasted through the winter. In 2005, all toads were in hibernation sites by 3 October and the ground was beginning to freeze by this time. In 2006, all toads were in hibernation sites by 10 October. We excavated each hibernation site between 14–23 October 2004, 3–6 October 2005, and 10–12 October 2006 to record data on the physical features of each site and to capture the toad to release it from its transmitter (Browne and Paszkowski, 2010). Hibernation sites ranged from mammal tunnels to peat hummocks and 68% of the toads in our study hibernated in communal hibernacula; see Browne and Paszkowski (2010) for full descriptions.

Timing of Hibernation

We tested the relationships between sex and size of toads with the dates of arrival at the hibernaculum and entry into the hibernation site. We considered the date of arrival to be when a toad was located within 25 m of its eventual hibernation site and remained within 25 m. Entry date was when a toad entered its eventual hibernation site and remained belowground. Because exact arrival/entry dates would have fallen between when we first observed a toad in the vicinity/belowground and the previous tracking encounter, we estimated all arrival/entry dates as the midpoint between the date when the toad was found in the vicinity of or within its hibernaculum and the date of the previous sighting.

We tested all data for normality, with the use of Kolmogorov–Smirnov one-sample tests, and for equal variance, using Levene's test, before using general linear models (GLM). We then used one-way ANOVA GLM to test if dependent variables (date of arrival, date of entry, distance between mid-September location and hibernation site, and straightness of movements) differed among study area-years (categories: park 2004, pasture 2004, boreal 2005, pasture 2006). If there were significant differences among area-years, we then ran analyses separately by area or year for that dependent variable. Sample size was slightly smaller for the arrival data than entry data because some of the toads were caught <25 m

from their hibernation site, so arrival date was not known.

We used ANCOVA GLM to determine if there were differences in arrival or entry dates for toads based on sex or SUL. SUL was not recorded for one male toad from the park area, so this individual was dropped from size analyses. To determine if larger toads made longer, straighter movements late in the season in traveling from foraging grounds to hibernation sites, we used an ANCOVA GLM to examine the effects of sex and body size (SUL) on the straight-line distance between a toad's location in mid-September (September 15, or the closest date of data collection to September 15) to its hibernation site. Our underlying assumption was that large distances in mid-September characterized toads that still remained on summer foraging grounds and small distances identified toads that were already traveling toward hibernacula. Mid-September was chosen because toads still exhibited a range of behaviors; 32% of toads had arrived in the vicinity of their hibernation sites, but the remainder were either en route or still relatively sedentary on foraging grounds. We also used an ANCOVA GLM to evaluate the effect of sex and body size on the straightness of movements to hibernation sites in mid-September (presuming that straighter paths indicate directed movements to known locations). We quantified movement patterns using a straightness index (straightness = D/L ; D = beeline distance, L = sum of move lengths), where a value of 1 indicates a perfectly straight path and values close to 0 have many turns (Benhamou, 2004).

We obtained data on temperature from Environment Canada from the Elk Island National Park (2004 and 2006) and Lac La Biche (2005) weather stations (Environment Canada, 2008). Mean minimum temperature was calculated for each week with the use of daily minimum temperature values. We used linear regression generalized linear models to examine the relationship between cumulative number of toads arrived at/entered into hibernation sites and mean minimum temperature and week of the year (a surrogate for day length) for each week. Correlations between week of the year and temperature were tested with the use of Pearson correlations.

All statistical analyses were computed with the use of SPSS version 15 (SPSS Inc., 1989–2006).

RESULTS

We determined the date of arrival at the hibernaculum for 41 individuals (park 2004: 2 males, 2 females; pasture 2004: 2 females; boreal 2005: 8 males, 10 females; pasture 2006: 6 males, 11 females), the hibernation entry date for 49 individuals (park 2004: 5 males, 5 females; pasture 2004: 2 females; boreal 2005: 9 males, 11 females; pasture 2006: 6 males, 11 females), and we tracked 41 individuals from mid-September to hibernation (park 2004: 2 males, 2 females; pasture 2004: 2 females; boreal 2005: 9 males, 9 females; pasture 2006: 6 males, 11 females). The dependent variables date of arrival ($Z = 1.037$, $n = 41$, $P = 0.233$), date of entry ($Z = 0.805$, $n = 49$, $P = 0.536$), distance between mid-September location and hibernation site ($Z = 1.210$, $n = 41$, $P = 0.107$), and straightness of movements ($Z = 1.163$, $n = 41$, $P = 0.134$) did not differ significantly from a normal distribution, and variance did not differ greatly among test groups (Levene's test: range for $P = 0.024$ – 0.876).

Mean date of arrival at the hibernaculum did not differ significantly among study area-years ($F_{3,37} = 1.902$, $P = 0.146$). However, the timing of entry was significantly different among study area-years ($F_{3,45} = 10.973$, $P < 0.001$). Toads entered hibernation sites significantly earlier at the boreal area in 2005 than at the park and pasture areas in 2004 and pasture area in 2006 (Tukey post hoc test: $P < 0.05$). We found no difference among area-years for distance between mid-September location and hibernation site ($F_{3,37} = 1.752$, $P = 0.173$) and straightness of movements ($F_{3,37} = 1.811$, $P = 0.162$).

For all area-years combined, males arrived in the vicinity of their hibernacula earlier than females (mean Julian day = 256 ± 3.12 SE, range = 239–276, $n = 16$ vs. mean Julian day = 267 ± 2.48 SE, range = 240–283, $n = 25$). However, toads were sexually dimorphic with respect to body size (females larger than males) and a GLM indicated that arrival date was significantly related to SUL and not sex when both factors were considered simulta-

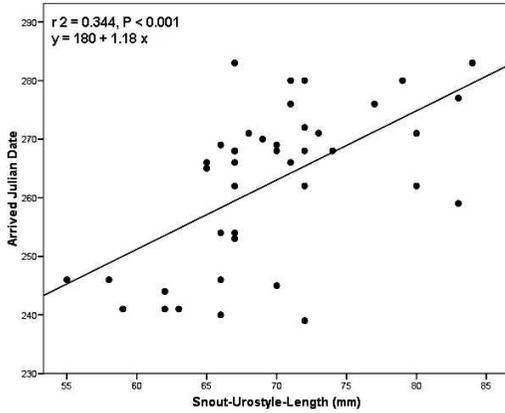


FIG. 1.—Large western toads arrived at hibernacula significantly later than small toads. A linear regression trend line was fit through the data with the use of SPSS (SPSS Inc., 1989–2006).

neously ($F_{2,38} = 11.7$, $P < 0.001$, SUL: $P = 0.001$, sex: $P = 0.138$; Fig. 1). Sex and body size did not influence entry dates in 2004 ($F_{2,17} = 1.204$, $P = 0.349$), 2005 ($F_{2,8} = 0.681$, $P = 0.519$), or 2006 ($F_{2,14} = 0.136$, $P = 0.874$).

For all area-years combined, female toads were farther from their hibernation sites in mid-September (mean distance = $93.5 \text{ m} \pm 17.9 \text{ SE}$, range = 0–317 m, $n = 23$), and moved along straighter paths (mean straightness = $0.771 \pm 0.0536 \text{ SE}$, range = 0.205–1.00, $n = 23$) than males (mean distance = $52.4 \text{ m} \pm 19.2 \text{ SE}$, range = 0–306 m, $n = 18$; and mean straightness = $0.560 \pm 0.0858 \text{ SE}$, range = 0.000–1.00, $n = 18$, respectively). However, as was true of arrival times, this pattern was driven by body size. Large toads were significantly farther from their hibernation sites in mid-September ($F_{2,38} = 3.800$, $P = 0.031$, SUL: $P = 0.032$, sex: $P = 0.489$; Fig. 2) and moved along straighter paths to reach their hibernation sites ($F_{2,38} = 6.033$, $P = 0.005$, SUL: $P = 0.014$, sex: $P = 0.226$; Fig. 3).

We examined the relationship between minimum and maximum temperatures and arrival and entry dates for each year (Fig. 4). The variables, mean minimum temperature and week of the year, were correlated with each other in 2004, 2005, and 2006 ($r = -0.771$, -0.991 , and -0.966 , respectively); therefore, they could not be included simultaneously as independent variables in gener-

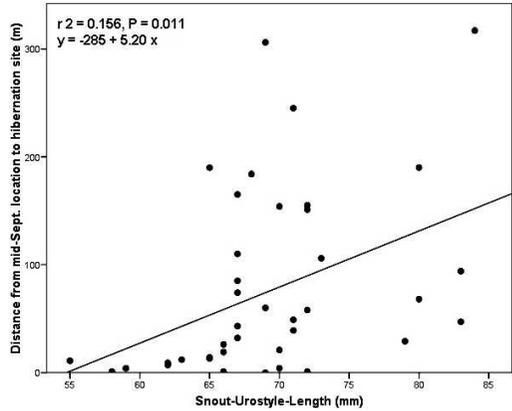


FIG. 2.—Large western toads were farther from hibernation sites in mid-September than small toads. A linear regression trend line was fit through the data with the use of SPSS (SPSS Inc., 1989–2006).

alized linear models. When examined individually, mean minimum temperature and week of the year were strongly correlated with the cumulative number of toads arriving at hibernation sites and entering sites in all three years, except for temperature, which was not significantly correlated with the number of toads that had arrived at hibernation sites in 2004 (Table 1).

DISCUSSION

Toads arrived at their hibernacula gradually from 27 August to 10 October. This date range

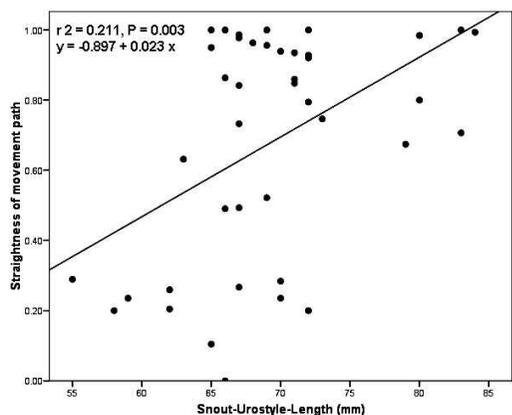


FIG. 3.—Large western toads moving to hibernation sites from their locations in mid-September followed straighter paths than small toads. A linear regression trend line was fit through the data with the use of SPSS (SPSS Inc., 1989–2006).

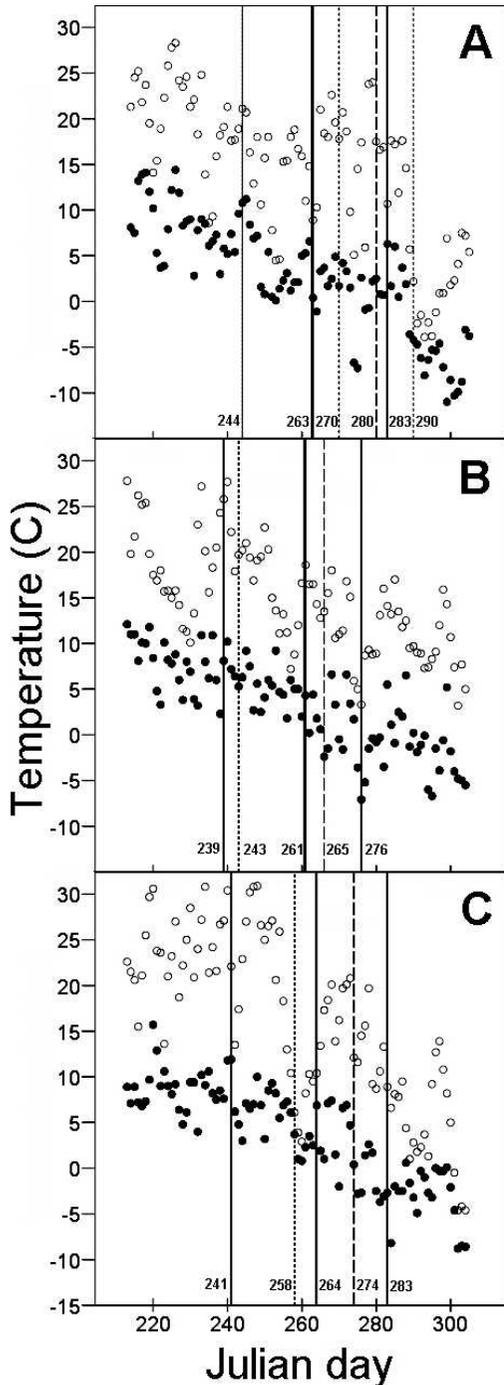


FIG. 4.—Minimum and maximum daily temperatures from August to October. Solid circles indicate minimum daily temperatures and hollow circles are maximum daily temperatures. Solid vertical lines indicate earliest, mean, and latest arrival dates ($n = 6$ in 2004, 18 in 2005, and 17

was very similar to that reported by Campbell (1970) for western toads in Colorado; Campbell reported that toads began moving to their hibernation sites in the last week of August and first two weeks of September, and by October most had entered hibernacula. In Oregon, western toads arrived at overwintering sites between 16 September and 10 November in 2002–2005 (Bull, 2006). Entry into hibernation sites was significantly earlier in 2005 at the boreal area (31 August–3 October) than in the Aspen Parkland areas in either 2004 or 2006 (26 September–16 October and 15 September–10 October, respectively). However, we cannot compare differences in arrival or entry dates among study areas or years independently because the variables study area and year are confounded.

We suspect temperature to be the main factor controlling the timing of entry into hibernation sites, although we cannot rule out a role for photoperiod in triggering hibernation. If photoperiod plays a large role in timing of movements to hibernacula, this could potentially be a future conservation concern in light of global climate change; if fall temperatures change significantly, then toads may arrive at their hibernacula too early (missing out on foraging opportunities) or too late (risk of freezing). Extra foraging time may be especially important in mild years, because energy reserves are depleted more rapidly during milder winters, which can cause higher rates of overwinter mortality (Reading, 2007). We were unable to determine whether arrival and entry dates at/into hibernacula were more tightly related with temperature or week of the year because these two variables were highly correlated, although at least in one year (2004), week of the year offered greater explanatory power than temperature.

Female toads arrived at their hibernacula later, were farther from their hibernacula in mid-September, and moved along straighter

←

in 2006). Dashed lines indicate earliest, mean, and latest entry dates ($n = 12$ in 2004, 20 in 2005, and 17 in 2006). Note, latest arrival and entry dates overlap in 2005 and 2006. Toads were tracked until day 297 in park and pasture areas in 2004 (A), 276 in boreal area in 2005 (B), and 285 in pasture area in 2006 (C).

TABLE 1.—Results of generalized linear models examining the influence of mean minimum temperature and week of the year on the cumulative number of toads arriving at and entering into hibernation sites.

Year	Independent variables	Arrival		Entry	
		Wald chi-square	P value	Wald chi-square	P value
2004	Temperature	2.336	0.126	4.304	0.038
	Week	22.400	<0.001	42.000	<0.001
2005	Temperature	80.928	<0.001	75.713	<0.001
	Week	55.560	<0.001	35.601	<0.001
2006	Temperature	46.460	<0.001	28.298	<0.001
	Week	45.771	<0.001	23.617	<0.001

paths than male toads; however, when body size was taken into consideration it became clear that this pattern was an artifact of females being larger on average than males. Smaller toads arrived at their hibernacula earlier, were closer to their hibernacula in mid-September, and moved along less straight paths than large toads, regardless of sex. Movement patterns differed between male and female western toads earlier in the season at our study areas. Female western toads moved to foraging grounds earlier in the season and were located farther from breeding ponds during July–August than male toads (Browne, 2010). This difference in movement timing early in the season can be explained by the fact that female toads left breeding ponds immediately after laying eggs, whereas male toads lingered at ponds longer, presumably to increase their chance of mating. We were not surprised that arrival date, distance between mid-September location and hibernation site, and straightness of movements was related to body size and not sex, as female and male toads require similar, specific conditions for overwintering and females were not located farther from hibernation sites in July–August than males (Browne, 2010).

Our observation that larger western toads arrived at hibernation sites later than smaller toads countered the behavior reported by Breckenridge and Tester (1961) for Canadian toads, where larger individuals entered hibernation at an earlier date. Although this study did not attempt to explain the pattern, Kelleher and Tester (1969) reported that large, adult Canadian toads from the same area in Minnesota accurately homed to their hibernation sites more frequently than small juveniles, so perhaps it also took longer for

young Canadian toads to select a hibernation site than more experienced individuals. All of the toads in our study were adults, so all would have successfully used at least one hibernaculum.

We offer two explanations for our observations that larger western toads arrived at hibernacula later, occurred farther from their hibernacula in mid-September, and moved along straighter paths. We propose that larger western toads are older individuals (western toads at our Aspen Parkland areas have been found to live up to eight years, and large toads tended to be older; Garrett, 2005), and that older individuals may be more familiar with the landscape and able to navigate along more direct routes to hibernacula. The ability to navigate along direct routes would allow large toads to remain at their foraging grounds later because they can travel quickly and efficiently to their hibernacula once they are stimulated by environmental cues to move. Remaining at good foraging grounds as late in the year as possible would be advantageous because individuals could continue active feeding and build body reserves for overwintering and reproduction. Likewise, large toads may be able to stay at foraging grounds later because they accumulate larger water and energy reserves, which may allow them to make long-distance movements, perhaps through inhospitable habitat, without stopping to feed or hydrate. If smaller toads must stop periodically, even in low-quality habitat patches, to obtain food or water as they move from their summer foraging grounds to hibernacula, their movement paths might be more tortuous and their progress slower. Chan-McLeod (2003) found that the probability that red-legged frogs (*Rana aurora*) in British

Columbia entered clear-cuts was related both to weather patterns (e.g., temperature and precipitation) and to frog body size.

CONCLUSIONS

Efficient timing of movements to hibernation sites may be critical for toads to maximize time on good foraging grounds but also ensure arrival at hibernation locations before temperatures become too cold for movement. Smaller toads arrived at the hibernacula earlier than larger toads, whereas entry date into hibernation sites was not related to body size. Arrival and entry dates were significantly related to temperature and/or the highly correlated variable week of the year. Our data show that larger (likely older) toads move to hibernation sites later in the year and move along straighter paths to reach these sites, suggesting that these individuals have superior navigational skills and/or larger energy/water reserves that allow them to make rapid, long-distance movements.

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