

State-wide survey for *Hygrotus diversipes* in Wyoming during 2012



Lusha Tronstad
Invertebrate Zoologist
Wyoming Natural Diversity Database
University of Wyoming
Laramie, Wyoming 82071
Tele: 307-766-3115
Email: tronstad@uwyo.edu
Website: <http://www.uwyo.edu/wyndd/>

Suggested citation: Tronstad, L.M. 2014. State-wide survey for *Hygrotus diversipes* in Wyoming during 2012. Report prepared for the Wyoming Game and Fish Department by the Wyoming Natural Diversity Database, University of Wyoming.

Cover photo by Lusha Tronstad showing a new location for *Hygrotus diversipes* discovered in 2012 and a photo of *Hygrotus* collected at the site.

Photo below by Cody Bish showing a lateral view of *Hygrotus diversipes*.



Abstract

Hygrotus diversipes is an aquatic beetle endemic to central Wyoming. This predaceous diving beetle appears to be rare. *Hygrotus diversipes* has been collected from only 12 sites, but is likely undersampled. We surveyed streams and ponds throughout the basins of Wyoming in 2012 to estimate the distribution of *H. diversipes*. We collected samples from appropriate streams and ponds in the Yellowstone River, Bighorn River, Wind River, Powder River, Little Missouri River, Belle Fourche River, Cheyenne River, North Platte River, Little Snake River, Great Divide, Bear River, and Green River Basins. We sampled 206 sites, and collected beetles at 74% of locations. We collected 33 genera and 62 species and subspecies of aquatic beetles, including 18 species of *Hygrotus*. We collected 4 female *H. diversipes* at only one location, at which the beetle had not previously been found. Specific conductivity (20,019 $\mu\text{S}/\text{cm}$) of the stream was 7 times higher than the mean specific conductivity of waters across the basins of Wyoming. *Hygrotus diversipes* appears to be restricted to small streams with relatively high concentrations of dissolved salts, in a relatively small region of central Wyoming. The year-to-year distribution of *H. diversipes* may be at least partially driven by the amount and distribution of spring precipitation in the region. Spring precipitation, especially in the form of snow, likely recharges shallow groundwater that is vital to *H. diversipes* habitat.

Introduction

Predaceous diving beetles (Dytiscidae) are the most diverse aquatic beetle family in the world, with over 3900 species described in 175 genera that live on all continents (Jach and Balke 2008). Dytiscid larvae and adults live in a variety of aquatic habitats, including lakes, ponds, streams, and wetlands. Eggs typically hatch in ~1 week (Larson et al. 2000) and beetles go through 3 life stages after hatching (holometabolus). Before pupating, the emerged larvae go through 3 larval instars. Larval development time likely depends on water temperature and final instar size. Pupation is a relatively short stage where the beetle makes a cell under an object (e.g., rock or log) along the margin of the water body. The adult stage generally lasts the longest and is the stage where predaceous diving beetles can disperse by flying among habitats. Dytiscids are generally good flyers that disperse to colonize new habitats, find overwintering areas, or leave less desirable habitats (e.g., drying ponds).

Hygrotus is a genus in the family Dytiscidae. *Hygrotus* are small beetles (2.1-5.6 mm length) typically found in exposed, standing water (i.e., lakes and ponds; Larson et al. 2000). Beetles in this genus occur from Alaska to Florida, but are most diverse on the prairies of British Columbia. Most *Hygrotus* beetles are thought to live one year (univoltine) with adults overwintering and mating the following spring and early summer. Many members of the genus live in unique habitats and may have special adaptations to do so. For example, *H. salinarius* has osmoregulatory adaptations for living in waters with high concentrations of salts (Tones 1978). The *Pedalis*-group consists of five species that live in unique habitats or restricted areas (Anderson 1983). For example, *H. pedalis* is known from only 6 counties in California, *H. thermarum* and *H. fontinalis* live in hot springs, *H. curvipes* occupy temporary habitats in southern California, and *H. diversipes* is known only from salty streams in central Wyoming.

Hygrotus diversipes was first collected from Dugout Creek northwest of Midwest, Wyoming (Figure 1) by Hugh Leech in 1964 who published a paper describing the new *Hygrotus* species in 1966 (Leech 1966). Anderson (1971, 1976, 1983) revised the genus and provided a key to distinguish species of *Hygrotus*. *Hygrotus diversipes* fits within the *Pedalis*-group (group IV), because of the modified profemora, mesofemora and mesotibia on males, and the shape of the aedeagus (male reproductive organ). The U.S. Fish and Wildlife Service (USFWS) listed *H. diversipes* as a Category II Candidate Species under the Endangered Species Act (ESA) in 1984, likely because the species had only been collected once at a single location.

In response to pipeline development, the Bureau of Land Management (BLM) surveyed for *H. diversipes* in 1985, 1988, and 1992. The BLM collected *H. diversipes* in 3 of 8 locations in 1985 (Dugout Creek, Cloud Creek at 33 Mile Road, and Dead Horse Creek), 0 of 16 locations in 1988, and 2 of 13 locations in 1992 (Cloud Creek at 33 Mile Road and Wildhorse Road; BLM unpublished data). Professional Entomological Services Technology, Inc. surveyed near the type location in 1992 and 1993, and collected *H. diversipes* in 2 of 9 locations (Dugout Creek and Hay Draw) both summers (Keenan and Howard 1995). The beetle was removed from the Category II Candidate Species list in 1996, but surveys for *H. diversipes* continued. Kelly Miller, a graduate student studying the systematics of beetles at that time, collected *H. diversipes* from Dugout Creek in 1995 and nearby Government Creek in 1996 (Miller 2002). In 2002, he surveyed eastern Wyoming for *H. diversipes* and located the beetle in 6 locations, 5 of which were new (Dugout Creek, unnamed pool in gulch east of Barnum, Flying E Creek, Teapot Creek, Conant Creek, and Sand Draw).

The USFWS received a petition to list 206 species, including *H. diversipes*, in July 2007 (Forest Guardians 2007). Another petition to emergency list 32 species, including *H. diversipes*, was sent to the USFWS in June 2008 (<https://www.casetext.com/case/wildearth-guardians-v-salazar-2/#.Uw0dB4U3crM>). The USFWS issued a "Not Warranted" 90-day decision for 165 species, including *H. diversipes*, in February 2009 (USFWS 2009). The petitioners filed suit to reverse this decision. A court decision issued in November 2011 by the District Court of Colorado found the declarant had no standing, and thus upheld the 2009 "Not Warranted" status.

Hygrotus diversipes was searched for again in 2010 and 2011 after the recent ESA action. We surveyed for the beetle at four previously known sites in 2010, and collected *H. diversipes* at 2 sites (Cloud Creek at Wild Horse Road and Dead Horse Creek; Tronstad et al. 2011). To estimate the distribution of *H. diversipes* in Wyoming, we created models to predict suitable habitat for the beetle. In 2011, we sampled 40 sites that the models predicted as suitable habitat, and we collected *H. diversipes* in one stream (Dead Horse Creek; Tronstad et al. 2011). WildEarth Guardians re-petitioned *H. diversipes* for ESA listing in 2013 (WildEarth Guardians 2013); this petition is currently under consideration by the U.S. Fish and Wildlife Service.

To more completely assess the distribution of *H. diversipes*, we collected beetles from appropriate streams and ponds throughout the basins of Wyoming in 2012. Predictive distribution models suggested that suitable habitat may be present in basins across the state (Tronstad et al. 2011). The models predicted that *H. diversipes* lives in intermittent streams with shallow groundwater, in areas with high soil conductivity, and in the warmest locations in Wyoming. Field observations confirmed that *H. diversipes* occupies prairie streams that have dried to a series of disconnected pools with high concentrations of dissolved salts. To estimate the current distribution of *H. diversipes*, we sampled over 200 sites in 10 Wyoming basins between May and July 2012.

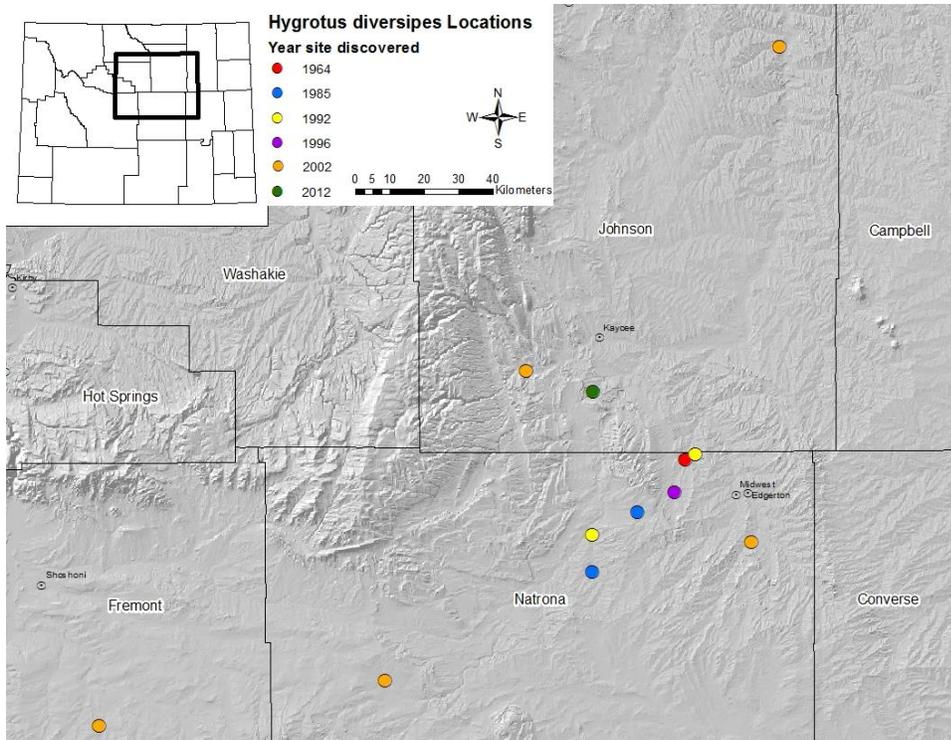


Figure 1. *Hygrotus diversipes* is known from 12 sites in central Wyoming (see inset map). The predaceous diving beetle was first discovered in 1964 and 11 other occupied sites have been found since that time, including one site documented in this report.

Methods

Predictive distribution models suggested that suitable habitat for *H. diversipes* existed in the Yellowstone River, Bighorn River, Wind River, Powder River, Little Missouri River, Belle Fourche River, Cheyenne River, North Platte River, Little Snake River, Great Divide, Bear River, and Green River Basins (Tronstad et al. 2011). In 2011 we attempted to sample specific stream reaches predicted suitable by the models, and found that the vast majority of such reaches were either inaccessible due to property ownership or were dry (and thus at least temporarily unsuitable for *H. diversipes*) at the time of sampling. Thus, in 2012 we took a broader approach in which we sampled in any publicly-accessible and inundated stream within the vicinity of streams predicted suitable by the model. We also sampled 7 sites on private ranches in the Thunder Basin Grassland Prairie Ecosystem Association with permission from the landowners. Additionally, we attempted to sample the 11 sites at which *H. diversipes* had been collected previously (Figure 1). All sampling occurred between May and July 2012.

We measured dissolved oxygen and water temperature at sampling sites with a Yellow Springs Instrument (YSI) Professional Optical Dissolved Oxygen probe, which was calibrated daily. Conductivity, oxidation-reduction potential, and pH were measured with a YSI Professional Plus Multiprobe, also calibrated daily. We recorded location and elevation with a GPS unit, described and photographed the habitat, and noted the riparian (vegetation at margin of water) and landscape vegetation, primary land use, and dominant stream substrate. We collected aquatic invertebrates using D-frame dip nets with 250 μm mesh. Invertebrates were preserved in ~75% ethanol and returned to the laboratory for identification. We identified all adult beetles in the samples using Merritt et al. (2008) and the family Dytiscidae using Larson et al. (2000).

Results

Basic water quality varied widely across the state. Water temperatures were generally warm (Table 1). The streams and ponds sampled contained fairly high concentrations of dissolved oxygen and many were supersaturated with oxygen. Waters sampled had relatively high concentrations of dissolved salts, and most were basic (pH >7). Oxidizing conditions occurred in most waters we sampled (oxidation reduction potential >200 mV).

Table 1. Mean values and the range of basic water quality measured at 206 locations across the basins of Wyoming compared to a tributary stream of Murphy Creek where we collected *Hygrotus diversipes* in 2012. Note that average conductivity of rivers in North America is ~284 $\mu\text{S}/\text{cm}$ (Wetzel 2001) and average conductivity of seawater is ~70,000 $\mu\text{S}/\text{cm}$.

Parameter	State-wide		Tributary to Murphy Creek
	Mean	Range	
Water temperature ($^{\circ}\text{C}$)	18.4	6.5-36.6	18.8
Dissolved oxygen (mg/L)	11.2	1.5-36.5	21.2
% Saturation dissolved oxygen	117	20.2-321	225
Specific conductivity ($\mu\text{S}/\text{cm}$)	2841	56.7-43,879	20,019
pH	8.5	7.0-10.7	7.54
Oxidation-reduction potential (mV)	290.4	-3.5-494.3	184.9

We drove >6000 miles and collected samples at 206 sites from 10 basins (Figure 2). Aquatic beetles were collected at 74% of sites (153 sites). Overall, we identified 33 genera and 62 species and subspecies of aquatic beetles across the state. Of these, we collected 18 species of *Hygrotus* in the basins of Wyoming, which represents a third of the known species of *Hygrotus* in North America (Larson et al. 2000).

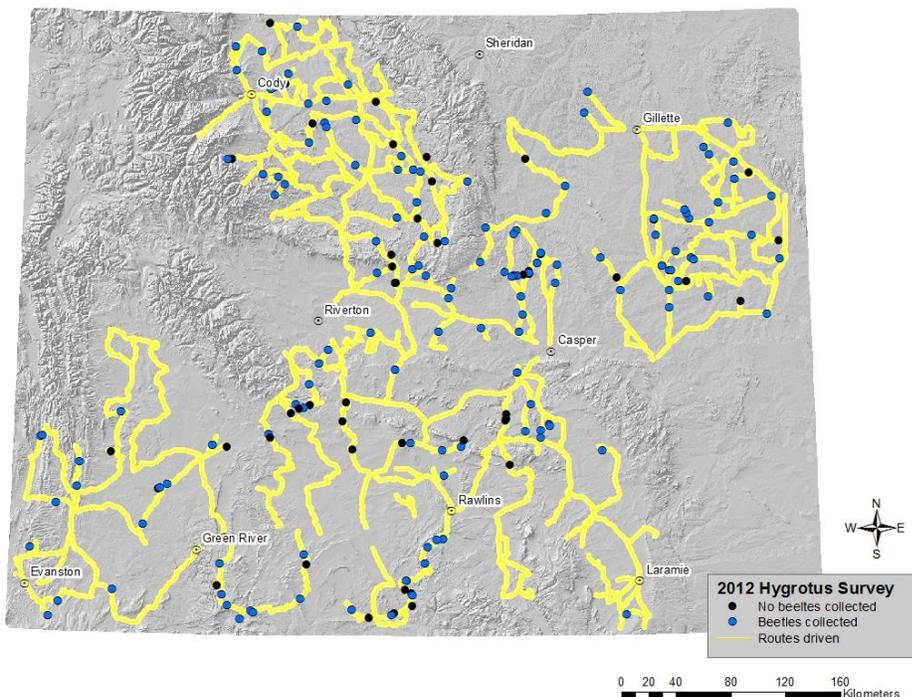


Figure 2. Routes driven and sites where samples were collected across the basins of Wyoming.

We collected *H. diversipes* at only one location in 2012; we caught 4 female *H. diversipes* in a tributary stream of Murphy Creek on 9 May 2012. *Hygrotus diversipes* is sexually dimorphic and females lack the sinuate profemur that males possess. Therefore, female *H. diversipes* are more difficult to identify and their diagnosis is less certain than male specimens. *Hygrotus diversipes* had not been collected at this site in the Powder River Basin previously. The stream flowed at a slow velocity and alkaline salts were deposited on the stream banks (see cover photo). The stream consisted of soft, fine sediments with algal mats floating on the water surface. Beetles were the dominant invertebrates in the stream. We collected 3 other beetles in the stream along with *H. diversipes* (*H. patruelis*, *H. nubilus*, and *Stictotarsus griseostriatus*). The specific conductivity of this tributary stream was 7x higher than the average value of other water bodies we sampled across the state (Table 1). Dissolved oxygen and % saturation were nearly 2x higher than the mean of other sites we sampled. Interestingly, the mean pH of streams and ponds in the basins were 10x higher than the tributary stream to Murphy Creek. The riparian vegetation consisted of sagebrush (*Artemisia* sp.), greasewood (*Sarcobatus* sp.), rabbitbrush (*Chrysothamnus* sp.), salt cedar (*Tamarix* sp.), and northern mixed prairie. Sagebrush, greasewood, and northern mixed prairie dominated the vegetation in the surrounding upland landscape as well.

The tributary of Murphy Creek increases the list of sites known to be occupied by *H. diversipes* to 12. Of the previously-known 11 sites, 7 were accessible and held water in 2012, and were sampled as part of our survey. We sampled Dugout Creek (7 May, 1 June, and 26 June), Dead Horse Creek (7 May, 1 June, and 26 June), Cloud Creek (2 locations; 7 May, 1 June, and 26 June), Government Creek (8 May), Teapot Creek (8 May), and Conant Creek (21 May). We did not collect *H. diversipes* at any of these 7 sites.

Discussion

Hygrotus diversipes appears to be restricted to only a relatively small portion of central Wyoming. Currently, *H. diversipes* has been collected from 11 locations within the Powder River Basin and 1 location in the Wind River Basin (Figure 1; Table 2). These 12 sites have resulted from 5 main survey efforts and a few ancillary field efforts, all taking place over a 50 year period (see Leech 1966, BLM unpublished data, Keenan and Howard 1995, Miller 2002, and Tronstad et al. 2011; see also Table 2). The net result of our state-wide surveys in 2011 and 2012 was only one new location occupied by *H. diversipes*.

The 2011 and 2012 surveys only collected *H. diversipes* in one location each year. In 2011, we collected the beetle in Dead Horse Creek (Tronstad et al. 2011), a site previously known to have been occupied. In 2012, we discovered *H. diversipes* in a tributary stream of Murphy Creek, a site the beetle was not previously known from but within the general known area. Both 2011 and 2012 were drought years and the dry conditions may have limited the distribution of the beetle. The year 2012 was an extreme drought year, and several of the sites previously known to be occupied by the beetle were dry by late June. Surveys during wetter years may reveal a wider distribution for *H. diversipes*. Spring precipitation is probably vital to *H. diversipes* habitat quality, because such precipitation recharges the shallow groundwater that is necessary to maintain these streams throughout the summer. Predictive distribution models suggested that *H. diversipes* inhabited streams with shallow ground water (Tronstad et al. 2011). More water likely percolates into the ground during spring because of lower temperatures and thus lower evaporation rates compared to summer. Precipitation in the form of snow probably recharges groundwater to a larger degree than rain, because a blanket of snow protects the melted water from evaporation. Additionally, drifted snow that accumulated in the stream bottoms throughout the winter are probably an important source of water during spring when drifts melt.

Table 2. All known sites, locations (Datum NAD 83), collectors, and dates where *Hygrotus diversipes* has been collected since the beetle's discovery.

Sites and Collectors	Locations and Dates
Dugout Creek	43.47795N, -106.41210W
H. Leech, California Academy of Sciences	July 1964
G. Dahlem, BLM	June 1985
L. Keenan and T. Howard, PEST, Inc.	August 1992
L. Keenan and T. Howard, PEST, Inc.	August 1993
K. Miller, Cornell University	July 1995
K. Miller, Cornell University	August 2002
Cloud Creek at 33 Mile Road	43.26375N, -106.65775W
G. Dahlem, BLM	June 1985
W. Fitzgerald, BLM	September 1992
Cloud Creek at Wild Horse Road	43.33211N, -106.65852W
W. Fitzgerald, BLM	September 1992
K. Swanson, University of Wyoming	July 2010
Dead Horse Creek	43.35316N, -106.51888W
G. Dahlem, BLM	June 1985
K. Swanson, University of Wyoming	July 2010
L. Tronstad, C. Bish, and K. Brown, WYNDD	May 2011
Hay Draw	43.48763N, -106.38641W
L. Keenan and T. Howard, PEST, Inc.	August 1992
L. Keenan and T. Howard, PEST, Inc.	August 1993
Government Creek	43.41602N, -106.43983W
K. Miller, Cornell University	August 1996
Unnamed pool by Barnum	43.64741N, -106.83006W
K. Miller, Cornell University	August 2002
Flying E Creek	44.25968N, -106.16591W
K. Miller, Cornell University	August 2002
Teapot Creek	43.32006N, -106.23851W
K. Miller, Cornell University	August 2002
Conant Creek	42.96911N, -107.95193W
K. Miller, Cornell University	August 2002
Sand Draw	43.05640N, -107.20176W
K. Miller, Cornell University	August 2002
Tributary to Murphy Creek	43.60800N, -106.65500W
L. Tronstad, C. Bish, and K. Hack, WYNDD	May 2012

To investigate the idea that spring precipitation may at least partially explain the distribution of *H. diversipes*, I plotted precipitation between March and May collected at Casper and Kaycee weather stations during the years when *H. diversipes* surveys occurred. I compared spring precipitation to the number of core sites where *H. diversipes* was found that year. I considered core sites to be all occupied sites that were discovered before 2000. Because the number of core sites searched differed among years, I also compared spring precipitation to the proportion of core sites where *H. diversipes* was collected that year. Both the number of core sites (Figure 3a) and the proportion of core sites (Figure 3b) where *H. diversipes* was collected were higher during years with more spring precipitation. Therefore, the distribution of *H. diversipes* appears positively correlated with spring precipitation.

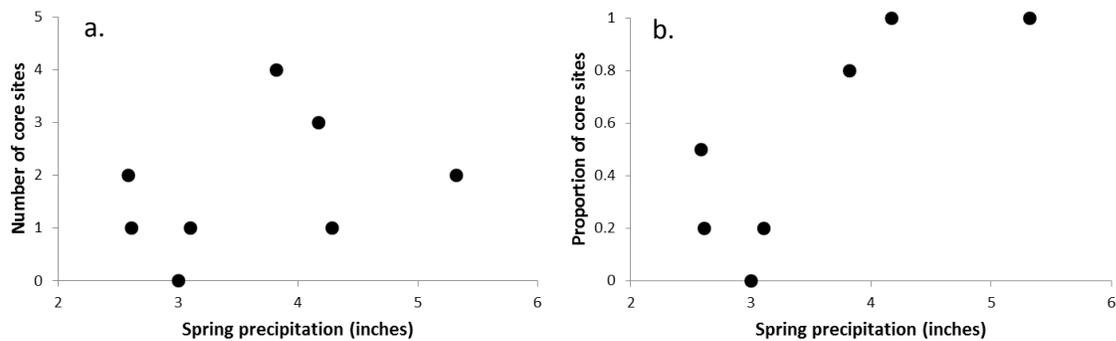


Figure 3. Spring precipitation compared to a.) the number of core sites and b.) the proportion of core sites where *H. diversipes* was collected during a given year.

Hygrotus diversipes has been collected only in streams with relatively high concentration of dissolved salts. *Hygrotus* beetles are thought to be lentic species (occur in standing water). Despite sampling in numerous ponds, *H. diversipes* has only been collected in streams. Most of these streams had dried to a series of disconnected pools when the beetles were collected. *Hygrotus diversipes* seems to specialize in small streams with little to no flow, a quality similar to ponds. Additionally, all the streams that *H. diversipes* lives in have white salts that precipitated around the margins. Salts in freshwater are primarily composed of the cations calcium, magnesium, sodium and potassium, and the anions bicarbonate, carbonate, sulfate and chloride (Wetzel 2001). Leech (1966) described the precipitated salts at Dugout Creek in 1964, and the 1985 BLM report stated that conditions at Dugout Creek, Cloud Creek and Dead Horse Creek all matched Leech's original description of Dugout Creek (BLM unpublished data). A high concentration of dissolved salts may at least partially determine the distribution of *H. diversipes*. We measured the specific conductivity of all waters we sampled in 2011 (Tronstad et al. 2011) and 2012. Based on these data, specific conductivity of streams where *H. diversipes* had been collected in the past (Table 3) had higher values than the average across the basins (Table 1), except for Government Creek. *Hygrotus diversipes* may select streams with higher conductivity, perhaps because these beetles have a competitive advantage in such environments. Invertebrates must have special osmoregulatory adaptations to survive in waters with high concentrations of dissolved salts. The adaptations of *H. salinarius* have been studied (Tones 1978), and several other species of *Hygrotus* can live in salty waters (Timms and Hammer 1988). Adult *Hygrotus* species in Wyoming (we collected 18 species) seem to occupy waters with higher specific conductivity (mean = 5000 $\mu\text{S}/\text{cm}$). In fact, we collected *H. unguicularis*, *H. tumidiventris*, and *H. patruelis* from the West Fork of Fiddler Creek in the Cheyenne River Basin with specific conductivity $\sim 28,000$ $\mu\text{S}/\text{cm}$ in 2012 and *H. masculinus* from a Chain Lake in the Great Divide Basin in 2011 with specific conductivity $\sim 25,000$ $\mu\text{S}/\text{cm}$ (Tronstad et al. 2011).

Like most adult dytiscids, adult *H. diversipes* are probably good flyers that can readily disperse among habitats (Tronstad et al. 2007). Dytiscids may disperse for many reasons, such as to find overwintering habitat or escape a drying pond or stream. Dytiscids vary in their ability to disperse, with some taxa flying often to track available habitat (Hilsenhoff 1986). Due to the temporary nature of some habitats that *H. diversipes* has been collected in, we expect that *H. diversipes* readily disperses among streams. Available habitat is likely dynamic in time and space, possibly varying with patterns of local precipitation. *Hygrotus diversipes* may not be found in the same location each year, as shown in Table 2. For example, *H. diversipes* has not been collected at Cloud Creek (33 Mile Road) since 1992 or Dugout Creek since 2002, despite recent searches. Cloud Creek at 33 Mile Road has been dry the last 3 years that we have surveyed, despite visiting throughout the summer (May – August). Dugout Creek has held water during

most of our visits, but water levels seemed to fluctuate more than other nearby streams. Rigorous monitoring of *H. diversipes* would require searches in multiple habitats, and possibly during more than one period in the summer (May – September).

Table 3. Mean specific conductivity of streams in 2011 and 2012 where *H. diversipes* had been collected in past surveys. Note that average conductivity of rivers in North America is ~284 $\mu\text{S}/\text{cm}$ (Wetzel 2001), and average conductivity of seawater is ~70,000 $\mu\text{S}/\text{cm}$.

Stream	Mean specific conductivity ($\mu\text{S}/\text{cm}$)	
	2011	2012
Dugout Creek	5420	5590
Dead Horse Creek	5300	8660
Cloud Creek	11,340	8020
Conant Creek		8850
Government Creek		2640
Teapot Creek		11,370

The distribution of *H. diversipes* may retract during drought years. Dytiscid beetles are known to survive drought by aestivating (reduced metabolic rate and activity during warm and dry periods) in damp or dry sediments, or by the adults dispersing to new habitats (Paul 1980, Garcia et al. 1990, Velasco and Millan 1998, Robson et al. 2011). I am aware of studies that have found adult dytiscids aestivating in sediments (Boulton 1989), but I am not aware of any studies showing that larval dytiscids have strategies to survive drying. Dytiscids in an Arizona desert stream survived drought by ovipositing eggs in habitats that would likely stay inundated long enough (~6 weeks) to allow the larvae to develop to adults (Gray 1981). Most dytiscids collected in intermittent streams in Australia used receding pools as refugia, but some adult dytiscids were also found under leaf litter, in a lake, or in the sediments of dried pools (Boulton 1989). Shallow water (<1 cm depth; Velasco and Millan 1998) and higher beetle densities (Yee et al. 2009) triggered dytiscids to fly to new habitats. Garcia et al. (1990) postulated that *Agabus disintegratus* aestivated in sediments instead of dispersing to permanent water to avoid competition. Twenty-two percent of these dytiscid beetles survived aestivation in the laboratory for 5 months (Garcia and Hagen 1987). *Hygrotus diversipes* may aestivate in sediments, because of the limited range of the species and the relatively dry conditions in the area. We may have collected fewer adult *H. diversipes* in 2011 or 2012 because adults were aestivating (e.g., buried in sediments or under rocks). However, nothing is known about how *H. diversipes* copes with dry conditions.

Hygrotus diversipes can only be identified in the adult stage. Although some species keys for *Hygrotus* larvae exist (Alarie et al. 1990, Barman 1999), *H. diversipes* larvae have not been paired with the adult stage. A number of important questions may be addressed once the larvae have been identified. For example, we currently do not know where *H. diversipes* lays eggs and rears larvae. We also do not know how long larval development lasts or the generation time for *H. diversipes*. Larvae cannot disperse among habitats, so larval rearing areas must remain inundated the entire period. Because larvae cannot move among habitats, protecting groundwater is probably vital to conserve the beetle. Larvae of *Hygrotus* can probably withstand higher concentrations of dissolved salts than adults (Tones 1978), so larval habitats may differ from adult habitats. We cannot learn more about the life cycle of *H. diversipes* until we identify the larval stage. Managing any species is exceptionally difficult when only a fraction of the life cycle is understood. Continued research into the basic biology of *H. diversipes* will yield important insights for scientists as well as resource managers.

Acknowledgements

Cody Bish, Kyle Hack, Ben Anson, Kelsey Brown, and Devin Baumer were instrumental in the field and the laboratory. Thanks to Dave Pellatz and the Thunder Basin Grassland Prairie Ecosystem Association for allowing us to sample water on several ranches. Comments from Gary Beauvais of WYNDD improved the report.

Literature Cited

- Alarie, Y, P. P. Harper, and R. E. Roughley. 1990. Description of the larvae of 11 nearctic species of *Hygrotus* Stephens (Coleoptera, Dytiscidae, Hydroporinae) with an analysis of their phyletic relationships. *Canadian Entomologist* 122:985-1035.
- Anderson, R. D. 1971. Revision of nearctic representatives of *Hygrotus* (Coleoptera: Dytiscidae). *Annals of the Entomological Society of America* 64:503-512.
- Anderson, R. D. 1976. A revision of the Nearctic species of *Hygrotus* groups II and III (Coleoptera: Dytiscidae). *Annals of the Entomological Society of America* 69:557-584.
- Anderson, R. D. 1983. Revision of the nearctic species of *Hygrotus* groups IV, V, and VI (Coleoptera: Dytiscidae). *Annals of the Entomological Society of America* 76:173-196.
- Barman, E. H. 1999. A key to the mature (third instar) larvae of Georgia species of *Hygrotus* Stephens (Coleoptera: Dytiscidae) with notes on the biology of *H. impressopunctatus* (Schaller) and *H. nubilus* LeConte. *Georgia Journal of Science* 57:109-112.
- Boulton, A. J. 1989. Over-summering refuges of aquatic macroinvertebrates in two intermittent streams in central Victoria. *Transactions of the Royal Society of South Australia* 113:23-34.
- Forest Guardians. 2007. A petition to list 206 critically imperiled or imperiled species in the mountain-prairie region of the United States as Threatened or Endangered under the Endangered Species Act. Available at: http://www.wildearthguardians.org/site/DocServer/petition_protection-206-species-r6_7-24-07.pdf?docID=1522&AddInterest=1103
- Garcia, R., and K. S. Hagen. 1987. Summer dormancy in adult *Agabus disintegratus* (Crotch) (Coleoptera, Dytiscidae) in dried ponds in California. *Annals of the Entomological Society of America* 80:267-271.
- Garcia, R., K. S. Hagen, and W. G. Voigt. 1990. Life history termination of summer diapause and other seasonal adaptations of *Agabus disintegratus* Crotch (Coleoptera, Dytiscidae) in the central valley of California USA. *Quaestiones Entomologicae* 26:139-150.
- Gray, L. J. 1981. Species composition and life histories of aquatic insects in a lowland Sonoran Desert stream. *The American Midland Naturalist* 106:229-242.
- Hilsenhoff, W. L. 1986. Life history strategies of some Nearctic Agabini (Coleoptera: Dytiscidae). *Entomologica Basiliensia* 11:385-390.
- Jach, M. A., and M. Balke. 2008. Global diversity of water beetles (Coleoptera) in freshwater. *Hydrobiologia* 595:419-442.
- Keenan, L. C., and T. Howard. 1995. Status report on the narrow-foot diving beetle *Hygrotus diversipes* Leech. Professional Entomological Services Technology, Inc., Broomfield, Colorado.
- Larson, D. J., Y. Alarie, and R. E. Roughley. 2000. Predaceous diving beetles (Coleoptera: Dytiscidae) of the Nearctic Region, with emphasis on the Fauna of Canada and Alaska. National Research Council of Canada Research Press, Ottawa, Ontario.
- Leech, H. B. 1966. The *Pedalis*-group of *Hygrotus*, with descriptions of two new species and a key to the species (Coleoptera: Dytiscidae). *Proceedings of the California Academy of Sciences* 33:481-498.
- Merritt, R. W., K. W. Cummins, and M. B. Berg, editors. 2008. *An Introduction to the Aquatic Insects of North America*, 4th edition. Kendall Hunt Publishing, Dubuque, IA.
- Miller, K. B. 2002. Report on the diving beetle *Hygrotus diversipes* Leech (Coleoptera: Dytiscidae). Cornell University, Ithaca, NY.

- Paul, A. R. 1980. Observations on the aestivating habits of *Agabus bipustulatus* (L.) (Col., Dytiscidae). Entomologist's Monthly Magazine 116:1-3.
- Robson, B. J., E. T. Chester, and C. M. Austin. 2011. Why life history information matters: drought refuges and macroinvertebrate persistence in non-perennial streams subject to a drier climate. Marine and Freshwater Research 62:801-810.
- Timms, B. V., and U. T. Hammer. 1988. Water beetles of some saline lakes in Saskatchewan. Canadian Field Naturalist 102:246-250.
- Tones, P. I. 1978. Osmoregulation in adults and larvae of *Hygrotus salinarius* Wallis (Coleoptera: Dytiscidae). Comparative Biochemistry and Physiology 60:247-250.
- Tronstad, L. M., B. P. Tronstad, and A. C. Benke. 2007. Aerial colonization and growth: rapid invertebrate responses to temporary aquatic habitats in a river floodplain. Journal of the North American Benthological Society 26:460-471.
- Tronstad, L. M., M. D. Andersen, and K. Swanson. 2011. Statewide survey for *Hygrotus diversipes* in Wyoming. Report prepared for the Wyoming Game and Fish Department and the Wyoming Governor's Office by the Wyoming Natural Diversity Database, University of Wyoming, Laramie. Available at: <http://www.uwyo.edu/wyndd/files/docs/reports/wynddreports/u11tro03wyus.pdf>
- U.S. Fish and Wildlife Service. 2009. Partial 90-day finding on a petition to list 206 species in the midwest and western United States as Threatened or Endangered with critical habitat. Federal Register 74:6122-6128. Available at: <http://www.gpo.gov/fdsys/pkg/FR-2009-02-05/pdf/E9-2358.pdf>
- Velasco, J., and A. Millan. 1998. Insect dispersal in a drying desert stream: effects of temperature and water loss. Southwestern Naturalist 43:80-87.
- Wetzel, R. G. 2001. Limnology: Lake and River Ecosystems. Academic Press, New York, NY.
- WildEarth Guardians. 2013. Petition to list the narrow-foot *Hygrotus* diving beetle (*Hygrotus diversipes*) under the Endangered Species Act. Available at: http://www.wildearthguardians.org/site/DocServer/Wyoming_diving_beetle_listing_petition.pdf?docID=11022
- Yee, D. A., S. Taylor, and S. M. Vamosi. 2009. Beetle and plant density as cues initiating dispersal in two species of adult predaceous diving beetles. Oecologia 160:25-36.