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DESCRIPTION OF FALL AND WINTER MOVEMENTS OF THE INTRODUCED AMERICAN BULLFROG (*LITHOBATES CATESBEIANUS*) IN A MONTANA, USA, POND

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***Abstract.*—American Bullfrogs (*Lithobates catesbeianus*) have been introduced across the globe, including in many northern latitude habitats where wetlands are ice-covered for part of the year. Because bullfrogs are less mobile at low temperatures, greater knowledge about their overwintering habitat may provide additional opportunities for control. Here, we described fall and early-winter movements and habitat associations for introduced juvenile bullfrogs in a pond within the Yellowstone River corridor near Billings, Montana, USA. We attached radio-transmitters to 13 juvenile bullfrogs and located individuals from 28 August to 10 December 2014. Bullfrogs moved greater distances in late summer and early autumn, and later during brief warming periods. Collectively, all bullfrog locations were distributed across a 15,384 m^2 area during the active season, but contracted to a 130 m^2 area in the east cove of the pond by the time the study site froze over. Our research provides evidence that managers in northern latitude regions like Montana may be able to use the long, cold winters to their advantage because the site-specific distributions of introduced bullfrogs contracted as temperatures decreased.**

Key Words.—aquatic invasive species; juvenile; northern latitude; radio telemetry; suppression; Yellowstone River

INTRODUCTION

Introduced American Bullfrogs (*Lithobates catesbeianus* [Shaw, 1802]; hereafter, bullfrogs) have been implicated in the declines of multiple amphibian and reptile species across the globe (Ficetola et al. 2007). Its large size, high mobility and fecundity, generalist eating habits, and role as a disease vector to other amphibians makes bullfrogs an extremely successful invader and a threat to biodiversity (Nentwig 2007). Currently, there are few feasible control options for bullfrogs, so populations are difficult to eradicate once established. Because bullfrogs are less mobile at low temperatures, greater knowledge about their overwintering habitat may provide additional opportunities for control.

Bullfrogs are a warm-adapted species, yet have successfully established in many northern latitude habitats across the globe that have ice cover during the winter (Bachmann 1969; Ficetola et al. 2007). In these colder habitats, bullfrog tadpoles and adults require permanent waters for overwintering because they cannot tolerate freezing or prolonged anoxia (Stewart et al. 2004). This strict habitat need suggests that bullfrogs in northern latitude habitats may be especially vulnerable to control efforts during the winter. Little is known about bullfrog overwintering behavior or habitat because visual encounters are rare when air temperatures fall below 15° C (Willis et al. 1956; Stinner et al. 1994). In the native range, several studies have documented that adult bullfrogs overwinter in areas with greater dissolved oxygen and warmer temperatures, such as pond inlets or near the shore (Stinner et al. 1994; Nie et al. 1999). Studies of other frog species also indicate that individuals prefer certain habitats for overwintering, display fidelity to specific overwintering sites, and make long-distance movements to suitable overwintering habitat (Kelleher and Tester 1969; Matthews and Pope 1999; Pilliod et al. 2002). Importantly, overwintering can be communal, with multiple individuals co-habiting a small area (Kelleher and Tester 1969). Given the site fidelity to overwintering habitats expressed by some amphibians and the high costs of long-distance movements to these habitats, it is likely that overwintering habitat is a critical resource that strongly influences vital rates (Pilliod et al. 2002). Understanding the overwintering habitats preferred by introduced bullfrogs may provide opportunities for effective control efforts, especially if individuals congregate in areas where the preferred microhabitat requirements are met.

Here, we describe fall and early-winter movements and habitat associations for introduced juvenile bullfrogs in the Yellowstone River corridor near Billings, Montana, USA. We focused on the juvenile life stage because demographic analyses indicate that juvenile survival has the greatest effect on population growth rates, so knowledge about juveniles will bolster control efforts (Govindarajulu et al. 2005). Bullfrogs were first documented in the Yellowstone River corridor in 1999

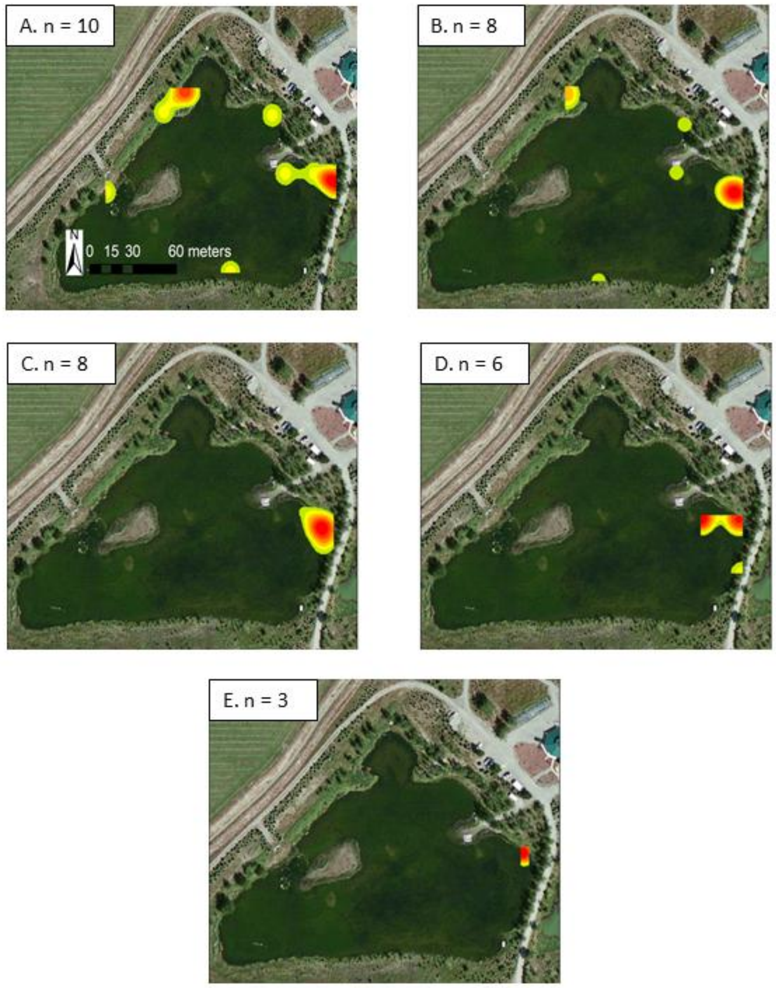

FIGURE 1. Kernel density estimates and sample size of American Bullfrog (*Lithobates catesbeianus*) locations in a pond complex near the Yellowstone River, Billings, Montana, USA on (A) 9 September, (B) 24 September, (C) 29 October, (D) 19 November, and (E) 10 December 2014. Warmer colors (red) indicate areas with the highest density of locations. Maps show 2015 World Imagery provided by Esri (Redlands, California, USA).

and by 2013 had spread to at least 58 sites spanning 107 km along the Yellowstone River (Sepulveda et al. 2015). This region has cold, dry winters and most waters are ice-covered November through March. The first freeze of the season typically occurs in early October, and subfreezing temperatures can occur into May. Because of the magnitude and duration of this cold, overwintering habitat is likely to be critical to the ability of bullfrogs to establish populations and spread to nearby areas where suitable habitat exists. Therefore, efforts to remove bullfrogs during the winter or to manipulate overwintering habitat may help managers to control introduced bullfrogs.

MATERIALS AND METHODS

This project was conducted in Will's Marsh, a reclaimed gravel quarry pond at the Audubon Conservation Education Center in Billings, Montana, USA, and adjacent to the Yellowstone River (elevation 952 m; latitude 45.742724°N, longitude 108.540560°W; Fig. 1). The surface area of Will's Marsh in the summer is 15,985 m^2, but recedes to < 10,000 m^2 in the winter.

***Radio tags*.—**To obtain a representative sample of juvenile bullfrogs, we dip-netted uniformly along the edge of the pond. We weighed (± 0.1 g) and measured the snout-vent length (SVL; ± 1 mm) of captured juveniles. We attached radio transmitters (BD-2, Holohil Systems LTD., Carp, Ontario, Canada) to bullfrogs using a lightweight belt harness made of flexible, plastic tubing (Burow et al. 2012). To minimize the effect on the behavior and health of bullfrogs, the transmitter and harness were < 10% of the weight of the bullfrog (Richards et al. 1994). Multiple capture and tagging events of new juvenile bullfrogs

TABLE 1. Summary data of each radio-tagged American Bullfrog (*Lithobates catesbeianus*) used in a study of wintering movements at a pond complex near the Yellowstone River, Billings, Montana, USA.

Frog #	SVL (mm)	Weight (g)	Initial release date	Last detection date	# Locations	Cumulative movement (m)	Net movement (m)	Tag status
1	63	35.0	26 Aug.	5 Nov.	10	75.6	32.2	Lost
2	65	39.5	26 Aug.	10 Dec.	11	365.7	111	Lost
3	68	35.5	26 Aug.	17 Sept.	2	13.5	13.5	Lost
4	70	46.1	27 Aug.	5 Nov.	10	71.2	11.3	Lost
5	75	41.9	24 Sept.	10 Dec.	6	75.9	19.2	Lost
6	80	68.3	27 Aug.	1 Oct.	5	213.4	131.5	Recovered
7	80	54.7	24 Sept.	5 Nov.	6	168.2	129.1	Lost
8	81	70.6	27 Aug.	17 Sept.	2	6.6	2.0	Recovered
9	84	75.0	27 Aug.	5 Nov.	10	145.6	74.6	Lost
10	84	88.0	27 Aug.	8 Oct.	5	208.8	65.1	Lost
11	85	55.6	24 Sept.	10 Dec.	7	107.5	47.4	Lost
12	87	80.9	27 Aug.	5 Nov.	10	102.2	13.6	Lost
13	88	84.5	27 Aug.	15 Oct.	6	355.4	233.5	Lost

were required because of short transmitter battery lives and tag loss. Capture and tagging events occurred on 28–29 August, 9 September, and 25–30 September 2014 (Table 1).

Surveys.—We located radio-tagged bullfrogs weekly from 25 August through 5 November 2014 and then biweekly until 10 December with a Lotek SRX 600 receiver (Lotek Wireless Inc., Newmarket, Ontario, Canada) and an H-type directional antenna (Telonics Inc., Mesa, Arizona, USA). Initial release locations and all subsequent locations were determined to the nearest 1 m using a global positioning system unit. When possible, we used visual observations to confirm the location of radio-tagged frogs. If we failed to detect a radio signal, we extended surveys to adjacent aquatic habitats within a 1-km radius. If we detected a radio signal in the same location for greater than one location survey, then we assumed the radio transmitter belt had broken off the bullfrog or that the bullfrog was dead. On these occasions, we only used location information for prior movements.

At each bullfrog location we recorded (1) water depth, (2) percentage cover of submerged and emergent aquatic vegetation based on visual estimates, (3) percentage mud and silt, sand, gravel, cobble, and boulder based on visual estimates, (4) water temperature, and (5) dissolved oxygen at the surface of the water and pond bottom. We used a multi-parameter meter (YSI Professional Plus, Yellow Springs, Ohio, USA) to measure water temperature and dissolved oxygen. If we could see radio-tagged bullfrogs, we collected these data within 0.5 m of that location. If we could not see the bullfrog, then we collected data at the point of the strongest signal. Because the majority of locations were in the water (94%), we restricted our descriptive analyses to aquatic habitats.

The study site froze over by 19 November 2014, so aquatic habitat data could not be collected during subsequent surveys. To describe the aquatic habitats of bullfrogs that were located on and after 19 November, we returned to Will's Marsh on 2 February 2015 and used an ice auger to expose location sites. We recorded aquatic habitat data at these location sites. To determine whether the microhabitat characteristics at these locations were consistent, we also collected habitat data at an additional 20 sites spaced at 25-m intervals around the perimeter of Will's Marsh. We randomly located sites within 0–16 m of the ice perimeter; a distance informed by amphibian locations in November and December.

Analyses.—We estimated bullfrog movements as the straight-line distance and straight-line distance standardized on a per-day basis between successive locations of an individual. We summed straight-line distances to describe the cumulative distance moved by each individual. We used the straight-line distance between the points of first location and final location to describe the net distance moved by each individual. Because of limited telemetry resolution, we disregarded all values < 1.0 m as being movements. We calculated cumulative and net distances using the point distance tool in ArcMap (v.10.2; Esri, Redlands, California, USA). To help visualize changes in bullfrog locations over time, we used the kernel density tool in ArcMap to make kernel density plots for all located individuals at each sampling event.

We tested for correlations of standardized straight-line distances between locations with average air and water temperatures during this period and Julian date of the location using Pearson's Product-Moment Correlation ($\alpha = 0.05$). Average air and water temperatures and Julian date were inversely correlated ($r = -0.83$ to -0.97, $P <$

TABLE 2. Summary of climate and habitat characteristics used by American Bullfrogs (*Lithobates catesbeianus*) in a pond complex near the Yellowstone River, Billings, Montana, USA. Weather data are for the period of 1 September–10 December 2014 and habitat data are for surveys that occurred weekly from 9 September to 11 November and then biweekly to 10 December 2014. Unless otherwise noted, habitat values indicate the median (range).

Month	September	October	November	December
Weather				
Air temperature (mean, °C)	16.1	12.3	0.1	0.6
Air temperature (min–max, °C)	-2 to 32.8	-4.4 to 27.8	-24.4 to 20.6	-25.0 to 13.9
Precipitation days (total, *N*)	8	4	10	11
Total precipitation (cm)	1.4	0.4	1.9	1.7
Snowfall days (total, *N*)	1	1	13	16
Total snowfall (cm)	< 0.3	< 0.3	33.5	21.3
Habitat				
Water depth (m)	0.5 (0.1–1.3)	0.8 (0.3–1.4)	0.9 (0.8–1.2)	-
Surface water temperature (°C)	20.8 (18.0–22.9)	12.9 (8.4–18.8)	9.7 (9.1–10.2)	-
Bottom water temperature (°C)	20.0 (17.1–22.9)	12.2 (7.6–18.8)	7.4 (7.1–7.9)	-
Surface dissolved oxygen (mg/L)	13.7 (9.8–18.8)	11.4 (7.2–14.7)	13.1 (11.7–17.2)	-
Bottom dissolved oxygen (mg/L)	14.0 (7.7–24.4)	10.5 (4.9–14.1)	8.4 (7.5–9.8)	-
Emergent vegetation (%)	11–25	0	0	-
Submergent vegetation (%)	11–25	51–75	76–100	-
Wood debris (%)	0	0	0	-
Mud, silt (%)	51–75	26–50	76–100	-
Sand (%)	26–50	11–25	1–10	-
Gravel (%)	11–25	11–25	1–10	-
Cobble (%)	1–10	1–10	1–10	-
Boulder (%)	0	0	0	-
Distance to pond edge (m)	2.7 (0.4–5.5)	4.0 (0.1–28.1)	6.4 (0.5–12.7)	7.4 (2.3–15.3)

0.01) and air and water temperatures were positively correlated (r = 0.91, P < 0.01), so we used principal components analysis to combine these metric into one axis that explained 94% of the variation. High values indicate colder temperatures and later dates. We also tested for correlation between bullfrog SVL and cumulative and net distance moved. We used descriptive analyses to assess changes in bullfrog habitat associations across the study period because we could not characterize aquatic habitats across the entire study period. Finally, we used nonparametric Wilcoxon tests (α = 0.05) in JMP (v. 10.0.2, SAS Institute Inc., Carey, North Carolina, USA) to test if the habitat characteristics at location sites from 19 November and 10 December 2014 were different from those at random sites.

RESULTS

***Temperatures*.—**Mean (± 1 SE) monthly air temperatures declined from 16.1° C (± 0.9) in September to 0.1° C (± 1.7) in November (Table 2). Subfreezing temperatures occurred on 12 and 13 September, 17 and 25 October, and consistently after 30 October. By 19 November, Will's Marsh was ice covered.

***Movement*.—**We radio-tagged 13 juvenile bullfrogs during the study period that were located more than once. The number of locations per survey date varied from 2–11, with five individuals having ≥ 10 locations each (Table 1). We located only one of 10 individuals radio-tagged in August and two of three individuals radio-tagged in September through December. We recovered three radio-tags that had detached (Table 2). No signal was detected from the other 11 radio-tags, indicating a dead battery or bullfrog movement beyond the surveyed region. Of the 106 radio-locations, we obtained visual observations 11 times, with the last visual observation on 22 October.

The distance frogs moved was variable through 29 October, but distances and variability then decreased in November and December (Fig. 2). Through 29 October, straight-line distances between locations varied from 1–242 m. The median (± 1 SE) standardized straight-line distance for this time period was 4.5 ± 1.1 m per day. In November and December, straight-line distances between locations varied from 1–24 m and the median standardized straight-line distance was 4.2 ± 1.3 m per day. Across the entire study period, median cumulative distance was 107.5 ± 31.7 and median net movement was 47.4 ± 18.7 m. Standardized straight-line distances and the principal component of temperatures and Julian date were inversely correlated such that bullfrog movements were greatest earlier in the fall and during warmer temperature periods (r = −0.60, P = 0.05).

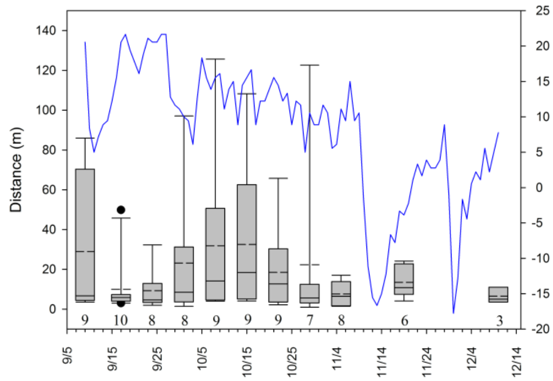

FIGURE 2. Box plot of the distribution of straight-line distances moved by radio-tagged American Bullfrogs (*Lithobates catesbeianus*) in 2014 between successive locations relative to the average air temperature (blue line). Box plots show the median value (solid horizontal line) and mean value (dashed horizontal line), box boundaries indicate the 25th and 75th percentiles, whiskers indicate the 5th and 95th percentiles, and filled circles indicate outliers. The value below each box indicates the number of radio-tagged bullfrogs located on each survey date. X-axis labels indicate date (month/day).

Bullfrog SVL was not correlated with cumulative distance (r = 0.16, P = 0.60) or net distance (r = 0.32, P = 0.29).

We located bullfrogs along the perimeter of Will's Marsh through 8 October and these locations (n = 69) occurred within an area of 15,384 m^2. Most locations occurred in the east and north coves. By 22 October, we located all but one bullfrog in the east cove and all locations (n = 37) were within 1,000 m^2 and 53% of these locations were within 130 m^2. Most radio-tagged bullfrogs remained or moved to the east cove of Will's Marsh during the study period (Fig. 2). Five bullfrogs, each located ≥ eight times, always occurred in this east cove. An additional five bullfrogs located along the north perimeter in September moved toward the east cove in October. Importantly, no bullfrog that was initially located in the east cove moved away.

Habitat.—Bullfrogs moved further away from the edge of the water with time (Table 2). We located bullfrogs within 6 m of the edge of the water early in the fall (28 August to 17 September), but later in the season we found them up to 15 m from the edge of the water. When bullfrogs were close to the banks during the first three weeks of the study, they were associated with shallow water and emergent vegetation. When bullfrogs moved away from the banks prior to 19 November, they occurred in deeper water with submerged vegetation (Table 2). Water temperatures and dissolved oxygen declined with time and by 5 November, we located bullfrogs in habitats with median (± 1 SE) surface and bottom water temperatures of 9.7 ± 0.2 and 7.4 ± 0.1° C and median surface and bottom dissolved oxygen concentrations of 13.1 ± 0.7 and 8.4 ± 0.3 mg/L. We located bullfrogs in habitats with silt and mud substrate through 5 November (Table 2).

In February, we characterized the habitats of bullfrogs that we located on 19 November and 10 December. Water depths below the ice ranged from 18–53 cm and bottom water temperature and dissolved oxygen concentration ranged from 0.1–1.7° C and 0.25–2.1 mg/L, respectively. All of these habitats had silt and mud substrate. Water depth, temperature, and dissolved oxygen at these six habitats did not differ from those at random sites (χ^2 < 1.35, P > 0.25). We also found no visual evidence (e.g., air-bubbles, temperature thermoclines) of localized groundwater or river water inflow at location sites.

DISCUSSION

The ongoing spread of introduced bullfrogs in northern latitude habitats, like the Yellowstone River floodplain, underscores the need for alternative management approaches. Current approaches include pond drying and direct removal during the warmer seasons. However, pond drying is not tractable in many invaded waters and direct removal is difficult because bullfrogs have high fecundity, density dependence, and are evasive (Adams and Pearl 2007). Our study suggests that targeted removal or suppression of bullfrogs in northern latitude habitats may be more effective in the late fall and winter because the distribution of radio-tagged bullfrogs in Will's Marsh greatly contracted with the onset of winter. Radio-tagged bullfrogs were distributed across a 15,384 m^2 area in the fall but then most clustered in a 130 m^2 area by the time the study site froze over. Targeting winter habitats where bullfrogs aggregate may increase the effectiveness of direct removal efforts with nets (Louette et al. 2013), lethal suppression agents like carbon dioxide (Abbey-Lambertz et al. 2014), or indirect approaches like habitat manipulation (Adams and Pearl 2007).

Despite the conservation threat that introduced bullfrogs pose to native species across the globe, little is known about their overwintering behavior in the field. Most research has occurred in the lab and focused on the physiological responses to winter temperatures and hypoxia (e.g., Stewart et al. 2004). These studies conclude that bullfrogs cannot tolerate freezing or prolonged anoxic conditions and therefore move to winter habitats with higher dissolved oxygen concentrations. In one of the few field studies that describes overwintering bullfrogs, six native adult bullfrogs were radio-tagged and their movement was tracked from October to April in two ponds in the Midwestern United States (Stinner et al. 1994). As was the case in our study, movement distance correlated with temperature and radio-tagged bullfrogs moved to a common overwintering location. These corroborating results suggest that clustered or communal overwintering may be a common attribute of introduced and native bullfrogs alike. Additional telemetry studies that monitor more individuals per site and that incorporate other habitats (e.g., riverine) are needed to confirm the generality of our result.

In a previous study, overwintering habitats of bullfrogs were characterized by high dissolved oxygen levels (Stinner et al. 1994), a factor that laboratory study demonstrated to be physiologically important (Stewart et al. 2004). Additionally, these habitats were fed by small streams, supported macrophyte communities, and were relatively shallow (< 1 m). In our study, however, we did not identify dissolved oxygen concentrations or other habitat characteristics that were unique to the confined area where bullfrogs were located in November and December. We suspect that this was due to our low sample size and short study duration (necessitated by the battery life of our radio transmitters), which limited observations to only as late as December. Macrophytes were present throughout Will's Marsh prior to ice cover and bullfrogs moved away from shallow habitats over time to deeper habitats further from shore. We also found no evidence of localized groundwater or river water inflow at location sites in the east cove of Will's Marsh. Because this overwintering site has a west-facing aspect, it is possible that it receives greater solar radiation than other areas of the pond. Greater solar radiation is predicted to result in less ice cover and more light and therefore warmer temperatures and higher dissolved oxygen levels (Stinner et al. 1994).

Though bullfrogs in our study site overwintered in a confined area, they were not torpid. We documented movement throughout November and December. Lithobatid species, including bullfrogs, are known to be active at low temperatures. Stinner et al. (1994) found that bullfrogs voluntarily moved during the coldest period of their study and others have observed volitional and forced movements of *L. pipiens* at near freezing temperatures (e.g., Cunjak 1986). Consequently, bullfrogs may still be able to evade direct removal efforts in the winter, particularly if disturbances like ice augers are required to access open water. Techniques that make these overwintering habitats unsuitable, such as manipulating carbon dioxide or the local introduction of fish piscicides, may prove effective especially if overwintering habitat is limited. Conversely, manipulating habitat so as to attract bullfrogs in the winter may also increase the effectiveness of direct removal and indirect suppression techniques.

***Conclusions*.—**Our research provides evidence that managers in northern latitude regions may be able to use the long, cold winters to their advantage because the site-specific distributions of introduced bullfrogs contracted dramatically as temperatures decreased. Further work is now needed to identify techniques that are especially effective and tractable for the direct removal or indirect suppression in winter environments. Further work is also needed to determine the specific habitat characteristics associated with overwintering habitat so that managers can apply suppression techniques to the numerous sites that bullfrogs have invaded at northern latitudes.

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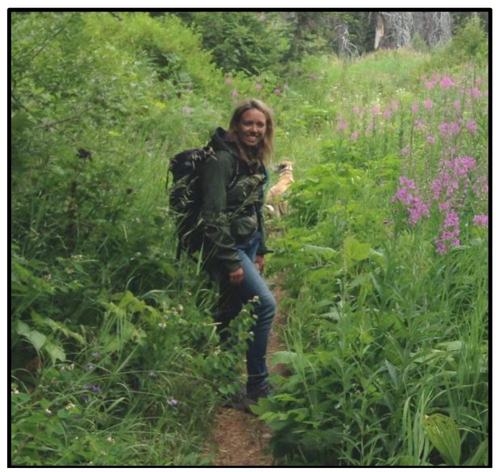

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