INVESTIGATING NON-INVASIVE SURVEY METHODS AND BUILDING A PREDICTIVE OCCUPANCY MODEL FOR HARLEQUIN DUCKS (*HISTRIONICUS HISTRIONICUS*) IN WESTERN MONTANA AND NORTHERN IDAHO

By

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Evaluating non-invasive survey methods and predicting breeding site-use of Harlequin Ducks (*Histrionicus histrionicus*) in Western Montana and Northern Idaho

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Harlequin Ducks (*Histrionicus histrionicus;* HADU) are an imperiled sea duck that breeds along white-water mountain streams, but challenges in surveying them have made it difficult to understand population trends in their Northern Rocky Mountain breeding population. In this study we had two objectives: (1) evaluate non-invasive survey methods for detecting HADU on their breeding grounds in Western Montana and Northern Idaho, and (2) develop an occupancy model to predict potential breeding stream use for HADU across the region. First, we assessed the efficacy of ground-based foot surveys (GBS), environmental DNA (eDNA), and camera traps to detect breeding HADU during time periods corresponding to the incubation and brood rearing phases of their annual cycle. GBS (0.51, SE: 0.108) and eDNA (0.49, SE: 0.146) had the highest mean detection probabilities during incubation season and time-lapse detection camera traps (0.16, SE: 0.067) were more effective than motion detection camera traps. We found that combining methods could improve our cumulative detection probability in a single visit to a stream; taking five eDNA samples in tandem with one GBS achieved a cumulative detection probability of 0.97 (SE: 0.037), emphasizing the power of combining methods. Second, we built an integrated species distribution model for breeding HADU using detection / non-detection data from GBS and eDNA samples collected from 2009 to 2024 across 1,025 one-mile stream segments. Our results indicated that stream geomorphology such as stream features like pools and braiding, human disturbance from changes to the landscape, and mean annual flow are important for predicting HADU site-use. Using posterior estimates from the occupancy model, we predicted site-use to streams within our sampling frame across the region. Predicted site use indicates that the northwest portion of the study area around Glacier National Park has the highest probability of site-use (0.29, SD: 0.07). To our knowledge this is the first large-scale statistical model for HADU site-use in Western Montana and Northern Idaho. By integrating findings from both chapters, we offer actionable strategies and recommendations for agencies to more efficiently detect and protect HADU.

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Investigating three non-invasive survey methods for detecting Harlequin Ducks (Histrionicus histrionicus) on their breeding grounds in the Northern Rockies

1.1 Introduction:

A longstanding challenge of ecology and management is obtaining the most valuable information from data collection and monitoring efforts (Nichols & Williams, 2006). This challenge requires careful allocation of limited resources to optimize data collection methods that address specific scientific and management goals (Nichols & Williams, 2006, Yoccoz, 2022). Population monitoring methods are constantly evolving as new technologies modify survey methodology and generate new types of data (Franklin et al., 2019; Golding et al., 2022; Iannino et al., 2024). However, the relevance and applicability of new survey methods is limited by our understanding of different factors that impact their efficacy. Understanding what factors impact method efficacy is especially relevant for species of conservation concern.

Harlequin Ducks (HADU; *Histrionicus histrionicus*) are a species of concern and difficult to survey given their life history, habitats they occupy, and low abundance. Although they have been monitored since the early twentieth century (Idaho Department of Fish and Game, n.d.; Montana Natural Heritage Program, 2024; Smith et al., 2023), the efficacy of these survey methods have not been evaluated. HADU are a northern hemisphere sea duck that exhibit strong site fidelity, with males following their female partners back to the female's natal stream to reproduce. They breed on rugged, fast-moving, whitewater streams in mountainous regions and fidelity to these streams creates regionally distinct breeding populations (Bengtson, 1972;

Robertson & Goudie, 2020). In the Northern Rocky Mountain breeding population (Montana, Idaho, Wyoming, and Alberta), monitoring efforts by multiple agencies and non-governmental organizations over the past century have documented declining numbers of HADU (Bate, Unpublished data; Idaho Department of Fish and Game, n.d.; Smith et al., 2023). These efforts include long-term annual monitoring of four breeding streams with historically large populations, as well as numerous single day surveys on other streams in the region every year (Bate, Unpublished data; Idaho Department of Fish and Game, n.d.; Smith et al., 2023). Additionally, roughly every five years since 2000, agencies coordinated pulses of high survey effort in priority areas to fill spatial data gaps (Bachen & Maxwell, personal communication, January 1, 2024; Montana Natural Heritage Program, 2024). Despite these efforts, outside of the four heavily monitored streams, inaccessibility of habitat and challenges associated with existing methodologies have limited the ability to obtain robust population estimates needed to inform management.

Monitoring methods for HADU have primarily relied on direct, in-person observations (Idaho Department of Fish and Game, n.d.; Montana Natural Heritage Program, 2024). However, because HADU inhabit inhospitable habitats, conditions outside the observer's control can make counts of these ground-based foot surveys (GBS) highly variable. For example, in high water, HADU often move into backwaters where they are unobservable (Hansen et al., 2019; Rine et al., 2022). High water also limits human access to streams, thereby negatively influencing detection. Using GBS, it is impossible to know whether a lack of detection is related to incomplete detection or a lack of bird occupancy. Adding to the complexity, behavior during different life history stages might affect the variability of GBS. The HADU breeding season can be broken into three distinct periods where behavior differs: breeding (~ late April – May), incubation (~June), and brood rearing (~July – mid September) (Kuchel, 1977; Reichel et al., 1995). During the incubation period, HADU only tend to forage and preen on the river for 2-4 hours a day in the afternoon and evening (MacCallum et al., 2021), whereas broods during the brood-rearing period spend much of the day in the stream. However, GBS are often completed when time allows, and surveys can span multiple life history phases and represent different distances or sections of streams. Furthermore, no one has identified the efficacy of a single GBS for any distance of survey, let alone during different life history stages. A better understanding of these complexities could provide a basis for improving interpretation of existing survey data (Bledsoe et al., 2022) and methodology for future surveys.

Two increasingly popular non-invasive methods for surveying wildlife occurrence are environmental DNA metabarcoding (eDNA) and remote, non-invasive cameras (camera traps) (Randler & Kalb, 2018; Thomsen & Willerslev, 2015). Both eDNA and camera traps could improve our understanding of HADU occurrence and abundance, but their efficacy has not yet been assessed for stream-residing waterfowl. eDNA allows researchers to assess species' presence by extracting small samples of DNA from substrates that the focal species interacts with, such as water (Ruppert et al., 2019). HADU spend substantial portions of each day on their breeding streams (Bengston, 1972) and applying eDNA methods might be especially useful for determining if they occupy streams that are otherwise difficult to survey (Sigsgaard et al., 2015). In comparison, camera traps allow for detection of species across greater time periods and overcome other methods' shortcomings that result from changes in animal behavior due to human presence (Burton et al., 2015). Camera traps can be deployed to detect motion or in a time-lapse mode, set to take photos at a pre-determined interval. Camera traps are not typically used on streams or on sea ducks. However, during the incubation period and the brood rearing period, HADU spend their days in a one mile stretch of stream where they forage downstream then fly or swim back upstream (Hansen et al., 2019). Due to HADU's restricted home range during these two periods, strategically placed cameras may be effective in detecting individuals.

Our objective was to understand the efficacy of three non-invasive HADU survey methods, GBS, eDNA, and camera traps across two distinct life stages, incubation and brood rearing. With all methods, we expected differences in detection probability between these two periods based on differences in HADU behavior or the abundance of ducks on the stream. Additionally, we expected stream characteristics, such as streamflow, to differentially impact HADU detection probability by method (Table 1). By understanding the process underlying the efficacy of each method, we determined how much effort was required to attain 80, 90, and 95 percent cumulative detection confidence per method and combination of methods. Identifying the most effective survey methods for these two time periods allows us to gain the highest quality information about HADU occupancy. Analysis of trade-offs in both effort and information gained allows us to provide recommendations on how best to implement these methods to improve our understanding of the status of Northern Rockies breeding population of HADU.

1.2 Methods:

1.2.1 Study Area:

The study area encompassed parts of the Rocky Mountains HADU breeding population in Montana and Idaho. Our boundary extended from the northeast boundary of Glacier National Park at the United States - Canada border, south along the Rocky Mountain front through the Gallatin National Forest to the Montana - Wyoming border and west to the Washington- Idaho border encompassing the Idaho panhandle (Figure 1).

We sampled known breeding streams throughout the study area. Breeding streams in the northern portion of the area are typically found at lower elevations (1000 - 2000m) within mesic forest dominated by cottonwoods (*Populus spp.*), hemlock (*Tsuga spp.*) and Western Red Cedar (*Thuja plicata*). In southern and eastern areas, breeding streams are found in more xeric conifer forests at higher elevations (up to 2500m) (Reichel et al., 1996).

1.2.2 Stream Selection:

We selected 10 streams from an initial list of 23 identified streams across western Montana and northern Idaho. Selected streams had high probable occupancy to facilitate studying the drivers of HADU detections; all study sites had confirmed breeding HADU in the last five to ten years (Idaho Department of Fish and Game, 2024; Montana Natural Heritage Program, n.d.). Streams varied in flow patterns, elevation, and vegetation cover (Appendix 1). Each selected stream was accessible to field personnel. Agency personnel sampled each stream twice during two separate field seasons in 2022 and 2023, and each sampling occasion occurred over a period of three consecutive days. The seasonal timing of sampling occasions was determined based upon stream elevation which influences HADU breeding phenology with lower elevation streams sampled earlier in the season when breeding occurs (MacCallum et al., 2021). We expected all ten streams to be occupied during the first sampling occasion and breeding attempts to occur on all ten streams in both years. However, success in the breeding attempts was required for the stream to be occupied during the second visit.

1.2.3 Field Methods:

During sampling occasions observers collected eDNA and deployed cameras for one day each. Additionally, GBS were conducted each day during sampling occasions (Table 2). For each stream visit, there were at least two designated primary observers, who surveyed all three days;

additional people may have joined for single days. The observers in this study included wildlife biologists, biological field technicians, interns, and volunteers who worked for, or were associated with Glacier National Park, the United States Forest Service, Montana Fish, Wildlife, and Parks, Idaho Department of Fish and Game, or Montana Audubon. All observers watched a training video and were given a hard copy of the protocol with documentation for identifying species and habitat variables to help enhance the quality of data they collected (Lewandowski & Specht, 2015). Population closure was assumed within each three-day visit, but not between visits. The timing of the first visit corresponded to when HADU with still viable nests would have been incubating (MacCallum et al., 2021). We expected to detect lone females who either did not breed, experienced a nest failure or were currently incubating; as such, a detection in this period would indicate attempted breeding and stream occupancy. The second visit occurred approximately three weeks later and corresponded to the brood rearing period; a detection in this period would indicate nest success.

1.2.4 Ground-based Foot Surveys (GBS)

GBS consisted of at least two observers walking upstream in the stream, when possible, looking for HADU. Observers surveyed unwalkable streams from the bank, taking turns watching the stream and walking through the brush so one person was always watching for HADU until it was safe to walk in the stream again (Hansen et al., 2019). Observers measured stream flow each day, at the start of the survey, using the float method (Robins & Crawford, 1954) and recorded data that included survey start and end time, number of HADU seen, the chick class, the number of observers, and data consistent with historical GBS (Appendix 2). Surveys were initiated between 07:00 and 10:00 and took varying amounts of time (six hours on average) to complete depending on the distance of the stream and the complexity of the terrain.

1.2.5 Environmental DNA (eDNA)

Observers collected eDNA samples while conducting a GBS, typically on the second day of each stream visit following the United States Forest Service's National Genomics Center for Wildlife and Fish Conservation protocol (Carim et al., 2016). Five liters of water was filtered, streamside, through a 1.5-µm-pore fiberglass filter (Carim et al., 2016). Observers collected eDNA at three different spatial scales (Figure 2) which allowed us to assess different spatial sampling strategies: samples were spaced at 250m for the first 1,500m of the survey reach and every 500m thereafter. Duplicate samples were collected at the sites corresponding to 1,000m spacing. eDNA samples were taken against direction of the stream flow. All samples were extracted at the National Genomics Center in Missoula, Montana, using a modified Qiagen DNEasy® Blood and Tissue Kit optimized for eDNA filters (Franklin et al., 2019). eDNA samples were analyzed for HADU DNA using a species-specific and sensitive quantitative polymerase chain reaction (PCR) assay developed by the National Genomics Center to detect a region of the HADU cytochrome c oxidase subunit I mitochondrial gene (Franklin et al. in prep). Extracts were then analyzed for the presence of HADU DNA in triplicate reactions using the optimized quantitative PCR assay conditions from Franklin et al. (in prep) on a QuantStudio 3 Real-Time PCR System (Life Technologies). A sample was determined to have a HADU detection if at least one of the triplicate reactions amplified HADU DNA. Negative controls were included in the DNA extraction process by including samples that had filtered distilled water and in the quantitative PCR analyses by using distilled water as a replacement of the DNA template. All samples were tested for inhibition by including a TaqMan Exogenous Internal Positive Control in the quantitative PCR reaction. A sample was considered inhibited if the mean cycle value (Ct) of the Internal Positive Control was more than one Ct delayed than the mean Ct of the

Internal Positive Control in the negative control reactions. To estimate the number of HADU DNA copies in each reaction (QeDNA), samples were analyzed alongside a seven-level standard curve (31 250, 6 250, 1 250, 250, 50, 10, and 2 copies per reaction) following the same conditions mentioned above with reporting requirements of efficiency between 90 and 110 percent and R^2 above 0.990. eDNA target copy numbers were then estimated by generating a linear regression from the amplification Ct values of the known starting quantities of DNA in standard curve and applying the regression to each Ct value of a reaction.

1.2.6 Camera Traps

Observers placed camera traps during the initial GBS within each sampling occasion. Two camera traps, one time-lapse and one motion detection, were placed each river mile (1,600m), starting at mile zero, along the surveyed reach of stream. Observers placed cameras on suitable pre-existing features, such as tree roots and logs, facing the stream within a 300-meter radius of the river mile (Figure 2). The 300-meter radius was pre-determined in ArcGIS Pro (Ersi Inc., 2022) prior to the survey. One camera was set to take photos every five minutes (time lapse) while the other camera was set to take motion trigger photos. Observers removed the camera traps during the second sampling occasion, approximately 3 weeks after deployment.

Photos were checked for HADU using a two-stage process. First, photos were processed by Microsoft MegaDetector AI (Beery et al., 2019) which identified empty images, objects in potential non-empty images and ascribed confidence values indicating whether the object was an animal, person, or vehicle. We then manually processed all photos with an AI detection confidence of 0.5 – 1 that were identified to contain an animal using Timelapse2 (v2.3.0.0, Greenberg et al., 2019). Animals in photos were identified to species. All photos were analyzed by one of two observers and all HADU and other waterfowl identified in photos were verified by an experienced observer. We also recorded the number of trap nights, camera angle to the stream (across = perpendicular to flow of the stream within 45 degrees; up or down = parallel to flow of stream within 45 degrees; or water-facing = where the camera was pointed downward at the stream such that the lateral angle could not be assessed), predominant stream feature (boulder, rapid, run, or pool), and the number of photos taken per day. This information was determined through photo assessment from each camera.

1.3 Statistical methods:

We confirmed each site was occupied by HADU if individuals were detected by at least one survey method during at least one day in each three-day sampling occasion. We used generalized linear mixed models, with a logit link, to investigate the detection probability of each method. We built six models, two for each method, and for each method we used a binary response variable representing detection / non-detection and specific covariates that we hypothesized affected the detection process for that method (Table 1). Before fitting models, we checked for correlation between covariates within each model. We considered variables to be independent if their R^2 value was less than 0.5 (max observed value = 0.818). We chose between correlated variables based on which variable was considered *a priori* to be more relevant to implementing best survey practices. We interpreted all covariates with a p-value < 0.1. For all models we used the lme4 package implemented in R 4.2.3 (Bates et al., 2015; R Core Team, 2023). We evaluated the intercept to understand the mean per-replicate detection probability of each method and used *p*-values of each covariate to determine significance in affecting HADU detection. Based on model results, we estimated the effort needed to reach different thresholds of cumulative detection confidence using each survey method. We calculated the number of replicates of each method that was necessary to achieve a cumulative detection to 0.8, 0.9, and 0.95 using the equation:

$$\hat{P} = 1 - \prod_{i=1}^{n} (1 - \hat{p}_i) \tag{1}$$

Where $\hat{P}$ is cumulative detection, $\hat{p}$ is our mean detection probability for a single replicate of a sample, and n is the number of replicates of each method or combination of methods (Canessa et al., 2012; Kéry, 2002; Loane et al., 1964). Finally, we calculated the cumulative detection probability when methods were combined (i.e. eDNA samples taken in tandem with a GBS).

1.3.1 Ground based foot survey models:

For the incubation and brood rearing seasons, we built separate, but identical, models relating detection of HADU in a GBS to the four covariates: pace, number of observers, streamflow, and mean QeDNA (Table 1). All covariates were scaled and centered. The model took the form:

$$Logit(y) = \beta_0 + \beta_1 X_{pace} + \beta_2 X_{number\ of\ observers} + \beta_3 X_{streamflow} + \beta_4 X_{meanQeDNA} \tag{2}$$

1.3.2 Environmental DNA models:

For the incubation and brood rearing seasons, we built separate, but identical, models relating detection of HADU with eDNA to the two covariates: streamflow and benthic substrate (Table 1). Our covariates account for variation at the sample location but not at the stream level; so, we included a random effect for each stream to account for variation within and between streams. Streamflow and wetted width were scaled and centered, and benthic substrate was included as a categorical variable. The model took the form:

$$Logit(y) = \beta_0 + \beta_1 X_{streamflow,j} + \beta_2 X_{benthic\ substrate,j} + \varepsilon_j \tag{3}$$

1.3.3 Camera trap models:

For the motion detection and time-lapse camera traps, we built separate, but identical, models relating detection of HADU in a camera trap to the four covariates: number of trap nights, camera angle to the stream, stream feature, and the average number of photos taken per day (Table 1). In both cases, models spanned the period between when incubation and brood surveys were conducted. Trap nights and average number of photos per day were scaled and centered, and camera angle to the stream and stream feature were categorical variables. The model took the form:

$$Logit(y) = \beta_0 + \beta_1 X_{trap\ nights} + \beta_2 X_{camera\ angle} + \beta_3 X_{stream\ feature} + \beta_4 X_{average\ number\ of\ photos\ per\ day} \tag{4}$$

<u>1.4 Results:</u>

1.4.1 Ground-based foot survey:

We completed 118 GBS over the two years; 50 occurred during the incubation period and 68 during the brood rearing period. The mean probability of detecting HADU using a GBS was similar between the two periods (0.51 and 0.45), but their covariate relationships differed.

During the incubation period, the mean probability of detecting HADU with a single, 5 km, GBS was 0.51 (95% CI: 0.31 – 0.71). Mean QeDNA and CFS exhibited positive relationships with detection ($p < 0.01$, $p = 0.094$, respectively; Appendix 3). Based on these relationships, if a stream was expected to have only a single breeding female and a streamflow less than 200 CFS, on a 5 km stream reach, 15 days of GBS would be needed to achieve an 80% confidence in the stream being unoccupied if no ducks are detected, or 27 days to achieve a 95% confidence. By contrast, if a stream was expected to have two to six single females and a streamflow is greater than 200 CFS, on a 5 km stream reach, 3 days of GBS would be needed to achieve an 80% confidence in the stream being unoccupied if no ducks are detected, or 6 days to achieve a 95% confidence (Table 3).

During the brood rearing period, the mean probability of detecting HADU with a single, 5 km, GBS was 0.45 (95% CI: 0.32 – 0.58). Mean QeDNA exhibited a positive relationship with detection while pace exhibited a negative relationship ($p = 0.091$, $p = 0.078$, respectively; Appendix 3). Based on these relationships, if a stream was expected to have only a single breeding female on a 5 km stream reach, 4 days of GBS would be needed to achieve an 80% confidence in the stream being unoccupied if no ducks are detected, or 7 days to achieve a 95% confidence (Table 3). Detection probability decreases with increased pace (Figure 3).

1.4.2 Environmental DNA:

We collected 717 eDNA samples over the two years; 312 samples during the incubation period and 405 samples during the brood rearing period. The mean probability of detecting HADU using eDNA differed between the two periods (0.49 and 0.27), but their covariate relationships were similar.

During the incubation period, the mean probability of detecting HADU at the mean CFS (214.81 ft^2/sec) in a cobble stream, taking a single eDNA sample was 0.49 (95% CI: 0.23 – 0.75). CFS exhibited a negative relationship with detection ($p = 0.0516$; Appendix 3). Based on this relationship, if a stream has a CFS in the range of 100-200, three eDNA samples would be needed to achieve an 80% confidence in the stream being unoccupied if no ducks are detected, or five to achieve 95% confidence (Table 4).

During the brood rearing period, the mean probability of detecting a HADU at the mean CFS (116.50 ft^2/sec) in a cobble stream, taking a single eDNA sample was 0.27 (95% CI: 0.11 – 0.53). CFS exhibited a positive relationship with detection ($p = 0.00208$; Appendix 3). Based on this relationship, if a stream has a CFS in the range of 100-200, four eDNA samples would be needed to achieve an 80% confidence in the stream being unoccupied if no ducks are detected, or six to achieve 95% confidence (Table 4).

1.4.3 Camera traps:

We deployed 198 cameras over the two years; 99 of the cameras were set to time lapse and 99 cameras were set to motion detection. Cameras were deployed for 4,454 trap nights and 2,325,060 photos (1,050,255 motion detection, 1,274,805 time-lapse) were collected. We processed all photos with AI detection confidence 0.5 – 1 (~30,000 photos) which took 85 hours (average 350 photos per hour). The mean number of photos collected per day on a motion detection camera was 486 and 864 photos on a time-lapse camera. The mean probability of detecting HADU using a camera trap was similar between motion detection and time-lapse (0.13 and 0.16), but their covariate relationships differed.

For a motion detection camera trap, the mean probability of detecting a HADU with a single camera pointed directly across the stream at a boulder, the most prevalent set up, was 0.13 (95% CI: 0.04 – 0.32) when deployed for 22 days. Trap nights had a positive relationship with detection, and more trap nights resulted in higher detection ($p = 0.0300$; Appendix 3). Based on this relationship, if a motion detection camera is deployed for 21 – 28 days, 12 cameras would be needed to achieve an 80% confidence in the stream being unoccupied if no ducks are detected, or 21 to achieve 95% confidence (Table 5).

For a time-lapse camera, the mean probability of detecting a HADU with a single camera trap pointed directly across the stream at a run, the most prevalent set up, was 0.16 (95% CI: 0.07 – 0.34) when deployed for 22 days. None of the four covariates were significant in predicting detection (Appendix 3).

1.4.4 Combing methods:

After analyzing each method, we calculated the cumulative detection probability of different combinations of these methods. The most effective combination for detecting HADU in a single day effort is combining a GBS with eDNA. During the incubation period observers can take five eDNA samples in tandem with a GBS to achieve a cumulative detection probability of 0.97 (95% CI: 0.87 – 0.99) (Figure 4). During the brood rearing season observers would need to take nine eDNA samples in tandem with a GBS to achieve a cumulative detection probability of 0.95 (95% CI: 0.80 – 0.99). Alternatively, observers can conduct two GBS, one during the incubation period and one during the brood rearing period, and set up four time-lapse game cameras for 22 days between the two visits to achieve a cumulative detection probability of 0.87 (95% CI: 0.76 – 0.96) (Figure 4).

1.4.5 Additional Analysis (lorelogram):

To determine adequate spatial distribution of eDNA samples, we assessed spatial independence of our eDNA samples using a lorelogram (Heagerty & Zeger, 1998; Iannarilli et al., 2019). Lorelograms account for dependencies between the mean and variance and enable us to quantify correlation in binary data (Iannarilli et al., 2019). For this analysis, we used 717 eDNA samples, along 10 streams, in 37 sample-days, with samples taken at scales ranging from 250-1000m (Figure 2). While all streams had eDNA detections in all years, we constrained our dataset of samples to sampling occasions where between 15 and 85% of samples yielded detections to ensure we had spatial variation in the sample to work with. We applied the lorelogram to our eDNA detection / non-detection data to quantify how the correlation between eDNA samples changed with distance between eDNA samples at 250m, 500m, 750m, and

1,000m distances between samples. We found that the eDNA detections were correlated for the first 750 – 1,000m then approached 0 at distances ≥ 1,000m apart (Figure 5).

1.5 Discussion:

This study quantified the detection probability of GBS, eDNA, and camera traps to determine occupancy of HADU on their breeding streams during incubation and brood rearing periods. The most longstanding survey method, single day GBS, had a detection probability of ~0.5 confirming biologists inclination that this method is not very effective. It is possible to attain a cumulative detection probability of >0.8 in a single-day effort with either multiple eDNA samples or by taking eDNA samples in tandem with a GBS. Effectively applying and combining methods requires both consideration of what covariates influence survey efficacy among methods and across seasons, and clear study objectives to guide method selection. We use this new understanding to provide recommendations for use of these approaches for HADU and similar stream-breeding waterbirds.

For all survey methods, stream condition and implementation covariates influenced survey efficacy. For GBS, variation among observer bias explained more variation in detection probability than stream conditions. While this variation among observers is concerning, studies on citizen science programs have shown that proper training for observers can help reduce variance and improve survey performance; though our observers were trained, future surveys could be improved with additional training methods (Lewandowski & Specht, 2015). For eDNA, streamflow had the greatest effect on HADU detection but opposite interactions between the two time periods; during the incubation period detection decreased with increasing streamflow and during the brood rearing period detection decreased with decreasing streamflow. This outcome suggests that streamflow potentially exhibits a quadratic relationship with detection probability.

During the incubation period, stream flow typically increases due to spring runoff which could flush DNA out of the system at faster rates (Barnes et al., 2014; Curtis et al., 2021; Shogren et al., 2017). However, during the brood rearing season stream flows are typically reduced with water remaining shallow, less turbid, or potentially drying up completely (Whitlock et al., 2017). Therefore, lower detection probability with lower streamflow could be explained by increased DNA degradation when exposed to higher temperatures and more UV from the sun and /or increased DNA absorption by the benthic substrate at reduced flows (Barnes et al., 2014; Fremier et al., 2019; Shogren et al., 2017; Strickler et al., 2015). For camera traps detection probability increased with deployment duration. We did not find that camera angle or stream feature significantly influenced either model, but our protocol did not result in enough variability in these two categories to adequately assess this relationship.

Detection probability varied between incubation and brood rearing seasons for GBS and eDNA. This could be explained by differences in behavior between the two time periods. Using GBS we detected a slight, although not statistically significant (0.06) decrease in average detection between the incubation period and the brood rearing period. Using eDNA we detected a 22% decrease in average detection between the incubation period and the brood rearing period. During the incubation period single females are distributed evenly across a stream which disperses DNA throughout the stream. During the brood rearing period, ducks are observed clustered together and the DNA may be more confined to certain reaches within the stream. This more patchy distribution of HADU along the stream may help explain the difference in eDNA detection between the incubation and brood rearing periods.

These differences in detection probability between incubation and brood rearing periods suggest different survey approaches may be needed depending on the objective. Data collected during the incubation period provides information about attempted breeding and stream occupancy. Data collected during the brood rearing season offers information about breeding success, since single females and females whose nests failed will have left the stream (MacCallum et al., 2021). Therefore, a lack of detection during the brood rearing period does not mean the stream was unoccupied during the incubation period and a detection during the brood rearing period is dependent on broods successfully fledging the nests. For example, if stream occupancy is of interest, it is better to survey during the incubation period. In contrast, if recruitment and nest success are of interest then surveying during the brood rearing season is better. We recommend that future surveys be planned for the period of interest depending on the study objectives. We also recommend that when making inference from historic survey data, the timing of the survey be considered.

Each survey method has information and resource effort trade-offs that are important to consider. First, GBS, unlike eDNA and camera traps, do not require post-processing and thus provide immediate presence information. Additionally, because observers count the number of individual ducks during GBS, they provide estimates of relative abundance. These benefits, however, come at the expense of increasing cumulative detection probability: to increase cumulative detection requires multiple days which quickly increases the resources needed. Second, enough eDNA samples can be collected in a single field day to achieve a degree of cumulative detection that is not possible with either GBS or camera traps. Five eDNA samples spread across a 5km reach will yield >95% (95% CI: 3 - 12 samples) cumulative detection probability during the incubation period. However, eDNA can only tell us presence or absence of HADU within a short portion of the stream; therefore, we cannot say for certain the extent of the stream occupied. Notably, our post-hoc analysis using a lorelogram found that our eDNA samples were spatially independent of one another at ~750 – 1,000 meters downstream which could indicate the distance of HADU DNA persistence. This outcome is consistent with some eDNA persistence studies in streams (Barnes et al., 2014; Fremier et al., 2019; Jane et al., 2015; Shogren et al., 2017), though a controlled experiment would be needed to verify this. Finally, camera traps can be deployed in otherwise hard to survey areas and multiple camera traps can be deployed or retrieved in a day, increasing cumulative detection probability. A notable drawback to camera traps is that they require two field days minimum—one to deploy and one to retrieve. Cameras also only provide presence or absence data as we cannot differentiate between individuals. Additionally, camera traps were the most labor and time intensive of the survey methods. Cameras require the most amount of time before, during, and after deployment per unit, and although detection probability increases with each day cameras were deployed, photo processing time also increased (Table 6). Because eDNA and cameras both require field days, if opting to use those methods, we recommend conducting a GBS simultaneously to provide both real-time and relative abundance data. If opting to use camera traps, we recommend using time-lapse cameras because it is not as prone to issues relating to trigger sensitivity.

This study provides a comprehensive understanding of the efficacy of non-invasive survey methods for monitoring stream-residing waterbirds and can inform techniques for improved monitoring of other species. Notably the life history of target species must be considered when applying any of these methods. Detection with eDNA could indicate different information depending on the species life history. For example, males of many stream residing waterbirds do not leave the females to raise the young alone or leave the streams altogether; therefore, an eDNA detection during brood rearing would confirm presence but does not confirm breeding success without visual confirmation of chicks, which GBS would provide. Importantly though, eDNA could help identify active territories and important areas for conservation action for species that uphold a territory, such as the Torrent Duck *(Merganetta armata),* American Dipper *(Cinclus mexicanus)*, or Blue Duck *(Hymenolaimus malacorhynchos*; Bakus, 1959; Eldridge, 1986; Ippi et al., 2018). Other life history characteristics such as multiple clutches or overlap in incubation and brood rearing season. (e.g. Spotted Sandpipers; *Actits maculari;* Reed et al., 2020) could impact inference of eDNA data. For other water dependent species who rely on water for prey, like ospreys *(Pandion heliaetus),* camera traps may be better than eDNA. Placement of camera traps could be tailored in ways that target shorelines which reduce photos triggered by water movement. Additionally, recent development in other non-invasive survey methods such as automated recording units (Shonfield & Bayne, 2017; Sidie-Slettedahl et al., 2015; Stewart, 2023) and infrared drones (Bushaw et al., 2021; Dundas et al., 2021; Mackell et al., 2024) may be a useful complement to methods presented in this study.

1.6 Management Implications:

With this study, managers in the Northern Rockies have gained a greater understanding of the efficacy of various HADU detection tools which can help increase their confidence in their population estimates in the future, ultimately allowing them to make the most informed management decisions. However, choice of methodology depends on monitoring objectives and available effort.

Method choice and timing is influenced by monitoring objectives. For example, for information about occupancy during attempted breeding it is better to survey during the incubation period, whereas for information about nest success, managers should survey during the brood rearing period.

For high detection probability in a single day the only options are to use eDNA. Combination of eDNA and GBS is both an efficient and effective approach for surveying HADU. Observers can reach a cumulative detection probability of >0.95 using only eDNA, however eDNA samples need to be spread throughout a stream therefore, we suggest also doing GBS. GBS in tandem with eDNA can help observers be more effective because GBS allow us to attain abundance data whereas eDNA can only give us presence / non detection data.

Cameras were the least effective method, and we do not generally recommend them for HADU surveys, however they may be useful in terrain where a GBS and eDNA are impractical due to challenging terrain. A single camera may be the best way to determine the presence of HADU across the season in select locations.

Finally, our study illustrates the value in combining methods for detecting cryptic, low abundance, waterbirds on streams and can inform a framework for a survey design for other stream residing species. However, if using this study as a framework, the method design needs to strongly consider the life history of the species of interest.

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1.7 Figures and Tables:

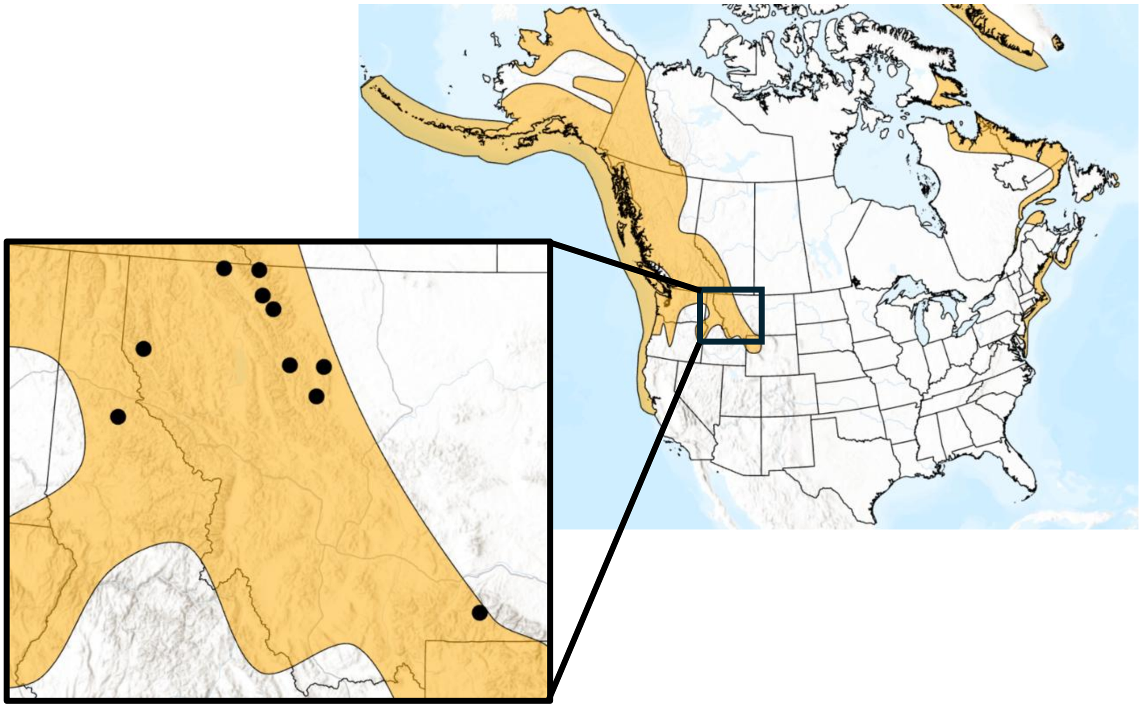

Figure 1: HADU North American range, with the study area in Western Montana and Northern Idaho and the selected breeding streams highlighted in inset map (BirdLife, 2022).

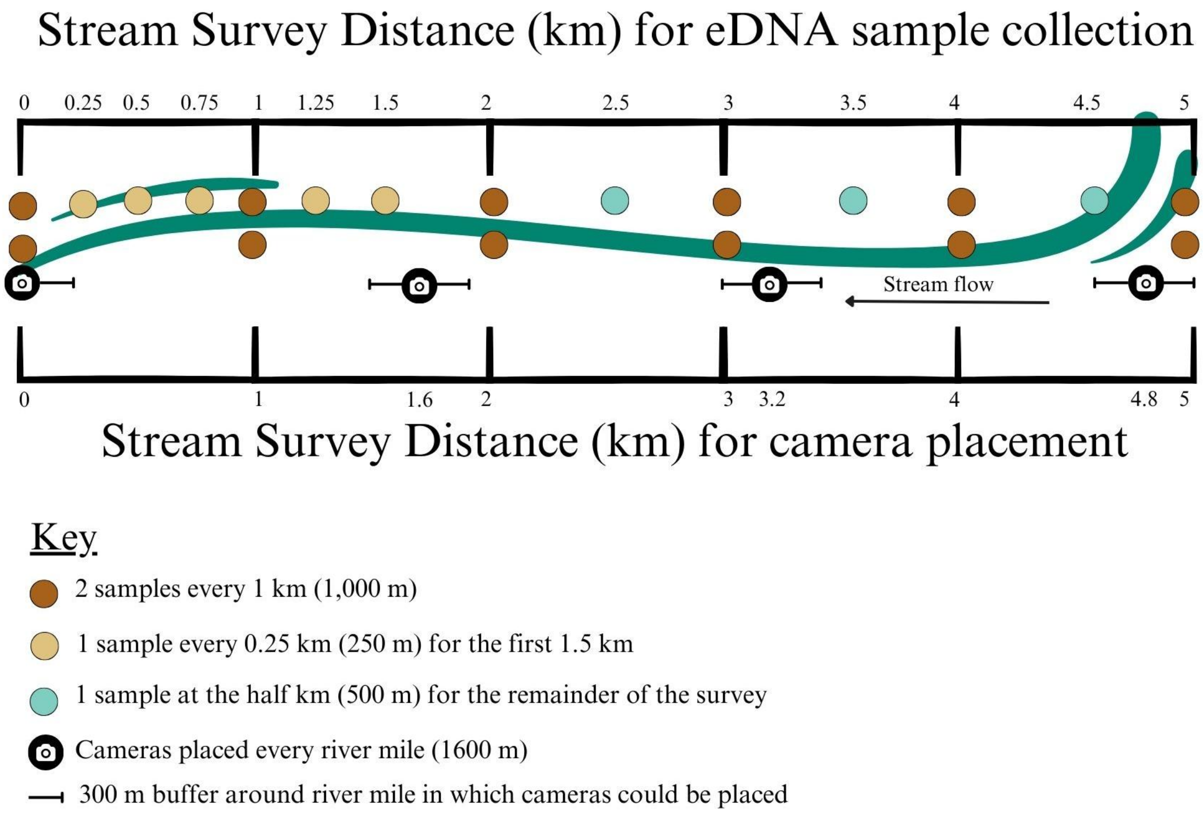

Figure 2: Detailed eDNA and camera trap sampling strategies.

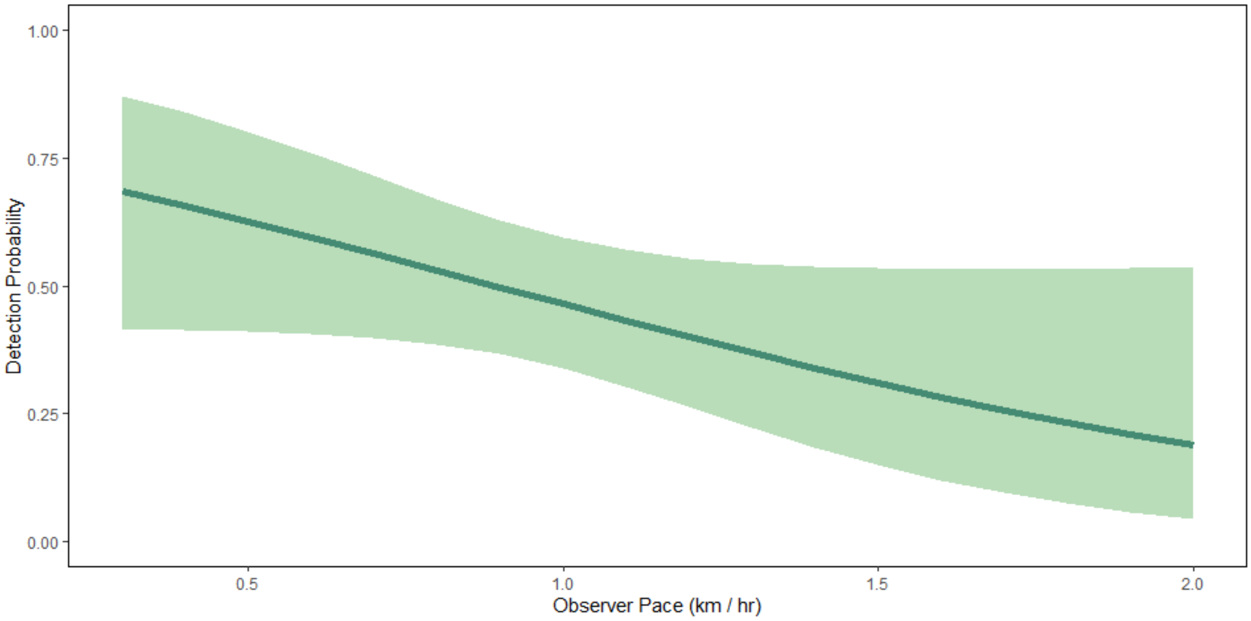

Figure 3: Observer pace vs detection probability for a single ground-based foot survey during the brood rearing season.

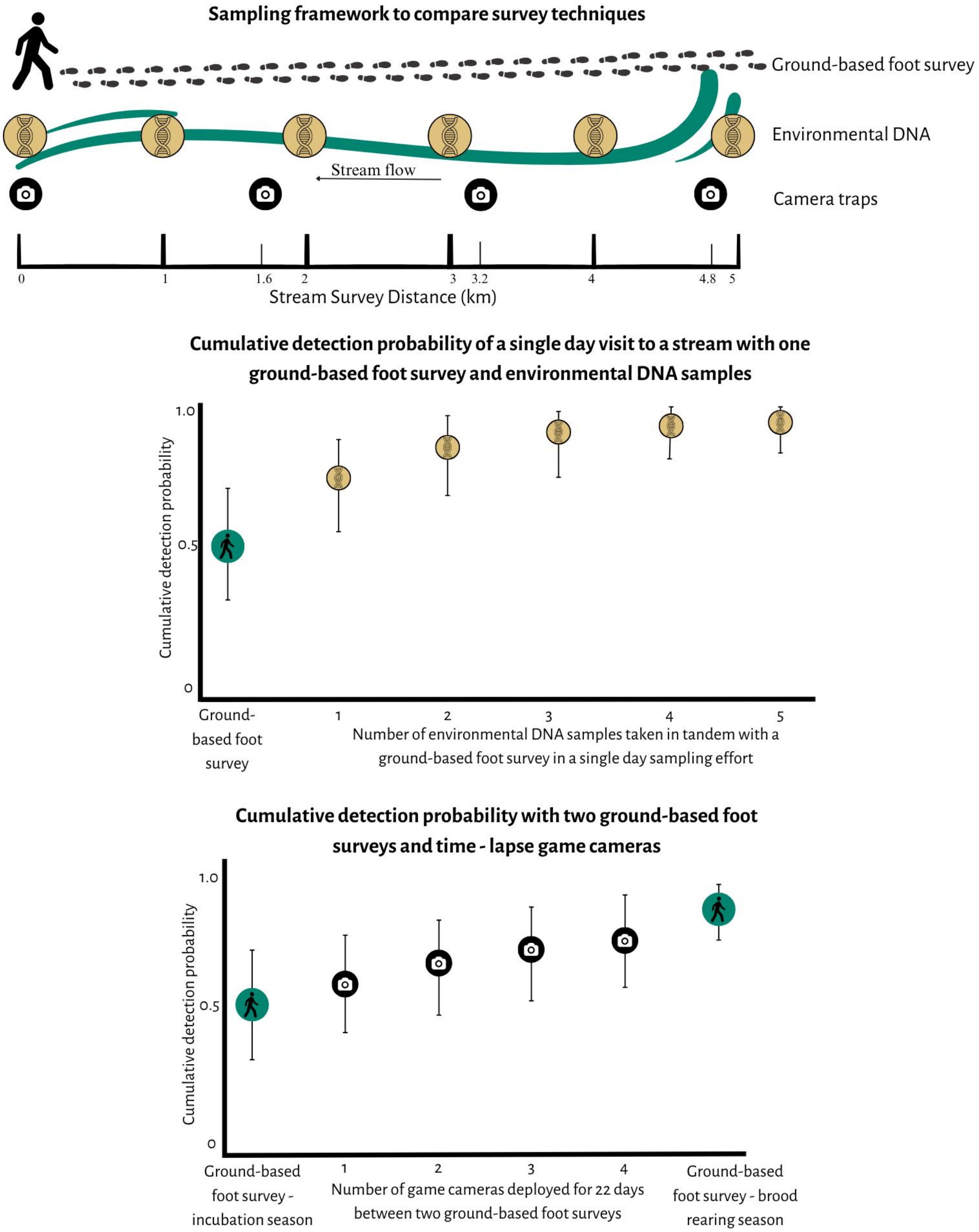

Figure 4: Graphical abstract of chapter 1. (Top) Sampling framework of the three non-invasive survey methods (ground-based foot surveys, environmental DNA, and camera traps) assessed in this chapter. (Middle) Graph showing how cumulative detection probability increases with every

additional environmental DNA sample taken in tandem with a ground-based foot survey in a single day sampling effort. (Bottom) Graph showing how cumulative detection probability increases with two GBS and every additional time-lapse game cameras.

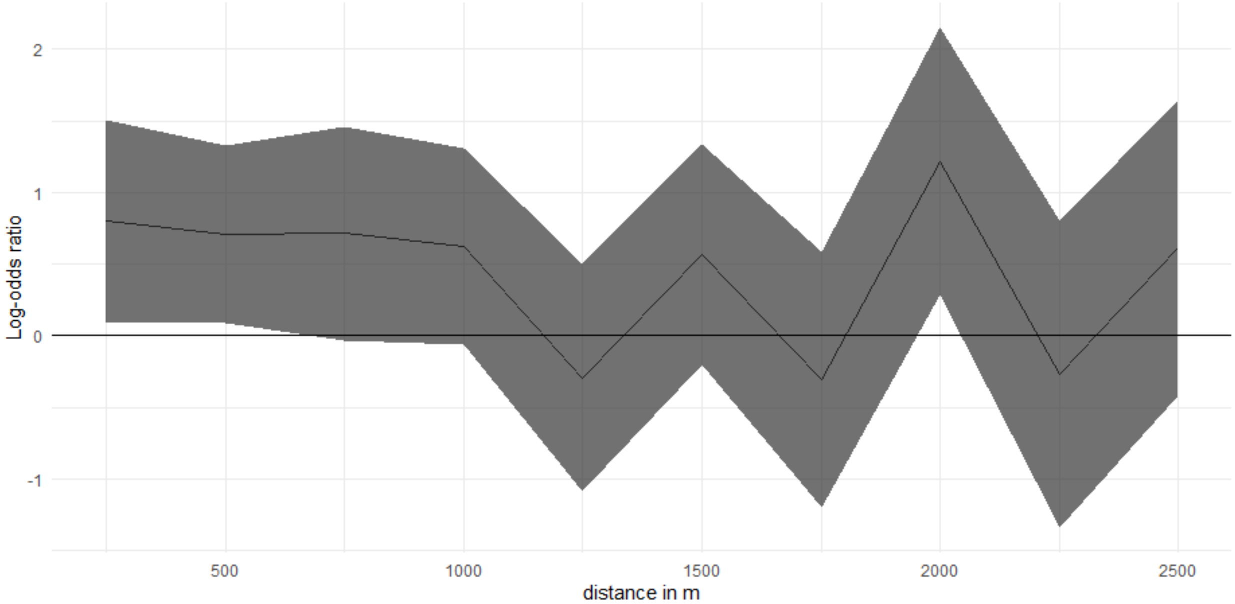

Figure 5: Lorelogram and 95% confidence intervals for distance between eDNA samples. Samples become spatially independent between 750 – 1,000m when 95% CI's cross 0.

Table 1: Model covariates: Name, units, hypothesis, mean, range, and standard deviation for all models.

Model	Covariate	Units	Hypothesis	Incubation Mean, Range, SD	Brood Rearing Mean, Range, SD
Ground-based foot survey	Pace	Total kilometers surveyed by the observation team during the survey / number of hours between start and end of survey (km/hr)	The quicker the pace observers are moving on a survey (higher pace value) detection probability will decrease because observers are spending less time observing for HADU.	0.84 km/hr 0.32 – 2.45 km/hr 0.373	1.03 km/hr 0.32 – 2.28 km/hr 0.412
	Number of observers	Number of observers during each survey	More observers on a survey may result in higher detection probability of detecting HADU because there are more people spotting ducks. However, more observers could also decrease detection if more observers result in HADU departing site prior to detection due to human disturbance.	3 observers 2 – 6 observers 0.894	3 observers 2 – 5 observers 0.712
	Streamflow	Cubic feet per second (CFS)	As CFS increases, navigating streams becomes more challenging and observers may be farther from the stream side, decreasing detection of HADU.	218.00 cfs 9.99 – 740.35 cfs 196.061	118.16 cfs 18.7 – 245.29 cfs 63.659
	Mean QeDNA	Mean number of copies of HADU DNA per liter of water filtered across all the eDNA samples taken on a stream during the sampling occasion that the GBS took place.	The higher the mean QeDNA is the higher the detection of HADU on a stream. Mean QeDNA is correlated with the observed high count (0.505) on each sampling occasion, and we used this metric instead of high count because it would be more independent of the method being assessed.	12.6 DNA copies / L 0.0 – 35.5 DNA copies / L 12.007	16.9 DNA copies / L 0.0 – 154.5 DNA copies / L 33.094

eDNA	Streamflow	CFS	Streamflow will have a negative relationship with detection because the faster the stream is flowing the quicker the DNA is washed from the stream.	214.8 cfs 15.5 – 653.1 cfs 168.126	116.5 cfs 29.2 – 245.3 cfs 65.223
	Benthic substrate	Boulder (> 10 inches across) or cobble (≤ 10 inches across)	As benthic substrates increase in size, it will have a positive relationship with detection and boulder will have the highest detection probability.	Cobble = 226 Boulder = 70 Na’s = 16	Cobble = 313 Boulder = 74 Na’s = 18
Camera traps	Trap nights	Number of nights the camera was deployed	Trap nights will have a positive relationship with detection and the longer cameras are left out, the higher the detection probability will be.	**Motion Detection Mean, Range, SD**	**Time Lapse Mean, Range, SD**
				22 nights 17 – 37 nights 3.509	22 nights 17 – 37 nights 3.549
	Average number of photos per day	Total number of photos taken divided by the total number of trap nights	Average number of photos taken per day will have a positive relationship with detection probability because the more photos that are taken the more likely a photo is to capture a HADU.	486 photos 0 – 4,379 photos 893.527	576 photos 0 – 1728 photos 335.041
	Camera angle to the stream	Upstream, downstream, across, down (direction unknown)	Camera angle to the stream may affect detections because angle affects viewshed. This covariate is one way we are hoping to quantify field of view.	Across = 59 Up = 27 Down = 10 Na’s = 3	Across = 64 Up = 20 Down = 9 Na’s = 6
	Stream Feature	Rapid, pool, run, and boulder	Stream feature may affect detection because there may be certain features that are more likely to detect HADU than others such as boulders which provide loafing habitat in which a duck may spend more time in front of a camera as opposed to a rapid where they	Boulder = 21 Rapid = 21 Run = 46 Pool = 8 Na’s = 6	Boulder = 18 Rapid = 30 Run = 40 Pool = 5 Na’s = 6

			may be hidden from the camera or harder to distinguish from the noise.		

Table 2: Sampling methods and strategies for assessing HADU occurrence.

Method	**Sampling occasion 1**	**Sampling occasion 2**	**Sampling interval**	**Explanation of sampling method**
Ground-Based Foot Survey	Days 1-3	Days 1-3	5-8 km stream reach	Observers walked upstream for five to eight kilometers looking for HADU. Observers collected data consistent with historical HADU surveys done in Montana (Hansen et al., 2019).
eDNA	Day 2	Day 2	Every 250 m for first 1,500 m then every 500 – 1,000 m	Filter 5 liters of water per sample following USFS National Genomics Lab protocol (Carim et al., 2016).
Camera Trap	Day 1	Day 3	Every 1600 meters	Two camera traps were placed every river mile of the survey stretch, one camera on a time-lapse set to take photos every 5 minutes and the other set to motion trigger. Cameras were deployed during the first visit and collected during the second visit.

Table 3: Expected number of HADU present and CFS range during the incubation and brood rearing periods and the mean detection probability of conducting a single GBS and the number of GBS needed to achieve a cumulative detection of 0.8, 0.9, and 0.95.

Time Period	**Expected number of HADU on stream**	**CFS range**	**Mean detection probability for a single GBS**	**95% CI**	**Number of GBS to achieve a cumulative detection of 0.8**	**Number of GBS to achieve a cumulative detection of 0.9**	**Number of GBS to achieve a cumulative detection of 0.95**
Incubation period	Low: 0 - 1	< 200 CFS	0.117	0.031 - 0.357	15 surveys (95% CI: 64 - 4 surveys)	21 surveys (95% CI: 91 - 6 surveys)	27 surveys (95% CI: 118 - 7 surveys)
	Medium: 2 - 6		0.316	0.131 - 0.589	6 surveys (95% CI: 16 - 2 surveys)	8 surveys (95% CI: 23 - 3 surveys)	10 surveys (95% CI: 30 - 4 surveys)
	High: 7 +		0.755	0.463 - 0.913	2 surveys (95% CI: 3 - 1 surveys)	2 surveys (95% CI: 5 - 1 surveys)	3 surveys (95% CI: 6 - 2 surveys)
	Low: 0 - 1	> 200 CFS	0.183	0.063 - 0.429	9 surveys (95% CI: 29 - 3 surveys)	13 surveys (95% CI: 41 - 5 surveys)	16 surveys (95% CI: 53 - 6 surveys)
	Medium: 2 - 6		0.467	0.272 - 0.675	3 surveys (95% CI: 7 - 2 surveys)	5 surveys (95% CI: 9 - 3 surveys)	6 surveys (95% CI: 12 - 3 surveys)
	High: 7 +		0.855	0.639 - 0.948	1 surveys (95% CI: 2 - 1 surveys)	2 surveys (95% CI: 3 - 1 surveys)	2 surveys (95% CI: 4 - 1 surveys)
Brood rearing period	Low: 0 - 1	Not statistically significant	0.379	0.253 - 0.524	4 surveys (95% CI: 6 - 3 surveys)	5 surveys (95% CI: 8 - 4 surveys)	7 surveys (95% CI: 11 - 5 surveys)
	Medium: 2 - 6		0.423	0.300 - 0.557	3 surveys (95% CI: 5 - 3 surveys)	5 surveys (95% CI: 7 - 3 surveys)	6 surveys (95% CI: 9 - 4 surveys)

	High: 7 +		0.515	0.353 - 0.671	3 surveys (95% CI: 4 - 2 surveys)	4 surveys (95% CI: 6 - 3 surveys)	5 surveys (95% CI: 7 - 3 surveys)

Table 4: CFS during the incubation and brood rearing period and the mean detection probably for a single eDNA sample and the number of eDNA samples needed to achieve a cumulative detection of 0.8, 0.9, and 0.95.

Time Period	**CFS range**	**Mean detection probability for a single eDNA samples**	**95% CI**	**Number of eDNA samples to achieve a cumulative detection of 0.8**	**Number of eDNA samples to achieve a cumulative detection of 0.9**	**Number of eDNA samples to achieve a cumulative detection of 0.95**
Incubation period	10 - 100	0.547	0.272 - 0.797	3 samples (95% CI: 2 - 6 samples)	3 samples (95% CI: 2 - 8 samples)	4 samples (95% CI: 2 - 10 samples)
	100 - 200	0.493	0.236 - 0.755	3 samples (95% CI: 2 - 6 samples)	4 samples (95% CI: 2 - 9 samples)	5 samples (95% CI: 3 - 12 samples)
	200 +	0.370	0.145 - 0.674	4 samples (95% CI: 2 - 12 samples)	6 samples (95% CI: 3 - 16 samples)	7 samples (95% CI: 3 - 21 samples)
Brood rearing period	10 - 100	0.321	0.118 - 0.627	5 samples (95% CI: 2 - 14 samples)	6 samples (95% CI: 3 - 19 samples)	8 samples (95% CI: 4 - 25 samples)
	100 - 200	0.411	0.169 - 0.704	4 samples (95% CI: 2 - 9 samples)	5 samples (95% CI: 2 - 13 samples)	6 samples (95% CI: 3 - 17 samples)

	200 +	0.571	0.272 - 0.824	2 samples (95% CI: 1 - 6 samples)	3 samples (95% CI: 2 - 8 samples)	4 samples (95% CI: 2 - 10 samples)

Table 5: Number of trap nights for a motion detection camera and the mean detection probably for a single camera trap and the number of cameras needed to achieve a cumulative detection of 0.8, 0.9, and 0.95.

Number of trap nights	**Detection Probability for a single motion detection camera**	**95% CI**	**Number of motion detection cameras to achieve a cumulative detection of 0.8**	**Number of motion detection cameras to achieve a cumulative detection of 0.9**	**Number of motion detection cameras to achieve a cumulative detection of 0.95**
1-7	0.005	0.000 - 0.095	378 samples (95% CI: 10030 - 17 samples)	540 samples (95% CI: 14349 - 24 samples)	703 samples (95% CI: 18668 - 31 samples)
7-14	0.015	0.002 - 0.117	123 samples (95% CI: 1313 - 14 samples)	175 samples (95% CI: 1878 - 19 samples)	228 samples (95% CI: 2443 - 25 samples)
14-21	0.051	0.013 - 0.177	37 samples (95% CI: 165 - 9 samples)	52 samples (95% CI: 236 - 13 samples)	67 samples (95% CI: 306 - 16 samples)
21-28	0.154	0.045 - 0.402	12 samples (95% CI: 39 - 4 samples)	16 samples (95% CI: 55 - 6 samples)	21 samples (95% CI: 72 - 7 samples)

Table 6: Effort per ground-based foot survey, eDNA sample, and camera trap.

	Pre-survey time required	Post processing time	Average time per sample	Number of field days
eDNA	None	3-6 months	20 min	1
Ground-based foot survey	None	None	6 hours	1
Motion detection camera trap	20 min	1.4 hr per day camera is deployed	20 min to set up 5 min to take down	2
Time lapse camera trap	20 min	2.5 hr per day camera is deployed	20 min to set up 5 min to take down	2

1.8 Appendix

Appendix 1: Streams selected for chapter 1, management area, elevation, forest type, distance surveyed, and survey dates.

Stream	**Management area**	**Elevation (m)**	**Dominant Forest Type**	**Survey Distance**	**Sampling Occasion Begin Dates 2022**	**Sampling Occasion Begin Dates 2023**
Rock Stream	Kootenai National Forest	703	Rocky mountain mesic montane mixed conifer forest (mesic – wet)	5 km	7/5/2022 & 7/26/2022	7/12/2023 & Not surveyed due to lack of water
Marble Stream	Idaho Panhandle National Forest	884	Rocky mountain mesic montane mixed conifer forest (mesic – wet)	8 km	7/18/2022 & 8/8/2022	7/17/2023 & 8/7/2023
Upper McDonald Stream	Glacier National Park	959	Rocky mountain mesic montane mixed conifer forest (mesic – wet)	8 km	7/18/2022 & 8/8/2022	7/17/2023 & 8/8/2023
Nyack Stream	Glacier National Park	1,189	Rocky mountain subalpine dry-mesic spruce-fir forest and woodland & recently burned forest	6.5 km	Not surveyed due to high water causing inaccessibility & 8/12/2022	7/25/2023 & 8/15/2023
Spotted Bear River	Flathead National Forest	1,234	Rocky mountain dry-mesic montane mixed conifer forest	8 km	8/1/2022 & 8/22/2022	Not surveyed due to ridge fire
Trail Creek	Flathead National Forest	1,234	Rocky mountain dry-mesic montane mixed conifer forest	5 km	7/27/2022 & 8/15/2022	7/31/2023 & 8/21/2023
Waterton River	Glacier National Park	1,335	Rocky mountain subalpine dry-mesic spruce-fir forest and woodland	5.5 km	8/3/2022 & 8/17/2022	8/2/2023 & 8/23/2023
North Fork Teton River	Helena-Lewis & Clark National Forest	1,495	Recently burned forest	5 km	7/25/2022 & 8/15/2022	7/31/2023 & 8/21/2023
South Fork Sun River	Helena-Lewis & Clark National Forest	1,523	Recently burned forest	8 km	8/1/2022 & 8/22/2022	8/7/2023 & 8/28/2023
Boulder River	Custer-Gallatin National Forest	1,551	Rocky mountain montane Douglas-fir forest and woodland	8 km	8/1/2022 & 8/22/2022	8/7/2023 & 8/28/2023

			& Rocky mountain lodgepole pine forest			

Appendix 2. Data collected during ground-based foot surveys.

Data	**Explanation**
Survey start and end time	What time survey started and ended
Time	When was the bird seen.
Species	Some agencies record all waterbirds and some only record HADU, for the agencies that record all species they record the species four letter code here.
Number of Birds	Number of birds observed during survey
Group Type	Female, Male, Brood (female and young), Juvenile (YOY w/o adult)
Chick Class	Class 1: Downy, no feathers visible, Class 2: Partly feathered, Class 3: Fully feathered, flightless
Coordinates	Recorded in decimal degrees.
Geographic Location	Geographical reference. Ex: Bend after cliff band, at 3 km mark.
Stream Location	Pool: Deep slow water; Rapid: Fast moving water, breaking waves; Run: Fast moving water, no waves; Riffle: Shallow and Turbulent; Cascade: "stair stepping"; Confluence: Two streams merge; Laminar: Extremely glassy flow; Eddy: Swirling water; Edge: Along Shoreline
Distance Away	How far away from the bird the observer is when they spot it.
Awareness	Is the bird aware of the observer?
Etho	Indicate behavior upon first visual observation of duck and subsequent changes throughout time if it's behavior changes if it notices you. FO = Foraging, PR = Preening, RE = Resting, DE = Defense, AL = Alert, DI = Disturbance, CO = Courtship, SO = social interaction, SW = Swimming, FL = Flying
Number of people on shore	How many people are around, excluding the observers.
Comments	Any extra comments about the observation.

Appendix 3: Model outputs

Model output for GBS incubation period:

	Estimate	Standard Error	Z Value	P Value
(Intercept)	0.056823	0.432327	0.131436	0.895431
Pace	-0.6688	0.622947	-1.07361	0.282998
CFS	0.709034	0.422919	1.676525	0.093635
Mean eDNA per L	1.91467	0.51708	3.702849	0.000213
Number of observers	-0.00667	0.409887	-0.01627	0.987018

Model output for GBS brood rearing period:

	Estimate	Standard Error	Z Value	P Value
(Intercept)	-0.17707	0.268461	-0.65956	0.509539
Pace	-0.5441	0.308862	-1.76162	0.078134
CFS	-0.20796	0.266971	-0.77895	0.43601
Mean eDNA per L	0.660941	0.391187	1.689578	0.091109
Number of observers	-0.02442	0.264062	-0.09248	0.926321

Model output for eDNA incubation period:

	Estimate	Standard Error	Z Value	P Value
(Intercept)	-0.04738	0.586641	-0.08076	0.935633
CFS	-0.29706	0.152646	-1.94606	0.051647
Benthic substrate boulder	0.237821	0.361699	0.657511	0.510852

Model output for eDNA brood rearing period:

	Estimate	Standard Error	Z Value	P Value
(Intercept)	-1.00275	0.563162	-1.78057	0.074982
CFS	0.530269	0.171856	3.08554	0.002032
Benthic substrate boulder	0.677552	0.395895	1.711444	0.086999

Model output for motion detection camera trap:

	Estimate	Standard Error	Z Value	P Value
(Intercept)	-1.90733	0.74526	-2.55928	0.010489
Camera angle - down	1.362877	0.941115	1.448152	0.147575
Camera angle - up	-0.64828	0.817218	-0.79328	0.427615
Stream feature - pool	1.485855	1.401916	1.059875	0.289202
Stream feature - rapid	0.691849	0.852967	0.811109	0.417303

Stream feature - run	-0.21167	0.915991	-0.23108	0.817249
Trap nights	0.621535	0.286416	2.17004	0.030004
Average number of photos per day	0.327987	0.261577	1.253885	0.209884

Model output for time-lapse camera trap:

	Estimate	Standard Error	Z Value	P Value
(Intercept)	-1.64531	0.490612	-3.3536	0.000798
Camera angle - down	-1.15153	1.140171	-1.00996	0.312515
Camera angle - up	-0.25821	0.667228	-0.38699	0.698767
Stream feature - boulder	0.656888	0.72034	0.911913	0.361814
Stream feature - rapid	0.746933	0.619972	1.204787	0.228286
Stream feature - pool	1.347471	1.057836	1.2738	0.202734
Trap nights	0.083013	0.266148	0.311906	0.755112
Average number of photos per day	0.386827	0.287584	1.345094	0.178595

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Chapter 2:

Where the ducks are: Predicting site-use of breeding Harlequin Ducks (*Histrionicus histrionicus*) in Western Montana and Northern Idaho

2.1 Introduction:

The ability to predict where species are beyond where they have been monitored is essential for efficient conservation and management of biodiversity (Guisan et al., 2013; Jetz et al., 2012; Sofaer et al., 2019; Villero et al., 2017). Reliable species distribution models (SDM) help managers decide where to use limited resources, identify and protect critical habitats, support legally binding environmental regulations, conserve rare species, and mitigate the spread of invasive species (Sofaer et al., 2019; Villero et al., 2017). For example, Albera Natural Park, on the Iberian Peninsula, used an SDM to define the core distribution areas and important connectivity corridors between isolated populations of the endangered Hermann's tortoise (*Testudo hermanni* subsp. *Hermanni)* when drafting their Special Protection Plan for the Natural Park (Villero et al., 2017). In another example, the United States Department of Agriculture Animal and Plant Health Inspection Service used an SDM to create predictive risk maps for the invasive European gypsy moth (*Lymantria dispar dispar*) to guide survey efforts to help detect and eradicate populations in the Pacific Northwest (Cook et al., 2019; Sofaer et al., 2019).

Survey efforts of Harlequin Ducks (HADU; *Histrionicus histrionicus*), a species of conservation concern with specialized habitat requirements, have only covered a small portion of their breeding range in Western Montana and Northern Idaho (Idaho Department of Fish and Game, 2024.; Montana Natural Heritage Program, 2024). HADU are a rare and cryptic sea duck, with strong site fidelity, who breed along rugged, fast-moving, mid-sized whitewater streams in mountainous regions. They require streams with little human disturbance and complex stream geomorphology, including braided channels, loafing rocks, rapids, deep pools for predator avoidance, streamside vegetation that provides nesting sites and predator protection, and backwaters to provide refuge for chicks (Bengtson, 1972; Cassierer et al., 1996; Kuchel, 1977; Reichel et al., 1996; Robertson & Goudie, 2020; Rodway et al., 1996). Despite being the focus of a mosaic of monitoring efforts by different agencies and non-governmental organizations, challenges accessing much of their habitat has limited implementation of widespread monitoring efforts. Thus, it remains unclear if recently observed declines on some breeding streams represent a regional trend.

Declines of HADU breeding pairs and broods in several annually monitored streams has prompted widespread concern about their status and trends in Western Montana and Northern Idaho (Bate, Unpublished data; Holmes et al., in prep; Idaho Department of Fish and Game, 2024.; Smith et al., 2023). These concerns are underscored by the constraints imposed on reproductive success resulting from males leaving the breeding grounds immediately after nests are established, preventing second nesting attempts if the first nest fails (Hansen, 2014; MacCallum et al., 2021). In the Northern Rockies, increasing human recreation and climate change-induced alterations to streamflow are hypothesized to threaten HADU (Cassierer et al., 1996; Hansen et al., 2019; Kuchel, 1977), each of which would present different management implications. However, the inaccessibility of their habitat and low detection probability make it difficult to understand the extent of declines across the region and to disentangle annual variability in reproductive success from growing climate change and human disturbance threats (Cassierer et al., 1996; Hansen et al., 2019; Hansen, 2014; Kuchel, 1977; Soulliere & Thomas, 2009).

An SDM could help support biologists who manage breeding HADU by identifying probable breeding streams beyond where surveys have been conducted in Western Montana and Northern Idaho. An integrated SDM is an approach that combines multiple datasets collected under different sampling schemes, and facilitates improved precision of estimates (Koshkina et al., 2017; Miller et al., 2019; Pacifici et al., 2019; Strebel et al., 2022). Sampling schemes can include repeated structured surveys, omnibus surveillance monitoring, opportunistic incidental observations, or citizen science programs (Isaac et al., 2020; Koshkina et al., 2017; Landau et al., 2022). By combining data types, an integrated SDM can leverage the strengths of each dataset and offset the weaknesses of others to create predictions of parameters informed by all available information (Landau et al., 2022). This approach is ideal for HADU in the Northern Rockies because the structured surveys traditionally used to monitor HADU by walking on foot along streams are sufficiently labor intensive that they have not been consistently conducted on many streams in the region (Montana Natural Heritage Program, 2024). While the data from these surveys facilitates accounting for low detection probability (Holmes et al., in prep) sampled sites represent limited variation in stream geomorphology relative to variation across the entire region. In complement, a much broader proportion of streams have other forms of detection / non-detection, presence-only or absence-only data, facilitating representation of a broader geographic area and variation in stream geomorphology. A robust integrated SDM could help biologists facilitate a multi-stakeholder monitoring strategy to inform HADU conservation. An integrated SDM could help prioritize spatially explicit management actions, such as restricting the frequency of stream crossings when planning the construction of new roads, closing access to critical foraging habitat areas during sensitive brood rearing times, or conducting vegetation management around breeding streams (Cook et al., 2019; Guisan et al., 2013).

We used an integrated SDM to build a predictive occupancy model of breeding HADU in Western Montana and Northern Idaho. To build our integrated SDM, we used our knowledge about HADU habitat requirements and behavior coupled with all the available survey and observation data collected across the region. Below, we explain how the resultant geospatial map product can guide survey strategies depending on the management or information objective. Ultimately, this model can be used to support managers in understanding broader patterns of region wide HADU site-use as well as associated habitat requirements.

2.2 Study Area:

The study area encompassed parts of the Rocky Mountains HADU breeding population in Montana and Idaho. Our boundary extended from the northeast boundary of Glacier National Park at the United States - Canada border, south along the Rocky Mountain front through the Gallatin National Forest to the Montana - Wyoming border and west to the Washington- Idaho border encompassing the Idaho panhandle (Figure 1).

We surveyed streams throughout the study area. Breeding streams in the Idaho panhandle and northwest Montana that encompass the Northern Rockies ecoregion are typically found at lower elevations (1000 - 2000m) within mesic forest dominated by cottonwoods (*Populus spp.*), hemlock (*Tsuga spp.*) and Western Red Cedar (*Thuja plicata*). In southern and eastern areas in Montana that encompass the Canadian and Middle Rockies ecoregions, breeding streams are found in more xeric conifer forests at higher elevations (up to 2500m) (Reichel et al., 1996; US EPA, 2015b).

2.3 Methods:

We built an integrated SDM to predict potential site-use of HADU breeding streams using available data, following an approach developed by Strebel at. al (2022). This approach enabled us to integrate multiple sources of detection / non-detection data by using an occupancy model where the different survey methods had their own detection functions (MacKenzie et al., 2002; Tyre et al., 2003). Then using the posterior beta estimates from our occupancy model, we predicted HADU site-use across sites that were never surveyed, and we used our presence only and absence only data to inform predictive constraints on the predictions by censoring unsuitable habitat and incorporating known breeding observations. Below we explain each data source and how it is used in the model. Then we explain our habitat covariates and our modelling framework.

2.3.1 Data sources:

Data type 1: Detection / non-detection data

Detection non-detection data came from structured ground-based foot surveys (GBS) and environmental DNA (eDNA). GBS were conducted between 2009 and 2024, eDNA was collected from 2015 to 2024 and both types of surveys were done between July and September in all years. We used data between July and September because it corresponds to the time after males leave the females to incubate (Hansen, 2014; MacCallum et al., 2021). Field effort conducted in 2024 was specifically sited to fill spatial gaps in the available data using single-visit surveys that combined eDNA sampling with a GBS (Holmes et al., in prep).

All GBS were completed by trained personnel who worked for Glacier National Park, the United States Forest Service, Montana Fish, Wildlife, and Parks, Idaho Department of Fish and Game, Montana Natural Heritage Program, or Montana Audubon. GBS consisted of at least two observers walking upstream in the stream. Observers surveyed unwalkable streams from the bank, taking turns watching the stream and walking through the brush so one person was always watching for HADU until it was safe to walk in the stream again (Hansen et al., 2019). GBS ranged from 5km to 10km in distance. The number of visits to a stream varied from one to six times in a year and some streams were sampled in multiple years. For our analysis, surveys were broken into 1,600-meter stream reaches (hereafter sites), which match the breeding home range of a female HADU (Hansen, 2014). Sites where HADU were detected were assigned 1's and sites that had no HADU detections were assigned 0's.

eDNA samples were taken in tandem with GBS in 2022 - 2024 with the same sites being re-surveyed in 2022 and 2023. eDNA samples from 2015 to 2021 were originally taken for fisheries projects that we analyzed for HADU. And each eDNA sample was considered as an individual replicate. eDNA samples were taken against direction of the stream flow. All samples were extracted at the National Genomics Center in Missoula, Montana, using a modified Qiagen DNEasy® Blood and Tissue Kit optimized for eDNA filters (Franklin et al., 2019). eDNA samples were analyzed for HADU DNA using a species-specific and sensitive quantitative polymerase chain reaction (PCR) assay developed by the National Genomics Center to detect a region of the HADU cytochrome c oxidase subunit I mitochondrial gene (Franklin et al. in prep). Extracts were then analyzed for the presence of HADU DNA in triplicate reactions using the optimized quantitative PCR assay conditions from Franklin et al. (in prep) on a QuantStudio 3 Real-Time PCR System (Life Technologies). A sample was determined to have a HADU detection if at least one of the triplicate reactions amplified HADU DNA. Negative controls were included in the DNA extraction process by including samples that had filtered distilled water and in the quantitative PCR analyses by using distilled water as a replacement of the DNA template. All samples were tested for inhibition by including a TaqMan Exogenous Internal Positive Control in the quantitative PCR reaction. A sample was considered inhibited if the mean cycle value (Ct) of the Internal Positive Control was more than one Ct delayed than the mean Ct of the Internal Positive Control in the negative control reactions.

Data type 2: Presence only data

Presence only data came from incidental HADU observations. Incidental observations were collected outside of a GBS between July and September from 2009 to 2024 and were censored to only include single females or broods. These data came from point observations submitted to agencies by other staff, visitors, or volunteers or citizen science (Idaho Department of Fish and Game, 2024.; Montana Natural Heritage Program, 2024) checklists submitted through eBird and iNaturalist. eBird and iNaturalist observations were verified by pictures and other users (*eBird Basic Dataset*, 2024; *iNaturalist*, 2024). These data, while not from a structured survey, represented places with observed breeding season occurrences; sites with these observations were fixed to high probability of occurrences in the predicted occupancy map.

Data type 3: Absence only data

HADU select for swift flowing montane streams, typically surrounded by conifer forested bank vegetation, with little human disturbance (Cassierer et al., 1996.; Marks et al., 2016). Therefore, we used the National Land Cover Database (NLCD) in Google Earth Engine to remotely classify the most common non-water landcover at every site in our study area within a 30 meter buffer of the stream (Gorelick et al., 2017; *National Land Cover Database (NLCD) 2021 Products | U.S. Geological Survey*, 2018). Sites that were classified as pasture / hay, cultivated crops, or barren land were considered non-viable HADU habitat. We constrained the sites the model was predicting to based on these criteria. Strebel et al. (2022), used similar absence-only data to inform the latent state of the occupancy model; this depends on having absence-only data in places with detection/non-detection data, a criteria our dataset did not meet.

We also set the occupancy probability of streams that were classified as stream order 7 through 9 to zero because we did not have any detection/non-detection data for those streams and use of those stream types for breeding is exceptionally rare in HADU.

Habitat covariates:

We modeled HADU site occupancy using a suite of a priori habitat covariates, all of which were derived from remotely sensed data. Covariates were selected based on eight a priori hypotheses around known habitat requirements important for breeding HADU (Table 1). Our hypotheses fell under four main categories: stream geomorphology, streamflow, forest cover, and human disturbance. We required that covariates were available for the entire study area and were remotely sensed. Lacking remotely sensed measures of some stream geomorphological characteristics such as measures of rapids, braiding, deep pools, benthic substrate, and aquatic invertebrate populations, we utilized the River Continuum Concept to identify proxy variables (Doretto et al., 2020; Vannote et al., 1980). This concept describes a river system as a continuous gradient of physical and biotic characteristic adjustments from the top of the headwaters downstream. Applying this concept, we used stream order, slope and sinuosity to represent stream geomorphology.

The Strahler Stream order, a system used to classify the position of a stream within a river system (headwater = stream order 1, the Amazon River, the largest river in the world = stream order 12), is thought to capture processes that are a proxy for measuring stream geomorphology variables (Doretto et al., 2020; Strahler, 1957; Vannote et al., 1980). HADU are known to breed near cold water streams that provide suitable foraging habitat and nesting opportunities, and maintain flows needed to support brood rearing through August (Cassierer & Groves, 1994; Reichel et al., 1996; Smith et al., 2023). In Montana and Idaho, stream order tends to be correlated with elevation where smaller order streams are higher in the mountains, often originating from glaciers or other snow fields, which are often colder (Carter et al., 1996). Furthermore, mid-sized streams (orders 4-6) tend to have the highest variability in temperature within a day which may lead to more diversity in aquatic invertebrates (Cummins & Klug, 1979; Vannote et al., 1980). The mechanism behind this process is that tree and shrub cover provide shade at different points of the day from the sun causing larger variation in daily temperature swings compared to small streams that are close to the consistent water source and large streams which are buffered from drastic temperature changes due to there being more water in the channel. In turn, this high variability in temperature creates optimal temperature ranges for multiple types of aquatic invertebrates which then may provide suitable foraging habitat for HADU (Minshall et al., 1983; Sitati et al., 2024; Vannote et al., 1980; Yates et al., 2018). Finally, stream order also explains the process of streams increasing in volume as they move away from their source and can be a proxy for annual flow (Hughes et al., 2010). While stream order captures broader scale variation in many aspects of stream geomorphology potentially relevant to HADU habitat, we sought to explain variation in stream slope and sinuosity at finer spatial scale through their inclusion as independent covariates.

Slope impacts water velocity (steeper slopes have faster water) which in turn affects sediment erosion and deposition. Faster moving streams have more capacity to move larger sediments like boulders and cobbles which are predominant in places where HADU are often observed (McCabe, 2011; Montgomery & Buffington, 1997; US EPA, 2015a). HADU are also typically found in streams with a diversity of stream features including rapids, runs, pools, riffles, and braiding (Cassierer & Groves, 1994; Reichel et al., 1996). Therefore, we hypothesized slope might help us explain some stream features that are not available using remote data because sites with steeper slopes may be indicative of sites that have rapids and steep drops where HADU are often observed (Montgomery & Buffington, 1997).

Sinuosity can be an indicator of other stream features like deep pools, braiding and benthic substrate. For example, more sinuous streams tend to be deeper and have more pools, whereas streams that are braided tend to have low sinuosity and both braiding and deep pools are known features of streams that HADU are typically found in (Bravard & Petit, 2009). Sinuosity's tie to benthic substrate is highly correlated with slope. Flatter streams tend to be more sinuous and have less velocity and therefore tend to have smaller benthic substrates and vice versa for steeper streams (Petrovszki et al., 2012; Schumm et al., 1972).

We used the coefficient of variation (CV) of the Julian day of peak stream flow at the Hydrologic Unit Code, level 10 scale (HUC10) watershed level from 1996 to 2024 to represent water variability. We were interested in gauging water variability because changing streamflow regimens due to climate change may be a key driver in HADU irregular levels of reproductive success (Cassierer et al., 1996; Hansen et al., 2019). For example, fluctuations in the timing of peak flow could result in nests washing out more regularly or conversely, streams drying up earlier leaving HADU chicks vulnerable to predation (Kuchel, 1977). We were interested in assessing whether water variability impacted HADU breeding streams because over time, streams that have high variability may lose their populations due to reoccurring nest and brood losses. We took the Julian day that had the highest CFS flows for the HUC10 watershed across a thirty-year period (1996 – 2024), then we calculated to CV of those days to determine variability in peak flow over time in each watershed.

We used the percent forest cover to represent vegetative protection from predators. HADU require vegetation to provide nesting habitat and refuge from predators (Bengtson, 1972;

Cassierer & Groves, 1994). Predators include Bald Eagles (*Haliaeetus leucocephalus*), aerial predators that may favor wider streams with less tree cover, and mink (*Neovison vison*), terrestrial predators that may raid nests (Heath et al., 2006). We took a 30-meter buffer from the center line of the stream to quantify tree cover around the streams (Arif et al., 2021; Sweeney & Newbold, 2014).

We used the human footprint index to represent human disturbance. The human footprint index is a measure of permanent modifications to the landscape which includes human settlement, agriculture, transportation, mining and energy production, and electrical infrastructure (Kennedy et al., 2019). We used the same 30-meter buffer that we used to calculate the percent tree cover to calculate the human footprint within the vicinity of the stream.

As a basis for deriving covariate values, we obtained all streams in Western Montana and Northern Idaho from the National Hydrography Dataset (NHD; Buto & Anderson, 2020), retained only named streams and split each stream into 1,600 meter line segments from the top of the headwater down, each representing a site. To obtain stream order, we spatially joined our 1,600 meter lines with the NHDPlusFlowlineVAA dataset and assigned each line a stream order based on the largest overlap (Buto & Anderson, 2020). To derive stream sinuosity, we took the total length of the line and divided it by the straight-line distance from the top to bottom of each line. We then buffered each streamline 30 meters on both sides to create site polygons. Then, to obtain minimum and maximum elevation, mean percent tree cover, the mode landcover classification, and the mean human footprint index, we used the NASA SRTM Digital Elevation 30m dataset, the Rangeland Analysis Platform to build a tree mask, the National Land Cover Database, and the CSP gHM: Global Human Modification dataset to clip values from each dataset to the site polygons from our shapefile (Allred et at., 2021;*CSP gHM*, n.d.; Farr et al., 2007; Jones et al. 2018; Jones et al. 2021; Kennedy et al., 2019; *NASA SRTM Digital Elevation 30m | Earth Engine Data Catalog*, n.d.; *NLCD 2021*, n.d.; Platform, n.d.; US EPA, 2015b; Robinson et al., 2019). To obtain slope, we used the maximum elevation, minimum elevation, and length in meters of each site to calculate the rise over run. To obtain variation in streamflow, we used the Headwaters Hydrology Project Streamflow Predictions API in R to get the Julian day of peak runoff at the HUC10 for 1996 to 2024 which we used to calculate the CV in timing of peak runoff (Hoylman, 2025). Finally, we derived streamflow (cubic feet per second; CFS) for each day a GBS or eDNA was collected, as the mean streamflow for the HUC10 on the day the survey was completed (Hoylman, 2025). Mean streamflow was used as a habitat covariate in our detection model. Continuous covariates were z-standardized and correlation was assessed and none of our covariates were highly correlated.

2.3.2 Statistical methods:

Within a Bayesian modeling framework, we used detection / non detection data in a site occupancy model to predict the probability of site-use given habitat covariates with hypothesized relationships to use. Detection probability was modeled separately for GBS and eDNA in relation to streamflow, which has a known effect on detection probability of both methods (Holmes, et al. in prep). We assumed closure across surveys for surveys conducted in the same site in the same year and due to strong breeding site fidelity of female HADU and breeding fidelity of offspring to their natal stream (Bengtson, 1972; Reichel et al., 1996; Smith et al., 2000). We generated posterior predictions of site-level occupancy probabilities of HADU from the final model for streams in our study area that were within our inclusion criteria.

Occupancy model

To estimate the probability of site-level occupancy, ψ_i, across all sites, we used a hierarchical Bayesian model incorporating our hypothesized habitat covariates. For each site *i*, the probability of occupancy ψ_i was modeled as a function of habitat covariates using logistic regression:

$$logit(\psi_i) = \epsilon_{streamOrder[i]} + \sum_{k=1}^{6} \beta_k X_{ik} \tag{5}$$

where, β_k represents the coefficient covariate value of the k^{th} site-specific habitat covariate, X_{ik}, parameter estimate on occupancy probability, and $\epsilon_{streamOrder[i]}$ represents a random intercept accounting for spatial variation among sites in different stream orders. All β_k were assigned un-informative priors (Normal (0, 10)). Stream orders were assigned autoregressive priors, with stream order one used as the reference category and given the prior logistic (0, 1). Stream orders two – six were given autoregressive normal priors ($\epsilon_j \sim N(\epsilon_{j-1}, \sigma^2_\epsilon)$). where σ^2 represents the variance in occupancy across stream orders. The occupancy state z_i was modeled as a Bernoulli process:

$$z_i \sim Bernoulli(\psi_i) \tag{6}$$

Where $z_i = 1$ if a site was occupied and $z_i = 0$ if a site is unoccupied.

Detection model

For each site *i* at visit *j*, the probability of detection $p_{i,j}$ was modeled as a function of survey type and streamflow using logistic regression:

$$logit(p_{i,j}) = (1 - st_i)(\gamma_1 + \gamma_2 f_{i,j}) + st_i(\gamma_3 + \gamma_4 f_{i,j}) \tag{7}$$

where, γ_1 and γ_3 represents the intercept for eDNA surveys and GBS, respectively. γ_2 and γ_4 represent the coefficient representing the effect of z-standardized CFS value of the i^{th} site on the j^{th} visit on detection probability. *st* represents the survey type. And *f* represents streamflow in CFS. γ_1 and γ_3 were assigned un-informative priors (logistic (0, 1)) and γ_2 and γ_4 were assigned un-informative priors (Normal (0, 10)). The observed detection y_{ij} followed a Bernoulli distribution:

$$y_{ij} \sim Bernoulli(p_{ij} * \ z_i) \tag{8}$$

where, *p* represents the detection probability, drawn from an uninformative prior (logit (0, 1)), ensuring that all possible values of *p* between 0 and 1 were equally likely before incorporating data.

We analyzed the data in R (R Core Team, 2023) and JAGS (Plummer, 2003) using the jagsUI package (Kellner, 2025). We sampled four MCMC chains for 200k iterations, and discarded the first 100k iterations as burn-in. We monitored convergence visually and via the Brooks-Gelman-Rubin statistic ($\hat{R}$; Brooks & Gelman, 1998). For each parameter described in the text we present medians, 95% Bayesian credible intervals, and when applicable, f, or the proportion of the posterior distribution on the same side of zero as the mean. We interpret f-values and a covariate was considered to have strong evidence of a relationship to occupancy if the proportion of a covariate's posterior distribution exceeding zero (f value) was greater than 0.9, some evidence of an effect if f was between 0.9 and 0.8, and no evidence of an effect if f was less than 0.8.

Predicting occupancy on un-surveyed sites:

To estimate occupancy probability at sites with no GBS or eDNA, we used mean posterior samples from the fitted model to generate predictions, confidence intervals, and standard deviations. For sites that were classified as open water, developed, forest, shrubland, herbaceous, or wetland using the NLCD, and were stream orders 1 – 6 occupancy probability was predicted using the estimated regression coefficients and site-specific standardized covariate values. All continuous covariates were z-standardized. Sites that were classified as agriculture or barren by the NLCD or stream orders 7 – 9 were fixed to 0. And sites that had incidental observations were fixed to 0.9 occupancy probability. Though HADU exhibit strong breeding and natal site fidelity, observed declines in the HADU breeding population inherently means that some historically occupied breeding streams are no longer occupied. Therefore, it is important to acknowledge that we modeled relative site-use and not true occupancy (Emmet et al., 2021).

2.4 Results:

We collated detection / non-detection data at 1,025 out of 59,179 one-mile sites across Western Montana and Northern Idaho, from 2009 to 2024 (Table 2). Our model converged and there was no evidence of lack of fit for covariates (Table 3).

In the model, there was strong support for negative linear effects of slope, sinuosity, and human footprint index on occupancy (f = 1, 0.939, and 0.967, respectively). There was some support for a positive effect of the CV in the Jullian date of peak runoff (f = 0.874) (Table 3, Figure 1, Figure 2). Stream order was used as an autoregressive random intercept and the model predicted the highest occupancy on filth order streams (Figure 3)

The model exhibited strong support for a positive effect of CFS on detection for eDNA and some support for a positive effect of CFS on detection for GBS (f = 1 and 0.878, respectively). The detection probability for GBS and a single eDNA sample on a first order stream, our intercept, was 0.12 and 0.45 respectively (GBS SD: 0.520 and 95% CI: 0.41 – 0.49; eDNA SD: 0.526 and 95% CI: 0.10 – 0.15).

Posterior distributions of the covariates used in the occupancy model were then used to predict occupancy across all sites and we found that the mean predicted occupancy across the entire study area was 0.10 (SD: 0.04, 95% CI: 0.04 – 0.21; Figure 4). Predicted occupancy varied spatially, with the northeast portion of the study area that encompasses Glacier National Park exhibiting the highest mean probability of occupancy at 0.29 (SD: 0.07, 95% CI: 0.18 - 0.44, Appendix 2). We found that the southern portion of the study area that encompasses the Beaverhead-Deerlodge National Forest has the lowest predicted mean probability of occupancy at 0.07 (SD: 0.04, 95% CI: 0.02 – 0.17).

2.5 Discussion:

This study used an integrated SDM to leverage multiple data sources, providing the first regional-scale statistical model that predicts site-use of HADU in Western Montana and Northern Idaho. Using available HADU detection / non-detection data from 2009 to 2024 on 1,025 one-mile stream sites, we modeled site-use in relation to remotely sensed habitat covariates. Four covariates (slope, sinuosity, mean human footprint index, and stream order) exhibited evidence of a strong effect of HADU site-use, and one covariate (CV of the Julian day of peak runoff) exhibited some evidence of an effect of HADU site-use. We used the posterior estimates from our occupancy model to estimate site use across all stream sites in the study area. Then, using these predicted metrics we created a predictive site-use map with the intention of creating a tool for biologists and land managers to support decision-making.

The model broadly reflects our knowledge of HADU's historic range in the region, validating what we knew about HADU while also identifying important areas to focus monitoring and management efforts (Idaho Department of Fish and Game, 2024.; Montana Natural Heritage Program, 2024). When we overlayed historic observations of HADU (observations from late 19th century to 2009) onto our predicted site-use map, we found streams with historic records had high predicted site-use whether or not they had contemporary observations (Figure 5). This suggests these streams may still be suitable habitat. For example, three national forests in Northern Idaho (Idaho Panhandle, Nez Perce-Clearwater, and Bitterroot) had HADU observations pre-dating the study period; the last 15 years have had few observations in these areas, yet our model still predicted these areas to be suitable for breeding HADU (Figure 6). The decline in observations could be due to lack of survey effort and not necessarily loss of HADU populations, as many areas with high predicted HADU site-use are hard to access.

Notably, both contemporary and historical survey efforts are variable across the region, which is important to consider when interpreting spatial patterns. We attempted to fill in these spatial data gaps in 2024 by analyzing 230 eDNA samples previously collected from fisheries projects and surveying streams where we have not seen HADU since before 2009 following recommended protocols by Holmes et al (in prep) (Figure 8, Figure 9). Despite these efforts, disparity in data between certain areas remained (Figure 8), making it difficult to disentangle whether low predictive site-use is a product of low survey effort, low site-use or both. Future monitoring could target these areas to disentangle these factors.

2.5.1 Remotely sensed habitat relationships:

We found that HADU site use was highest on stream orders three through five, consistent with previous studies (Morneau et al., 2008; Rine et al., 2022; Figure 3). Mid-sized streams may offer the most suitable conditions for the cold, clear streams, and suitable foraging habitat that HADU require. For example, lower order streams may dry up or become too shallow to provide refuge from predators, despite generally being colder, and larger order streams may be too warm for HADU. Mid-sized streams have enough water to provide suitable habitat yet are still relatively cold. Mid-sized streams are also thought to have higher aquatic invertebrate diversity than smaller order streams which may provide suitable foraging habitat for HADU (Cummins & Klug, 1979; Doretto et al., 2020). This diversity, coupled with the fact that HADU are visual feeders may also explain why they tend to prefer the clear water of mid-order streams (MacCallum, 2001). The turbidity of larger order streams may limit visibility, compromising HADU foraging ability.

Slope and sinuosity, while related to stream order at broad scales (Vannote et al., 1980), further refined our model of HADU site use, presumably by reflecting processes that relate to more fine scale effects of benthic substrate and unquantified stream features preferred by HADU (e.g. rapids, runs, pools, riffles, and braiding). We found opposite relationship of slope and sinuosity to site use than we expected. Typically, as streams become less steep they become more sinuous (Miller, 1988). Our results show that HADU prefer less steep streams, as well as those that are less sinuous. Since none of these covariates measure specific stream features directly (i.e. exact benthic substrate, number of pools, rapids and waterfalls), future work to quantify these important habitat characteristics using remotely sensed data could be beneficial.

We found strong evidence for a negative relationship between HADU breeding site-use and human disturbance. Human footprint index is a measure of permanent anthropogenic stressors on the landscape (human settlement, agriculture, transportation, mining and energy production, and electrical infrastructure; Kennedy et al., 2019) and therefore our results are indicative of human disturbance from development negatively impacting HADU site-use, and do not directly quantify or implicate disturbance from recreation (e.g. people with boats, fishing, or swimming). For example, two well-known areas that have high recreation, but different human footprint index values are the Lower Rattlesnake Creek near Missoula, Montana and Upper

McDonald Creek in Glacier National Park. The lower section of Rattlesnake Creek is part of a popular, high-use, recreational area where locals and visitors flock every summer to go hiking and fishing. Lower Rattlesnake Creek, however, is surrounded by neighborhoods, roads, and trails and it has a mean human footprint index of 0.59 and a mean probability of site-use of 0.01. In comparison, Upper McDonald Creek in Glacier National Park is also known for having extremely high recreation as is parallels the famous Going-to-the-Sun Road that roughly three million people drive every summer. McDonald Creek is highly accessible to park visitors and people love to swim and fish at the many pullouts along the road. Despite the high visitation, it has a mean human footprint index of only 0.015 and a mean probability of site-use of 0.77. It is important to distinguish the different types of disturbance because there is the assumption that all forms of human disturbance are bad for HADU, and there is growing concern about the impact from human recreation (Cassierer et al., 1996; Hansen, 2014; HADU working group, personal communications, 2025). As of now, there are no direct studies examining human recreation impacts on breeding HADU site-use. Given concern related to the potential threat of recreation as more people are recreating on streams which used to see little to no use, research into impacts on HADU would be informative for management (Idaho Department of Parks and Recreation, 2023; Lant, 2024; Unites States Forest Service, 2025).

We found weak evidence for a positive relationship with the CV in the Julian day for peak streamflow and HADU site-use. Our results indicate that HADU potentially prefer slightly less predictable watersheds for when peak runoff happens year to year. We have two ideas as to why this pattern was observed: (1) by using a single peak runoff day rather than identifying a multi-day high water period, we may not have identified the most consequential high water period of the season for breeding HADU; (2) if high water is temporally more variable (more early or late dates), it is potentially less likely to interfere with the incubation period when nests are at risk of being washed out resulting in reproductive failure. Other measures that may represent inter-annual variability more precisely might be using a window of time in which streamflow is highest such as a week or ten days, or looking at how high the peak in streamflow was relative to the median flow (Smith & Boers, 2023).

We did not find evidence of a relationship between HADU site use and mean percent tree cover. Mean percent tree cover was used as a proxy variable for protection and did not include riparian vegetation composed of shrubs such as willow, so may have been an underestimation of the actual provided vegetation protection.

Management Implications:

The objective of this study was to build a predictive site-use map to provide a foundation for building a more robust HADU monitoring program in the Northern Rockies. Below we provide recommendations for different uses of this model depending on the information or management objective:

1. *Determine region wide known species distribution:* This model could help biologists and managers prioritize where to conduct surveys and/or resampling eDNA to determine whether HADU are using certain streams. To understand regional species distribution with high confidence requires broad spatial coverage with high detection (Murphy & Smith, 2021). To decide where to sample, we recommend first using our model to identify streams with high predicted site-use that have historic records of breeding HADU but where HADU have not been detected in recent years. Second, the model could identify areas with high probability of site-use that are easily accessible but have never been surveyed. Finally, depending on time and resources, the model could identify

more difficult to access areas with high probability of site-use that have never been surveyed. This approach provides an effort-sensitive approach to improving information about distribution. To achieve high detection probability, we recommend using methods from Holmes et. al (in prep), where observers collect six eDNA samples (one every kilometer) in tandem with a GBS. This method has a mean cumulative detection probability of 95% (95% CI: 0.85 – 0.99).

Two additional sources of occupancy data, pre-existing eDNA samples and targeted outreach, could supplement new survey efforts or provide data related to distribution in situations where resources are limited and structured surveys are not feasible. HADU share many of the same habitat requirements as well-studied trout species in Montana and Idaho (e.g. Bull Trout, *Salvelinus confluentus*; Yellowstone cutthroat trout, *Oncorhynchus clarckii bouvieri*; and Westslope cutthroat trout *Oncorhynchus clarcii lewisi;* Rieman & McIntyre, 1993) and preexisting eDNA samples may be available for analysis through the eDNAtlas (Yates et al., 2018). If sampling pre-existing eDNA we recommend identifying streams using the approach described above and selecting streams with multiple eDNA samples since cumulative detection probability increases with each sample; Holmes et al. (in prep) found that eDNA detection probability varies with streamflow and suggests taking between six and nine samples on a stream. Finally, if re-sampling eDNA, we recommend only using samples that were collected between June and July because that corresponds to the single female and early brood rearing season where occupancy is expected to be the most relevant to understanding breeding populations (MacCallum et al., 2021). Additionally, targeting outreach to encourage reporting of HADU observations by visitors and other staff can supplement other HADU occurrence data (Kelling et al., 2019; Stenhouse et al., 2020).

2. *Evaluating regional changes in use of breeding streams:* This model could help biologists and managers prioritize where to conduct surveys to evaluate fluctuations in HADU use of breeding streams (Elzinga et al., 1998). Evaluating changes in use of breeding streams requires knowledge of locations where streams had been used by HADU historically, but have been locally extirpated (Robinson et al., 2018). However, populations could also be colonizing new breeding streams. As such, evaluating change in use of breeding streams would require broad spatial coverage with high detection, repeated over time (Block et al., 2001). Information about changes in use is more actionable when those changes are assessed with respect to potential causal factors (Scheele et al., 2018). We suggest using the model to identify a sample of higher predicted use streams that represent the variation in factors hypothesized to be causing changes. For example, understanding effects from recreation or wildfire on HADU occupancy could help inform management actions on other streams experiencing similar pressures. Management actions could include options like seasonal boating closures in sensitive areas or conducting vegetation management to help forests around important breeding streams be more resilient to wildfire (Montana's State Wildlife Action Plan, 2025). If, alternatively, what is desired is an assessment of whether streams that were known to be used by breeding HADU historically are still used by HADU, then known historic occurrences should be used to identify sites for monitoring instead of the predicted site use map. After identifying a set of breeding streams to be resampled, similar to region wide known species distribution, we would

recommend monitoring streams with one effective visit by following the protocol laid out by Holmes et al. (in prep).

3. *Evaluate trends in Abundance on breeding streams:* Evaluating trends in abundance requires counts of HADU over time (Ficetola et al., 2018; Wauchope et al., 2019). The model from this work could be used to identify potential important breeding streams across the region of interest that could be a part of a monitoring program where the selected streams are re-visited both within a season and across years on a regular basis. If there is interest in making inference about the trends in the region based on the collected data, the selected streams must be representative of that region (Fedy et al., 2015). We would recommend following the HADU survey protocol laid out by Holmes et al. (in prep), determining the appropriate amount of GBS survey effort that would be required to achieve a high detection probability based on the stream condition of the selected streams. Holmes et al. (in prep) found that streamflow, the expected number of HADU on a stream, and timing significantly affected the detection probability of a GBS. For example, to achieve a 0.9 cumulative detection probability on a stream with a streamflow greater than 200 CFS, with an estimated two to six HADU, during the incubation period (late June – July), biologists would need to conduct five GBS within a year. Then to get abundance trends over time, the surveyed streams would need to be revisited at a regular interval across years (Wauchope et al., 2019).

4. *Mitigating effects of development:* Managers are often tasked with reviewing project proposals (e.g. development of new roads and structures or logging operations) and

assessing the potential impact of the project on species of concern (Emerson et al., 2022; US EPA, 2013). This model could be used to determine if the proposed project falls within HADU breeding habitat. We recommend using the high detection protocol laid out by Holmes et al. (in prep) to survey any stream with a predicted probability of site use greater than 0.1. This threshold should ensure monitoring of 85% of potential HADU sites. To give the highest probability of detection, we recommend completing these surveys in early July when females are incubating or chicks are just fledging, and single females are still on the stream (MacCallum et al., 2021). If HADU are detected actions to mitigate impacts on breeding HADU include: maintaining a 100m buffer zone around the stream, avoiding road placement in the valley bottoms, restricting the frequency of stream crossings, building bridges instead of using culverts, minimizing turbidity through management of runoff from upslope worksites, and conducting work outside of HADU breeding season (Montana's State Wildlife Action Plan, 2025).

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2.7 Figures and Tables:

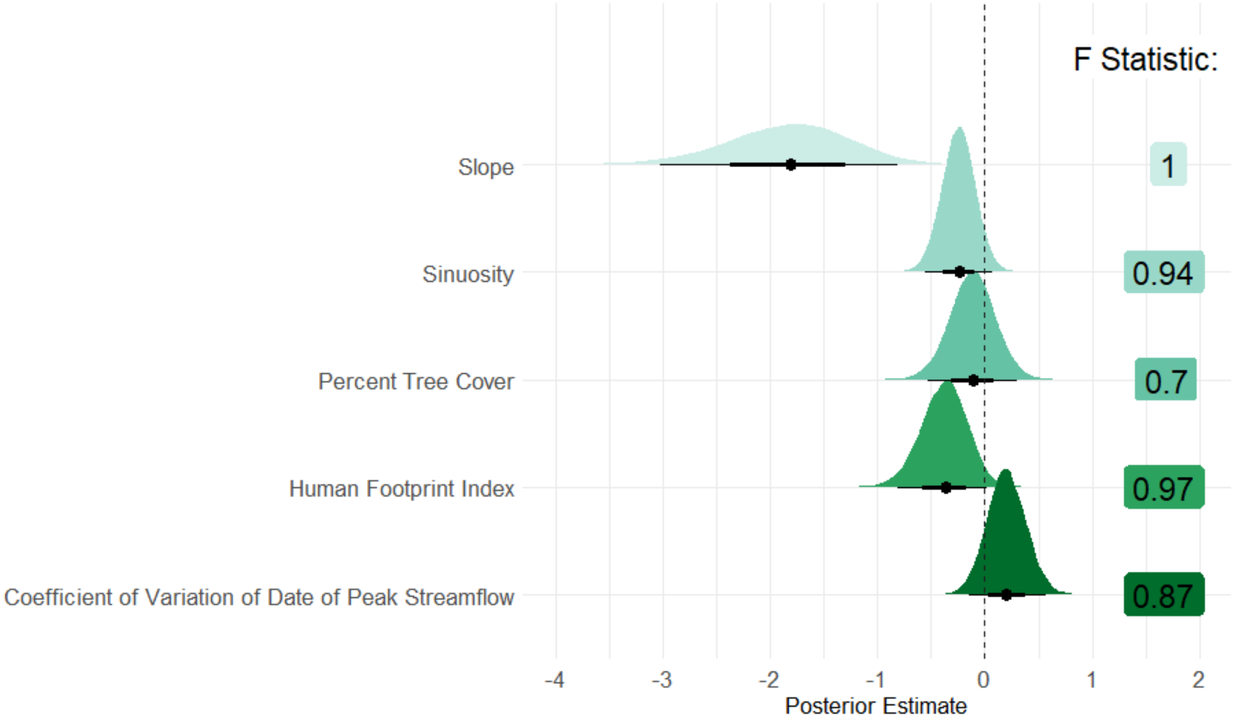

Figure 1: Posterior distributions of covariates included in occupancy model are represented in green. 50% confidence intervals are indicated by dark black line and 95% confidence intervals are indicated by thin black line. f statistic is listed on the right which indicates how much of the posterior distribution is on the same side of 0.

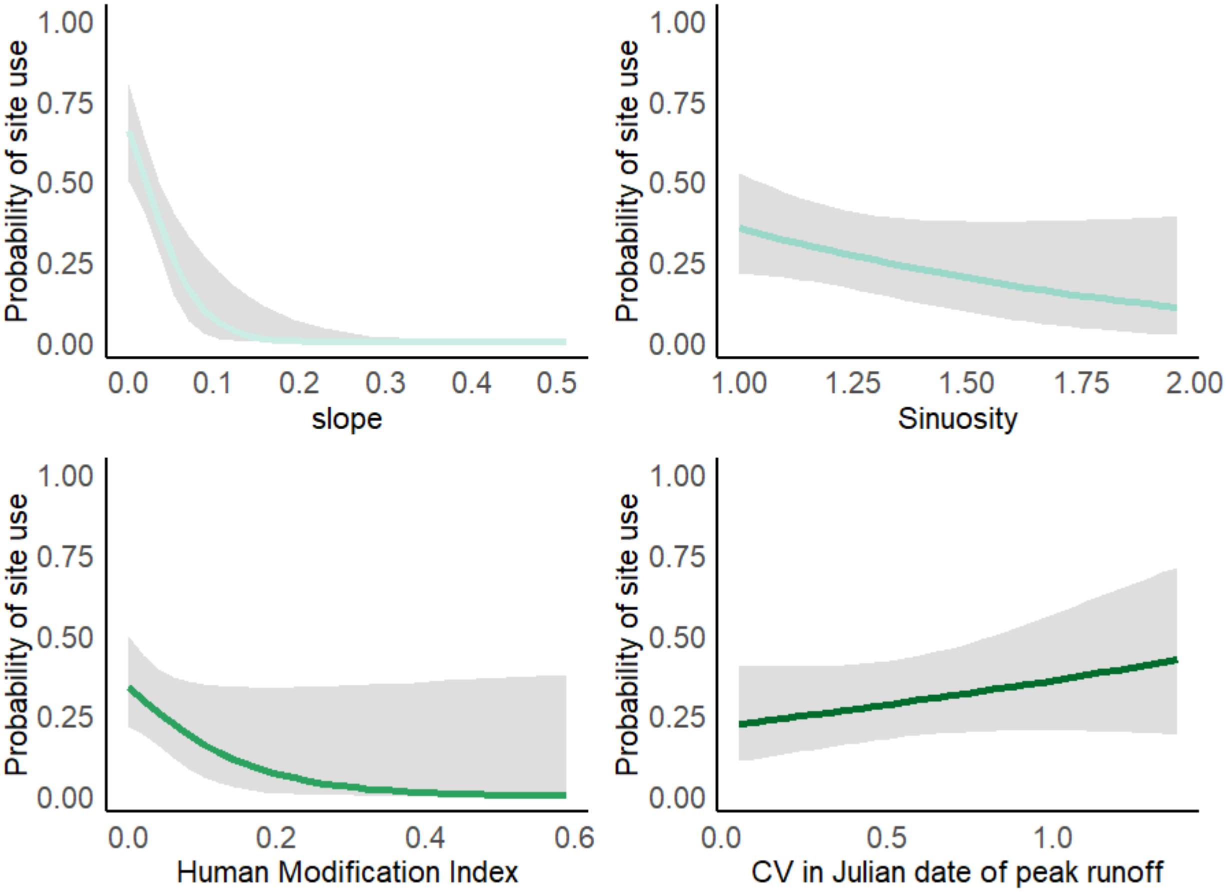

Figure 2: Covariate effect plots showing the effect of the covariates that had strong or some evidence of an effect on occupancy (slope, sinuosity, mean human modification index, and the CV in Jullian data of peak flow) on the probability scale.

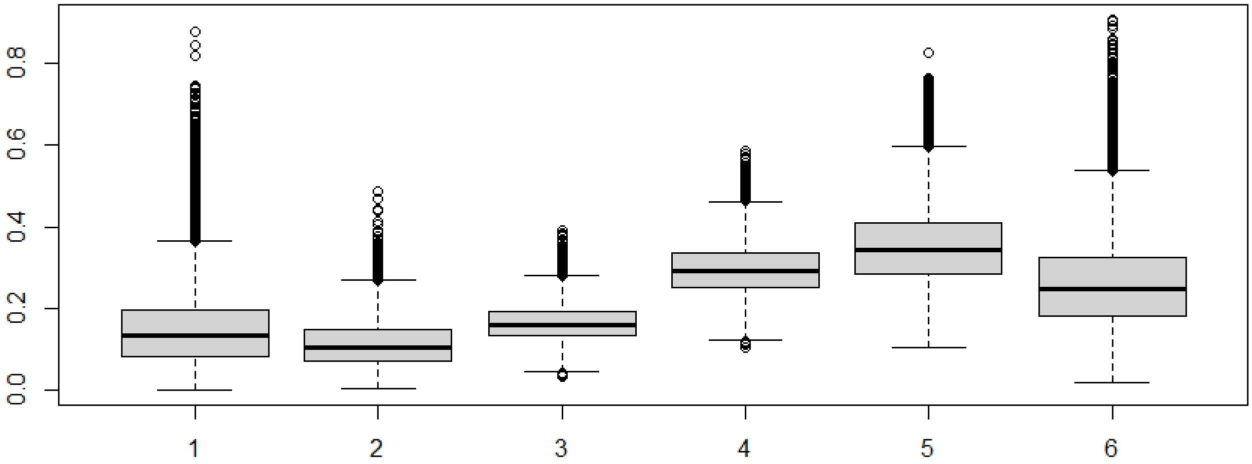

Figure 3: Estimates of occupancy for each stream order and its 95% confidence intervals.

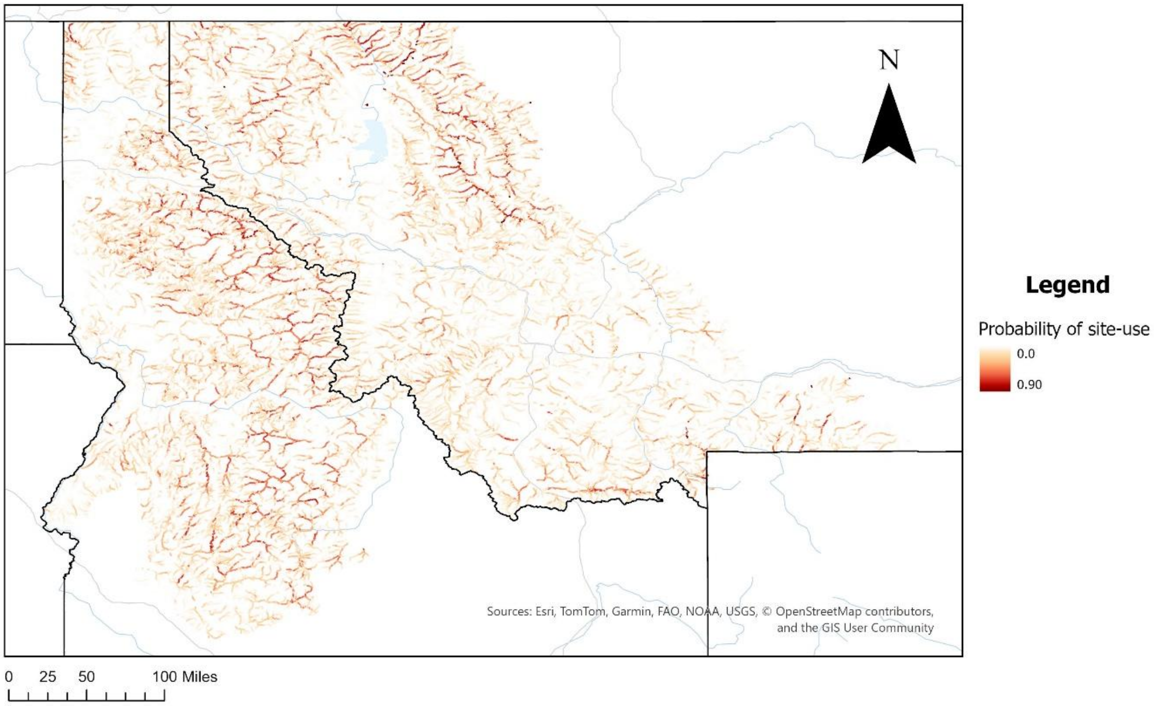

Figure 4: Predictive HADU site-use map across Western Montana and Northern Idaho. Darker red indicated high probability of site-use.

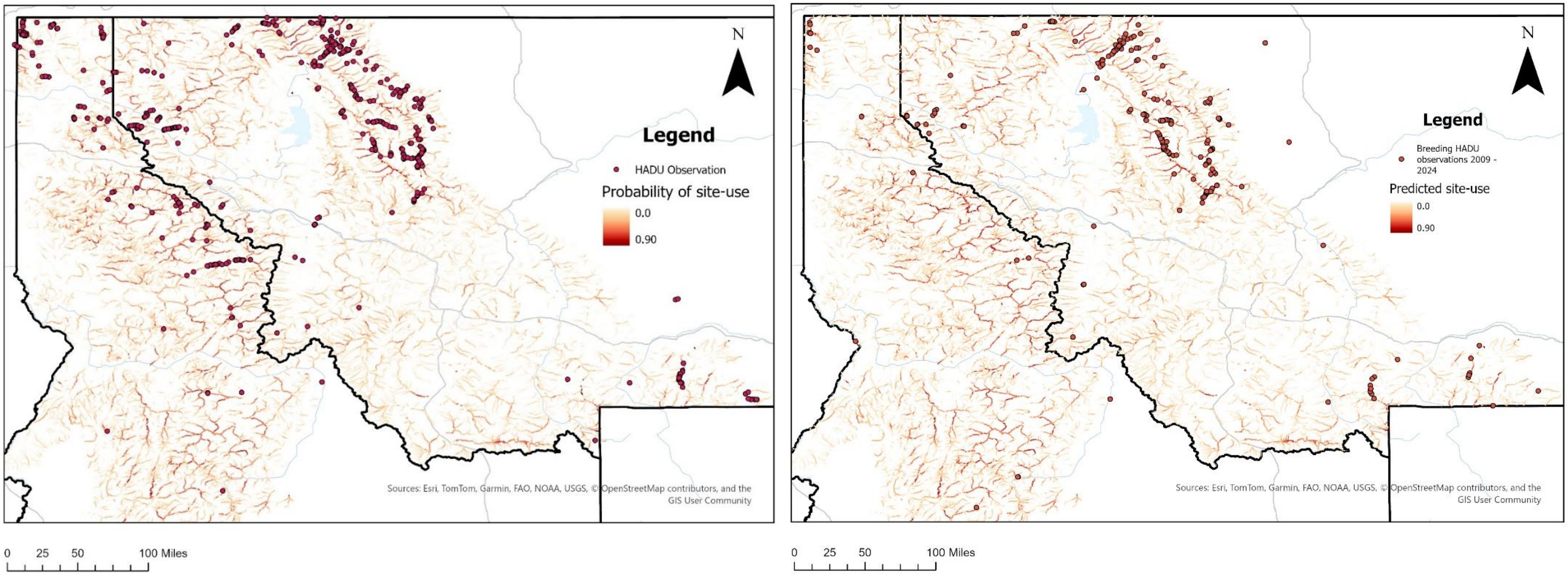

Figure 5: Predictive HADU site-use map across Western Montana and Northern Idaho with confirmed breeding observations of HADU from 1874 to 2009 on the left and breeding observations of HADU from 2009 to 2024 on the right.

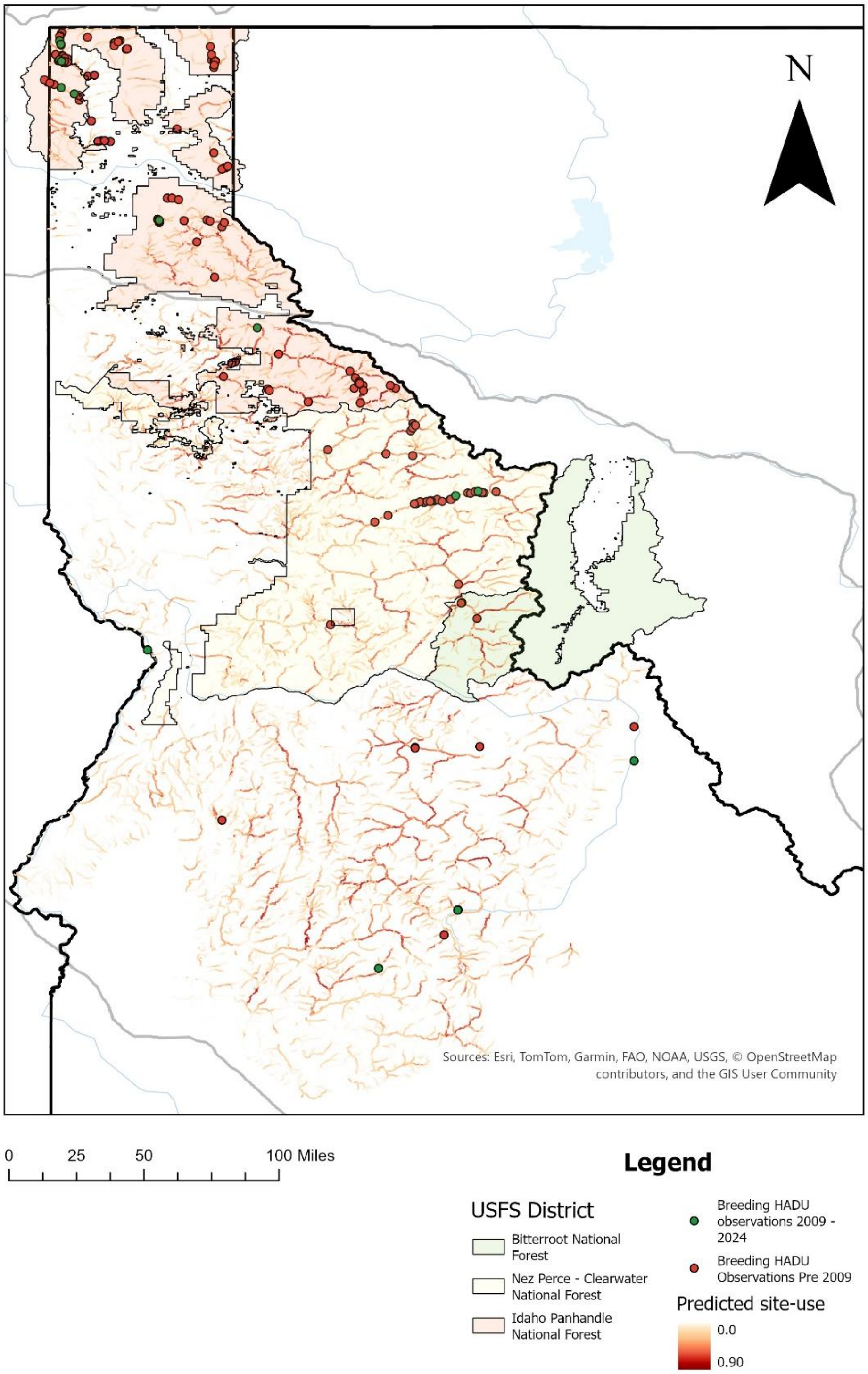

Figure 6: Map of Idaho with the Bitterroot, Nez Perce – Clearwater, and Idaho Panhandle National Forests overlaid with the results from the predictive site-use model and historic observations of breeding HADU in red and breeding observations from 2009 – 2024 in green.

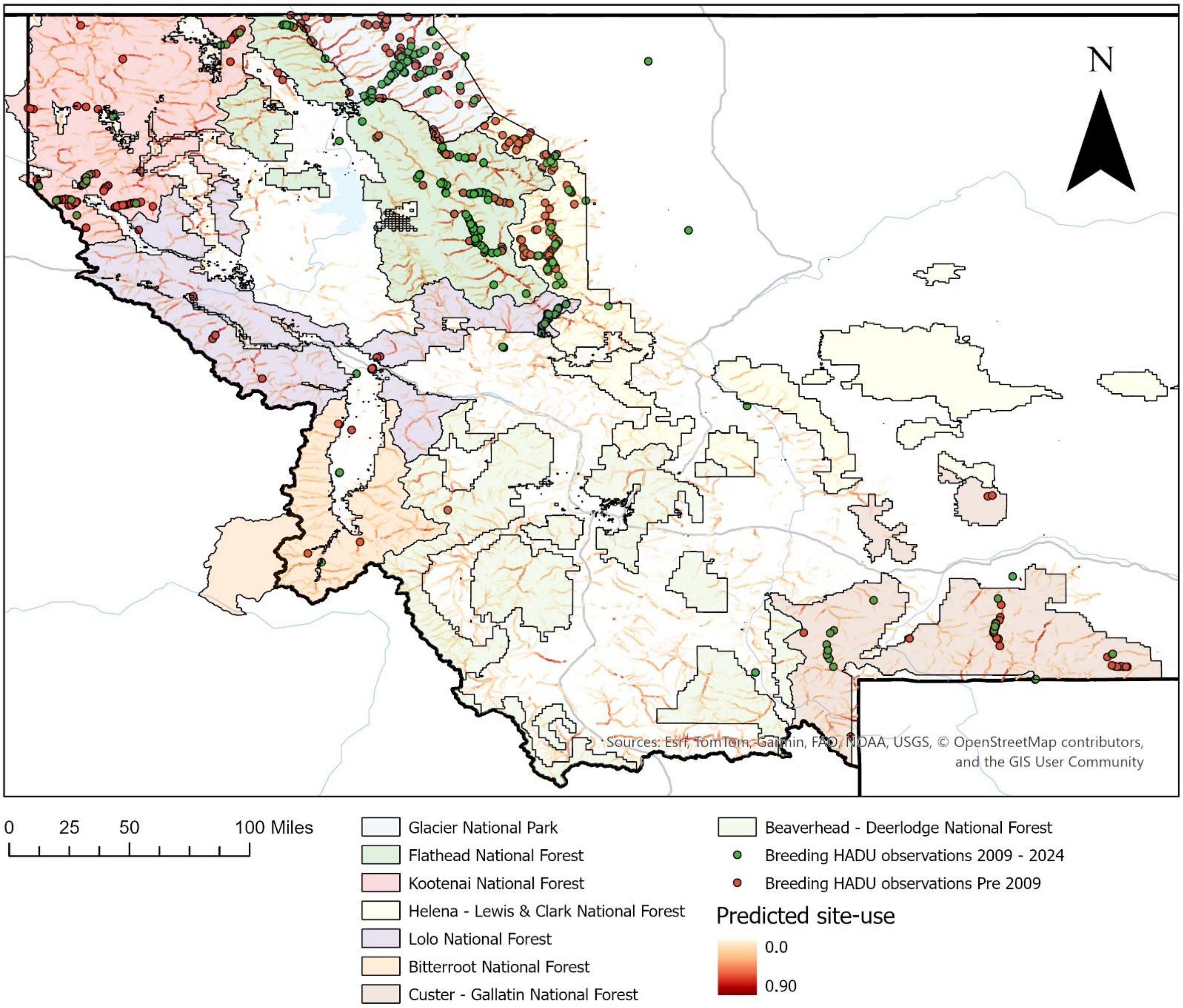

Figure 7: Map of Western Montana with National Forests and Glacier National Park overlaid with the results from the predictive site-use model and historic observations of breeding HADU in red and breeding observations from 2009 – 2024 in green.

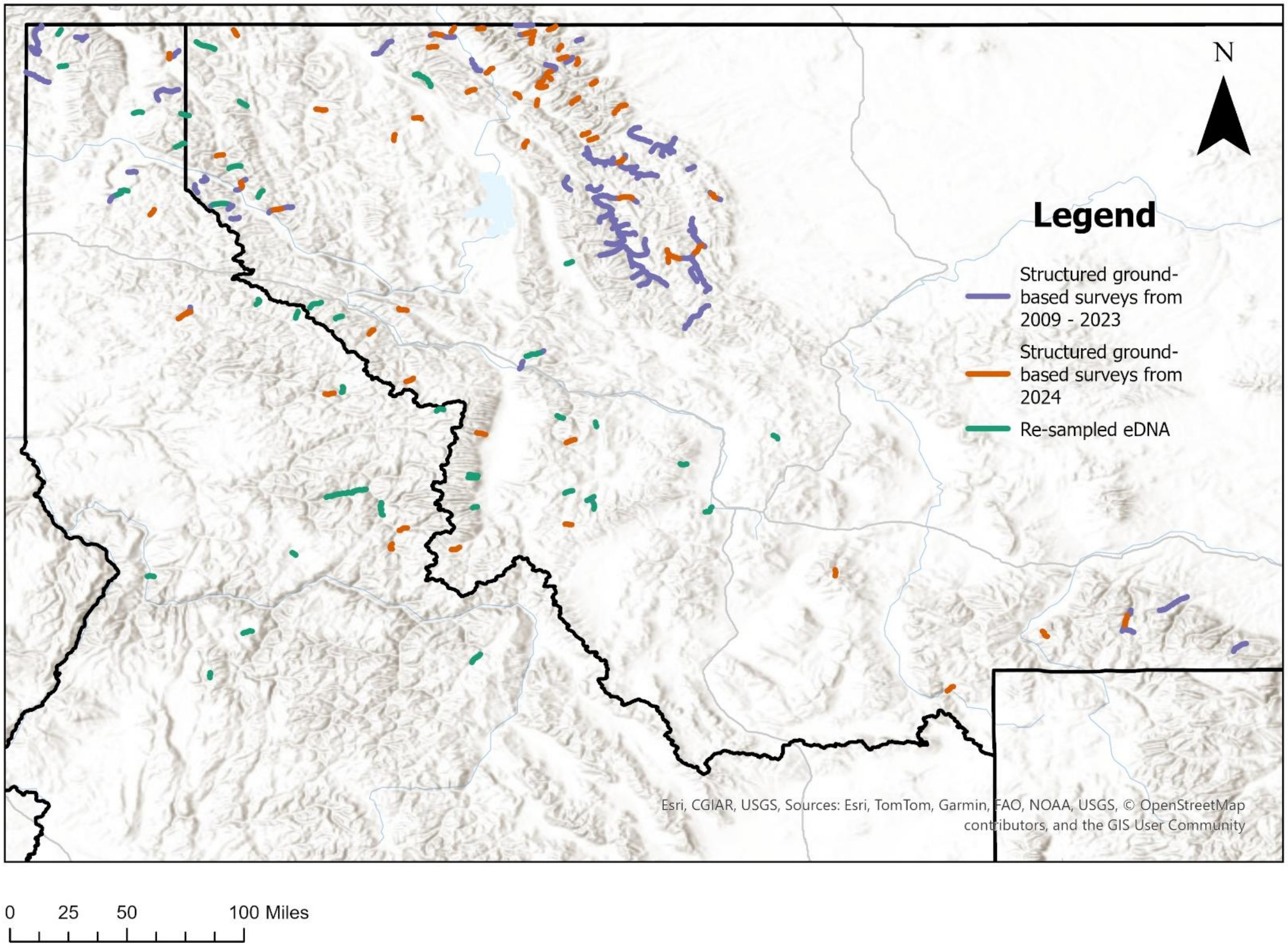

Figure 8. Survey Effort: Map showing all detection / non-detection data included in the occupancy model. All GBS conducted between 2009 – 2023 are highlighted in purple. GBS collected in 2024 for this study are highlighted in brown. Streams where eDNA was analyzed from previously collect fisheries projects are highlighted in green.

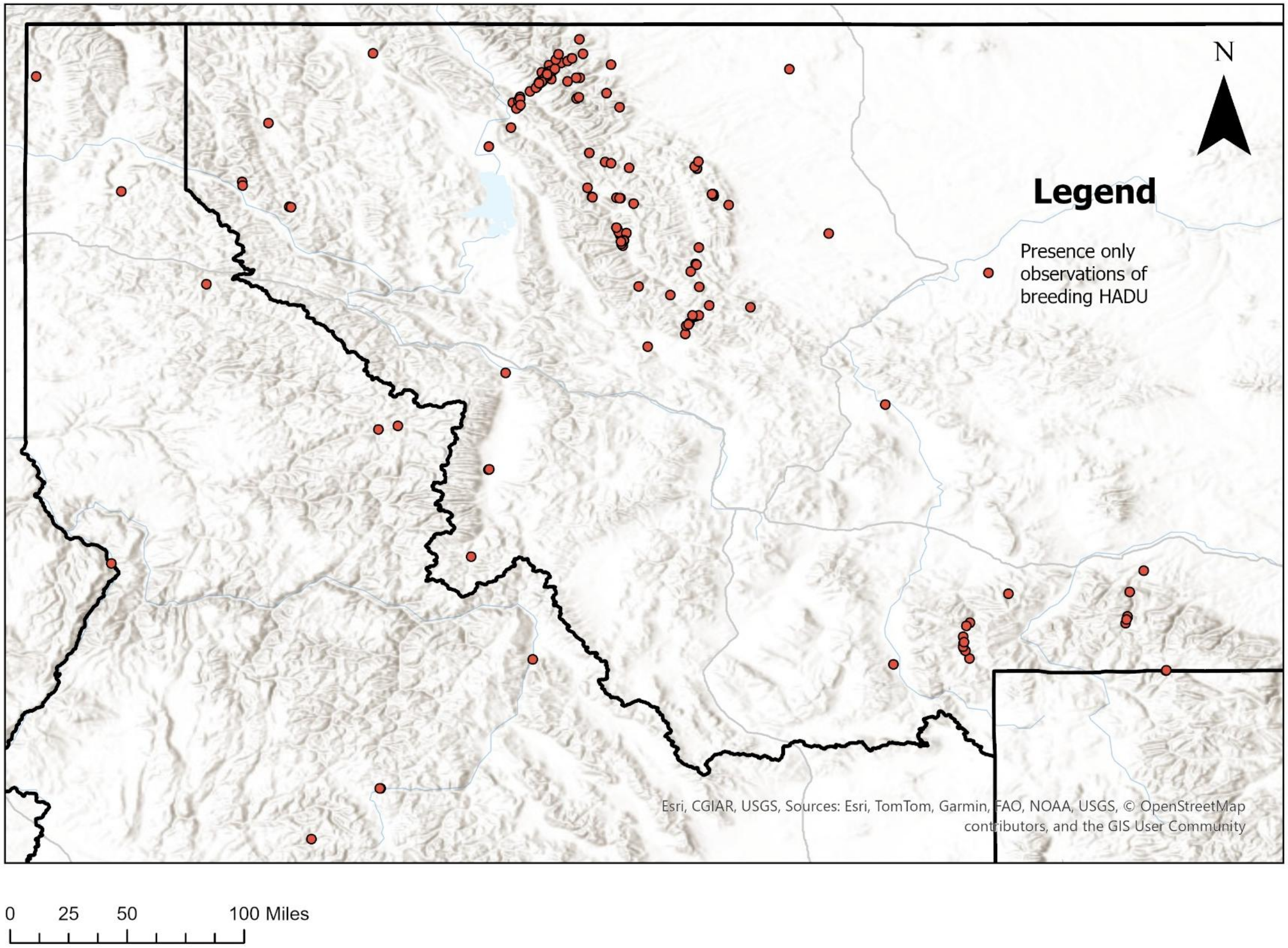

Figure 9: Presence only observations of HADU. These points come form incidentals and citizen science observations.

Table 1: Hypotheses and selected covariates.

Category	**Process**	**Hypothesis**	**Covariate**
Streamflow	Water Variability	Streams with high variability in the timing of peak runoff are less likely to be occupied by HADU due to the increased risk of nests washing out during the incubation period or streams drying during the brood rearing season leading to loss of protective habitat from predators. Streams with more consistent flow (lower seasonal variability) are more suitable for HADU occupancy, as they provide stable nesting and brood-rearing conditions.	CV in the Julian day of peak stream flow
	Mean Annual Flow	HADU prefer mid-sized streams (3rd – 5th order) because these streams provide suitable foraging habitat and nesting opportunities. Smaller streams may lack the consistent flow needed to support brood rearing, while larger streams may be too turbulent for foraging.	Stream Order`
Forest	Protection	Streams with higher percentages of forest cover have increased HADU occupancy because dense forest cover provides essential refuge from predators and buffers against human disturbance, creating safer breeding environments.	Percent tree cover
Disturbance	Human disturbance	HADU occupancy will be lower in streams within basins experiencing higher levels of human disturbance, due to potential loss of breeding habitat, increased noise, and recreational activity, which can disrupt nesting behavior and reduce brood-rearing success.	Mean human foot print index
Stream Geomorphology	Benthic Substrate	HADU occupancy will be higher in streams with boulder and cobble substrates, as these features provide increased loafing habitat in the middle of the stream and are indicative of favorable streamflow patterns that enhance foraging opportunities (River continuum theorem).	Stream order and slope
	Temperature (water and air)	HADU occupancy will decrease in streams with temperatures above 10°C, as they are cold-water habitat specialists. Colder streams may limit invertebrate productivity and indicate delayed snowmelt, which could restrict early access to nesting sites. However,	Stream order

		moderate to low temperatures are likely optimal for HADU.	
	Stream Oxygen	HADU occupancy will decrease with lower levels of stream oxygen, as reduced oxygen availability may negatively impact invertebrate productivity limiting foraging opportunities and habitat quality for nesting and brood-rearing.	Stream order
	Channel complexity	HADU occupancy will increase in streams with more channel complexity because it provides better habitat for both foraging and predator protection.	Slope and sinuosity

Table 2: Summary of sites with GBS data only, eDNA data only, and sites with both GBS and eDNA detection / non detection data.

Type of detection / non detection data	**Number of sites with HADU detections**	**Total number of sites with detection / non detection data**
GBS only	60	701
eDNA only	9	154
Both GBS and eDNA	47	170

Table 3: Mean probabilities of each parameter in the occupancy model and mean standardized effect sizes for covariates. Asterisk represents covariates whose 95% credible interval did not overlap zero. f represents the portion of the posterior distribution that had the same sign as the mean effect with f > 0.9 indicating strong evidence of an effect and 0.8 > f < 0.9 indicating weak evidence of on occupancy. $\widehat{R}$ is our MCMC chain convergence.

Parameter	**Mean**	**SD**	**2.5 %**	**97.5 %**	***f***	$\widehat{R}$
Occupancy						
*Slope	-1.840	0.567	-3.031	-0.807	1.000	1.000
Sinuosity	-0.241	0.157	-0.550	0.065	0.939	1.000
% tree cover	-0.110	0.211	-0.532	0.301	0.701	1.000
Human foot print index	-0.377	0.215	-0.817	0.025	0.967	1.000
CV in timing of peak flow	0.206	0.181	-0.144	0.566	0.874	1.000
*Stream order 1	-1.968	0.820	-3.793	-0.533	0.995	1.000
*Stream order 2	-2.216	0.660	-3.695	-1.135	1.000	1.000
*Stream order 3	-1.669	0.327	-2.340	-1.057	1.000	1.000
*Stream order 4	-0.896	0.308	-1.497	-0.293	0.998	1.000
Stream order 5	-0.649	0.420	-1.453	0.205	0.938	1.000
Stream order 6	-1.116	0.609	-2.317	0.106	0.966	1.000
Detection						
*Intercept eDNA	-0.194	0.080	-0.352	-0.038	0.992	1.000
*CFS eDNA	0.253	0.070	0.119	0.391	1.000	1.000
*Intercept GBS	-1.952	0.103	-2.155	-1.752	1.000	1.000
CFS eDNA	0.107	0.091	-0.075	0.283	0.878	1.000

2.8 Appendix:

Appendix 1: Mean occupancy for each stream order on the probability scale with its standard deviation and 95% confidence intervals.

Stream order	Mean occupancy	SD	2.5 %	97.5 %
1	0.123	0.694	0.022	0.195
2	0.098	0.659	0.024	0.149
3	0.159	0.581	0.088	0.191
4	0.290	0.576	0.183	0.335
5	0.343	0.603	0.190	0.409
6	0.247	0.648	0.090	0.324

Appendix 2: Land managing agency, district, and the mean probability of HADU site-use with its 95% credible intervals and standard deviation.

Agency	District	Mean Probability of Occupancy and 95% CI	SD
Glacier National Park	Glacier National Park	0.293 (0.18 – 0.44)	0.070
USFS - Montana	Flathead National Forest	0.169 (0.09 – 0.28)	0.052
	Helena – Lewis & Clark National Forest	0.120 (0.06 – 0.21)	0.040
	Custer Gallatin National Forest	0.076 (0.03 – 0.15)	0.033
	Kootenai National Forest	0.128 (0.06 – 0.23)	0.045
	Beaverhead-Deerlodge National Forest	0.076 (0.02 – 0.17)	0.039
	Lolo National Forest	0.101 (0.05 – 0.19)	0.038
USFS – Montana and Idaho	Bitterroot National Forest	0.097 (0.04 – 0.18)	0.036
USFS - Idaho	Nez Perce – Clearwater National Forest	0.129 (0.06 – 0.23)	0.046
	Idaho Panhandle National Forest	0.134 (0.07 – 0.23)	0.043
Montana Fish Wildlife and Parks	All of Montana in study area	0.103 (0.04 – 0.21)	0.046
	Region 1	0.133 (0.06 – 0.24)	0.048
	Region 2	0.081 (0.03 – 0.18)	0.041
	Region 3	0.079 (0.02 – 0.19)	0.046
	Region 4	0.191 (0.10 – 0.32)	0.057
	Region 5	0.083 (0.04 – 0.16)	0.034
Idaho Department of Fish and Game	All of Idaho in study area	0.108 (0.05 – 0.21)	0.043

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