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Research Article

Combining non-invasive survey methods increases cumulative detection probability for breeding harlequin ducks *Histrionicus histrionicus*

Holli A. Holmes¹✉, Hannah M. Specht², Lisa J. Bate³, Kristina Smucker², Casey McCormack⁴, Cara Staab⁵, Thomas W. Franklin⁶, Dan Bachen⁷, Bryce Maxell⁷, Allison J. Puchniak Begley² and Joshua J. Millsaugh⁸

¹University of Montana, Missoula, MT, USA

²Montana Fish, Wildlife, and Parks, Helena, MT, USA

³Glacier National Park, West Glacier, MT, USA

⁴Idaho Department of Fish and Game, Coeur d'Alene, ID, USA

⁵United States Forest Service, Retired, Denver, CO, USA

⁶National Genomics Center for Wildlife and Fish Conservation, United States Forest Service Rocky Mountain Research Station, Missoula, MT, USA

⁷Montana Natural Heritage Program, Helena, MT, USA

⁸University of Montana and State University of New York College of Environmental Science and Forestry, Missoula, MT, USA

Correspondence: Holli A. Holmes (holli.holmes@umconnect.umt.edu)

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The effective implementation of new technologies for wildlife population monitoring is limited by knowledge of factors that impact their efficacy. Population monitoring of harlequin ducks *Histrionicus histrionicus* on their breeding streams in Montana and Idaho in the Northern Rocky Mountains, has historically relied on ground-based foot surveys (GBS), which have produced variable count data, making it hard to decipher trends in stream occupancy and population size. We quantified the detection probability of GBS and compared it to two additional non-invasive technologies, environmental DNA (eDNA), and camera traps (time-lapse and motion-detection) for detecting breeding harlequin ducks. We surveyed for harlequin duck presence on 10 occupied streams during incubation and brood rearing in 2022 and 2023 using GBS, eDNA, and camera traps. We found that a single 5-km GBS had a mean detection probability of 0.51 (95% CI: 0.31–0.71) and varied with the relative abundance of harlequin ducks, streamflow, and survey pace, but not between incubation and brood-rearing periods. Both eDNA and camera traps proved effective in detecting harlequin ducks, particularly when replicated across space (multiple samples of eDNA along a stream reach) or time (camera traps deployed over several weeks). It is important to note that eDNA and camera traps only provide presence/absence data, while GBS provides relative abundance. Combining methods proved particularly effective; we estimated a cumulative detection probability > 0.95 for a single-day survey effort by collecting eDNA samples spread throughout a stream reach in tandem with a GBS. Utilizing and combining these non-invasive survey techniques could also be used to effectively detect other low density, cryptic, waterbirds occupying stream habitats.

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Introduction

A longstanding challenge of ecology and management is obtaining the most valuable information from data collection and monitoring efforts (Nichols and Williams 2006). This challenge requires careful allocation of limited resources to optimize methods that address specific scientific and management goals (Nichols and Williams 2006, Yoccoz 2022). Population monitoring methods are constantly evolving as new technologies emerge 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 to address any particular question is limited by our understanding of different factors that impact their efficacy (Mackenzie and Royle 2005).

Factors that affect efficacy of survey methods for estimating occurrence and abundance of wildlife include environmental variables that relate to habitat, and behavioral variables unique to the species (Watson et al. 1999, Manning 2011). These are exemplified well in low density stream-residing waterbirds, which can be masked by dense vegetation, cryptic coloration, variable stream conditions, and predator avoiding behaviors (e.g. diving) (Johnsgard 1966, Kear 1975, Cerón and Trejo 2012, D'Amico et al. 2020). Species listed with special conservation and population designations often occur in low densities and can require an adapted species-specific monitoring protocol to adequately detect individuals (Nichols and Williams 2006). Understanding factors that impact method efficacy is especially relevant for identifying and implementing appropriate survey methodology.

Harlequin ducks *Histrionicus histrionicus* are a Northern Hemisphere sea duck and females exhibit strong breeding site fidelity to their natal stream while males follow their partner to reproduce. They breed on dynamic, fast-moving, whitewater streams in mountainous regions and fidelity to these streams creates regionally distinct breeding populations (Bengtson 1972, Robertson and Goudie 2020). In the Northern Rocky Mountains (Montana, Idaho, Wyoming, and Alberta), breeding populations of harlequin ducks are listed as a species of concern, special concern, or greatest conservation need due to their low abundance, vulnerability to climate change impacts, and habitat loss (Government of Alberta 2011, Oakleaf and Patla 2013, Idaho Department of Fish and Game [IDFG] 2024b, Montana Natural Heritage Program [MTNHP] 2024). Furthermore, they are especially difficult to survey given their life history, habitat use, and low abundance. Breeding observations have been recorded since the early twentieth century (Smith et al. 2024, IDFG 2024b, MTNHP 2024) and regular surveys conducted since the 1980s. Monitoring efforts by multiple agencies and non-governmental organizations over the past century have documented declining numbers of harlequin ducks in Montana,

Idaho, and Alberta while the population in Wyoming appears stable (Bate unpubl., Oakleaf and Patla 2013, Smith et al. 2024, IDFG 2024b, MTNHP 2024). These efforts include long-term annual monitoring of four breeding streams with historically large populations (Bate unpubl., IDFG 2024b, Smith et al. 2024). Other monitoring data in the region includes numerous single-day brood count surveys on other streams in the region. Although, the efficacy of these survey methods has never been evaluated and these surveys may be better suited for understanding long-term trends in stream occupancy rather than actual population trends (MTNHP 2024). Challenges associated with existing methodologies, access, and agency resources limit the ability to obtain robust population estimates needed to inform conservation status and management and has lead both Montana and Idaho to list harlequin ducks as a species of greatest conservation need (Montana Fish, Wildlife, and Parks [FWP] 2015, IDFG 2024c, FWP 2025).

Monitoring methods for harlequin ducks have primarily relied on direct, in-person observations (Cassierer et al. 1996, IDFG 2024b, MTNHP 2024). However, counts from these ground-based foot surveys (GBS) have been noted to be highly variable on the same stream reaches even just days apart due to aspects of bird behavior or stream conditions outside the observer's control. For example, during seasonally high water associated with snow melt, human access to streams is limited and harlequin ducks often move into calmer backwaters where they often go undetected, thereby negatively influencing detection (Hansen et al. 2019, Rine et al. 2022). Furthermore, differences in detections could be driven by variation in availability and occupancy corresponding to different portions of the breeding season and behavior. The harlequin duck breeding season can be classified into three distinct periods where behavior differs: mating and nest prospecting (~ late April–May), incubation (~ June), and brood rearing (~ July–mid-September) (Kuchel 1977, Reichel et al. 1995). During mating and nest prospecting, pairs move larger distances on their breeding streams and unmated individuals may move between streams altogether (Kuchel 1977, Reichel et al. 1997), making it hard to determine whether a detection of an adult harlequin duck indicates a potential breeding effort associated with that stream. After the mating period, males migrate back to the Pacific Coast, leaving the females to incubate eggs and raise hatched ducklings (Wiggins 2005). During the incubation and brood-rearing periods, harlequin duck females and their broods are more closely tied to their breeding streams and typically spend their days within a stretch of stream approximately 1600 m long, where they forage while drifting downstream and then fly or swim back upstream (Hansen et al. 2019). During incubation, female harlequin ducks only tend to forage and preen on the river for 2–4 hours a day in the afternoon and evening

and are otherwise hidden on their nests (MacCallum et al. 2021), often located along streambanks or islands, whereas broods during the brood-rearing period spend much of the day in the stream. However, throughout the season, as some clutches fail or broods are lost, the opportunities for detection also decline as females that have experienced reproductive failure migrate back to the coast earlier than those who successfully reproduced (Wiggins 2005, MacCallum et al. 2021). GBS are often completed when time allows, across inconsistent sections of streams, and span multiple periods of the breeding season, thereby representing different information about the population. Given this complexity, a better understanding of the efficacy of a single GBS for detecting the occurrence of harlequin ducks for any distance of survey could provide a basis for improving interpretation of existing survey data (Bledsoe et al. 2022), and methodology for future surveys.

Two increasingly utilized non-invasive methods for surveying wildlife occurrence are environmental DNA (eDNA) and stationary cameras (camera traps) (Thomsen and Willerslev 2015, Randler and Kalb 2018). Both eDNA and camera traps could improve our understanding of harlequin duck occurrence and abundance, but their efficacy has not yet been assessed for stream-residing waterfowl. eDNA allows researchers to assess species' presence by extracting their DNA from the environment within their associated habitats, such as water (Mason et al. 2025) or soil (Allen et al. 2023). Harlequin ducks spend substantial portions of each day on their breeding streams during the brood-rearing period (Bengston 1972), and applying eDNA methods could 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 visual 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 pre-programmed to a motion trigger or a time-lapse mode. Motion trigger mode collects images when animal movement is detected, while time-lapse mode collects a series of photos at a programmed interval. Camera traps have not typically been used on stream habitats to detect waterfowl. However, due to harlequin ducks' restricted home range during incubation and brood rearing (Hansen et al. 2019), strategically placed cameras may be effective in detecting individuals.

Our objective was to evaluate the efficacy of three non-invasive harlequin duck survey methods: GBS, eDNA, and camera traps across two distinct stages of the breeding season: incubation and brood rearing, when birds are generally confined to areas on their breeding stream. With all methods, we expected differences in detection probability between these two periods based on differences in harlequin duck behavior or the abundance of birds on the stream. Additionally, we expected stream characteristics, such as streamflow, to differentially impact harlequin duck 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 combinations of methods. Identifying effective survey strategies for these two time periods will facilitate survey design decisions to improve our understanding of the status of the Northern Rockies breeding population of harlequin ducks.

Material and methods

Study area

The study area encompassed parts of the Rocky Mountain harlequin duck breeding population in Montana and Idaho. Our boundary extended from the northeast boundary of Glacier National Park at the US–Canada border, south along the Rocky Mountain front through the Gallatin National Forest to the Montana–Wyoming border, and west through the Idaho Panhandle National Forest to the Washington–Idaho border (Fig. 1).

We sampled known breeding streams throughout the study area. Breeding streams in the northern portion of the study area are typically found at lower elevations (1000–2000 m a.s.l.) 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 typically found at higher elevations (up to 2500 m a.s.l.) within more xeric conifer forests dominated by Douglas-fir *Pseudotsuga menziesii*, western larch *Larix occidentalis*, grand fir *Abies grandis*, and lodgepole pine *Pinus contorta* (Reichel et al. 1996).

Stream selection

We selected 11 study sites on 10 streams from an initial list of 23 identified streams across western Montana and northern Idaho with high probable breeding season occupancy by harlequin ducks. All study sites were between 5 and 8 km in length and had confirmed breeding harlequin ducks in the previous five to ten years (IDFG 2024a, MTNHP 2024). Using probable occupied sites facilitated a study design focused on assessing drivers of detection. Streams varied in flow patterns, elevation, and vegetation cover (Supporting information).

Field methods

Field personnel sampled each site twice during each of two separate field seasons in 2022 and 2023. Each sampling occasion consisted of three consecutive survey days of the same stream reach. GBS were conducted each day during sampling occasions, whereas observers deployed cameras and collected eDNA on only one day each sampling occasion (days 1 and 2, respectively). For each sampling occasion, at least two designated primary observers 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 US Forest Service, Montana Fish, Wildlife, and Parks, Idaho Department of Fish and Game, or the Montana Audubon Society. All observers

Table 1. Model covariates: name, units, hypothesis, mean, range, and standard deviation for all models. NA=not available.

Model	Covariate	Units	Hypothesis	Incubation mean (SD; range)	Brood rearing mean (SD; range)
Ground-based foot survey	Pace	Total distance surveyed by the observation team divided by the survey duration (km h ⁻¹)	Higher observer pace reduces detection probability because less time is spent scanning for ducks.	0.84 (0.373; 0.32–2.45)	1.03 (0.412; 0.32–2.28)
	No. of observers	No. of observers during each survey	More observers can increase detection but may also decrease it if ducks are disturbed and leave.	3 (0.894; 2–6)	3 (0.712; 2–5)
	Streamflow	Cubic feet per second (CFS; ft ³ s ⁻¹)	Higher CFS makes streams harder to navigate, reducing detection probability.	218.00 (196.061; 9.99–740.35)	118.16 (63.659; 18.7–245.29)
	Mean QeDNA	Mean no. of copies of harlequin duck DNA per liter of water filtered across all the eDNA samples taken on a stream during the sampling occasion (DNA copies l ⁻¹)	Higher mean QeDNA increases detection probability. Mean QeDNA is correlated with the observed high count (r=0.505) on each sampling occasion; we used this metric because it is more independent of the survey method being assessed.	12.6 (12.007; 0.0–35.5)	16.9 (33.094; 0.0–154.5)
eDNA	Streamflow	CFS (ft ³ s ⁻¹)	Faster streamflow decreases detection because DNA is transported away more quickly.	214.8 (168.126; 15.5–653.1)	116.5 (65.223; 29.2–245.3)
	Benthic substrate	Boulder (> 10 in. across) or cobble (≤ 10 in. across)	Larger benthic substrates increase detection because DNA settles more quickly in finer substrates and boulder will have the highest detection probability.	Cobble=226 Boulder=70 NA=16	Cobble=313 Boulder=74 NA=18
Camera traps	Trap nights	No. of nights the camera was deployed	More trap nights increase detection, as longer camera deployment raises the chance of capturing ducks.	Motion-detection mean (SD; range) 22 (3.509; 17–37)	Time-lapse mean (SD; range) 22 (3.549; 17–37)
	Average no. of photos per day	Total no. of photos taken divided by the total no. of trap nights	Higher daily photo counts increase detection probability by providing more opportunities to capture ducks.	486 (893.527; 0–4379)	576 (335.041; 0–1728)
	Camera angle to the stream	Upstream, downstream, across, down (direction unknown)	Camera angle influences detection by affecting the field of view.	Across=59 Up=27 Down=10 NA=3	Across=64 Up=20 Down=9 NA=6
	Stream feature	Rapid, pool, run, and boulder	Stream features influence detection; ducks are more likely to be seen on boulders than in rapids.	Boulder=21 Rapid=21 Run=46 Pool=8 NA=6	Boulder=18 Rapid=30 Run=40 Pool=5 NA=6

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 and Specht 2015). Since harlequin ducks have a restricted home range during incubation and brood rearing (Hansen et al. 2019), population closure (i.e. no change in the no. of ducks occupying the survey section) was assumed within each three-day sampling occasion, but not between incubation and brood-rearing periods.

The seasonal timing of sampling occasions was designed to correspond to the incubation period and the brood-rearing period; timing was determined based upon site elevation which

influences harlequin duck breeding phenology, with lower elevation sites sampled earlier in the season when breeding occurs (MacCallum et al. 2021). The timing of the first sampling occasion corresponded to when harlequin ducks with active 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 on recess from incubating; as such, a detection in this period would indicate attempted breeding and site occupancy. The second sampling occasion occurred approximately three weeks later and corresponded to the brood-rearing period; a detection in this period would indicate one or more females were still

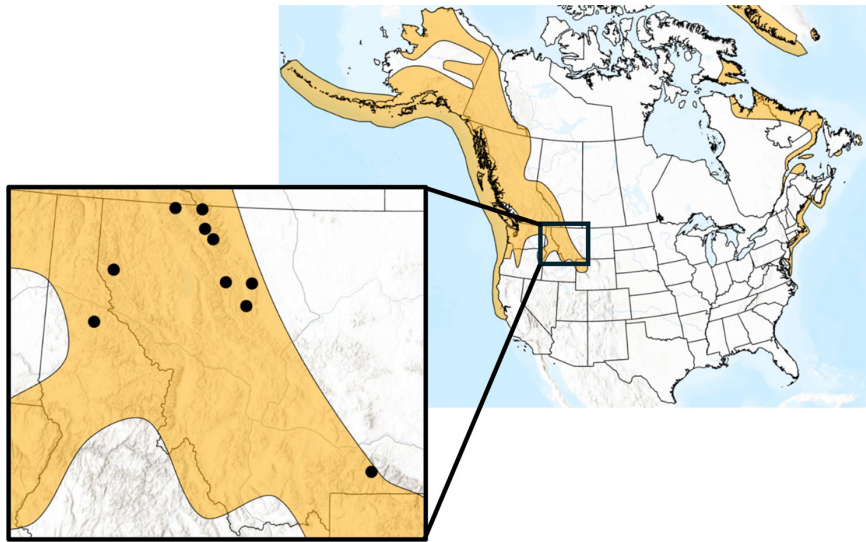


Figure 1. Harlequin duck North American range displayed in orange, with the study area in western Montana and northern Idaho and the selected breeding streams denoted by black circles in inset map (BirdLife International and Handbook of the Birds of the World 2022).

present on the site likely with a brood. We expected all 11 sites to be occupied by incubating females during the first sampling occasion in both years. However, reproductive success during the incubation period was required for the site to be occupied during the second, brood-rearing visit.

Ground-based foot surveys (GBS)

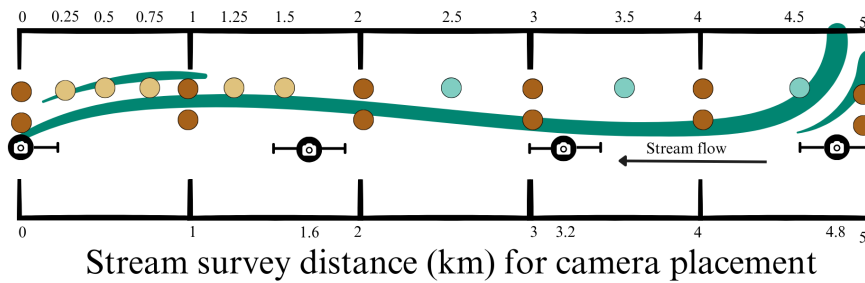
Ground-based foot surveys (GBS) consisted of at least two observers walking upstream together within the stream channel and continuously searching for harlequin ducks, while stream conditions and terrain allowed. When observers encountered unwalkable streams or sections of streams, one observer would maintain continual observation while the other observer navigated the forest beside the stream until making connection back with the stream (Hansen et al. 2019). Observers measured streamflow each day, at the start of the survey, using the float method (Robins and Crawford 1954) and recorded data that included survey start and end time, number of harlequin ducks seen, the duckling class, the number of observers, and data consistent with historical GBS (Supporting information). Surveys were initiated between 07:00 and 10:00 h and took varying amounts of time (six hours on average) to complete depending on the length of the stream segment and the complexity of the terrain.

Environmental DNA (eDNA)

Observers collected water samples for eDNA analysis while conducting a GBS, typically on the second day of each sampling occasion following the US Forest Service's National Genomics Center for Wildlife and Fish Conservation (NGC) protocol (Carim et al. 2016). Five liters of stream water were filtered, streamside, through a 1.5 μm -pore fiberglass filter and stored in silica desiccant (Carim et al. 2016). Observers collected water samples at three different spatial scales (250, 500, and 1000 m; Fig. 2), which allowed us to assess different

spatial sampling strategies. Samples were spaced at 250 m for the first 1500 m of the survey reach and every 500 m thereafter. Duplicate samples were collected at the sites corresponding to 1000 m spacing. eDNA water samples were collected from downstream to upstream within a site. All samples were extracted at the NGC in Missoula, MT, using a modified Qiagen DNEasy Blood and Tissue Kit optimized for eDNA filters (Franklin et al. 2019). eDNA samples were analyzed for harlequin duck DNA using a species-specific and sensitive quantitative polymerase chain reaction (PCR) assay developed by the NGC to detect a region of the harlequin duck cytochrome *c* oxidase subunit I mitochondrial gene (Franklin et al. unpubl.). Extracts were then analyzed for the presence of harlequin duck DNA in triplicate reactions using the optimized qPCR assay conditions from Franklin et al. (unpubl.) on a QuantStudio 3 Real-Time PCR System (Life Technologies). A sample was determined to have a harlequin duck detection if at least one of the triplicate reactions amplified harlequin duck DNA. Negative controls were included in the DNA extraction process by including samples that had filtered distilled water and in the qPCR analyses by using distilled water as a replacement of the DNA template in a triplicate reaction. All samples were tested for inhibition by including a TaqMan Exogenous Internal Positive Control (IPC) in the qPCR reaction. A sample was considered inhibited if the mean cycle value (Ct) of the IPC was more than one Ct delayed than the mean Ct of the IPC in the negative control reactions. To estimate the number of harlequin duck DNA copies in each reaction (QeDNA), samples were analyzed alongside a seven-level standard curve (31 250, 6250, 1250, 250, 50, 10, and 2 copies per reaction) following the same conditions mentioned above with reporting requirements of efficiency between 90 and 110% and R^2 above 0.990. eDNA target copy numbers were then estimated by generating a linear regression from the amplification Ct values

Stream survey distance (km) for eDNA sample collection



Key

- 2 samples every 1 km (1,000 m)
- 1 sample every 0.25 km (250 m) for the first 1.5 km
- 1 sample at the half km (500 m) for the remainder of the survey
- Ⓢ Cameras placed every river mile (1600 m)
- 300 m buffer around river mile in which cameras could be placed

Figure 2. Spatial sampling design for eDNA and camera traps on a 5-km stream segment.

of the known starting quantities of DNA in standard curve and applying the regression to each Ct value of a reaction.

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 (1600 m), starting at mile zero, along the surveyed site. Observers placed cameras on suitable pre-existing features, such as tree roots and logs, facing the stream within a 300 m radius of the river mile (Fig. 2). Cameras were given a 300 m radius to allow for some flexibility in river location to minimize false detections by moving water (i.e. camera placed just below rapid where water is calmer). The 300 m radius was pre-determined in ArcGIS Pro (Esri Inc. 2022) prior to the sampling occasion. One camera took photos every 5 min (time-lapse) while the other camera took motion-triggered photos. Observers removed the camera traps during the second sampling occasion, approximately 3 weeks after deployment.

Photos were checked for harlequin ducks 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 (ver. 2.3.0.0; Greenberg et al. 2019). Animals in photos were identified to species. Additionally, a random subset of 10 000 photos with a detection confidence less than 0.5 were processed by a reviewer to assess the rate of false negatives. All photos were preliminarily analyzed by one of two observers to isolate images with harlequin ducks and other waterfowl species. Images containing waterfowl were then reviewed and 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°; up or down=parallel to flow of stream within 45°; or water-facing=where the camera was pointed downward at the stream such that the lateral angle could not be assessed; Supporting information), predominant stream feature (boulder, rapid, run, or pool), and the number of photos taken per day. This information was determined through photo review and assessment from each camera.

Statistical methods

We confirmed each site was occupied by harlequin ducks 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 ver 4.2.3 (Bates et al. 2015, www.r-project.org). 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 harlequin duck 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 were necessary to achieve a cumulative detection to 0.8, 0.9, and 0.95 using the equation:

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

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 (Loane et al. 1964, Kéry 2002, Canessa et al. 2012). Finally, we calculated the cumulative detection probability when methods were combined (i.e. eDNA samples taken in tandem with a GBS).

Ground-based foot survey models

For the incubation and brood-rearing periods, we built separate, but identical, models relating detection of harlequin ducks 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:

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

Environmental DNA models

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

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

Camera trap models

For the motion-detection and time-lapse camera traps, we built separate, but identical, models relating detection of harlequin ducks 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:

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

Results

Ground-based foot survey

We completed 118 GBS on 11 sites over the two years; 50 occurred during the incubation period and 68 during the brood-rearing period (Supporting information). The mean probability of detecting harlequin ducks using a GBS was similar between the two periods (0.51 and 0.45), but their covariate relationships differed.

During the incubation period, harlequin ducks were detected on 27 surveys and the mean detection probability of a single, one day, 5-km GBS was 0.51 (95% CI: 0.31–0.71). To achieve a mean cumulative detection probability > 95%, five GBS would be required ($P=0.96$, 95% CI: 0.85–0.99; Fig. 3). Mean QeDNA and CFS exhibited positive relationships with detection ($p < 0.01$, $p = 0.094$, respectively; Fig. 3, Supporting information). Based on these relationships, we predicted the mean number of GBS required to achieve 80, 90, and 95% cumulative detection probabilities under different stream scenarios. For example, 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 (see the Supporting information for tables with different stream scenarios for each method across both periods).

During the brood-rearing period, harlequin ducks were detected on 31 surveys and the mean detection probability of a single 5-km GBS was 0.45 (95% CI: 0.32–0.58). To achieve a mean cumulative detection probability > 95%, five GBS would be required ($P=0.95$, 95% CI: 0.86–0.99; Fig. 3). Mean QeDNA exhibited a positive relationship with detection while pace exhibited a negative relationship ($p=0.091$, $p=0.078$, respectively; Fig. 3, Supporting information).

Environmental DNA

We collected 717 eDNA samples over the two years; 315 samples during the incubation period and 403 samples during the brood-rearing period. The mean probability of detecting harlequin ducks at a single eDNA sampling point within a site using eDNA differed between the two periods (0.49 and 0.27), but their significant covariates were similar, however their relationship was opposite.

During the incubation period, harlequin ducks were detected in 155 eDNA samples. The mean detection probability at the mean CFS (214.81 ft³ s⁻¹) at a cobble site, taking a single eDNA sample was 0.49 (95% CI: 0.23–0.75). To achieve a mean cumulative detection probability > 95%, six eDNA samples collected throughout a 5-km site would be required ($P=0.96$, 95% CI: 0.79–0.99; Fig. 4). CFS

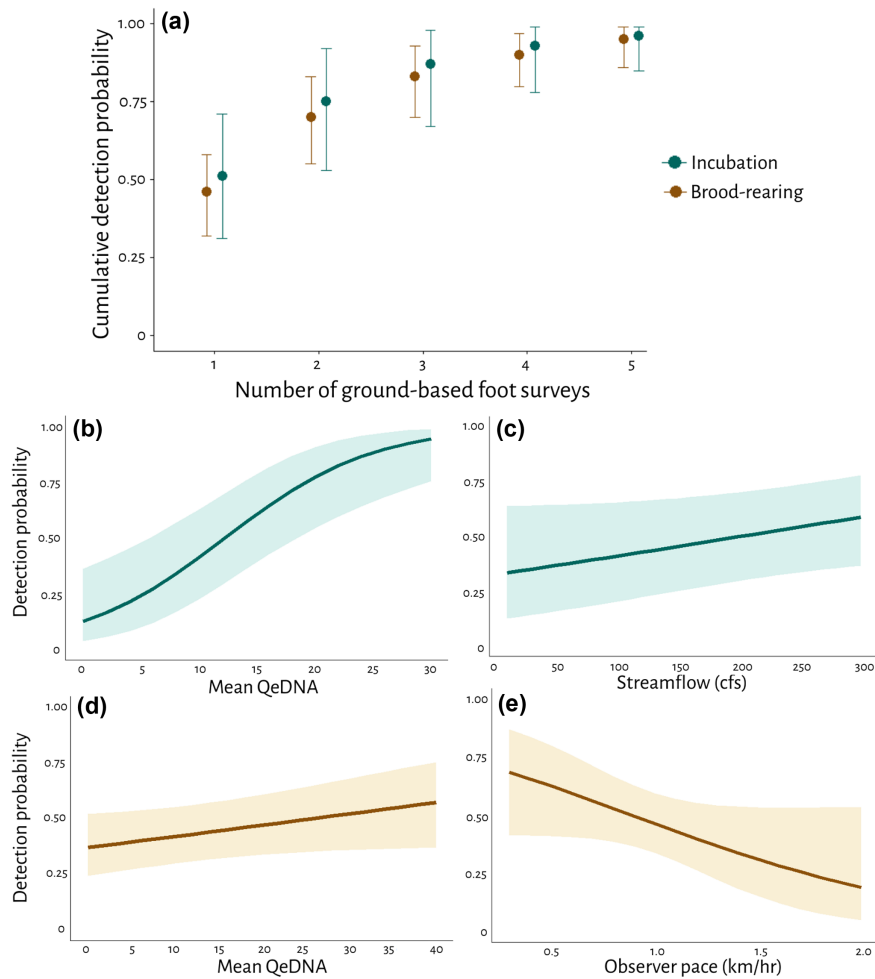


Figure 3. Modeled relationships between detection probability of a single, 5-km ground-based foot survey (GBS) and modeled covariates. (a) Cumulative detection probability versus the number of GBS conducted when all covariates are held at their mean for both the incubation and brood-rearing periods. (b) Effect plot showing how mean QeDNA affects detection probability during the incubation period. (c) Effect plot showing how streamflow affects detection probability during the incubation period. (d) Effect plot showing how mean QeDNA affects detection probability during the brood-rearing period. (e) Effect plot showing how observer pace affects detection probability during the brood-rearing period.

exhibited a negative relationship with detection ($p=0.0516$; Fig. 4, Supporting information).

During the brood-rearing period, harlequin ducks were detected in 194 eDNA samples and the mean detection probability at the mean CFS ($116.50 \text{ ft}^3 \text{ s}^{-1}$) at a cobble site, taking a single eDNA sample was 0.27 (95% CI: 0.11–0.53). To achieve a mean cumulative detection probability > 95%, 12 eDNA samples collected throughout a 5-km site would be required ($P=0.95$, 95% CI: 0.74–0.99; Fig. 4). CFS exhibited a positive relationship with detection ($p=0.00208$; Fig. 4, Supporting information).

Camera traps

We deployed 198 cameras over the two years, with an equal split (99 each) between time-lapse and motion-detection settings. Cameras were deployed for 4454 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 harlequin ducks using a camera trap was similar between motion-detection and time-lapse (0.13 and 0.16), but their covariate relationships differed.

For motion-detection camera traps, harlequin ducks were detected on 20 cameras in 327 photos and the mean detection probability with a single camera pointed directly across the stream at a boulder for 22 days, the most prevalent set up, was 0.13 (95% CI: 0.04–0.32). To achieve a mean cumulative detection probability > 95%, 35 camera traps would be required along a 5-km site ($P=0.95$, 95% CI: 0.69–0.99; Fig. 5). Trap nights had a positive relationship with detection, and more trap nights resulted in higher detection ($p=0.0300$; Fig. 5, Supporting information).

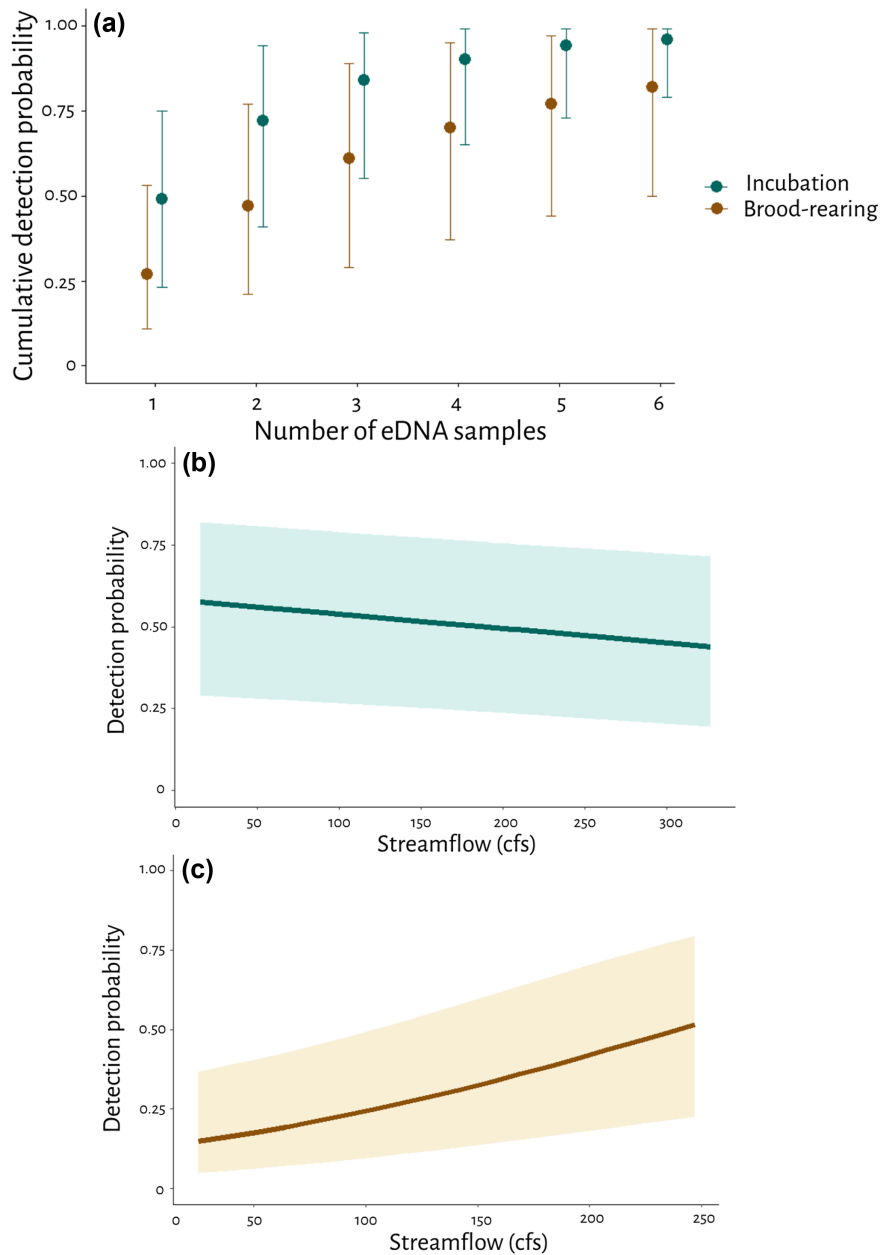


Figure 4. Modeled relationships between detection probability of a single eDNA sample and modelled covariates. (a) Cumulative detection probability versus the number of eDNA samples collected when all covariates are held at their mean for both the incubation and brood-rearing periods. (b) Effect plot showing how mean streamflow (CFS) effects detection probability during the incubation period. (c) Effect plot showing how mean streamflow (CFS) affects detection probability during the brood-rearing period.

For time-lapse camera traps, harlequin ducks were detected on 22 cameras in 387 photos and the mean detection probability with a single camera trap pointed directly across the stream at a run for 22 days, the most prevalent set up, was 0.16 (95% CI: 0.07–0.34). To achieve a mean cumulative detection probability > 95%, 21 camera traps would be required along a 5-km site ($P=0.95$, 95% CI: 0.78–0.99; Fig. 5). None of the four covariates were significant in predicting detection (Fig. 5, Supporting information).

To assess rates of false negatives we reviewed 10 000 randomly selected photos with a detection confidence > 0.5

and found harlequin ducks in 3 photos for a false positive rate of 0.0003.

Combining methods

After analyzing each method individually, we calculated the cumulative detection probability of different combinations of these methods. The most effective combination for detecting harlequin ducks in a single-day effort is to combine a 5-km GBS with eDNA. During the incubation period observers can take five eDNA samples in tandem with a GBS to achieve a mean cumulative detection probability of

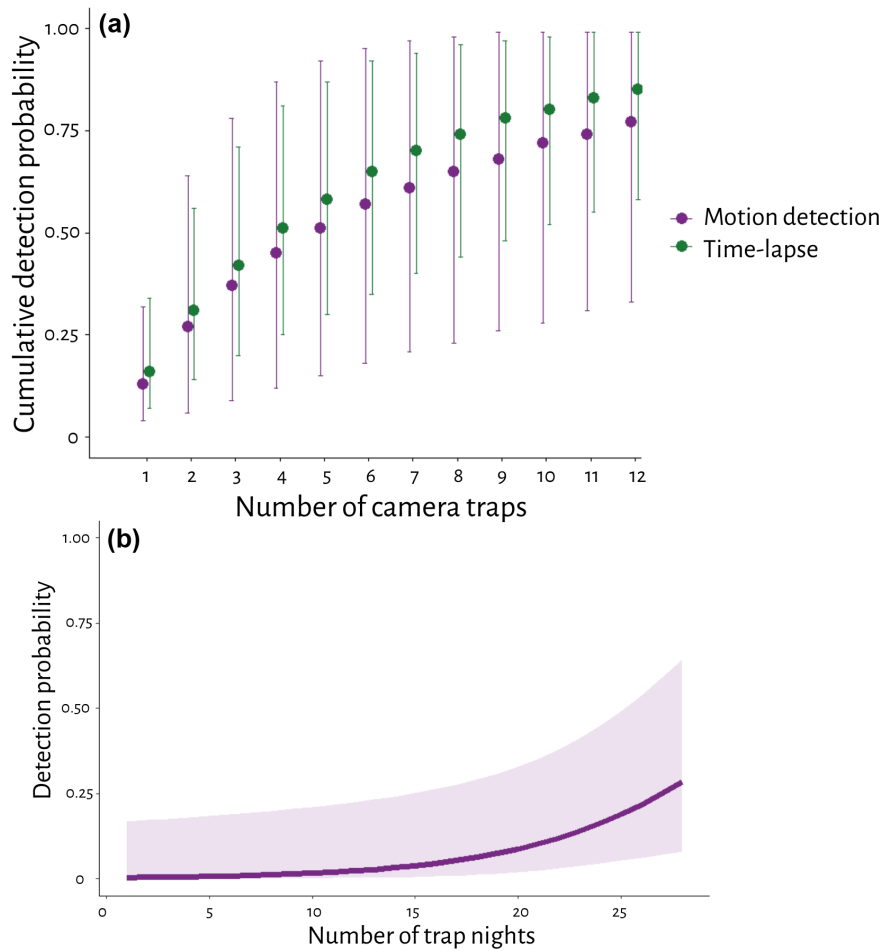


Figure 5. Modeled relationships between detection probability of a single, 22-day camera deployment and modeled covariates. (a) Cumulative detection probability versus the number of cameras deployed for 22 days when all covariates are held at their mean for both motion-detection and time-lapse camera traps. (b) Effect plot showing how mean number of trap nights affects detection probability for motion-detection camera traps.

0.97 (95% CI: 0.87–0.99; Fig. 6). During the brood-rearing period, 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 5-km 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 mean cumulative detection probability of 0.87 (95% CI: 0.76–0.96; Fig. 6).

Additional analysis (lorelogram)

To determine adequate spatial distribution of eDNA samples, we assessed spatial independence of our eDNA samples using a lorelogram (Heagerty and 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 pairs of samples taken at distances from each other ranging from 250–1000 m (Fig. 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 250, 500, 750, and 1000 m distances between samples. We found that the eDNA detections were correlated for the first 750–1000 m then approached 0 at distances ≥ 1000 m apart (Fig. 7).

Discussion

This study quantified the detection probability of GBS, eDNA, and camera traps to determine occupancy of harlequin ducks 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 and validated previous concerns that this method may

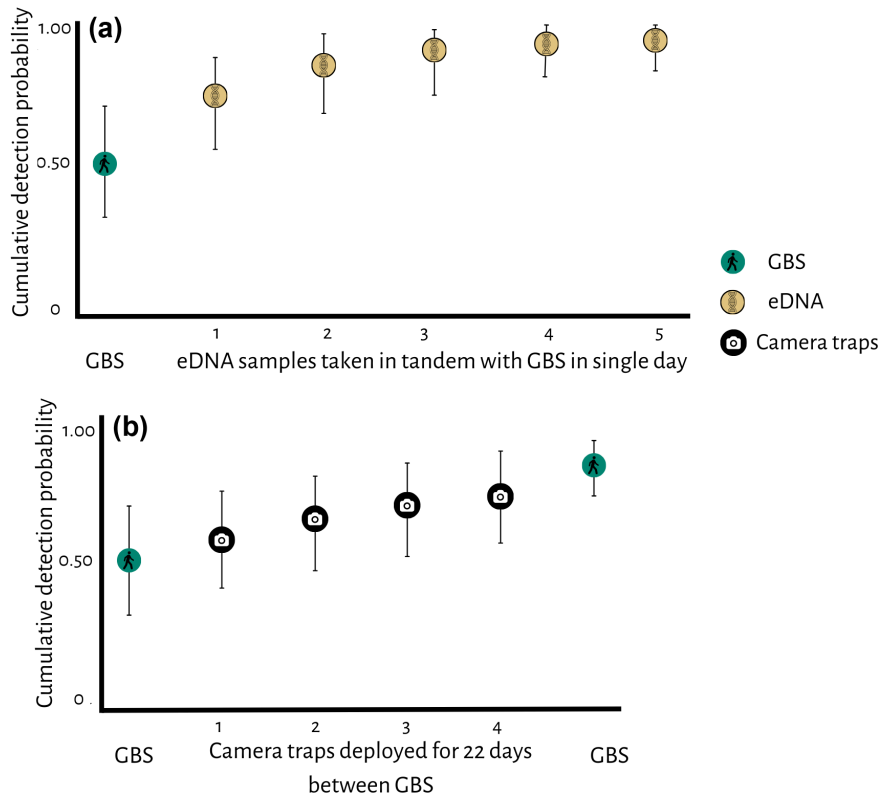


Figure 6. Cumulative detection probabilities of combined survey approaches: (a) Graph showing cumulative detection probability increasing with each additional environmental DNA sample taken in tandem with a ground-based foot survey in a single-day sampling effort during the incubation period. (b) Graph showing cumulative detection probability increasing with two GBS – one during incubation and one during brood rearing – and with each additional time-lapse game camera.

underrepresent the presence of harlequin ducks on streams. It is possible to attain a cumulative detection probability of > 0.95 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 periods, and clear study objectives

to guide method selection. We use this new understanding to provide recommendations for the use of these approaches for harlequin ducks and similar stream-residing waterbirds.

For all survey methods, stream condition and implementation covariates influenced survey efficacy. For GBS, differences among observers explained more variation in detection probability than stream conditions. While there

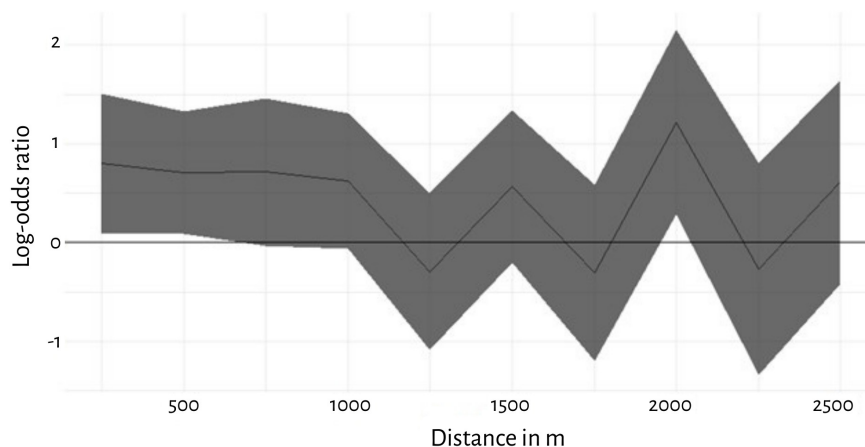


Figure 7. Lorelogram and 95% confidence intervals for distance between eDNA samples. Samples become spatially independent between 750 and 1000 m when 95% CI's cross 0 on the y-axis.

was a discrepancy among observers, studies of 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 and Specht 2015). For eDNA, streamflow had the greatest effect on harlequin duck detection but showed opposite interactions between the two time periods: during the incubation period, detection increased with decreasing streamflow and during the brood-rearing period detection increased with increasing streamflow. This outcome suggests that streamflow potentially exhibits a quadratic relationship with detection probability over the breeding season. During the incubation period, streamflow typically increases due to spring runoff which could dilute and/or flush DNA out of the system at faster rates resulting in less genetic material captured on the filter (Barnes et al. 2014, Shogren et al. 2017, Curtis et al. 2021). However, during the brood-rearing period streamflows are typically reduced with water remaining shallow, less turbid, or potentially drying up completely. Therefore, lower detection probability with lowered streamflow could be explained by decreased DNA transport from the source individuals and increased DNA degradation when exposed to higher temperatures and more UV from the sun, and/or increased DNA settling into the benthic substrate at reduced flows and therefore not being available in the water column at high enough concentrations for detection (Barnes et al. 2014, Strickler et al. 2015, Shogren et al. 2017, Fremier et al. 2019). 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 periods for GBS and eDNA. This result could be explained by differences in harlequin duck behavior between the two time periods. Using GBS, we detected a slight (0.06) decrease in mean 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 may be distributed more randomly 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 patchier distribution of harlequin ducks along the stream may help explain the difference in eDNA detection between the incubation and brood-rearing periods. DNA only persists for limited temporal and spatial periods before degrading or diluting enough to be undetectable using eDNA, making a patchier distribution of harlequin ducks harder to detect.

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 provide information about attempted breeding and stream occupancy. Data

collected during the brood-rearing period offer 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 and breeding attempt are of interest, it is more effective to survey during the incubation period, and we recommend conducting surveys during this period to establish a baseline of stream occupancy across a region of management interest. In contrast, if nest success or potential recruitment is of interest then surveying during the brood-rearing period is more effective. We recommend that future surveys be planned for the period of interest depending on study objectives. We also recommend that when making inferences from historical 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 probability 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. Six eDNA samples spread across a 5-km reach will yield > 95% (95% CI: 3–12 samples) cumulative detection probability during the incubation period. Additionally, following the collection protocol for eDNA is relatively easy, and the standardized protocol eliminates observer bias and allows anyone to collect samples, not just trained biologists. However, eDNA can only tell us the presence or absence of harlequin ducks within a short spatial and temporal portion of the stream; therefore, we cannot say for certain the extent of the stream that is occupied. Notably, our lorelogram analysis found that our eDNA samples were spatially independent of one another at ~ 750–1000 m downstream which could indicate the transport distance at which harlequin duck DNA persists at detectable levels. This outcome is consistent with some eDNA persistence studies in streams (Barnes et al. 2014, Jane et al. 2015, Shogren et al. 2017, Fremier et al. 2019), though a controlled experiment would be needed to verify this result. 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 a minimum of two field days – 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 time before, during, and after

deployment per unit, and although detection probability increases with each day cameras are deployed, photo-processing time also increases (Table 2). 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 they are not as prone to issues related to trigger sensitivity.

This study provides a comprehensive understanding of the efficacy of non-invasive survey methods for monitoring harlequin ducks, a stream-residing waterbird, and can provide a framework to inform techniques for improved monitoring of other species. Notably, many stream-residing waterbirds globally are monitored by a similar GBS method (Siegfried et al. 1975, Ullrich 2007, Cerón and Trejo 2012, D’Amico et al. 2020, Malham 2023) and, if resources are available, using eDNA or camera traps in tandem with already existing protocols may be a useful tool for increasing confidence in stream occupancy state. Importantly the application and inference of these methods must be informed by the life history of the target species and species specific modifications may be needed for optimal implementation. For example, unlike harlequin ducks, males of many stream-residing waterbirds are territorial and reside on their territories year-round. These include species such as the torrent duck *Merganetta armata*, dippers (American dipper *Cinclus mexicanus*, white-throated dipper *Cinclus cinclus*), blue duck *Hymenolaimus malacorrhynchos*, African black duck *Anas sparsa*, and Salvadori’s teal *Salvadorina waigiensis* (Bakus 1959, Kear 1975, Ball et al. 1978, Eldridge 1986, Cardona and Kattan 2021, Ippi et al. 2018, Magoolagan and Sharp 2018). Therefore, an eDNA detection during brood rearing would confirm presence but does not confirm breeding success without visual confirmation of chicks, which GBS can provide. Importantly though, eDNA could help identify active territories and priority areas for conservation action.

Thoughtful placement of camera traps could also prove useful for territorial species. For example, a camera trap could be placed in a known occupied territory and may be able to capture information on brood success if chicks are captured in photos, information that the presence of eDNA does not provide and may be missed by GBS. For other species that rely on water for prey but are not always on a stream (e.g. ospreys, *Pandion heliaetus*), placement of camera traps could be tailored to target shorelines, reducing photos triggered by water movement and capturing diving and foraging behaviors. Additionally, recent development of other non-invasive

survey methods such as automated recording units (Slettedahl et al. 2015, Shonfield and Bayne 2017, Stewart 2023) and infrared drones (Bushaw et al. 2021, Dundas et al. 2021, Mackell et al. 2024) may be useful complements to methods presented in this study.

Management implications

This study provides wildlife managers in the Northern Rockies with a greater understanding of the efficacy of various harlequin duck detection tools which can help increase their confidence in their ability to detect trends in occupancy and maximize efficient use of limited resources, ultimately allowing them to make more informed management decisions. The choice of methodology and timing depends on monitoring objectives and available resources. 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.

To achieve high detection probability in a single-day effort, eDNA sampling is recommended. A combination of eDNA and GBS is also both an efficient and effective approach for surveying harlequin ducks. Observers can reach a mean cumulative detection probability of > 0.95 using only eDNA, however eDNA samples need to be spread throughout a stream so are easily paired with GBS. This approach has the added benefit of attaining count data whereas eDNA can only offer presence/non detection data.

eDNA has proved to be a powerful tool when resources or funding is limited. eDNA samples also contain DNA from other species that interact with the water, enabling the detection of multiple species from a single field sample (Chen et al. 2025). One eDNA sample can be analyzed for up to eight total species and samples can be submitted and archived in research repositories for further inventory investigation (Carim et al. 2020). Water samples that were originally collected for eDNA analysis of other aquatic species of interest can be reanalyzed for harlequin duck DNA with no new field time and no additional collection costs. When thoughtfully selected, these archived samples could provide deeper insight into areas with marginal habitat, difficult access, discontinuous GBS data, and provide valuable information on additional taxa of interest, such as fish and amphibians. Furthermore, due to eDNA’s standardized protocol it does not have observer bias and allows for samples to be taken by a wider array of people who might not be trained in harlequin duck identification (e.g. fish biologists, citizen scientists, hydrologists).

Table 2. Effort per ground-based foot survey, eDNA sample, and camera trap.

	Pre-survey time required	Post-processing time	Average time per sample	No. 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 h per day camera is deployed	20 min to set up 5 min to take down	2
Time-lapse camera trap	20 min	2.5 h per day camera is deployed	20 min to set up 5 min to take down	2

Cameras were the least effective method, and we do not generally recommend them for harlequin duck surveys; however, they may be useful where a GBS or eDNA is impractical due to challenging terrain. Cameras may be the best way to determine the presence of harlequin ducks across the season in select locations, such as areas of aggregation (e.g. stream junctures with larger rivers where broods may aggregate at the end of the brood-rearing period prior to migration). If deciding to use camera traps, we recommend using time-lapse. However, if you choose to use motion-detection cameras, be aware that rapids will trigger your camera, and these are best placed on sections with calmer water.

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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Author contributions

Holli Holmes: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Funding acquisition (supporting); Investigation (lead); Methodology (equal); Project administration (lead); Resources (equal); Software (lead); Supervision (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Hannah Specht:** Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Funding

acquisition (supporting); Investigation (equal); Methodology (equal); Project administration (supporting); Resources (supporting); Software (supporting); Supervision (supporting); Validation (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Lisa Bate:** Conceptualization (equal); Funding acquisition (equal); Investigation (supporting); Methodology (supporting); Project administration (supporting); Resources (supporting); Supervision (supporting); Writing – review and editing (supporting). **Kristina Smucker:** Conceptualization (equal); Funding acquisition (equal); Methodology (supporting); Project administration (supporting); Resources (supporting); Writing – review and editing (supporting). **Casey McCormack:** Conceptualization (equal); Funding acquisition (equal); Investigation (supporting); Methodology (supporting); Project administration (supporting); Resources (supporting); Supervision (supporting); Writing – review and editing (supporting). **Cara Staab:** Conceptualization (equal); Funding acquisition (equal); Methodology (supporting); Project administration (supporting); Resources (supporting); Writing – review and editing (supporting). **Thomas Franklin:** Data curation (supporting); Methodology (supporting); Resources (supporting); Validation (supporting); Writing – review and editing (supporting). **Dan Bachen:** Conceptualization (supporting); Data curation (supporting); Methodology (supporting); Writing – review and editing (supporting). **Bryce Maxell:** Conceptualization (supporting); Data curation (supporting); Methodology (supporting); Writing – review and editing (supporting). **Allison Puchniak Begley:** Conceptualization (supporting); Methodology (supporting); Resources (supporting); Writing – review and editing (supporting). **Joshua Millsbaugh:** Conceptualization (supporting); Formal analysis (supporting); Funding acquisition (equal); Investigation (supporting); Methodology (supporting); Project administration (supporting); Resources (supporting); Software (supporting); Supervision (supporting); Validation (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.2v6wwq039> (Holmes et al. 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

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