

Inferring bird communities on remote freshwater lakes through time-lapse imagery

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Abstract

Assessing bird diversity and associated ecological patterns in remote freshwater lakes presents challenges that require innovative approaches. Here, we evaluated the utility of time-lapse images from camera traps for this purpose using two lakes in Haida Gwaii, British Columbia, Canada. We consider four key factors: (1) manual versus automated image processing, (2) data validation through in-person observations, (3) the ability of time-lapse data to capture known ecological patterns, and (4) variation in sampling effort. We find that (1) MegaDetector, a common AI approach, is not effective at detecting birds from time-lapse images—necessitating manual screening, (2) relative bird abundances were correlated between time-lapse and in-person observer data, (3) time-lapse data capture previously documented ecological variation in space and time, and (4) sampling effort per camera trap can be, under certain scenarios, scaled down, but camera trap position and time-lapse frequency greatly influence bird detectability. Our research builds on the few previous studies that use time-lapse imagery to detect birds, and our work is the first to focus on detecting ecological patterns on freshwater lakes in remote landscapes. Camera trap technologies can shed light on avifauna in remote freshwater lakes, but additional developments are needed to maximize utility of such applications.

Key words: avian diversity, camera traps, freshwater habitats, ornithology, remote sensing, time-lapse imagery

Résumé

L'évaluation de la diversité et des modèles écologiques de l'avifaune des lacs d'eau douce isolés présente actuellement des défis nécessitant des approches innovatrices. Conséquemment, nous avons mesuré l'efficacité de la chronocinématographie (*time-lapse imagery*) obtenue via des pièges photographiques installés aux abords de deux lacs d'Haida Gwaii en Colombie-Britannique au Canada. Notre analyse tient compte de quatre facteurs clés: (1) la détection manuelle ou automatisée des images, (2) la validation des données par des observations en personne, (3) la capacité de la chronocinématographie à capturer des modèles écologiques connus et (4) la variation de l'effort d'échantillonnage. Nous avons constaté que: (1) MegaDetector, une approche IA courante, n'est pas efficace pour détecter des oiseaux à partir de la chronocinématographie et une détection manuelle est ainsi nécessaire. (2) Les données d'abondances relatives d'oiseaux provenant de la chronocinématographie sont corrélés avec les données issues d'une présence sur site. (3) Les données chronocinématographiques capturent les variations écologiques spatiales et temporelles déjà documentées. (4) L'effort d'échantillonnage par piège photographique peut dans certains scénarios être réduit, mais la position du piège photographique et la fréquence de la prise d'image influencent grandement la détectabilité des oiseaux. Par ailleurs, notre recherche permet d'enrichir des résultats d'études antérieures portant sur la détection de l'avifaune à l'aide de la chronocinématographie et elle est pionnière en matière de détection de modèles écologiques sur des lacs d'eau douce de régions isolées. De plus, nous déterminons de quelle manière les technologies de pièges photographiques peuvent mettre en lumière la structure et la diversité de l'avifaune de lacs d'eau douce isolés et expliquons quels sont les développements supplémentaires nécessaires permettant de maximiser l'utilité de ces applications. [Ceci est une traduction fournie par l'auteur du résumé en anglais.]

Mots-clés : Avifaune, diversité, chronocinématographie, habitats d'eau douce, pièges photographiques, ornithologie, télé-détection

Introduction

Understanding and conserving ecosystems relies on the accurate and seasonally representative repeated assessment of biodiversity assemblages (Williams et al. 2002; McNellie et al. 2020; Mooney et al. 2020). Such monitoring is particularly challenging in remote areas, where comprehensive information about community diversity, assemblage dynamics, and species interactions is often lacking. Conventional biodiversity assessment and monitoring rely primarily on direct observations by on-the-ground observers (Beng and Corlett 2020). Given the logistical challenges of extended in-person presence in the field (Gomez and Pourquié 2009; Basset et al. 2012), especially at remote sites, these conventional efforts are usually short (e.g., days or weeks in a single season) and thus offer only a snapshot of any given location. As such, conventional assessment methods in remote areas can be misleading when attempting to understand changes in seasonal abundances (e.g., migratory animals), episodic visits (e.g., large home ranges), or “cryptic” animals (e.g., nocturnal).

To overcome the challenges of conventional in-person biodiversity assessments, researchers have increasingly turned to remote sensing tools, including environmental DNA (eDNA), acoustic recording devices (e.g., song meters), citizen (or community) science initiatives (Beng and Corlett 2020), and camera traps. These tools can, in theory, provide continuous, year-round monitoring for certain species, albeit with their own sets of limitations. For instance, even though eDNA offers a powerful tool for detecting the presence of organisms (Rees et al. 2014; Beng and Corlett 2020), it often cannot—at least not without continuous intensive effort—provide accurate assessment of abundances or some temporal changes (Valentini et al. 2016; Deiner et al. 2017). When it comes to acoustic recordings, a major limitation is the obvious inability to assess non-vocalizing species. And while citizen science initiatives can be extremely useful, they also can be unreliable in some contexts (Dickinson et al. 2010) and are typically heavily biased toward accessible areas (Geurts et al. 2023), making them infeasible for remote ecosystems.

For some taxa, camera traps provide a solution to the problems facing remote assessments (Caravaggi et al. 2017; Frey et al. 2017; Augustine et al. 2018; Burgar et al. 2018; Jacques et al. 2019). Indeed, camera traps are now commonly used to assess wildlife distributions, abundances, behaviour, and community structure (Rovero et al. 2013; Meek et al. 2014; Burton et al. 2015). The typical approach is to use passive infrared motion sensors that “trigger” the camera to take a photo (Marcus Rowcliffe et al. 2011). To date, the vast majority of studies using these camera traps have focused on mammals (e.g., ~94% in the meta-analysis of Burton et al. 2015), with relatively few focusing on avian species (O'Brien and Kinnaird 2008; Pascalis et al. 2018; Qianwen et al. 2018; Fontúrbel et al. 2020; Sun et al. 2021). The comparatively few studies employing camera traps to monitor avian communities tend to focus on terrestrial bird species, often those of large body size (O'Brien and Kinnaird 2008; Scheideman et

al. 2017; Whitworth et al. 2018; Nykänen et al. 2023). Studies targeting aquatic bird species remain scarce, with most focusing on monitoring seabird colonies (Pascalis et al. 2018; Black 2019). To our knowledge, no study has yet attempted to use camera traps to seasonally characterize and monitor aquatic bird species on freshwater lakes. This approach presents unique challenges, including increased distance of the target animal from the camera, presence of waves, reflections on the water surface, and moving animals (compared to nesting sites).

Given their role as indicators of specific environmental changes (Jørgensen et al. 2016), and recent changes in bird phenology in response to global climate change (Hurlbert and Liang 2012), characterizing and tracking freshwater avian assemblages in remote areas is critical for their conservation (Neate-Clegg et al. 2020). As an example, migratory birds spend about 25%–30% of their annual cycle in transit between breeding grounds and wintering areas (Bonter et al. 2009). These temporary stopovers can be important for successful migration, and yet they can be hard to monitor in person owing to the short and sometimes unpredictable occurrence in both space and time (Sillett and Holmes 2002). Further, information on freshwater birds can be important for answering ecological and evolutionary questions. For instance, in our study system, non-breeding Common Loons (*Gavia immer* (Brünnich, 1764)) are present at Drizzle Lake (Haida Gwaii, BC) in large numbers (up to 89 individuals per day) in July (Reimchen and Douglas 1980, 1984, 2021; Reimchen 1994). During their 4–6-week peak stopover, as a group, these birds consume approximately 105 000 threespine stickleback (*Gasterosteus aculeatus* Linnaeus, 1758) and thus exert strong selection pressures that dramatically shape the ecology and evolution of the stickleback (Reimchen 1994; Reimchen and Bergstrom 2023). Yet these relatively short but significant bird stopovers are likely unknown for countless other lakes that do not have onsite year-round observers.

We anticipated that a time-lapse (rather than a trigger) approach would be necessary because birds on lakes often will be too distant or small to trigger motion detectors—as is known in other contexts (Pascalis et al. 2018; Black 2019; Naqvi et al. 2022; Leorna and Brinkman 2024). For such imagery to be a valuable tool in avifauna monitoring, several factors should be evaluated. First, we would hope for rapid image processing given the very large number of photographs potentially taken. Second, the data collected should be comparable to that obtained through conventional in-person observation methods (Kenney et al. 2024). Third, the data should capture ecological patterns of species richness and abundance (e.g., variation in time and space) that are, based on previous work, known to be present. Finally, it would be useful to know the extent to which effort-per-site could be scaled back to enable scaling up the number of sites monitored. Our study site offers an excellent setting to address these factors.

Question 1: A potential limiting factor when using time-lapse approaches can be transforming the raw images into

usable data (Kellenberger et al. 2020). That is, when each photo must be manually reviewed and classified, projects that gather millions of images can become unmanageable (Fennell et al. 2022). One approach to overcome this limitation is the use of crowd-sourcing platforms (e.g., MammalWeb and Zooniverse), where members of the public can screen images (Swanson et al. 2016; Hsing et al. 2018). However, this approach requires data types that engage and maintain public interest, as well as considerable effort to ensure data quality. Another approach is the use of machine learning and computer vision to sort through blank images (Fennell et al. 2022; Leorna and Brinkman 2022). Such Artificial Intelligence (AI) approaches use different methodologies, such as convolutional neural networks (CNNs) or region-based CNNs (R-CNNs), to detect and classify animals and humans in camera trap images through learning to recognize unique patterns and shapes. AI workflows have been used to label images with species identifications (Tabak et al. 2019; Schneider et al. 2020) and identify individual animals (Halloran et al. 2015; Schneider et al. 2019). Further, tandem AI-human approaches are used to increase the efficiency of human image labellers by removing blanks and creating bounding boxes around likely animals (e.g., Clarfeld et al. 2023). One of the most commonly applied and easily accessible AI tools is MegaDetector (Beery et al. 2019), a pre-trained image detection model capable of identifying broad groups of objects (animals, people, vehicles). Given that the utility of this model has not yet been evaluated in freshwater settings to identifying images containing animals from images that do not, we here ask: *to what extent can MegaDetector detect images of birds on lakes?*

Question 2: If we assume that data collected by a human observer is closer to the “truth”, comparing such boots-on-the-ground data to that from camera traps speaks to the quality of inferences about absolute abundances, such as how many birds are present at any given time. However, even if camera traps are poorly suited for such “absolute” inferences, perhaps they are still valuable at inferring relative differences between times or places. Therefore, we here ask: *can data collected by a human observer validate data collected from camera traps?*

Question 3: Based on long-term monitoring (Reimchen and Douglas 1980, 1984, 2021; Thomas E. Reimchen pers. obs.), we know that birds on our focal lakes exhibit several different patterns. First, our two study lakes have different bird communities, with Drizzle having more Common Loons and Boulton having more Hooded Mergansers (*Lophodytes cucullatus* (Linnaeus, 1758)). Second, bird communities change with seasons where, for example, Common Loons are much more abundant in July than in August (Reimchen and Douglas 1984). Third, birds are generally more abundant in the morning than mid-day, most obviously for Common Loons at Drizzle (Reimchen and Douglas 1984). We therefore here ask: *to what extent are camera traps effective in capturing known ecological patterns?*

Question 4: The above considerations revealed that, for certain types of ecological questions relating to aquatic birds, time-lapse imagery can be a useful tool (details below). As is often the case, the main challenge lies in the amount of effort

required to manually sort through the images (Greenberg et al. 2019; Leorna and Brinkman 2024). In our particular case, the AI approach employed was ineffective (details below), and so, time-consuming manual screening was necessary. In such cases, considerable effort would be saved by reducing the number of images taken (or screened) without compromising robust inferences. We therefore finally ask: *how does variation in survey effort influence the conclusions derived from camera traps?*

Materials and methods

Study area

Haida Gwaii, BC, Canada, offers an excellent opportunity to evaluate the utility of camera traps for remote sensing of bird communities and diversity on lakes. Located approximately 100 km off the mainland of British Columbia, Haida Gwaii is situated along a major migratory corridor and serves as seasonal habitat for a number of aquatic avian species (Bellrose 1980). Our study centers on two ecologically significant lakes: Drizzle and Boulton (Fig. 1). Both lakes have been studied intensively over the last four decades (Reimchen and Douglas 1980, 1984, 2021; Reimchen 2000; Reimchen and Nosil 2001a, 2001b, 2002, 2006).

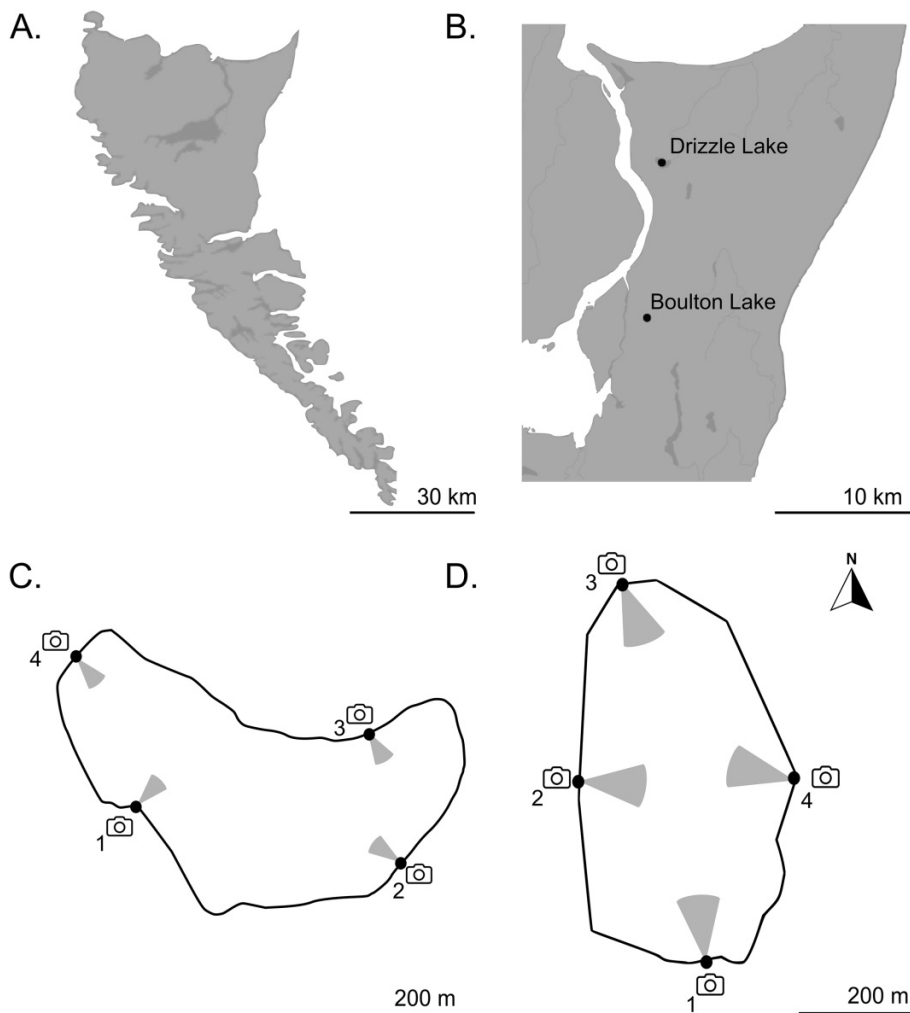
One of our focal lakes, Drizzle (53°56'N, 132°05'W), has been an Ecological Reserve since 1973 and has long served as a benchmark for assessing ecological and evolutionary change. This 1.15 km² lake is located in the northeast corner of Graham Island in a sphagnum bog and coniferous forest (Reimchen and Douglas 1980). The approximately hour-long hike through a bog makes this lake infrequently visited apart from some members of our research team. Our other focal lake, Boulton (53°47'N, 132°06'W), is also located on Graham Island ~20 km from Drizzle Lake. This 0.20 km² lake lies in an area of mixed muskeg and coniferous forest (Reimchen 1980).

Data collection and analyses

In 2017, camera traps were deployed on 10 July at Drizzle Lake and on 12 July at Boulton Lake. On each lake, four Reconyx (Holmen, WI, USA) PC900 hyper fire professional covert camera traps equipped with lithium-ion batteries were strategically mounted along the shoreline in hopes of capturing as much of the lake surface as possible (Fig. 1). Each camera trap was mounted approximately 1 m high on a tree facing the lake. We programmed photographs at set time intervals: every 5 min between 4:30 am and 10:55 pm, thus ensuring images throughout daylight hours, as well as during dawn and dusk. We also enabled motion triggers, so we could consider images of birds from both motion-triggered images and time-lapse images (Leorna and Brinkman 2022). The cameras were set up to take photos until the batteries died, which was between 11 November and 2 December (see Suppl. Mat. for detailed end dates).

To estimate the maximum detection distance from our images, we used available information on bird size (e.g., body length) and the corresponding apparent size of the selected size measure (i.e., number of pixels measured in ImageJ) to estimate the distance between the camera and the bird us-

Fig. 1. Maps depicting the location and estimated captured area for each camera trap. Base maps were obtained from iMapBC (<https://www2.gov.bc.ca/gov/content/data/geographic-data-services/web-based-mapping/imapbc>) and modified using Inkscape. Panel (A) is Haida Gwaii. Panel (B) is Graham Island with focal lakes identified. Panel (C) is Drizzle Lake with approximate viewshed area for each camera. Panel (D) is Boulton Lake with approximate viewshed area for each camera. Note that depictions of camera viewsheds are not to scale.



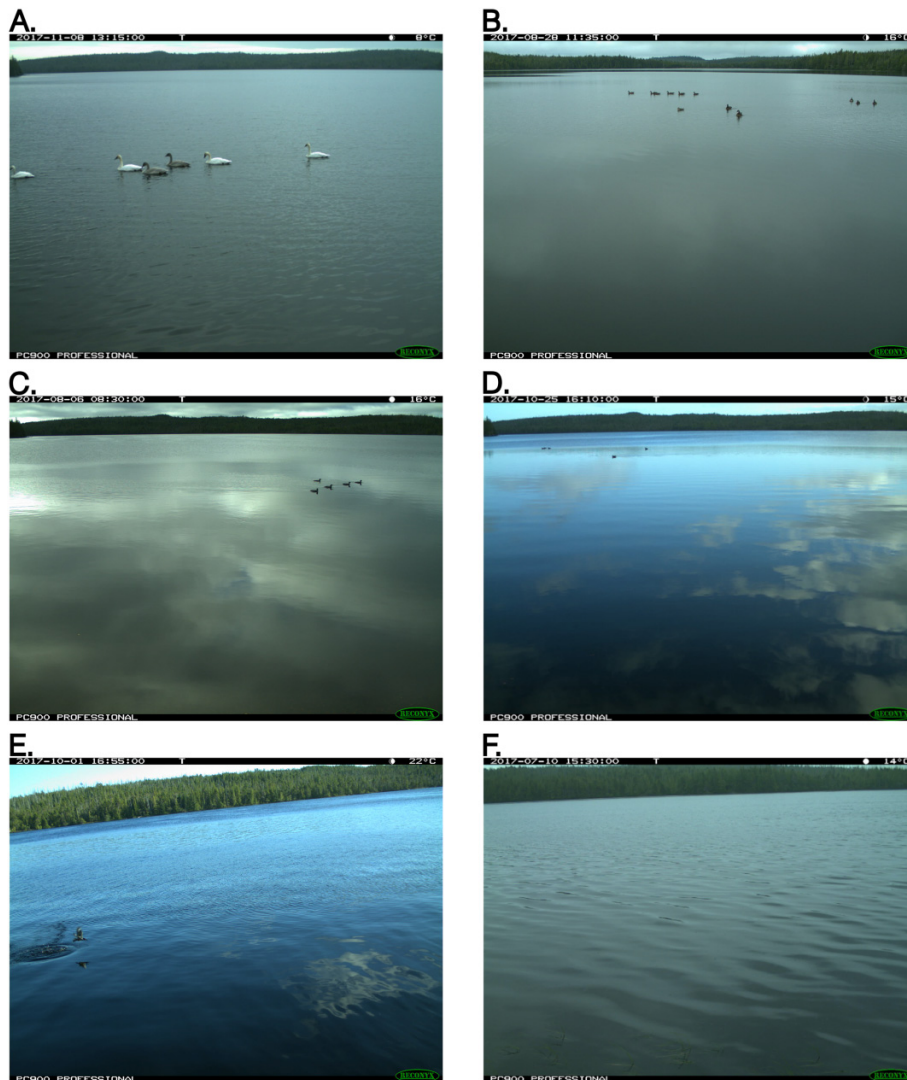
ing a photogrammetric technique developed by [Leorna et al. \(2022\)](#). Then, to estimate an average viewshed area for our cameras, we used this maximum detection distance and the angular field of view (~ 37.7 degrees for our cameras) to approximate the area sampled in the camera viewshed using the equation for the area of a circle ([Leorna et al. 2022](#)). Using this information, we can also estimate the surface area of the lake that is captured by each camera trap. We estimate that our camera traps are capturing between 2% and 9% of the lake surface on Drizzle Lake, and 11% and 50% of the lake surface on Boulton Lake. We provide a range estimate because, depending on weather conditions and other factors, we can sometimes identify birds from a further distance.

We first manually screened all images to identify those containing birds ([Fig. 2](#)). We then went back to every photo that had a bird present and identified (when possible) each to species and counted the number present in the photo. The identification step is expected to be highly dependent on resolution of camera trap images, so accurate identifica-

tions are much more likely to be obtained using high-quality equipment. When birds were too far away to be identified to species, they were still counted and labelled as “unidentified”. All subsequent analyses were conducted in the R environment version 4.3.2 ([R Core Team 2023](#)).

To what extent can MegaDetector detect images of birds on lakes? We estimate that, on average, about 40 images can be screened for bird presence in a minute, which means that our $\sim 200\,000$ images took about 83 h and 20 min just for initial screening to identify the fraction containing birds. AI approaches such as computer vision have been used as a solution to this sort of problem of removing blank images in other contexts ([Fennell et al. 2022](#)). For our data, we used the pre-trained MegaDetector v4.1 image detection model (release 2020.04.27; based on Faster R-CNN architecture) to detect birds (labelled as “animal” by the detection model) in the camera trap images ([Beery et al. 2019](#); [Microsoft 2020](#)). This model does not identify species, but rather sorts through blank images. We ran all images (motion-triggered and time-

Fig. 2. Examples of photographs captured by time-lapse camera traps at Drizzle Lake in 2017. Panel (A): 6 Trumpeter Swans (*Cygnus buccinator*). Panel (B): 12 Canada Geese (*Branta canadensis*). Panel (C): 5 Common Loons (*Gavia immer*). Panel (D): 5 unidentified birds. Panel (E): 1 Belted Kingfisher (*Megaceryle alcyon* (Linnaeus, 1758)). Panel (F): no birds evident.



lapse) collected from Drizzle Lake to see the extent to which MegaDetector could identify images that contained birds. Images were processed in their native resolution (2048×1536 px). We ran images at a confidence threshold of both 0.1 and 0.8.

To assess the use of MegaDetector in identifying images with birds, we calculated commonly used metrics. Accuracy calculates the ratio of all correct predictions out of all instances. Precision calculates the ratio of true positives to total positives. Recall calculates the ratio of true positives to all conditional positives. F1 uses precision and recall to apply a harder penalty when one measure improves at the expense, and specificity is the proportion of negative instances that are correctly identified by the system (Kutugata et al. 2021). The relevant equations are

$$(1) \quad \text{Accuracy} = \frac{\text{TP} + \text{TN}}{\text{TP} + \text{TN} + \text{FP} + \text{FN}}$$

$$(2) \quad \text{Precision} = \frac{\text{TP}}{\text{TP} + \text{FP}}$$

$$(3) \quad \text{Recall} = \frac{\text{TP}}{\text{TP} + \text{FN}}$$

$$(4) \quad F_1 = \frac{2\text{TP}}{2\text{TP} + \text{FP} + \text{FN}}$$

$$(5) \quad \text{Specificity} = \frac{\text{TN}}{\text{TN} + \text{FP}}$$

where TP is true positives, TN is true negatives, FP is false positives, and FN is false negatives.

Given the low-degree of congruence between human- and MegaDetector-labelled images with birds in our specific study system (see Results), we henceforth only consider human-labelled data to address our remaining questions. Furthermore, because motion-triggered images were ineffective at regularly detecting birds (see Results), we only report images that were collected by time-lapse moving forward.

Table 1. Confusion matrix presenting the results of MegaDetector at detecting images with birds in them compared to human observers.

		A				B	
		Human				Human	
		Bird	No bird			Bird	No bird
MegaDetector	Bird	1282 (54.6%)	50 689 (36.1%)	MegaDetector	Bird	209 (8.9%)	6183 (4.4%)
	No bird	1064 (45.3%)	89 766 (63.9%)		No bird	2137 (91.1%)	134 272 (95.6%)

Note: Percentages represent proportion of those detected by the human observer, so columns sum to 100%, but not rows. Table A is using a MegaDetector threshold = 0.1, and Table B is using a MegaDetector threshold = 0.8.

Can data collected by a human observer validate data collected from camera traps? Avian abundance surveys were conducted for 10 consecutive days (10 July to 20 July 2017) at Drizzle Lake. Because of logistical constraints, this process could not be repeated at Boulton Lake. To obtain daily loon counts on the lake, the observer made full lake counts (with binoculars) every 30 min from dawn until mid-morning (10 am), as well as intermittently near mid-day (10 am–2 pm) and in the evening (7 pm–10 pm). All observations were made from a shoreline location (53.934177°N, 132.082024°W) that allowed observation of 97% of the lake surface. Because some proportion of aquatic birds were foraging (and thus submerged), multiple sequential scans were made until a maximum count was replicated on multiple sequential scans (further details in Reimchen and Douglas 2021). Because Common Loons are so abundant in July at Drizzle Lake (Reimchen and Douglas 1980, 1984, 2021) and because they are so important for inferences regarding natural selection on stickleback fishes (Reimchen 1994; Reimchen and Bergstrom 2023), we use their maximum count on any single visual scan of the lake as a daily reference baseline for comparison with human-labelled time-lapse data collected from camera traps during the same 10 days. For the time-lapse data, we also use the maximum count of loons for the same day. We calculated the Pearson's correlation coefficient as a measure of correspondence between the maximum number of loons captured by the time-lapse images and a human observer, with maximum daily values as the data points. We repeat this exercise using camera trap images labelled by TER, an expert in Haida Gwaii avifauna, and a less experienced human labeller owing to the likely importance of background knowledge of the study system.

To what extent are camera traps effective in capturing known ecological patterns? We considered the effectiveness of camera traps in detecting already-known (i.e., already published or documented for our sites) ecological patterns (see Introduction). As described above, we used human-labelled time-lapse images to answer this question. First, using the corresponding functions from the “vegan” package version 2.6.6.1 (Oksanen et al. 2024), we compared bird communities between our two focal lakes by calculating various indices (Morris et al. 2014) of biodiversity and community assemblages (species richness, Shannon–Wiener index, Jaccard similarity index, Bray–Curtis dissimilarity index, and percentages of the most common species). Second, we examined seasonal patterns by comparing the numbers of observations of key species in different months (July through November). Finally, we examined diurnal patterns for Common Loons

by totalling the number seen across all images throughout the day.

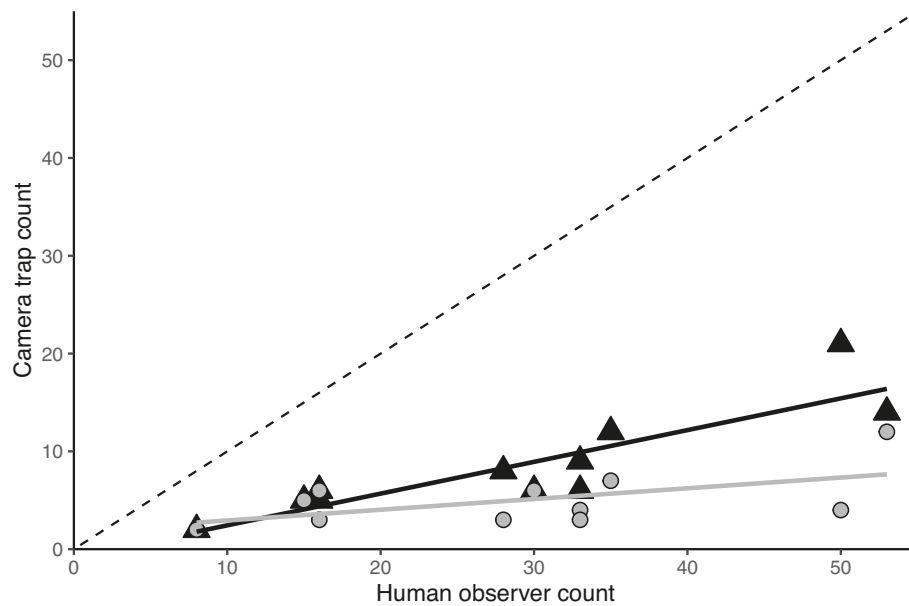
How does variation in survey effort influence the conclusions derived from camera traps? If we are to scale up the use of time-lapse imagery, it would be helpful to reduce the number of images taken or screened—because manual screening is time consuming, and MegaDetector is not effective (details below). We attempt to address this possibility by subsampling the number of images screened and comparing the results to the full dataset. Subsampling methods used include camera position, camera number, and random subsampling of total number of images. We first considered the use of a single camera trap per lake rather than the actual four. Similarly to Question 3, for each camera, we calculated species richness, Shannon diversity, percentage of bird observed, and the percentage of Common Loons observed. We next used subsampling across all images with 500 repetitions for random removal of 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, 90% of the images. Here, we only use the data from Drizzle Lake to answer these questions because we had more data available to test subsampling methods.

Results

We screened a total of 119 557 time-lapse images from Drizzle Lake, of which 1.5% had birds present and 118 003 time-lapse images from Boulton Lake, of which 1.2% had birds present. Of the 3185 images with birds present, confident identification to species was possible for 11% (192 images) at Drizzle and 10% (141 images) at Boulton. In addition, 24% (621) of images were motion-triggered at Drizzle Lake of which 21% had birds that could be identified to the species level, and 1% (17 images) were motion-triggered at Boulton Lake, of which none were identified to the species level. We note that the low rate of bird observations in motion-triggered images is largely because glare from the sun was picked up by the motion sensors.

To what extent can MegaDetector detect images of birds on lakes? We ran all of the images from Drizzle Lake through MegaDetector v4.1. Of the 142 801 images (here including motion-triggered images), 2347 were identified by a human as having birds present. Even at its lowest confidence threshold (0.1), MegaDetector missed ~45% of those images and 36% of the images flagged by MegaDetector were false positives (Table 1). The model performed poorly across the suite of labelling performance metrics evaluated: *precision* = 0.025; *accuracy* = 0.638; *recall* = 0.546; *specificity* = 0.639; and *F1-score* = 0.047. At a high confidence threshold (0.8), MegaDetec-

Fig. 3. Daily maximum count (on a single visual scan) of Common Loons (*Gavia immer*) by an onsite human observer (x-axis) and by human-labelled camera trap images (y-axis) on Drizzle Lake. Each point is a single day from 10 July to 20 July in 2017. The dashed line corresponds to identical numbers inferred from the two methods: that is, the one-to-one line. Black triangles are data from images labelled by an expert in avifauna in Haida Gwaii (TER). Grey circles are data from images labelled by a biologist that has less experience in Haida Gwaii avifauna.



tor missed 91% of images containing birds and had a 4% false positive rate (Table 1). Even though the *accuracy* (0.942) and *specificity* (0.956) increased at this higher threshold, *precision* (0.033), *recall* (0.089), and *F1-score* (0.048) remained poor. Although MegaDetector performed better on images that were motion-triggered (Table S1), as noted above, motion triggers only represented a fraction (sometimes a small fraction) of the images that contain birds. Given the low-degree of congruence between human- and MegaDetector-labelled images (for our specific study system), from this point forward, we only consider human-labelled data (from time-lapse images) to address our remaining questions.

The above summary included both the time-lapse images and also any image that happened to have been motion-triggered. Closer examination of these two categories confirmed our intuition that triggers would not be appropriate for our application due to both false positives and false negatives (see above). Moving forward, we only report images that were collected by time-lapse as this method better reflects future applications.

Can data collected by a human observer validate data collected from camera traps? On average, human-labelled camera trap images detected $20 \pm 10\%$ (mean \pm SD) of the maximum number of Common Loons detected by an onsite observer (Fig. 3). As such, our current camera trap setup was not effective for inferring the absolute number of birds on a lake; yet it provided a reasonable index of relative differences in abundance. In particular, there was a positive relationship between the maximum number of Common Loons seen by an onsite observer and the maximum number captured by camera traps (across the 11 days), although the correlation between observation types was marginally non-significant

($r = 0.56$, $p = 0.07$). This relationship became significant (Fig. 3; $r = 0.87$, $p < 0.005$) when time-lapse images were screened by TER, who is an expert on Haida Gwaii avifauna. When images are screened by an expert, camera traps detected, on average, $30 \pm 7\%$ of the maximum number of Common Loons captured by a human observer.

To what extent are camera traps effective in capturing known ecological patterns? We first considered differences between Drizzle Lake and Boulton Lake. As expected (Reimchen and Douglas 1980, 1984, 2021; TER pers. obs.), the number of Common Loons detected was much higher on Drizzle (265 total detections, 53.97% of the total avifauna identified to the species level) than on Boulton (36 total detections, 7.27%), whereas the number of Hooded Mergansers showed the opposite pattern (Drizzle: 10 total detections, 2.05%; versus Boulton: 392 total detections, 79.19%) (Fig. 4). Camera traps recorded a total of 11 different bird species at Drizzle Lake and 12 different bird species at Boulton Lake, with the Shannon–Wiener index slightly higher at Drizzle (4.97) than at Boulton (4.65). Overlap in species composition was also similar based on Jaccard similarity (0.891) and Bray–Curtis dissimilarity (0.803).

Second, we considered seasonal community differences expecting that Common Loons would be more abundant in July than the other months (Reimchen and Douglas 1980, 1984, 2021; TER pers. obs.). Species richness was relatively consistent between July and November at Drizzle Lake but not at Boulton Lake (Table 2). For instance, we detected five species in each month at Drizzle Lake (except six in August), whereas, depending on the month, we detected between three and eight species at Boulton Lake. Species diversity, which includes variation in abundance, however, showed more vari-

Fig. 4. Bird species and relative abundances captured by camera traps (and counted a posteriori by an expert on the photos) on Boulton Lake (top panel) and Drizzle Lake (bottom panel) by date and time of day. Colours represent the different species and size of circles, and the size of points represents the number of birds captured by the camera traps. Each dot represents a single photograph. Bird species included are Bald Eagle (*Haliaeetus leucocephalus* (Linnaeus, 1766)), Belted Kingfisher (*Megaceryle alcyon*), Bufflehead (*Bucephala albeola* (Linnaeus, 1758)), Canada Goose (*Branta canadensis*), Common Loon (*Gavia immer*), Common Merganser (*Mergus merganser*), Duck, Great Blue Heron (*Ardea herodias* Linnaeus, 1758), Hooded Merganser (*Lophodytes cucullatus*), Mallard (*Anas platyrhynchos* Linnaeus, 1758), Red-breasted Merganser (*Mergus serrator*), Red-throated Loon (*Gavia stellata*), Ring-necked Duck (*Aythya collaris* (Donovan, 1809)), Scaup, and Trumpeter Swan (*Cygnus buccinator*).

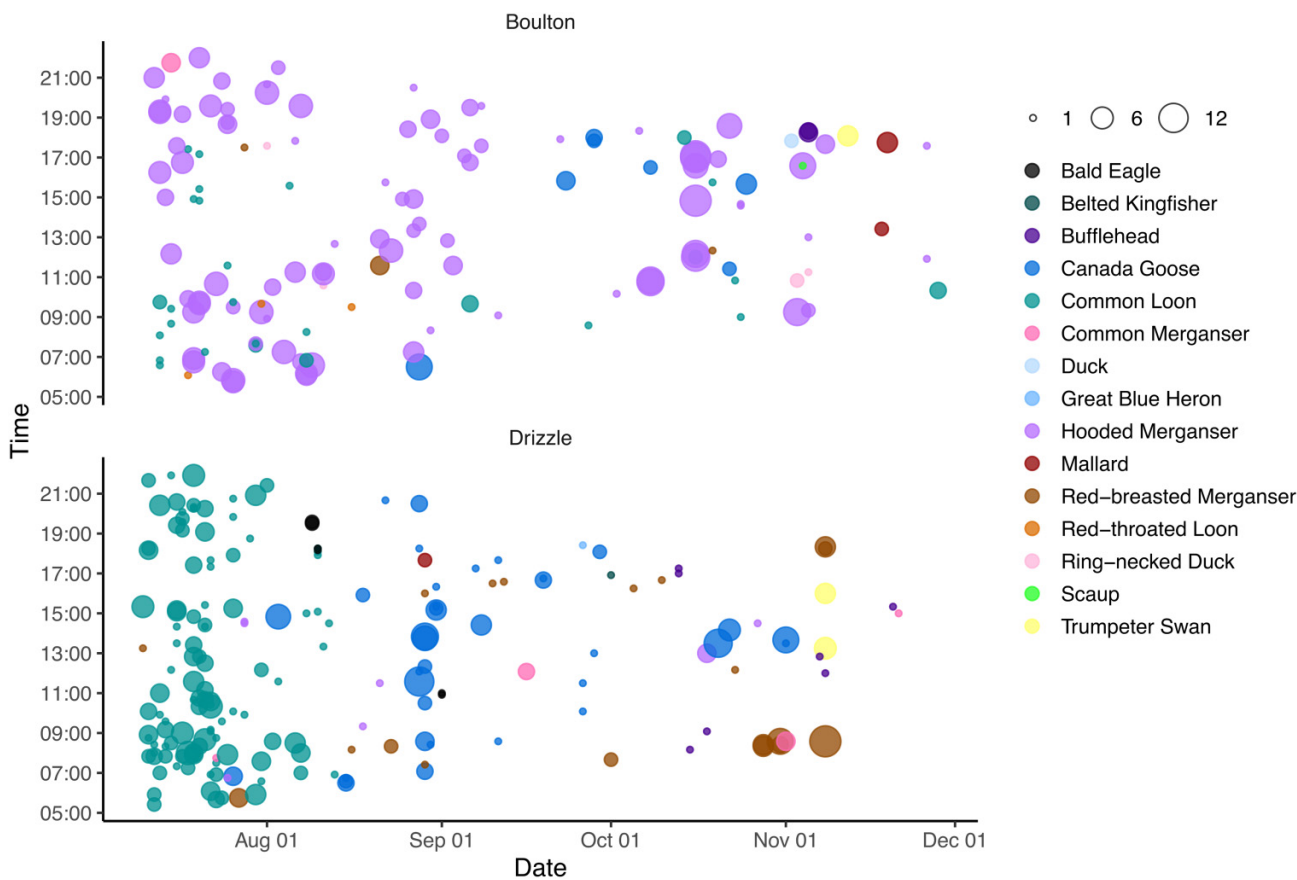


Table 2. Diversity metrics (species richness and Shannon diversity) calculated from human-labelled camera trap images for both Boulton Lake and Drizzle Lake for each month of deployment.

	Species richness		Shannon diversity	
	Boulton	Drizzle	Boulton	Drizzle
July	5	5	3.66	4.42
August	6	6	3.37	3.47
September	3	5	2.61	2.58
October	4	5	2.74	2.45
November	8	5	2.56	2.10

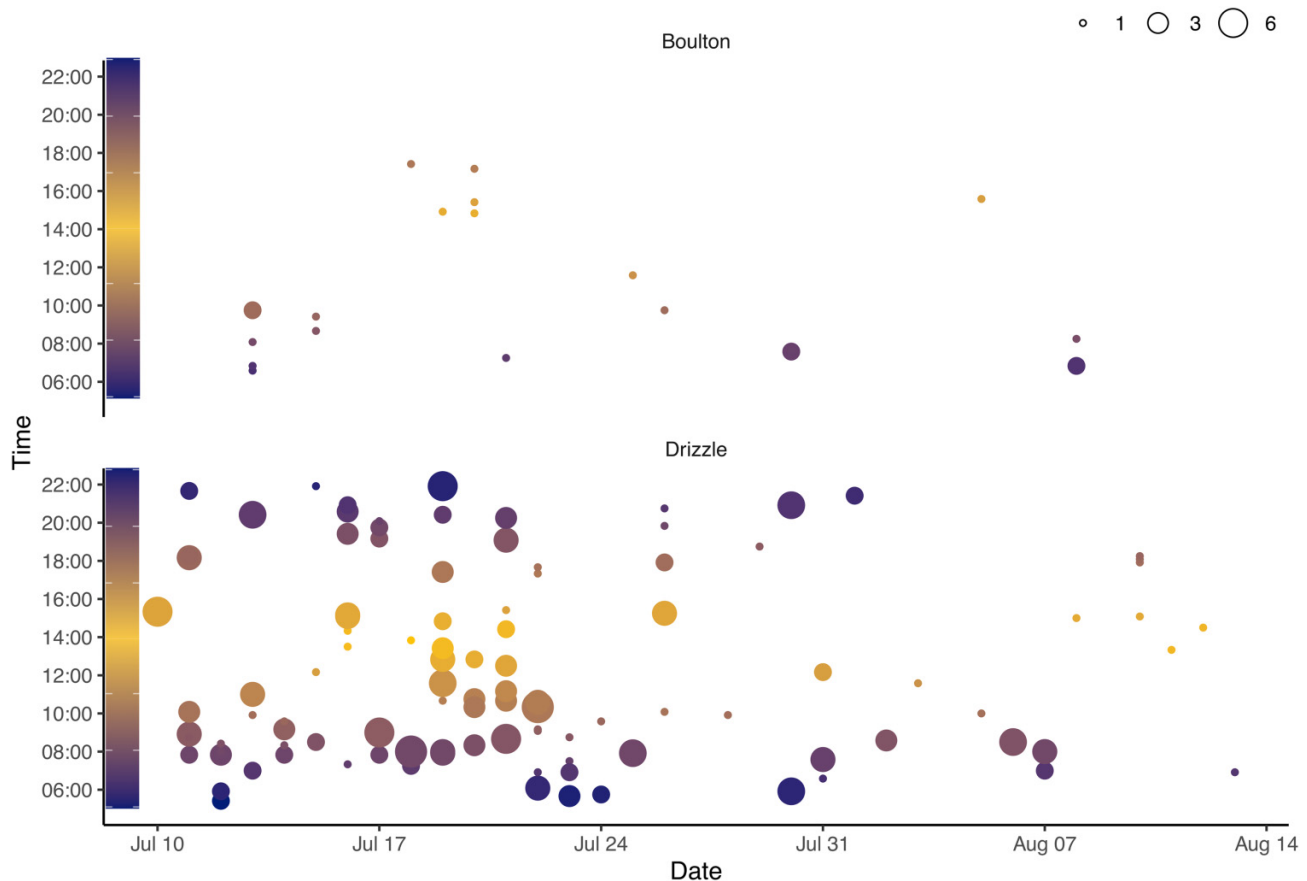
ation between months at Drizzle (Shannon diversity = 2.10–4.42) than at Boulton (Shannon diversity = 2.56–3.66), with a steady decrease in both cases toward lower diversity later in the year (Table 2). Most importantly, Common Loons were detected much more frequently in July than in the later months (Figs. 4 and 5).

Finally, we considered diurnal patterns in birds on the lakes, where previous work pointed toward higher abundances in the morning than during the rest of the day

(Reimchen and Douglas 1980). Taking Common Loons as an exemplar (Fig. 5), 53% of observations at Drizzle Lake were captured between 5 am and 10 am, 25% were captured between 5 pm and 10 pm, and only 22% were captured between 11 am and 5 pm. On Boulton Lake, the corresponding numbers were 68%, 9%, and 23%.

How does variation in survey effort influence the conclusions derived from camera traps? Here, we found considerable variation among cameras (Fig. 6). For example, at Drizzle Lake, camera

Fig. 5. Common Loons (*Gavia immer*) detected by camera traps (and counted a posteriori by an expert on the photos) on Boulton Lake (top panel) and Drizzle Lake (bottom panel) by date and time of day. Size of the points represents the number of Common Loons detected on each photo. Each dot represents a single photograph. The colour gradient represents the amount of sunlight with solar noon in bright yellow and dusk and dawn in dark blue.



2 recorded eight different species, whereas the other cameras recorded four, five, or six species (Table S2). Although camera 2 captured 25% of bird observations, it only captured 9% of Common Loon observations (Table S2). Similarly, at Boulton Lake, camera 2 recorded six different species, whereas camera 4 recorded three species. However, camera 3 recorded 34% of all bird observations, whereas camera 1 only recorded 11% of all bird observations. We next considered the use of fewer images overall by randomly removing different percentages of images from the full dataset. In this case, outcomes became increasingly variable as more images were deleted (Fig. 7)—as expected. However, even when half of the images were deleted at random, 66% of the replicates yielded a detection rate (percentage of images with birds in them) that was within one SD of the true value.

Discussion

The deepest ecological insights will probably always require (or at least strongly benefit from) detailed observations by experienced personnel residing onsite for extended periods of time. This type of effort is rare these days and would be, regardless, limited to a small number of focal locations (Holmes and Sherry 2001; Grant and Grant 2002; Reimchen

and Douglas 2021). As such, remote assessment methods have been suggested as a way of scaling up focal site observations to a greater number of locations for longer periods of time (Steenweg et al. 2017; Oliver et al. 2023). Here, we demonstrate the utility of time-lapse images from camera traps as a tool for assessing bird communities on freshwater lakes in remote areas. In particular, our approach was able to capture known ecological patterns related to variation in community assemblages between lakes, seasons, and times of day. The approach is not without constraint, however, because it generates a large number of images that are time-consuming to screen manually.

To what extent can MegaDetector detect images of birds on lakes?

We might expect AI to not be as effective at identifying wildlife in time-lapse images as it would be in motion-triggered images—because time-lapse settings essentially expand the viewshed area to include animals that are farther away and so would not trigger the camera (Hamel et al. 2013; Moeller et al. 2023). Indeed, Leorna and Brinkman (2022) found that MegaDetector performed much better when detecting barren-ground caribou (*Rangifer tarandus* Linnaeus,

Fig. 6. Subsetting images from Drizzle Lake by camera trap. Each dot represents a single photograph. The different colours represent species, the size of the dots, the number of birds on the photo, and each panel a different camera. Bird species included are Bald Eagle (*Haliaeetus leucocephalus*), Belted Kingfisher (*Megasceryle alcyon*), Bufflehead (*Bucephala albeola*), Canada Goose (*Branta canadensis*), Common Loon (*Gavia immer*), Common Merganser (*Mergus merganser*), Duck, Great Blue Heron (*Ardea herodias*), Hooded Merganser (*Lophodytes cucullatus*), Mallard (*Anas platyrhynchos*), Red-breasted Merganser (*Mergus serrator*), Red-throated Loon (*Gavia stellata*), Ring-necked Duck (*Aythya collaris*), Scaup, and Trumpeter Swan (*Cygnus buccinator*).

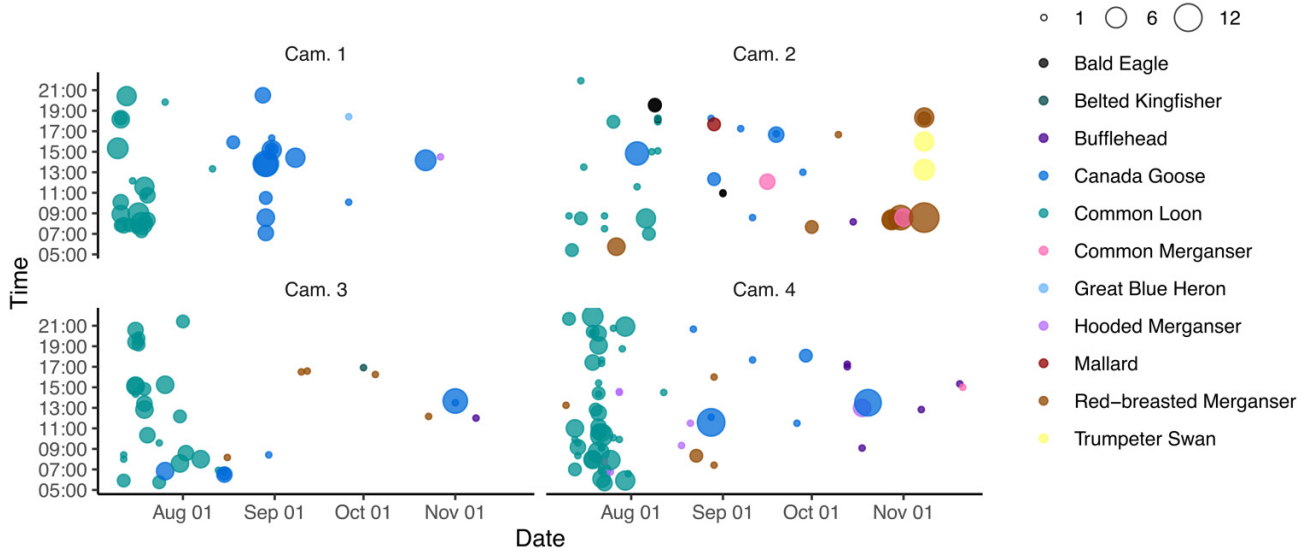
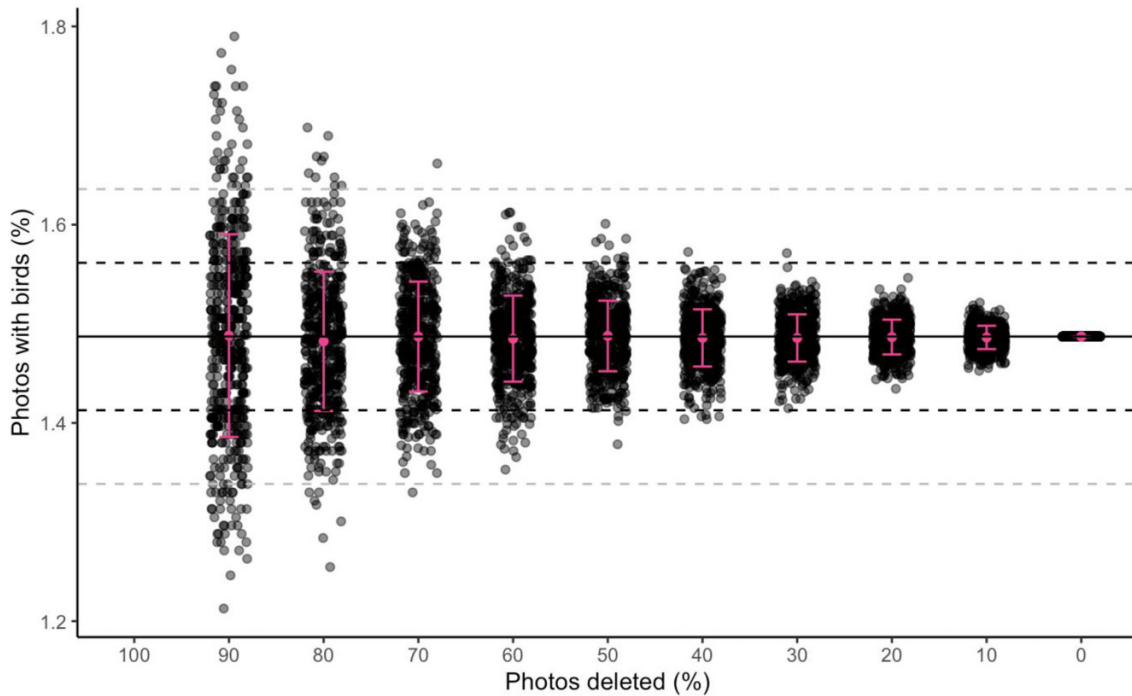


Fig. 7. Random subsampling of camera trap images with 500 repetitions for Drizzle Lake. Pink dots represent the mean number of birds for each subsampling proportion, and error bars represent standard deviations. The solid line is the true percentage of images containing birds, the black dotted lines are $\pm 5\%$ from the true percentage of images containing birds, and the grey dotted lines are $\pm 10\%$ of the true percentage of images containing birds.



1758) from motion-trigger images ($\geq 94.6\%$ accuracy) as compared to time-lapse images ($\leq 61.6\%$ accuracy). Similarly, we found that MegaDetector performed better at detecting images with birds on motion-triggered images compared to

time-lapse images (Table S1); yet motion-triggers captured fewer images of birds overall. MegaDetector likely performed poorly for two reasons. First, birds on time-lapse images occur at much greater distances making detection difficult. Second,

freshwater lakes present additional challenges compared to other types of environments where AI has proven useful because lakes can be particularly visually complex and variable, with waves and reflections creating ever-changing contexts on which an animal must be detected.

Overall, MegaDetector v4.1 performed poorly for our application: with a high rate of false positives and false negatives (Table 1). The high frequency of false positives means that, even if we were to adopt a MegaDetector workflow with few false negatives (see Results), a substantial number of images would still need to be manually processed. Yet if we increase the confidence threshold to the point where false positives are few, many images that actually do have birds in them are missed. We recommend that researchers using camera traps on lake habitats use caution when applying AI and machine learning approaches developed for terrestrial habitats as a tool to sort through blank images, as they are likely to return a high degree of false positive and false negative results. However, new versions of MegaDetector are continuously being developed (e.g., MegaDetector v6 was recently released), so as the technology continues to improve, further tests will be warranted. As such, future work that trains a model using deep learning specifically for lake habitats would presumably increase the accuracy and precision of the process, and further enhance the efficiency and scalability of the work discussed here (Chalmers et al. 2023; Penn et al. 2024). Furthermore, to achieve automated bird classification (i.e., species identification) on freshwater lakes, this new model would need to be developed using a very large training dataset (Chalmers et al. 2023; Schneider et al. 2023).

Can data collected by a human observer validate data collected from camera traps?

Comparison of the camera trapping approach with the gold-standard survey technique (in-person observation with an experience observer) revealed that camera traps recorded (to a resolution where identification was possible) only a subset of the individuals of a common and abundant bird species—in contrast to the onsite observer. For instance, the maximum daily number of Common Loons seen on Drizzle Lake at any given time by the camera traps was about 20% of the daily maximum seen by the onsite observer (Fig. 3). As such, the time-lapse data did not effectively capture the absolute numbers of birds on the lake. However, as described above, our camera traps are only capturing a fraction of the lake's surface area, whereas the human observer estimates capturing 97% of the lake surface area (TER, pers. obs.). In addition, camera traps are also capturing only a fraction of time (7.2 min per day) compared to a human observer (6–10 h per day). Presumably, scaling up the number of cameras (dependent on lake area) could potentially reduce the disparity between cameras and in-person observers—yet such scaling would probably require detailed in-person observations that negate the remote and continuous monitoring advantage of camera traps. Further, on larger lakes, it will remain difficult to use camera traps to capture the offshore area, although such efforts could be improved by developing floating stands for the cameras (McCleery et al. 2014; Frederick et al. 2016).

Given this uncertain correspondence between human observations and camera trap data, we henceforth focus on inferences related to relative (rather than absolute) abundances.

To what extent are camera traps effective in capturing known ecological patterns?

Even though camera traps captured fewer birds (see above section) in our study design compared to the onsite observer, maximum daily counts were strongly correlated between the camera traps and the onsite observer (Fig. 3). This result suggests that relative comparisons are likely to be useful and informative. Of course, with optimized experimental designs (e.g., camera trap locations) and statistical tools that account for coverage and uncertainty, absolute abundance estimates can be generated (Gilbert et al. 2021). For now, however, we focused on the extent to which relative comparisons could be an effective tool for capturing ecological patterns. We specifically consider how human-labelled time-lapse images compare to previous insights obtained through detailed long-term onsite surveys for our study area (Reimchen and Douglas 1980, 1984, 2021; TER pers. obs.).

First, previous work has shown that Common Loons are more frequent on Drizzle Lake than on Boulton Lake, whereas Hooded Mergansers show the opposite pattern (Reimchen and Douglas 1984; TER pers. obs.). This difference arises because Boulton Lake is shallow and primarily littoral, habitats preferred by Hooded Merganser, while Drizzle Lake is deeper, larger, and primarily limnetic, habitats favoured by Common Loon (Reimchen and Douglas 1980; Reimchen 1994). Our time-lapse data faithfully recovered this insight (Fig. 4). For example, we found 265 detections of Common Loons at Drizzle Lake and only 36 at Boulton Lake. However, we found 10 detections of Hooded Mergansers at Drizzle Lake, but 392 at Boulton Lake.

Second, previous onsite observations indicated a replicated yearly trend for a peak presence of non-breeding Common Loons at Drizzle Lake in July, where they come to forage (Reimchen and Douglas 1980, 2021). Our camera trap findings also align with this seasonal trend, where we observe a peak presence of Common Loons at Drizzle in July and very few observations in subsequent months (Figs. 4 and 5). For example, cameras detected 236 occurrences of Common Loons in July at Drizzle Lake, but only 25 occurrences in subsequent months (August, September, October, November). We also detected a seasonal turnover in the most common species at Drizzle Lake, as was documented previously (Reimchen and Douglas 1984). In July, Common Loons were most common; in August, Canada Geese (*Branta canadensis* (Linnaeus, 1758)) were most common, and, in September and October, Hooded Mergansers were most common. Camera trap data also suggest a change from previous observations. For instance, historical data from human observations (Reimchen and Douglas 1984) showed that Red-throated Loons (*Gavia stellata* (Pontoppidan, 1763)) were common at Drizzle Lake throughout the summer, yet the camera traps did not record this species. However, previous work has suggested a steady decline in the number of Red-throated Loons since the 80s at Drizzle Lake (Reimchen and Douglas 2021).

Third, we know from onsite observations that Common Loons tend to exhibit diurnal patterns where they tend to arrive near dawn and reach peak abundances around mid-morning (Reimchen and Douglas 1984). Our time-lapse data reveal a similar trend, where Common Loons were more abundant early in the morning than at midday (Fig. 5). For example, 53% of Common Loon observations at Drizzle Lake were captured between 5 am and 10 am. This is similar to known patterns where Common Loons arrive at the lake in small groups at dawn to forage with numbers increasing until mid-morning (Reimchen and Douglas 2021).

How does variation in survey effort influence the conclusions derived from camera traps?

We next considered how we might reduce the intensive photo sorting effort in a study like ours by asking what would happen if we had fewer camera traps or fewer images per camera. Based on the data collected for our system, we do not recommend reducing the number of camera traps—because the different cameras provided different information in terms of both bird diversity and relative abundances (Figs. 6 and S1; Tables S2 and S3). The most striking example was camera 2 on Drizzle Lake, which captured more species than the other cameras (Fig. 6; Table S1). In particular, it was the only camera to capture large numbers of Common Mergansers (*Mergus merganser* Linnaeus, 1758), Red-breasted Mergansers (*Mergus serrator* Linnaeus, 1758), and Trumpeter Swans (*Cygnus buccinator* Richardson, 1831). We suspect this is because the south region of the lake where camera 2 is positioned is most protected from the strong southeast winds that can be particularly important in fall (TER pers. obs.). Camera 2 is also the camera that recorded the lowest numbers of Common Loons (Fig. 6), perhaps because Common Loons and Mergansers do not overlap much seasonally (Reimchen and Douglas 1984).

These fine-scale habitat differences captured by the camera traps are similar to conclusions drawn from studies that used camera traps to assess terrestrial mammal diversity. For instance, it has been repeatedly shown that cameras along trails tend to have higher capture rates for certain species than do camera traps at random locations (Larrucea et al. 2007; Kolowski and Forrester 2017). Camera placement that increases detectability of certain species can provide useful information, but it can also introduce data biases that misrepresent certain species (Fonteyn et al. 2021). Overall, the rate of capture for a given species is determined by the abundance of a species in a given location and its likelihood of being photographed at that location (Fonteyn et al. 2021). As such, decisions relating to camera position should consider such aspects, while also considering the goal of the research questions. For example, in our case, using fewer cameras would probably be acceptable for smaller lakes, provided that they are not positioned facing the sun, which reduces visibility. Indeed, none of the cameras on the 8 ha Boulton Lake stood out like camera 2 on the 112 ha Drizzle Lake (Fig. S1).

Perhaps more likely, our 5 min intervals per camera trap might be unnecessary. For example, randomly deleting half of the photographs from our dataset had only a minimal ef-

fect on the total number of images containing birds. Thus, we could have increased the time interval between photographs (Leorna and Brinkman 2024), or programmed the cameras for lower frequency recording during periods of less interest, such as mid-day or late fall. We note that this subsampling (random, systematic, or targeted) could take place prior to camera placement (via programming the cameras) or afterward (by screening only some of the images). The later approach might seem the safest and most flexible but—in reality—the frequency at which we took images meant that the batteries ran out after only 4 months or so. Hence, longer deployments will necessitate reduced sampling via programming as opposed to during processing.

Conclusion

We recommend several experimental design choices when using camera traps to assess and monitor birds on freshwater lakes. First, as using camera traps in lake habitats is still in its infancy, we recommend collection of high-quality ecological data from the study system of interest by an onsite observer and experienced naturalist. The data collected in this classical manner serves as a critical baseline reference against which to proof data collected by camera traps, and which can be used to inform the optimal camera trap design—such as the number of traps, placement locations, and the optimal times and intervals for data collection. Once this approach is adopted more broadly, and the relative strengths and weaknesses of camera traps are better characterized for freshwater environments, this recommendation will be less important. Second, different aspects of data collection through camera traps can be further optimized depending on the hypotheses researchers hope to address. For example, if researchers are interested in investigating spatial patterns, the number of sites should be maximized compared to other parameters such as photo frequency or number of cameras per site. For larger sites, however, more numerous camera traps placed in more diverse locations are more likely to capture the diversity of birds on that lake. Third, we encourage the development of new deep-learning models that are specifically trained for birds on freshwater lakes, which could reduce the effort and time dedicated to manual image sorting. Finally, although not assessed in our study, the deployment of video (as opposed to photograph) camera traps might improve bird detection, and thus also makes a more direct comparison to a human observer. However, this approach is likely to create additional data storage challenges.

In summary, our study demonstrates the utility of camera traps as one effective tool for assessing bird diversity on lakes. It is important to note that we are not advocating for the replacement of direct observers in the field. We also recognize that other remote sensing methods may be able to complement the data obtained from camera traps (e.g., autonomous recording units, eDNA, citizen science initiatives). However, none of these methods replace the expertise and first-hand knowledge of an onsite observer. Remote sensing tools, including camera traps, thus should be viewed as complementary approach to, rather than a substitute for, conventional natural history methods.

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Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

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Methodology: SS, GEH

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Competing interests

The authors declare there are no competing interests.

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Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjz-2024-0084>.

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