

RESEARCH ARTICLE

The Purr-fect Catch: Using accelerometers and audio recorders to document kill rates and hunting behaviour of a small prey specialist

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Funding information

Natural Sciences and Engineering Research
Council; W. Garfield Weston Foundation;
Institut Nordique du Québec

Handling Editor: Graziella Iossa

Abstract

1. Characterizing variation in predator behaviour and, specifically, quantifying kill rates is fundamental for parameterizing predator-prey and food web models. Yet, current methods for recording kill rates of free-ranging predators, particularly those that consume small-bodied (<2 kg) prey, present a number of associated challenges.
2. In this paper, we deployed custom-adapted acoustic recorders and tri-axial accelerometers on free-ranging Canada lynx *Lynx canadensis* to assess the capacity of biologging devices to continuously document individual hunting behaviour, including prey selection and kill rates, on a predator that specializes on prey weighing <2 kg.
3. Automated classification of acoustic recordings captured 87% of snowshoe hare kills that were identified through snow-tracking (26 of 31 kills). Classification of detailed acceleration recordings summarized over minutes, instead of seconds, captured consumption of snowshoe hare *Lepus americanus*, but not smaller species, at high accuracy ($F1 = 0.96$).
4. By summarizing acoustic and accelerometer data from free-ranging lynx, we demonstrate the capacity of these devices to document within- and between-individual variation in diet composition (ranging from 40% to 80% snowshoe hares) and daily feeding bouts (ranging from 0 to 3.5 bouts per day).
5. We suggest that acoustic recorders provide a promising method for characterizing several aspects of predator hunting behaviour including prey selection and chase outcomes, while broad-scale accelerometer-based behavioural classifications provide hare kill rates and fine-scale non-hunting behavioural information. Combined, the two technologies provide a means to remotely document both kills and feeding events of small-bodied prey, allowing for individual-based exploration of functional responses, predator-prey interactions and food web dynamics at temporal scales relevant to environmental change.

KEYWORDS

acoustics, biologging, Canada lynx, hunting behaviour, kill rates, *Lynx canadensis*, predator-prey ecology, tri-axial accelerometer

1 | INTRODUCTION

Predator kill rates are an important element of many fundamental theories in ecology. Whether the interest is in documenting functional responses, predator–prey interactions or population and food web dynamics, understanding and estimating kill rates and hunting success is a necessary component (Kalinkat et al., 2013; Lima, 2002; McGhee et al. 2013). In addition to kill rates, estimates of hunting success, kleptoparasitism and scavenging in natural systems are key to predator energy budgets (Pagano et al., 2018), species interactions (Gorman et al., 1998; Peers et al., 2020) and food web dynamics (Focardi et al., 2017; Wilson & Wolkovich, 2011). While current methodological approaches provide estimates of kill rates and predator behaviour summarized at the population level and over seasonal time frames (Lake et al., 2013; O'Donoghue, Boutin, Krebs, Zuleta, et al., 1998), there is considerable interest in documenting predator responses to environmental change at the individual level across short temporal scales (e.g. days, weeks; Bolnick et al., 2011; Pettorelli et al., 2015).

Kill rates are traditionally measured through direct observation, which is restricted to species that are observable from one location thanks to small size (Uiterwaal et al., 2017) or open habitats (Honer et al., 2002). Tracking is also common but is labour-intensive, and often only produces an average population kill rate across a season or year (O'Donoghue, Boutin, Krebs, Zuleta, et al., 1998). A recent major advancement that reduces the need for direct observation involves identifying kill sites through spatial and temporal clustering of GPS locations (Merrill et al., 2010). Although an improvement, this approach still requires visits to kill sites to confirm and identify prey, even after the technology has been validated (McPhee et al., 2012). Additionally, cluster analyses only identify large prey kill sites where the predator spent more time at the site (e.g. hours to days) than other locations (Bacon et al., 2011). This results in missing small prey kills and an overrepresentation of large prey items in predator diets (Jansen et al., 2019; Leighton et al., 2020). Thus, to date, there is no available method for quantifying kill rates of small prey specialists beyond intense field effort (e.g. direct observation, kill site investigations, scat collection).

Recent advances in biologging technology provide opportunities to remotely record behaviour, including hunting, of free-ranging organisms. Accelerometers, which can record acceleration multiple times per second, have been used to calculate activity–time budgets (Williams et al., 2014), energetic costs (Masello et al., 2017) and kill rates of cryptic carnivores (Petroelje et al., 2020). However, two major issues impede the widespread application of accelerometers for quantifying kill rates. First, classifications of acceleration work best for behavioural states consisting of repetitive motions, like walking or wing beats (Shepard et al., 2008). But, the only clear, repetitive motion during feeding (jaw movement; Iwata et al., 2012) is often not captured by collar-attached accelerometers. As such, attempts at classifying feeding behaviour with accelerometers are often associated with high error (e.g. 0.34 sensitivity in bobcats, Petroelje et al., 2020; 0.68 precision in polar bears, Pagano et al., 2017). Second, automated classifications often require species- and context-specific observational data to train the models (Campbell et al., 2013; Pagano et al., 2017), which for many cryptic species is not attainable.

Recently, interest has grown in using camera collars to capture individual behaviour, but the size of battery needed to power these units limit their application to large animals and short duration observations (e.g. 1.1 kg collars record 10 s/5 min for 36 weeks: Thompson et al., 2012; 2.0 kg collars record 0.5–1 min/2 min for 4–14 hr/day for 5–10 days: Pagano et al. 2018). Acoustic recorders, which require less power to operate, might serve a similar purpose for smaller species (5.5 g recorded for 24 hr; Couchoux et al., 2015). While stationary remote acoustic monitoring has provided novel approaches for documenting species presence, distribution and abundance (Hannay et al., 2013), activity levels (Lawson et al., 2019) and conspecific interactions (Manna et al., 2014; Welch et al., 1992), recent attachment of recorders directly to animals has provided novel approaches for recording individual behaviour (Ilany et al., 2013; Lynch et al., 2013) including that of predators (Wijers et al., 2018) and humans (e.g. diet, Mirtchouk et al., 2016). As such, acoustic recorders hold great potential to circumvent challenges associated with other methods (Studd et al., 2019; Wijers et al., 2018), and to directly measure hunting behaviour of small- and medium-sized predators.

Here, we assess the capacity of small acoustic recorders and accelerometers to characterize hunting success and kill rates of Canada lynx *Lynx canadensis* (hereafter lynx), a boreal small prey specialist. Lynx (~10 kg) occupy large home ranges in densely forested habitats, making them difficult to observe in the wild. In the northern part of their range, their diet is primarily composed of snowshoe hares, a relatively small-bodied prey (<2 kg), along with smaller red squirrels *Tamiasciurus hudsonicus* (200 g) and birds (grouse, Canada Jays *Perisoreus canadensis*, <550 g; O'Donoghue, Boutin, Krebs, Zuleta, et al., 1998). The short handling times required to consume these prey preclude the use of GPS cluster analysis to identify kill sites as the majority of clusters are located at resting or grooming sites. However, lynx provide an ideal species to test these technologies thanks to the ease at which kill sites can be found through snow-tracking. Lynx therefore present an interesting and important case study for the usefulness of biologging technologies to document kill rates and hunting success of free-ranging predators since, if these devices prove useful for identifying kills of small prey by a medium-sized carnivore, they could enable a more complete picture of predatory behaviour and diet for predators of all sizes.

2 | MATERIALS AND METHODS

This research conformed to the guidelines of the American Society of Mammalogists (Sikes & Mammalogists, 2016) and was approved by the McGill University, University of Alberta and Trent University Animal Care and Use Committees, and by the Yukon Government Scientists and Explorers and Yukon Government Wildlife Research Permits (Supplementary Materials 1.1).

2.1 | Biologger deployment

Canada lynx were live-trapped in southwestern Yukon (61°N, 138°W) between November and April over five winters (2015–2020) in

conjunction with a 45-year long-term monitoring and ecological research project (Krebs et al., 2018). We used custom-made box traps (Kolbe et al., 2003) baited with meat (road kill), scented lures (castor, skunk essence) and visual attractants (tinsel, compact discs). Once captured, lynx were transferred to a wooden crate and transported to a local veterinary clinic (~45 km) where they were chemically immobilized (Supplementary Materials 1.2). For all lynx over 6 kg (mean mass = 10.1 kg), standard body measurements were taken, and a GPS collar (fix rate: 15–30 min; Telemetry Solutions remote download model, 350 g, $N = 5$; or Followit Iridium GPS, 245 g, $N = 34$) with externally mounted self-powered accelerometer (Technosmart Axy 3 or 4; 8 g; $N = 39$) and acoustic recorder (EDIC-mini tiny E60-1200h, 35 g, $N = 27$; or SOROKA-14E, 28 g, $N = 12$) was attached (see Supplementary Materials 2.1, Figures S1 and S2 for collar design). Assembled collars were less than 5% of the weight of each animal (Telemetry Solutions: ~393 g, ~4%, mean lynx = 10.0 g; Followit: ~281 g, ~3%, mean lynx = 10.2).

2.2 | Snow-tracking

To confirm that biollogger-identified hunting behaviour was capturing real events, each winter we visited GPS locations from the previous 2 days, and recorded whether lynx were feeding, travelling, sitting or bedded down according to the tracks or prey remains in the

snow. At kill sites, we identified prey species according to remaining fur or feathers, and whether it was a fresh kill (only fresh tracks, signs of a chase) or scavenging event (older or other predator tracks). Locations were labelled as unknown when tracks/behaviour were not discernible. For analysis, we categorized each GPS location as 'kill' or 'no kill' and combined all consecutive locations within each category as a single 'snow tracking event'.

2.3 | Acoustic data

Two different models of acoustic recorders (EDIC-mini and SOROKA-14E) were used over the study with slightly different recording settings (see Supplementary Materials 1.1). At selected settings and battery size, EDIC-mini recorded for up to 25 days and SOROKA-14E recorded for up to 49 days. Acoustic data were downloaded as 600 MB–2GB.wav files for analysis.

Classification and processing of audio files involved multiple steps (Figure 1). We first listened to and transcribed a subset of lynx audio files ($n = 18$; 24.75 days; Figure 1: A1). This established that chewing (bone crunching sounds; Supplementary Materials 4) and chases (Supplementary Materials 5, 6) generated unique and distinguishable sounds (Figure 1: A2). We confirmed that our interpretation of chewing sounds was correct with video of free-ranging lynx (Supplementary Materials 7) and correlation with kill

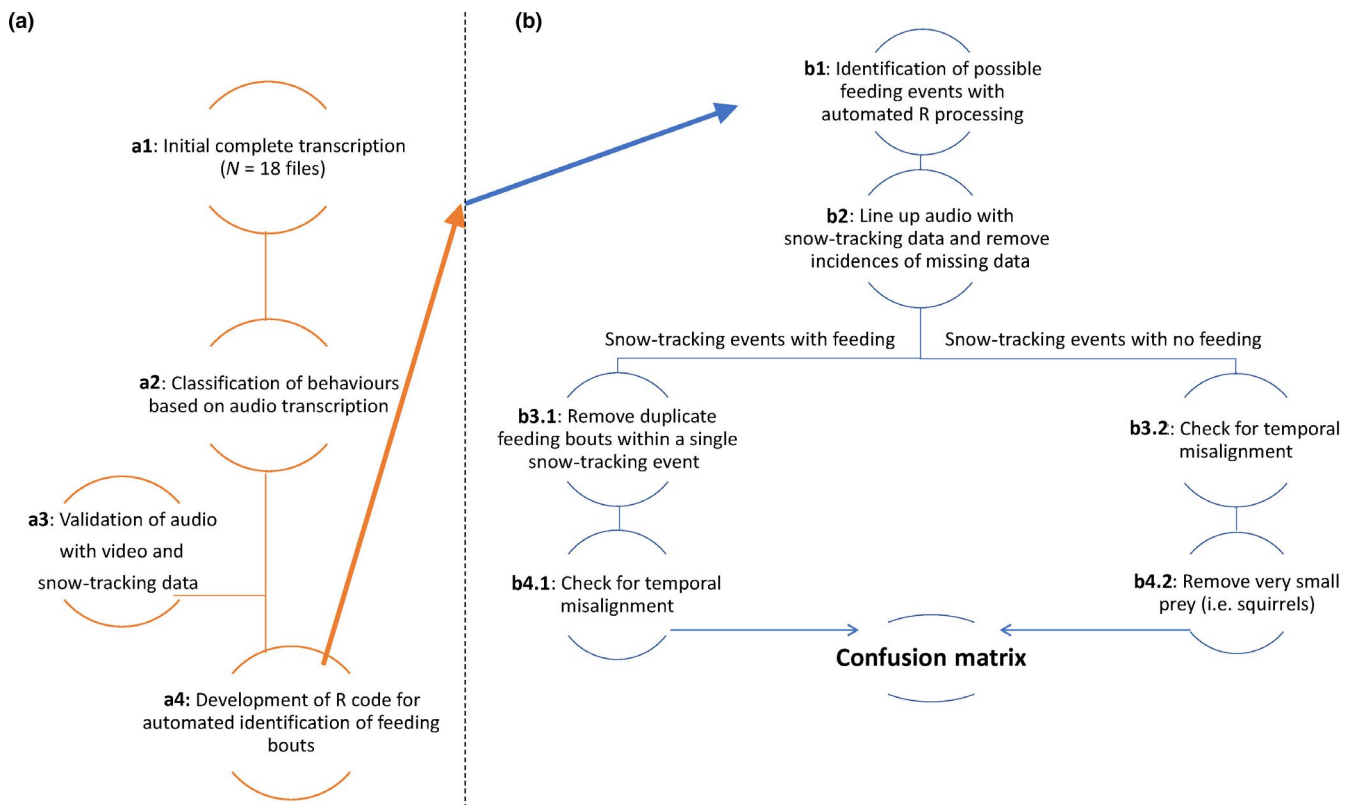


FIGURE 1 Methodological approach to generating an automated classification of meals from acoustic data. Panel a displays the initial processing required to generate the automated R code used to identify feeding events. In the second stage of analysis (panel b), feeding events identified using our automated process were further manually processed before inclusion in the final dataset (confusion matrix)

sites identified by snow-tracking (Supplementary Materials 2.2; Figure 1:A3).

We then developed in two steps an automated classification aimed at classifying all audio into feeding and not feeding (Figure 1: A4). First, we determined which acoustic metrics identified chewing from other behavioural states. Using three hundred and sixty 15-s audio clips of chewing, grooming, walking and not moving from six lynx (15 clips/behaviour/lynx), we calculated spectral properties, peak frequency, number of bursts, number of syllables, mean amplitude of syllables, mean amplitude of whole clip and loudness using *SEEWAVE* and *SOUNDGEN* packages in R (Anikin, 2019; Sueur et al., 2008). Comparing these metrics between behavioural states revealed that clip loudness and mean amplitude of syllables were distinct enough to isolate chewing (Supplementary Materials, Figures S3 and S4). Second, using 3-day segments of audio from 11 lynx for which we had manually identified all feeding events (i.e. continuous chewing over several minutes), we calculated loudness and amplitude for every 15 s across the 3 days and built a classification algorithm around three criteria. For each lynx, a clip was labelled as chewing when (a) the loudness was in the *a* percentile or higher of all audio clips, and (b) the mean amplitude was in the *b* percentile or lower of all audio clips. Finally, (c) a feeding event required *c* audio clips within a 10-min window to be classified as chewing. To determine which thresholds generated a classification model that best predicted training data, we calculated F1, precision and recall for each of the 6,408 models run across a range of values for *a* (0.5–0.95 by 0.05 increments), *b* (0.1–0.95 by 0.05 increments) and *c* (5–40 clips) parameters (Figure S5).

We tested the accuracy of our top model by assessing whether the modelled feeding events matched known kill sites from snow-tracking (Figure 1b). After lining up extracted feeding events with snow tracking events using *fuzzyjoin* in R (Robinson, 2020) and removing any cases where no tracks were found during snow-tracking, we divided snow tracking events into two subgroups, namely those with identified feeding events and those without (Figure 1 B2). When multiple audio feeding events occurred at a single snow tracking event, we manually combined the feeding events into a single event (Figure 1 B3.1) and adjusted false negatives caused by slight time misalignment (Figure 1 B4.1, Supplementary Materials 2.3). We checked for time misalignment of events with no feeding (Figure 1 B3.2) and removed any kills that could not have been identified in our 10-min window due to very short feeding times ($N = 2$ squirrels; Figure 1 B4.2). Once data were cleaned, we used a confusion matrix (Velez et al., 2007; package *CARET* in R: Kuhn, 2008) to calculate the proportion of predicted feeding events that correspond to true snow tracking kills (recall); the proportion of predicted non-feeding events that correspond to non-feeding snow tracking events (specificity); the proportion of snow tracking kill events that the model predicted (precision); F1; and overall accuracy.

Lastly, to measure hunting success, we generated an automated classification of chases. Using the fully transcribed audio files as validation data, we determined that chases were distinguishable as the loudest sounds (Figure S3). Using *SEEWAVE*, we calculated the mean amplitude of sound over 2 s for each second of recording, and

extracted all sounds that were louder than 30% (in all years except 2019–2020) or 20% (SOROKA-14E recorders in 2019–2020 due to microphone adjustment) of the maximum amplitude recorded in that file. This threshold captured 94.5% of 109 chases along with some misclassification of non-chase behaviour (<1% of audio files, ~33 of 8,931). Although the error is relatively small, a purely automated process would generate a substantial overestimate of chases. Thus, to generate an accurate measure of hunting effort and success, we paired this automation with a manual post-processing of tagged events to confirm chases.

2.4 | Accelerometer classification

Accelerometers recorded acceleration continuously at a 1-Hz (2015–2017) or 10-Hz (2017–2020) sampling frequency within a ± 8 g range. Prior to generating a model to identify feeding events, we used continuous behavioural observations of tagged free-ranging lynx to determine the most common behavioural states that needed to be included in the model to minimize misclassification. By locating and observing lynx (24 hr on four individuals) using very high frequency (VHF) telemetry, we determined that lynx spend 95% of their time in one of four states (chewing, not moving, grooming and walking; see Figure 2 for example accelerometer profiles), often expressing each state for 15 min or longer at a time. For our classification model, we generated training data for these four behavioural states for 10 lynx (2,300–3,200 min per state) according to whether the individual was travelling (GPS) and the sound level on the acoustic recorders, denoting whether individuals were inactive or active (Figure 3; Supplementary Materials 3.1 and 3.2 for clock drift correction). For our models, these training data were subsampled using a 2-min sliding window with a stride of 1 min. Direct observations were not used for training data as most lynx were not observable, and even with those that were observable, we could not collect enough direct observations to use as training data.

For classification, we separated 1-Hz ($n = 5$ lynx) and 10-Hz ($n = 5$) accelerometer data, and for each frequency we explored two machine learning algorithms using Python (Figure 3; green-dashed line). One algorithm was a one-dimensional convolutional neural network (1d-cnn) model implemented using the Keras and TensorFlow libraries that we ran on the raw data (see Supplementary Materials 3.3). The second was a random forest (scikit-learn library; Pedregosa et al., 2011) that operated on a suite of time-series features generated using the *tsfresh* library (Christ et al., 2018). We removed as many features as possible without compromising the cross-validation scores to minimize computational cost of the model (see specifications in Supplementary Materials 3.3). We ran and compared classifications on only the heave axis with those on all three axes. This revealed that models using only the one axis outperformed those that included multiple axes, especially with the 1d-cnn models (Supplemental Materials 3.5, Table S1). Thus, all reported classifications use only the heave axis. Performance of all classifications ($n = 4$; both algorithms for

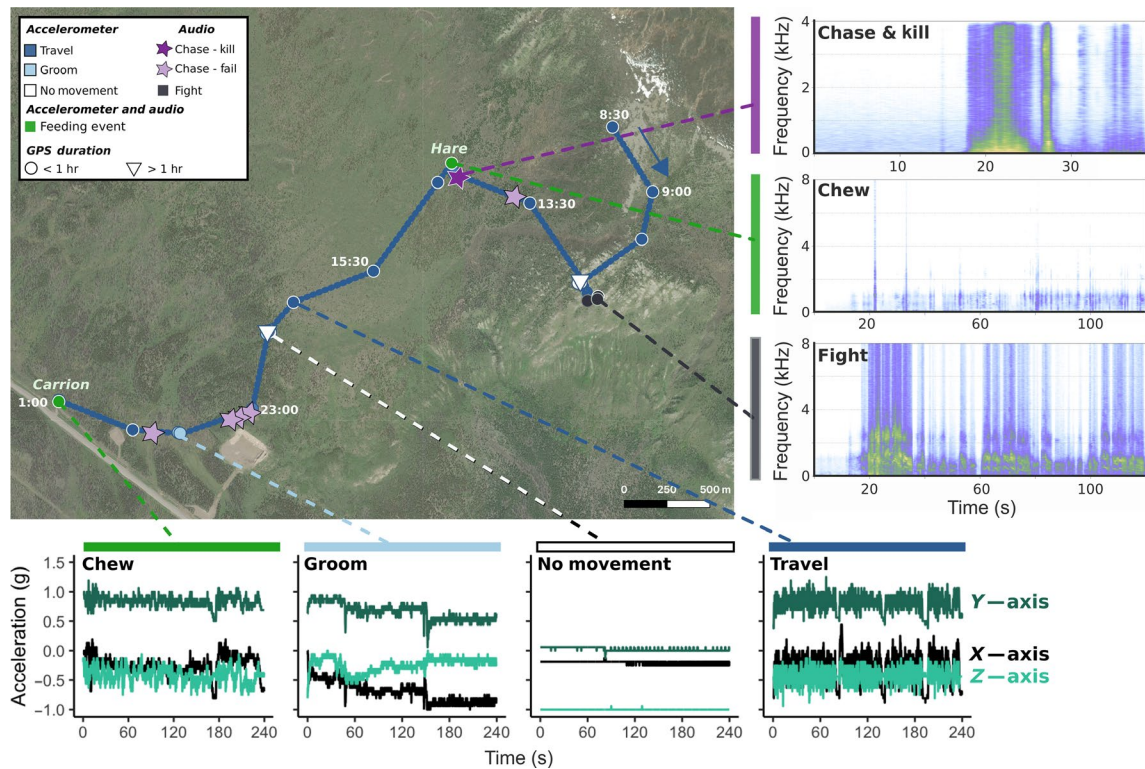


FIGURE 2 Example GPS track and behaviour of a male lynx over a day. Locations illustrate the acoustic (right) and acceleration (bottom) signatures of each behaviour that is extractable from the biologging devices. For acceleration, signatures for the X (black), Y (dark teal) and Z (light teal) axes are shown

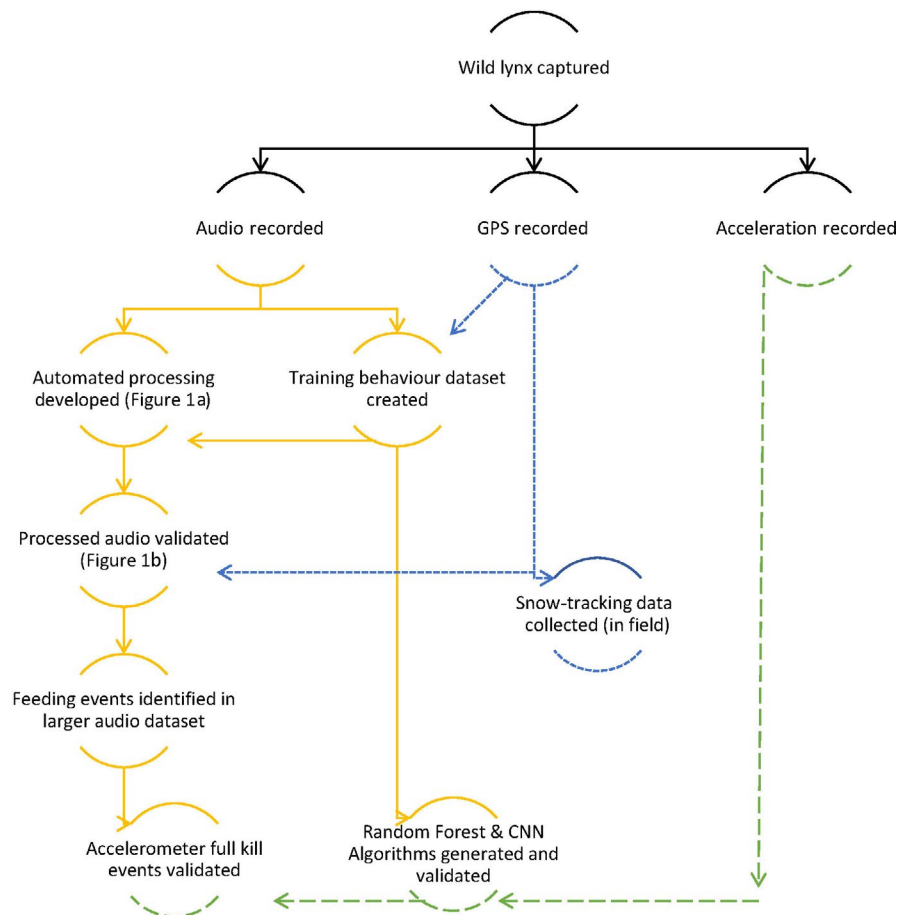


FIGURE 3 Schematic of the methodological workflow for extracting kill rates from accelerometers, acoustic recorders and GPS collars deployed on free-ranging lynx. Colours and line types represent which data types were used in each step: orange solid lines represent audio data; blue-dotted lines represent GPS data; and green-dashed lines represent accelerometer data

1 and 10 Hz) was calculated using a 'leave one lynx out' cross-validation method where the model was built using training data from all lynx but one, and then validated on the training data from that remaining lynx.

To calculate kill rates, we validated the accelerometer classifications at the scale of feeding events in addition to the scale of the classification (i.e. 2-min windows). We defined a feeding event as consecutive occurrences of chewing with no gaps greater than 10 min (see Supplementary Materials 3.4). Using all manually confirmed feeding events in the audio files ($n = 269$; mean per lynx = 19) as known events, we calculated precision and recall of the accelerometer classification. As the classification generated lots of false short feed events, we tested how accuracy was impacted if we applied a threshold requirement in the duration of a feeding event. For a range of threshold durations (2 to 24 min), we relabelled accelerometer-identified feeding events that were shorter than the threshold as not feeding, and calculated F1 scores for the accelerometer classification's ability to identify (a) all known feeding events in the audio, (b) all snowshoe hare feeding events and (c) all snowshoe hare feeding events in the audio with durations longer than the threshold (Figure S6). This validation used the accelerometer classification that did not include training data for that lynx (i.e. leave one out), and included lynx ($n = 4$) and known feeding events that were not used for training (56.6% of feeding events; Figure 3). These additional lynx were included here as an independent sample of the efficacy of applying the classification to new data.

2.5 | Lynx hunting behaviour

To demonstrate potential ecological data that can be generated from the above classifications, we processed all audio and accelerometer data for 13 lynx for which we had data from both devices. For each chase identified by our semi-automated classification, we recorded duration (<1 to 39 s; mean = 6.0 s), prey species from vocalization and whether it was successful (Figure 4). Chases were successful if followed by a death-associated vocalization of the prey (66% of 331 successful chases; Figure S7; audio clip Supplementary Materials 5 and 6), or if chewing occurred within 10 min with no subsequent chases (91% of 331 successful chases). We excluded any running that was not a sprint (i.e. high step rate) to minimize the inclusion of non-chase behaviour. Since the output of this semi-automated classification generated similar chase success rates as previously documented through snow tracking (O'Donoghue, et al., 1998), we believe that the majority of hunting attempts were captured including those from ambush beds. For all feeding events, we recorded prey type (prey vocalization), feeding duration and whether the event was a new kill (preceded by a chase), a stolen kill (preceded by vocalizations of other predators and no chase; Supplementary Materials 8) or scavenging (no chase or lynx vocalizations). We calculated the proportion of different prey types in lynx diets categorized as follows: snowshoe hare kill (hare vocalizations prior to feeding and/or any feeding longer than 15 min), red squirrel kill (squirrel vocalizations prior to feeding), stolen, scavenging or other (unidentifiable prey vocalization or

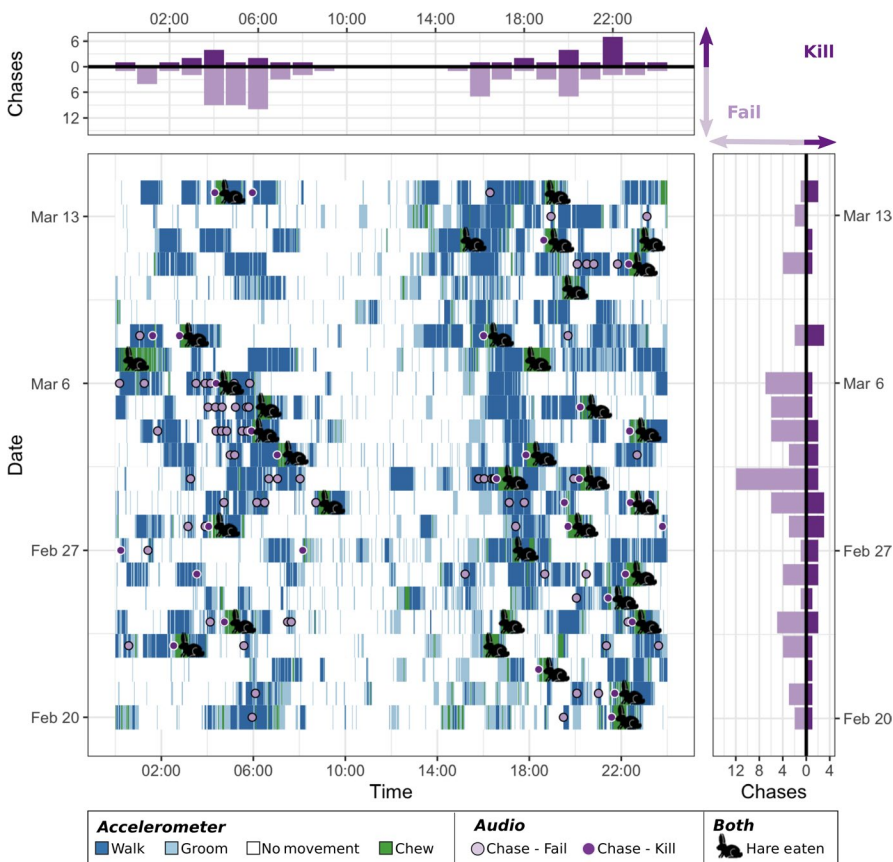


FIGURE 4 Example actogram of a male lynx illustrating continuous behavioural classification over 1 month from a combination of accelerometer and audio devices

no vocalization with feeding <15 min). We calculated the average number of feeding events per 2-day periods.

3 | RESULTS

3.1 | Audio data

Over the five seasons of the study, we collected 14,470 hr (spanning 693 lynx-days) of audio data from 39 collars and 26 individual lynx. We visited 4,682 lynx GPS points through snow tracking and identified 129 kills (81% hare, 14% red squirrel and 4% avian spp.). These points clustered into 158 snow tracking events lasting 14–1,020 min, but only 34 kills corresponded with audio due to faulty recorders ($N = 8$ collars and $N = 5$ individual lynx). Our top model labelled a clip as chewing when loudness fell in the upper 25th quantile and amplitude fell in the lower 40th quantile of all clips in the file, and labelled a series of clips as a feeding event when there was >6.25 min of chewing in a 10-min window. Our automated model tagged 113 feeding events from 971 hr of audio. After aligning and cleaning ($N = 13$ duplicates removed), 31 feeding events occurred during snow-tracking data: 26 aligned with a snow tracking kill, leaving 5 false positives (Table 1). There were 46 snow tracking events that did not correspond to a feeding event in audio after cleaning ($N = 2$ small prey removed; Figure 1 B4.2). These included five kill sites (i.e. false negatives), all of which were females known to be travelling with another lynx (Table 1). The overall accuracy of the confusion matrix was 0.87 with high recall (0.87), specificity (0.87), precision (0.87) and F1 (0.87). Our automated classification of chase behaviour tagged 16,745 sound clips, of which manual post-processing confirmed 1,316 were unsuccessful chases, 331 were successful chases (i.e. ended in a kill) and 15,098 were not chases.

TABLE 1 Confusion matrix of the number of predicted events (feeding and not feeding) from audio (columns) that corresponded with snow tracking kill sites and non-kill sites (rows)

	Snow-tracking: kill	Snow-tracking: no kill
Audio: feeding	26	5
Audio: no feeding	5	41

TABLE 2 Performance metrics of accelerometer classification models at identifying feeding events with durations >15 min for each model type and acceleration sampling frequency. Overall precision, recall, F1 scores and sample size are presented, along with the range of F1 scores for individual lynx

Model type	Frequency	Support	Precision	Recall	F1	F1 range
Random forest	1 Hz	108	0.99	0.94	0.96	0.92–1
	10 Hz	118	0.94	0.98	0.96	0.83–1
CNN	1 Hz	108	0.74	0.88	0.80	0.53–1
	10 Hz	118	0.69	0.91	0.78	0.54–0.96

3.2 | Accelerometer classification

Classification of accelerometer data into four behavioural states at 2-min resolution produced overall F1 scores >0.80, but there was variation in accuracy between sampling frequencies and classification algorithms (Table S1; Supplementary materials 3.5). Accuracy at classifying chewing at this 2-min resolution was higher with the random forest ($F1 = 0.82$ – 0.90 dependent on sampling frequency) than the CNN ($F1 = 0.79$ – 0.81) algorithm. At the scale of feeding events, the accuracy of the classification algorithm varied depending on the threshold used for how long feeding must occur in order to be considered a feeding event (Figure S4). A classification that included all events with durations greater than 2 min generated high incidences of false positives (feeding events that did not exist in audio). Increasing the duration threshold reduced false positives while increasing false negatives (feeding events in audio that were missed). A feeding duration threshold of 15 min produced the highest F1 score when classifying all feeding events ($F1 = 0.90$; Figure S6a), only snowshoe hare feeding events ($F1 = 0.93$; Figure S6b) or only snowshoe hare feeding events with a duration equivalent or longer than the threshold ($F1 = 0.97$; Figure S6c). This threshold captured 90% of hare kills, stolen meals and scavenging, but captured only 6% of red squirrel and other species kills (Figure S8). At this threshold, 1-Hz and 10-Hz sampling frequencies were similarly successful at identifying hare feeding events (Table 2). The random forest models were more successful than the CNN models at identifying feeding events both at the individual device level (Table S1) and across all devices (RF: $F1 = 0.96$; CNN: $F1 = 0.78$ – 0.80 ; Table 2).

3.3 | Variation in lynx hunting behaviour

Both audio recorders and accelerometers provided individual data that captured variation in hunting behaviour (Figure 4). According to audio data of 13 individual lynx (six females and seven males), at the increase/peak phase of the snowshoe hare cycle, the individual proportions of feeding events that were hare kills ranged from 40% to 80% (Figure 5a), while red squirrel kills ranged from 0% to 27%. If scavenging events or stolen prey are assumed to be snowshoe hares, as suggested from our snow tracking and from previous lynx diet research in the study area (O'Donoghue et al., 1997), then feeding events comprised of snowshoe hares ranged from 70% to 100%. Both devices showed that lynx eat an average of 1.2 large prey items

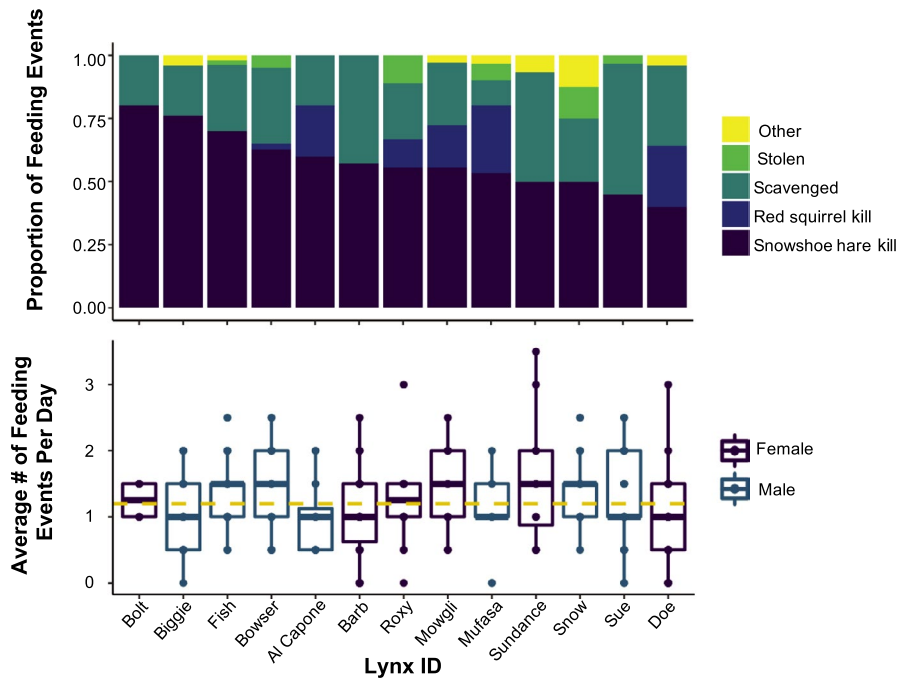


FIGURE 5 Variation in (a) feeding composition and (b) average number of feeding events per day for 13 individual lynx (six females and seven males) in winter. Feeding composition was determined through audio data. Average feeding events per day were calculated from both accelerometers and acoustic recorders across 2-day periods for individual male (blue) and female (purple) lynx along with the population average (1.2 feeding events per day; dashed line)

(hare) per day (Figure 5b). The variation was greater within individuals (2-day average ranging from 0 to 3.5 feeding events) than across individuals (individual means varied from 0.97 to 1.5 feeding events).

4 | DISCUSSION

Using audio recorders and accelerometers, we were able to document chases, kills, scavenging events and feeding events of free-ranging Canada lynx, a cryptic mesocarnivore and small prey specialist of the boreal forest. Although similar behavioural metrics have been documented in larger carnivores using GPS cluster analyses (e.g. Williams et al., 2014), these key hunting metrics have remained unattainable for the majority of carnivores (71.9% are small prey specialists; calculated from Carbone et al., 1999) due to the limited time spent at a kill site (<1 hr) relative to other locations (grooming: ~1 hr, sleeping: >1 hr). As such, predator studies have had low detection rates of short feeding events (25% chance of detecting GPS clusters less than 9 hr long; Vogt et al. 2018) which often leads to not considering prey <2 kg in their results (McLean et al., 2005; Svoboda et al., 2013). As such, the biologging methodologies presented here are a substantial advance in the capacity to continuously document kill rates and detailed hunting behaviour for predators of any size without intensive field work related to kill site investigations or scat collection, but particularly for carnivores that specialize on small-bodied vertebrate prey.

We found that audio recorders accurately captured predator kill rates, while also providing additional information on prey type, hunting success, intraspecific aggression at kill sites and post-kill behaviour. Audio recorders have been used to document feeding behaviour in herbivores (Kikuchi et al., 2014; Studd et al., 2019), and here we show that they are also well-suited for use on predators, although

recording duration and battery size will depend on body size. In addition to chases and feeding events, we were often able to identify the prey species (for 66% of kills) according to prey vocalizations, which is a major advantage over GPS and accelerometer approaches that require kill site visits for prey information (McPhee et al., 2012). Another advantage of audio that we found is the ability to identify occurrences of scavenging or kleptoparasitism, as well as the potential to quantify social dynamics (solitary or cooperative hunting; not validated here) according to the frequency and type of vocalizations between individuals. The capacity of audio recorders to provide these extra details improves quantification of predator hunting behaviour and provides new opportunities to explore the role of cooperation, competition and scavenging in predator success and predator-prey interactions.

Despite these considerable advantages, there are some drawbacks to the use of acoustic data. The sound quality varied considerably between devices and across deployments, partially due to variation in rehousing and attachment to collars, but also from damage sustained post-deployment. This contributed to some error in our automated classification as the fit of our universal thresholds varied with the quality of the acoustic file generating more false positives in some files than others. We also had five snow tracking kills that were not captured by the classification. Manual listening of the audio revealed that one had some evidence of chewing (although it was unclear), while four had no evidence of chewing. In all cases, these events stemmed from three female lynx that consistently hunted in a group (two or three individuals), so we suspect the snow tracking kill was primarily consumed by another individual. In addition, although very short feeding times (>10 min) could be identified through manual processing of audio files, our automated algorithms did not capture these events, demonstrating that despite the large value of this technology for identifying kills of small prey, very small prey (e.g. squirrels, small birds) may still

be missed. Thus it seems that our classification was capturing all hare feeding events, but was imperfect for quantifying group hunting success, and consumption of very small prey (<0.5 kg). Another major drawback for this technology is that extracting additional information like chase success or prey type required a substantial amount of manual processing (~1 hr/day of audio). Moreover, because this technology is not currently produced commercially for wildlife applications, it required considerable troubleshooting with high device failure rates in the first couple years; >50% of devices failed to record at all, or broke within the first 3 days of deployment, mostly due to water or physical damage from lynx claws.

Independent of the acoustic recorders, we successfully quantified kill rates using accelerometers with higher accuracy than has been previously achieved. Although behavioural classification of acceleration is becoming common practice, feeding of terrestrial predators has proven difficult (e.g. Glass et al., 2020; Pagano et al., 2017; Wijers et al., 2018). Our success here results from considering behavioural signals over longer time periods (minutes) than are often used for classifications (seconds; Nuijten et al., 2020). For lynx, we found that the clear and consistent distinction between feeding and grooming was the posture; during feeding, lynx consistently maintained a crouched posture over the carcass (see Supplementary Materials 7), while during grooming, they adjusted posture every couple of minutes. Although the boost in classification accuracy that we achieved for feeding over other studies may seem moderate (~10%), such error in classification can translate into substantial over- or underestimation of kill rates (i.e. a doubling) due to the rarity of feeding events in most large predators (<5% of the day in lynx).

However, the use of accelerometers to characterize hunting behaviour also had limitations. First, similar to the audio, our classification was most accurate when using long time windows (2 min), which reduced the ability to extract short feeding events (<15 min). Therefore, although these methods greatly improve what can be achieved through GPS clustering (Jansen et al., 2019; Leighton et al., 2020), our automated classifications still miss identifying consumption on the smallest prey (squirrels and birds; Figure S8). Second, accelerometer classification algorithms require considerable amounts of observational data for training. As use of captive animals or surrogate species often increases error in the classification (Campbell et al., 2013; Pagano et al., 2018), collecting data on the focal species in the field remains a major challenge. Because free-ranging lynx are difficult to observe (most individuals avoided observers), we had to infer behavioural states from a combination of GPS and audio data. While successful, the deployment of additional biologging technology increases costs, data management and processing requirements. Finally, achieving sufficiently low error to accurately quantify kill rates is challenging. We attempted several combinations of statistics, time windows and algorithms, of which only the two presented here produced promising results. A universal approach does not seem to exist so each classification requires considerable time investment to determine the best metrics and algorithm to use. This should be considered when selecting accelerometers, and biologgers in general, for studying behaviour.

Ultimately, we found that the combination of acoustics and accelerometry provided the best results. Although each technology individually generates unprecedented information about predator behaviour, we found that the most complete quantification was produced from a combination of the two. Audio data provided chase and prey details and accelerometers provided an efficient method for identifying hare kills. Despite the focus of this study on hunting behaviour, both devices also provide additional behavioural and environmental information, which can refine our understanding of predator behaviour, predator-prey interactions and social dynamics. We documented substantial intraspecific variation in both prey selection and kill rates, something that has been unattainable for free-ranging small prey specialists. We believe that the fine-scale (minute by minute) data that can be collected by these technologies continuously over long time periods (weeks to months) will provide unprecedented insight about the lives of cryptic terrestrial species, including but not limited to their hunting behaviour.

ACKNOWLEDGEMENTS

The authors thank Agnes MacDonald for long-term access to her trapline, and to the Champagne and Aishihik First Nations for allowing them to conduct work on their traditional territory. Funding was provided for this project by the Natural Sciences and Engineering Research Council, W. Garfield Weston Foundation and Institut Nordique du Québec.

AUTHORS' CONTRIBUTIONS

E.K.S. and M.M.H. conceived the initial idea of capturing hunting behaviour with accelerometers and S.B. suggested the use of acoustics; All the authors contributed to developing those ideas and provided comments on earlier drafts; E.K.S., A.K.M. and R.E.D. developed the field-based methods and collected the data; E.K.S., J.F.S. and RED completed the analyses; E.K.S., R.E.D. and A.K.M. wrote the paper.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/2041-210X.13605>.

DATA AVAILABILITY STATEMENT

Data used in this manuscript can be found on Figshare at <https://doi.org/10.6084/m9.figshare.14210735>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Studd EK, Derbyshire RE, Menzies AK, et al. The Purr-fect Catch: Using accelerometers and audio recorders to document kill rates and hunting behaviour of a small prey specialist. *Methods Ecol Evol*. 2021;00:1–11. <https://doi.org/10.1111/2041-210X.13605>