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ORIGINAL ARTICLE

Evaluating camera traps as an alternative to live trapping for estimating the density of snowshoe hares (*Lepus americanus*) and red squirrels (*Tamiasciurus hudsonicus*)

Petra Villette[1] · Charles J. Krebs[2] · Thomas S. Jung[3]

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Abstract Live trapping is one of the methods typically used to estimate population densities of small mammals, but this is labor-intensive and can be stressful to individuals. We assess the use of camera trap hit (detection) rates as a noninvasive alternative to live trapping for estimating population densities of snowshoe hares (*Lepus americanus* (Erxleben, 1777)) and red squirrels (*Tamiasciurus hudsonicus* (Erxleben, 1777))—two common small (≤1.5 kg) mammal species in the boreal forests of northern North America. We compared hit rates from camera trapping to live trapping mark-recapture density estimates and asked if the hit window—the length of time used to group consecutive videos together as single detections or "hits"—has an effect on the correlation between hit rates and live trapping density estimates. The relationship between hit rate and population density was sensitive to hit window duration for red squirrels with R^2 values ranging from 0.41 to 0.68, and a 5-min hit window generated the highest value. R^2 values for snowshoe hares ranged from 0.70 to 0.90, and a 10-min hit window generated the highest value, but hares were live trapped and filmed only at very low densities. Our results indicate that camera trapping is a robust means for estimating the density of red squirrels, but the appropriate hit window duration must be determined empirically if camera trapping data are to be used to monitor populations of this species. Additional live trapping and filming of snowshoe hares is required to better assess camera trapping of this species.

Keywords Camera trapping · Density estimation · *Lepus americanus* · Snowshoe hare · Red squirrel · *Tamiasciurus hudsonicus*

✉ Petra Villette
petra.villette@gmail.com

Charles J. Krebs
krebs@zoology.ubc.ca

Thomas S. Jung
thomas.jung@gov.yk.ca

[1] Laboratoire Chrono-Environnement, UMR 6249 Université de Bourgogne Franche-Comté, La Bouloie-UFR Sciences et Techniques, 16 Route de Gray, 25030 Besançon Cedex, France

[2] Department of Zoology, University of British Columbia, #4200-6270 University Blvd, Vancouver, BC V6T 1Z4, Canada

[3] Yukon Department of Environment, P.O. Box 2703, Whitehorse, Yukon Y1A 2C6, Canada

Introduction

Snowshoe hares *Lepus americanus* (Erxleben, 1777) and red squirrels *Tamiasciurus hudsonicus* (Erxleben, 1777) are small mammals (1–1.5 kg and 250 g, respectively) that are important prey species in the North American boreal forest, and both species can experience dramatic fluctuations in population density (Boonstra et al. 2001; Krebs et al. 2013). The population densities of these species are often assessed using live trapping and mark-recapture methods, but live trapping is known to cause significant physiological stress in both snowshoe hares (Boonstra and Singleton 1993) and red squirrels (Bosson et al. 2012), and can be labor-intensive, driving up costs.

Camera traps are a potential alternative to estimating population densities of small mammals. Camera traps (cameras that take photographs or record videos in the absence of a human operator) have been used to observe wildlife since the 1920s (reviewed in O'Connell et al. 2011), and we have used them successfully to estimate population densities of red-backed voles (*Myodes rutilus*) and deer mice (*Peromyscus maniculatus*) (Villette et al. 2016). Cameras are less invasive than live trapping, can be cheaper to operate in the long-term by minimizing the amount of time in the field (Rovero and Marshall 2009), and can operate continuously in remote and extreme conditions (McCarthy et al. 2008). There are other noninvasive methods for estimating the densities of our focal species, like snowshoe hare fecal pellet densities (Krebs et al. 1987; Murray et al. 2002) and red squirrel auditory point counts (Mattson and Reinhart 1996), but these methods have their own limitations (Murray et al. 2005; Efford and Dawson 2009) and can require considerable effort.

Estimating densities with camera traps is relatively straightforward when the focal species features markings that allow for the identification of individuals; photographic "capture" histories can be constructed for individuals and these can then be used with mark-recapture models to estimate densities (e.g., Karanth 1995). Estimating densities when individuals cannot be identified has proven more challenging; approaches include mark-resight studies (e.g., fisher *Martes pennant*; Jordan et al. 2011) and simply using detection or "hit" rates as an uncalibrated index of density (e.g., European pine marten *Martes martes*; Manzo et al. 2011). More complex treatments of hit rate data include Rowcliffe et al.'s (2008) random encounter model, which utilizes daily movement rates and camera detection areas in a gas model to estimate densities from hit rates.

Random encounter models (REMs) have been used to estimate the densities of captive muntjac *Muntiacus reevesi*, water deer *Hydropotes inermis*, and red-necked wallabies *Macropus rufogriseus* (Rowcliffe et al. 2008), wild Harvey's duiker *Cephalophus harveyi* (Rovero and Marshall 2009), and wild Irish hares *Lepus timidus hibernicus* and European hares *Lepus europus* (Caravaggie et al. 2016). REM density estimates in these studies appear comparable to estimates obtained through other means (a park-wide census in the case of Rowcliffe et al. (2008), and line transect distance sampling in the case of Rovero and Marshall (2009) and Caravaggie et al. (2016)), but REMs rely on the assumption that animal movement across the landscape is random, and they are dependent on some measure of movement rate which is not always known for the focal species in question (e.g., Rovero and Marshall 2009) or for the focal species in the study area (e.g., Caravaggie et al. 2016). In addition, focal species may be rare or cryptic, necessitating the use of bait to increase the probability of detection (e.g., red fox *Vulpes vulpes,* Vine et al. 2009), which would violate the assumption of random movement across the landscape.

In light of these limitations, there remains a need to develop camera trapping methods for situations in which REMs are not applicable (e.g., bait is necessary for detection, or daily movement rates are unknown). Calibrating hit rates with density estimates obtained through another method (e.g., live trapping or distance sampling) is one way to approach this gap, and the one we have adopted here. We compared snowshoe hare and red squirrel baited camera trap hit rates to population density estimates obtained through live trapping and mark-recapture models to determine if hit rates can be used to obtain density estimates comparable in accuracy and precision to what we would obtain using live trapping for these two species. We predicted that hit rates and live trapping density estimates would strongly correlate for both species.

We also addressed the question of how to define a hit. Conventions for counting photographs or videos vary between studies; some have grouped consecutive photos or videos together when they appear to be of the same animal (e.g., Rowcliffe et al. 2008; Caravaggie et al. 2016), others have used camera delay settings to prevent multiple photographs or videos being generated by a single encounter (e.g., Manzo et al. 2011), while others have used what we will call a hit-window convention and counted consecutive photographs or videos as a single hit when they occurred within a specific time range of each other (e.g., Rovero and Marshall 2009). In comparing hit rates to live trapping density estimates of northern red-backed voles (*Myodes rutilus*) and deer mice (*Peromyscus maniculatus*), we have found that the correlation between hit rates and live trapping density estimates can be sensitive to the hit-window used (Villette et al. 2016), and we predicted that the correlation between hit rates and live trapping densities estimates of snowshoe hares and red squirrels would exhibit similar sensitivity.

Materials and methods

Study sites

We conducted live and camera trapping for both species in the Kluane Lake Region (61° N, 138° W) of southwest Yukon, Canada, in May to August of 2010–2012. The forest in this region is predominantly white spruce (*Picea glauca*) with some trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*). The dominant shrub is the gray willow (*Salix glauca*), followed by bog birch (*Betula glandulosa*), shrubby cinquefoil (*Potentilla fruticosa*), and soapberry (*Shepherdia canadensis*). Abundant groundcover plants include *Lupinus arcticus*, *Anemone parviflora*, *Mertensia paniculata*, and *Achillea millefolium* (Turkington et al. 2002). Snowshoe hares and red squirrels are among the most common mammals in the region and have been subject to intensive population study there (e.g., Hodges et al. 2001). The trapping girds are placed such that they are accessible (within 500 m of vehicle access), spaced at least 1 km apart, and occupy spruce forest habitat; they have been in operation for at least 26 years as part of long-term ecological experiments and monitoring programs in the region, and the live traps are left out permanently on the grids.

As in Villette et al. (2016), the general procedure was to conduct a 2-day camera trapping session using 15–16 cameras on a grid, followed by a 2- or 3-day live trapping session on that grid. Our experimental unit was a grid; a hit rate for a given camera trapping session was calculated using the footage from all of the cameras operating during that camera trapping session pooled together (see below).

We camera-trapped and live-trapped snowshoe hares on five permanent grids: Jacquot North grid and Jacquot South grid were located on Jacquot Island, which is approx. 5 km^2 in area and located at the north end of Kluane Lake. Both Jacquot grids consisted of 100 stations laid out in a 10 × 10 fashion with stations 30 m apart, covering an area of 7.29 ha. Single capture, hare-sized live traps (Tomahawk Live Traps, Hazelhurst, WI) were located at every other station (A1, B2, A3, B4, etc.) for a total of 50 trapping stations, and the traps were situated under trees for protection from the rain. The remaining three grids, Chitty grid, Sulfur grid, and Silver grid, were located on the mainland, 40–60 km southeast of Jacquot Island, adjacent to the Alaska Highway. These three grids consisted of 400 stations laid out in a 20 × 20 fashion with stations 30 m apart, covering an area of 32.49 ha. Live traps were located at alternating stations along the A, B, G, H, M, N, S, and T rows (A1, B2, A3, B4, etc.) and at D20, F20, I1, K1, P20, and R20 for a total of 86 trapping stations. Silver grid and Jacquot South were located in dense spruce forest with dense undergrowth and considerable deadfall; the remaining grids were located in open spruce forest with less undergrowth and deadfall.

We camera-trapped and live-trapped red squirrels on seven permanent grids. Agnes grid and Chitty grid were located in open spruce forest with little shrub cover, while Lloyd, Sulfur, Kloo, GPC, and Joe were located in denser forest with considerable undergrowth and shrub cover. The Chitty and Sulfur squirrel grids were subsets of their respective hare grids, and all seven squirrel grids are located within 50–500 m of the Alaska Highway. Each grid consisted of 100 stations laid out in a 10 × 10 fashion, with stations 30 m apart; 50 squirrel-sized live traps (Tomahawk Live Traps, Hazelhurst, WI) were located at every other station (A1, B2, A3, B4, etc.), under spruce trees for protection from the weather.

Remote cameras

We used three Bushnell Trophy Cams (model 119,455) and 11 SG550 ScoutGuard cameras equipped with 2GB memory cards, and 20 SG560 ScoutGuard cameras equipped with 8GB memory cards. All three models are equipped with an infrared lamp for filming at night, and a passive infrared detector for detecting motion, and had similar specifications (e.g., trigger speed, detection distance). The cameras were set to record a 60-s video when triggered, and the delay option was set to the lowest possible setting for all cameras (videos could be recorded as little as 1 s apart in the Bushnells, and 1.2 s apart in the ScoutGuards). Motion sensitivity in all cameras was set to high. The two camera models performed similarly in controlled field tests (data not shown), and no distinction was made between videos taken from the different models in subsequent analyses.

Camera trapping sessions were 2 days long and involved 15–16 cameras placed on a grid such that, within a summer, a given trapping station on a grid was not camera-trapped twice. On squirrel grids, we did not place cameras at adjacent trap stations during a camera trapping session, and therefore, cameras were always at least 60 m apart. At the selected stations, we secured one camera trap to a tree 1–2 m from the trap entrance and 10–30 cm above ground; we placed the camera traps directly in front of the live traps where possible, but when a clear view of the live trap entrance was not possible, or when a live trap could not be moved or rotated to face the camera without removing it from tree cover, we placed the camera traps to the side. All live traps on the grid were baited at the beginning of the camera trapping session (alfalfa cubes for hares and peanut butter for squirrels), and all live traps were locked open for the duration of the camera trapping sessions.

Live trapping

Hare live trapping sessions consisted of 3 days of trapping conducted immediately after the camera trapping sessions. We limited live trapping to 3 days because longer trapping sessions can cause weight loss in captured individuals (Hodges et al. 2001). We replenished the alfalfa where needed and placed a slice of apple in every live trap in the evening of the first day of live trapping when the live traps were set. We checked the live traps the morning of the second trapping day and closed them for the day to prevent red squirrels from getting trapped; live traps were reset the evening of the second trapping day. We checked live traps again the morning of the third day, emptied them of any bait, and closed them. We conducted only one night of live trapping during Jacquot South session 2 and Jacquot North session 2 due to heavy rainfall.

Squirrel live trapping sessions consisted of 2 days of trapping. We rebaited traps with peanut-butter and set them at 07:00 the morning of the first day of live trapping; live traps were checked at 08:30 and 10:00, and again at 11:30 at which time they were locked open. Trapping resumed on the second day at 7:00 at which time live traps were rebaited and set. Traps were checked at 08:30 and 10:00 and emptied of peanut butter and closed during the last trap-check at 11:30.

Captured animals were tagged using numbered fingerling fish tags, and their mass, sex, and reproductive status were recorded. All live trapping was carried out under protocols approved by the University of British Columbia's Animal

Care Committee and followed the standard animal care principles of the American Society of Mammalogists (Sikes et al. 2011).

Squirrel densities were estimated using the spatially-explicit capture-recapture method (Efford 2004) as implemented in DENSITY 4.4 (Efford et al. 2004, http://www.otago.ac.nz/density) with a maximum-likelihood estimate of recapture distances when sample sizes were large. We used the default parameters for DENSITY 4.4 for all estimates and set the buffer width to 100 m. The majority of hare trapping sessions (11 of 16) yielded too few data to estimate densities using spatially-explicit capture-recapture models, and therefore, all hare densities were estimated using the number of individuals live trapped during a trapping session (minimum number alive or MNA) divided by the average effective grid area, calculated from historical live trapping. Effective grid areas were 56.6 ha for Silver, 63.5 ha for Sulfur, 60 ha for Chitty, and 16.5 ha for both Jacquot grids. Krebs et al. (1986) suggest that MNA estimates are likely close to true population size when snowshoe hare densities are low.

Statistical analyses

All statistical analyses were done in R version 2.14.2 (R Development Core Team 2012, www.R-project.org). To address our first question of whether hit window has an effect on the correlation between hit rates and live-trapping-based population density estimates, we calculated hit rates for each camera trapping session using multiple different hit windows. The smallest hit window we used was a 1-min hit window; for the majority of the dataset, in which each video is 1 min in duration, this is equivalent to treating each video as an independent hit. There were 38 instances (17 during squirrel filming, 21 during hare filming) in which a camera malfunctioned and generated videos that were shorter than 60 s; in these instances, if these shorter videos were of the same species and were taken within 1 min of each other, they were counted as a single hit. For 37 of these malfunctioning cameras, the number of "extra" videos obtained because of the malfunction is less than 5, but in one case, 27 extra videos were generated.

Applying a hit window of longer duration (for example, 5 min) involved grouping videos as a single hit when they were obtained by the same camera, featured the same species, and were taken within 5 min of each other. We used hit windows of 1, 5, 10, 30, 60, 90, 120, 150, 180, 210, 240, 720, and 1440 min. Hit rates were calculated for each camera trapping session as the total number of hits of the species obtained during the first 48 h of the camera trapping sessions by all of the cameras, divided by the total effort in camera-days (the number of 24-h periods each camera was operational for during that filming session, summed together). In instances in which a camera's memory card filled in less than 48 h, we determined the amount of time the camera was operational using the time stamp of the last video made by that camera. Cameras that experienced lamp failures at any point during a camera trapping session were excluded from that session's hit rate calculations.

We used multiple linear regression to determine if live-trapping-based population density estimates could be predicted by hit rates for snowshoe hares and red squirrels. Initial hare models included a weather rank variable based on the estimated amount of precipitation falling during the trapping session, as well as a hit rate—weather rank interaction term. For the two Jacquot grids, weather rank was based on Environment Canada precipitation data recorded at the Burwash airport; if the total precipitation for the 3 days of the trapping session was 0, the session was assigned a rank of 0, between 0.1 and 10 mm a rank of 1, and >10 mm a rank of 2. For all other grids, ranking was based on Environment Canada precipitation records averaged from the Burwash and Haines Junction airports. Both live-trapping-based population density estimates and hit rates were tested with log-10 and square-root transformations to check for linearity for hares and red squirrels, and grid type (small or large) was also included as a random effect in initial hare models.

The week of the year during which the trapping session was conducted, and a hit rate-week interaction term was included in the initial models used for the red squirrel data. Grid and year were included as random factors in both hare and squirrel initial models.

Backward stepwise model simplification was done using the stepAIC function of the MASS library (Venables and Ripley 2002), followed by manual backward simplification using partial F-tests, for each species and each hit window. For models that did not simplify to a single explanatory variable, included variables were assessed for multicollinearity; where multicollinearity between hit rate and another variable was found, hit rate was retained in the model and the other variable removed.

Results

A total of 573 videos (range 0–118 videos per day) of snowshoe hares were obtained in 432 camera-days of filming effort (Table 1). A total of 1349 videos (range 9–149 videos per day) of red squirrels were obtained in 361.3 camera-days of effort (Table 2). Filming effort for hare sessions ranged from 14.2–30 camera-days, and squirrel filming session effort ranged from 14 to 30 camera-days, where 1 camera-day represents one functioning camera deployed for 24 h.

A total of 64 snowshoe hares were live-trapped in this study; the minimum number of individuals alive (MNA) on a grid ranged from 0 to 15, with estimated densities ranging from 0 to 0.91 animals/ha (Table 1). A total of 361 individual

Table 1 Summary of video counts, filming effort, the number of individuals trapped (MNA or minimum number alive), and live trapping-based density estimates (animals/ha) for snowshoe hares (*Lepus americanus)* by grid

Grid	Session	Session date	Videos	Camera-days	Cameras	MNA	Estimated density
Chitty	1	29-Jun-11	2	28	14	0	0
	2	12-May-12	14	30	15	3	0.05
	3	14-Jun-12	8	28	14	0	0
	4	12-Aug-12	43	28	14	9	0.14
Silver	1	13-Aug-11	3	14.2	12	1	0.02
	2	06-Jun-12	0	30	15	0	0
Sulfur	1	31-Jul-11	22	30	15	5	0.08
	2	15-May-12	3	26	13	1	0.02
	3	16-Jun-12	8	24	12	2	0.03
	4	12-Aug-12	15	24	12	3	0.05
Jacquot North	1	20-Jun-11	117	30	15	15	0.91
	2	07-Aug-11	34	28	14	3	0.18
	3	01-Aug-12	101	28	14	4	0.24
Jacquot South	1	22-Jun-11	54	28.5	15	11	0.67
	2	07-Aug-11	31	26	13	3	0.18
	3	03-Aug-12	118	29.3	15	12	0.73
Average			35.8	27.0	13.9	4.5	0.21
Total			573	432	222		

red squirrels were live trapped, with densities ranging from 2.12–4.99 animals/ha (Table 2). There were two instances in which hares were filmed during a camera trapping session but not live-trapped during the subsequent trapping session.

Hit rate was the best predictor of estimated population density for all hit windows for hares and red squirrels; including additional variables and interaction terms did not significantly improve fit for any of the hit windows for squirrels, and additional variables and interaction terms that did significantly improve fits for hares were collinear with hit rate and therefore not retained in the final models. Including grid or year as a random effect did not improve model fit for any hit window

Table 2 Summary of video counts, filming effort, the number of individuals trapped (minimum number alive, MNA), and mark-recapture density estimates (animals/ha) with 95% confidence limits for red squirrels (*Tamiasciurus hudsonicus)* by grid

Grid	Session	Session date	Videos	Camera-days	Cameras	MNA	Estimated density	95% Confidence limits
Agnes	1	07-Jun-11	149	30	15	50	4.85	(3.53, 6.22)
	2	08-Jul-12	109	29.7	15	45	3.79	(2.81, 5.15)
Chitty	1	18-May-11	9	15	8	21	2.15	(1.34, 3.27)
	2	20-May-12	92	22.1	13	23	2.95	(1.84, 4.70)
GPC	1	17-May-11	18	14	7	16	2.38	(0.64, 5.91)
	2	05-Jun-12	83	29.6	15	17	2.12	(1.20, 3.74)
Joe	1	13-Jun-11	117	28.9	15	34	3.81	(2.64, 5.49)
	2	08-Jul-11	143	29.8	15	52	4.87	(3.65, 6.48)
Kloo	1	06-Jul-11	95	28	14	31	2.85	(1.88, 3.83)
	2	28-Jun-12	118	28	14	35	3.45	(2.46, 4.79)
Lloyd	1	06-Jul-11	120	23.4	12	32	2.98	(2.29, 4.64)
	2	04-Jul-12	129	27.1	14	36	4.99	(3.02, 8.27)
Sulfur	1	02-Jul-11	84	26.2	14	32	2.54	(1.70, 3.60)
	2	24-Jun-12	74	29.5	15	35	2.98	(2.12, 4.18)
Average			95.7	25.8	13.3	32.8	3.34	
Total			1340	361.3	186			

for hares or squirrels, and including grid type did not improve model fit for any hit window for hares. Log-transforming density estimates maximized the correlation between hit rates and densities for both hares and red squirrels, such that the final model for each hit window for both species was a simple linear regression of hit rate on log-transformed population density estimates.

For hares, hit window had some effect on goodness-of-fit, with R^2 ranging from 0.70–0.90 (Fig. 1). The highest R^2 value was obtained with a hit window of 10 min, but R^2 values for all hit windows between 1 and 240 min were similar. For red squirrels, R^2 values ranged from 0.42–0.68. A hit window of 5 min generated the highest R^2 value (Fig. 1), but this does not differ much from the 1-min hit window (R^2 of 0.64) or the 10-min hit window (R^2 of 0.65). The regressions for all of the hit windows were statistically significant for both hares and red squirrels; the 10-min hit window was selected as the best model for both hares and red squirrels, based on model selection procedures suggested by Burnham and Anderson (2002).

The regression models were significant for hares ($F_{1,14}$ = 123.6, p < 0.001, Fig. 2, Table 3) and squirrels ($F_{1,12}$ = 26.03, p < 0.001, Fig. 3, Table 3). Slope estimates were significant for hares (t_{14} = 9.1, p < 0.001) and squirrels (t_{12} = 5.10, p < 0.001), and the intercept was significantly different from zero for squirrels (t_{12} = 0.19, p = 0.014) but not for hares (t_{14} = −1.87, p = 0.08).

Discussion

Our study is the first attempt to use motion-detecting cameras to estimate snowshoe hare and red squirrel population densities. The data suggest that camera-generated hit rates may be an accurate means of estimating the density of red squirrels,

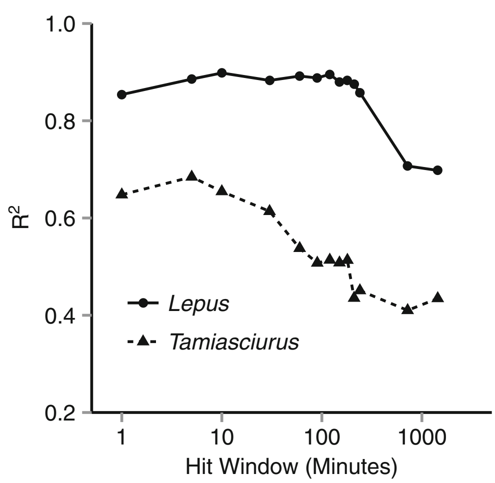

Fig. 1 R^2 values for linear regressions between live-trapping-based population density estimates and hit rates calculated using different hit window lengths for snowshoe hares (*Lepus americanus*) and red squirrels (*Tamiasciurus hudsonicus*), Kluane Lake, Yukon, 2011–2012

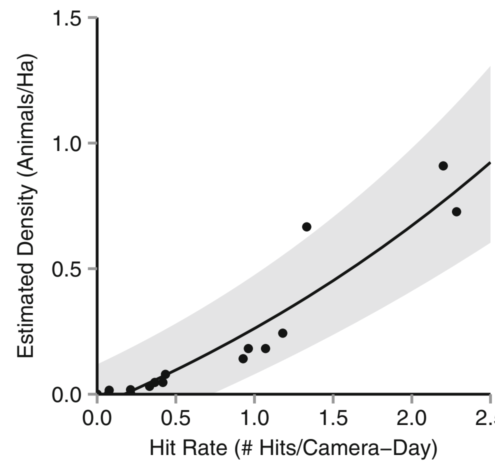

Fig. 2 Relationship between hit rates and log-transformed live trapping density estimates for snowshoe hares (*Lepus americanus*) at Kluane Lake. Hit rates were calculated using 5-min hit windows. *Each point* represents a 2-day filming session followed by a 3-day live trapping session. *Solid line* indicates linear regression (R^2 = 0.90), *error bars* are ±1 S.E., and *dashed lines* represent 95% prediction intervals

demonstrating that camera trapping may be viable alternative to live trapping this species. Low snowshoe hare densities prevent us from fully assessing camera trapping as a means of estimating population densities for this species, but the strong correlation between hit rates and live trapping density estimates at low densities suggests that cameras may be a viable alternative given additional testing at higher densities.

The use of hit windows to group videos that occur within a short time frame and probably represent a single encounter should have an effect on the correlation between estimated population density and hit rates when there is heterogeneity in the amount of time individuals spend around traps. If some individuals spend more time around traps than others, then the number of videos generated in a set amount of time is due not only to population density but also due to variation in behavior. This is especially relevant to the investigation presented here because we used bait to lure the animals to the traps; differences in food quality or food availability within home ranges could lead to some individuals spending more time around traps consuming bait than others, and in the case of snowshoe hares, competition for high quality food could result in subordinate individuals being excluded from traps by dominant individuals (Sinclair 1986). In the case of red squirrels, which are highly territorial in this region (Smith 1968; Price et al. 1986), the placement of traps and cameras relative to territory boundaries may influence the duration and frequency of visits by this species. For these reasons, we expected hit rate to have a large influence on the relationship between hit rate and estimated population density for both snowshoe hares and red squirrels.

Our expectations regarding the effects of hit window duration were met for red squirrels; the correlation between hit rate and population density was sensitive to hit window duration.

Table 3 Linear regressions to predict trap-based population density estimates (animals/ha) from camera trapping hit rates (hits/day) for snowshoe hares (*Lepus americanus)* and red squirrels (*Tamiasciurus hudsonicus*)

Species	Regression equation	Sample size	Mean squared error	Slope standard error	R^2
Lepus	Log_{10}(estimated density + 1) = 1.79 + 0.90(hits/day)	16	0.0022	0.011	0.90
Tamiasciurus	Log_{10}(estimated density) = 0.18 + 0.11(hits/day)	14	0.0067	0.021	0.68

Hit rates were calculated using a 5-min hit window for squirrels and a 10-min hit window for hares

Decreasing correlation between hit rates and population density with longer hit windows may be due to the relatively high densities at which red squirrels were observed; as mentioned above, red squirrels in this region are highly territorial, but trespassing is common (Boon et al. 2008), and more squirrels on a grid could increase the chances of more than one squirrel visiting a trap. Longer hit windows may group videos produced by different individuals together, under-representing the number of squirrels visiting the traps and reducing the correlation between estimated population density and hit rate.

If we use a 5-min hit window, hit rates account for 68% of the variation in red squirrel live trapping density estimates. While there is also considerable scatter in these data, the model-predicted densities for each hit rate fall within their respective live-trapping-based population density estimate's 95% confidence interval, and the 95% prediction interval of the model encompasses most of the 95% confidence intervals of the live-trapping-based population density estimates (Fig. 1). Why only 68% of the variation can be accounted for by hit rates may be related to the hit window itself; using a 5-min hit window for the entire dataset assumes that the 5-min hit window is the "best" way to account for any hit rate inflation without under-representing visits for all filming sessions on all grids.

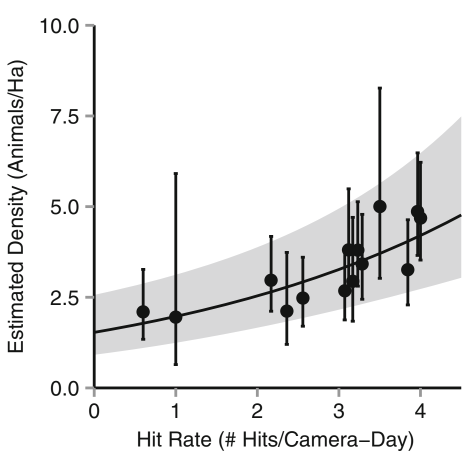

Fig. 3 Relationship between hit rates and log-transformed live-trapping-based population density estimates for red squirrels (*Tamiasciurus hudsonicus*) at Kluane Lake. Hit rates were calculated using 5-min hit windows. Each point represents a 2-day filming session followed by a 2-day live trapping session. *Solid line* indicates linear regression (R^2 = 0.68), *dashed lines* represent 95% prediction intervals. *Error bars* are ±1 S.E. for density estimates

But, as suggested above, heterogeneity in trap visitation behavior in squirrels may be related to population density; longer hit windows may group different visits together on high-density grids but may be less likely to do this on lower-density grids because fewer squirrels are present to visit traps.

We obtained an even stronger correlation between hit rates and density estimates for snowshoe hares; if we use a 10-min hit window, hit rates account for 90% of the variation in snowshoe hare live trapping density estimates, and unlike red squirrels, this correlation is relatively insensitive to hit-window duration. However, the densities at which we trapped and filmed snowshoe hares were very low; snowshoe hares densities have reached as high as 4.4 animals/ha at the peak of their population cycle in this region (Krebs et al. 2013), and it is unclear if we would find a similar correlation at higher densities. As such, we cannot assess if hit rates are a robust means of assessing the population density of this species and suggest conducting live trapping and mark-recapture at higher densities to better address this question. In terms of the utility of camera trapping for assessing low population densities, camera trapping appears comparable to other index approaches; our maximum correlation between hit rates and live trapping density estimates was similar to that reported for fecal pellet densities and live trapping density estimates of snowshoe hares in other locations (Murray et al. 2002).

While the low densities at which we trapped snowshoe hares limits our ability to comment on the use of hit rates for estimating higher densities, it does highlight a management application of camera trapping: At very low densities, camera trapping detected snowshoe hares when live trapping did not. This could be of particular interest when trying to delineate species ranges (Mori et al. 2014) or monitor endangered species.

In terms of effort, our live trapping and camera trapping protocols required similar effort. A hare live trapping session of 3 days, including prebaiting the traps beforehand, takes approximately eight to nine person hours, while camera trapping, including setting up and retrieving cameras, viewing video footage and recording relevant information, took between 6 and 10 person hours per session depending on the amount of footage obtained. Squirrel live trapping was more labor-intensive; 2 days of trapping took approximately 20 person hours, while camera set-up, retrieval, and footage viewing took between 10 and 15 person hours per session. Camera trapping required considerably less time in the field as setting up and retrieving the cameras typically took 2–2.5 person hours, and the time required to train someone to view and score footage was also less than that required for small mammal handling. In light of the recent proliferation of camera trapping software packages and programs (e.g., Bubnicki et al. 2016; Niedballa et al. 2016), we anticipate that footage processing will only become more rapid. Currently, the ScoutGuard SG560 camera can be purchased for approx. 100 USD/unit, and squirrel- and hare-sized tomahawk traps can be purchased for 33 USD/unit and 75 USD/unit, respectively, but since fewer cameras are required than traps, total equipment costs for camera trapping are lower than for live trapping. In summary, camera trapping and live trapping as conducted here are similar in terms of effort, but camera trapping has lower equipment costs and requires less field work.

These results and the results presented in Villette et al. (2016) together suggest that hit rates are a possible alternative for estimating densities of small mammals in the boreal forest when the appropriate hit window is used. That hit window appears to be especially important for red squirrels and northern red-backed voles may be due to these species activity patterns; red squirrels are diurnal and northern red-backed voles are active around the clock, which may allow for greater variation in the time spent around traps compared to snowshoe hares and deer mice, both of which tend to be nocturnal (Gilbert et al. 1986; Larsen and Boutin 1994; Feierabend and Kielland 2014).

Further work is needed to develop this method. The squirrel densities observed during this investigation (1.9–5.0 animals/ha) are fairly representative of the range of densities that have been observed in this region, but densities have been as low as 0.3 animals/ha and collecting additional footage and trapping data at lower squirrel densities would be prudent. As mentioned above, additional trapping and filming of snowshoe hares at higher densities is required for a thorough assessment of camera traps as a method of density estimation for this species.

When Rowcliffe et al. (2008) developed their random encounter model, they suggested that sampling area would not affect the rate of encounters between animals and cameras, and we assumed here that grid size would have no effect on hit rates and analyzed the Jacquot Island hare data and mainland hare data together. Testing this assumption would be prudent; note that there is low overlap in densities between Jacquot Island and the mainland (densities from the mainland ranged from 0 to 0.14 animals/ha, while densities on the island ranged from 0.18–0.9 animals/ha), and collecting additional data from both grid sizes such that there is greater overlap in densities between the two sites would allow for the confirmation that sampling area does not have a significant effect on hit rates.

In addition, determining if the relationships between hit rates and population density found in Kluane can be applied to different areas in the boreal forest, and applied in different seasons, is vital. Calibrating the relationship between hit rates and estimated population density at each location in which one wishes to collect population density information would be cost-prohibitive in many cases, therefore determining if the models we have presented here can be applied to camera data collected in other habitats is critical. The camera models we used are rated to operate in subzero temperatures, and performance did not appear to be affected by cold or wet weather, but confirming this before camera trapping in winter would be prudent. We did not detect seasonal effects here, but low sample size may limit our ability to detect seasonal variation in hit rates. In summary, we suggest that the following two studies are needed to validate this approach. First, do the relationships presented here extend linearly for the whole possible range of hare and squirrel densities? Second, can models developed in the Kluane region for estimating snowshoe hare and red squirrel densities from camera trapping be applied to populations in other regions?

The results obtained in this study and that of Villette et al. (2016) are encouraging because they indicate that it may be possible to census small mammals with cameras, without the necessity of the more difficult and invasive effort of live trapping, marking, and releasing animals.

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