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Can camera trapping provide accurate estimates of small mammal (*Myodes rutilus* and *Peromyscus maniculatus*) density in the boreal forest?

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Estimating population densities of small mammals (< 100 g) has typically been carried out by intensive livetrapping, but this technique may be stressful to animals and the effort required is considerable. Here, we used camera traps to detect small mammal presence and assessed if this provided a feasible alternative to livetrapping for density estimation. During 2010–2012, we used camera trapping in conjunction with mark–recapture livetrapping to estimate the density of northern red-backed voles (*Myodes rutilus*) and deer mice (*Peromyscus maniculatus*) in the boreal forest of Yukon, Canada. Densities for these 2 species ranged from 0.29 to 9.21 animals/ha and 0 to 5.90 animals/ha, respectively, over the course of this investigation. We determined if 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 rate and population density. The relationship between hit rate and density was sensitive to hit window duration for *Myodes* with R^2 values ranging from 0.45 to 0.59, with a 90-min hit window generating the highest value. This relationship was not sensitive to hit window duration for *Peromyscus*, with R^2 values for the tested hit windows ranging from 0.81 to 0.84. Our results indicate that camera trapping may be a robust method for estimating density of small rodents in the boreal forest when the appropriate hit window duration is selected and that camera traps may be a useful tool for the study of small mammals in boreal forest habitat.

Key words: camera trapping, density estimation, hit window, *Myodes rutilus*, *Peromyscus maniculatus*, Yukon

Tracking changes in the densities of small mammals, such as northern red-backed voles (*Myodes rutilus*) and deer mice (*Peromyscus maniculatus*), in the boreal forest is of interest to scientists and managers because while small rodents (< 100 g) constitute a minor fraction (4%—Boonstra et al. 2001) of the vertebrate biomass in that food web, their importance is disproportionately greater than suggested by their biomass (Krebs et al. 2014). In addition, both northern red-backed voles and deer mice can exhibit dramatic fluctuations in population density, and the mechanisms producing these fluctuations are not fully understood (Gilbert and Krebs 1991). Currently, small mammal population densities are often estimated with livetrapping and mark–recapture methods (e.g., Falls et al. 2007; Stradiotto et al. 2009; Krebs et al. 2011), but livetrapping can cause physiological stress in naïve voles and mice (Harper and Austad 2001; Fletcher and Boonstra 2006) and can require considerable effort and money—efforts that may not be sustainable at the spatial or temporal scales required to test hypotheses or inform management. Thus, there exists a need to develop means to monitor small mammal populations that requires less effort and can be applied across large landscapes over long time frames.

Camera trapping has become a popular method for monitoring wildlife (O'Connell et al. 2011; Meek et al. 2014b) and has been used to estimate population densities of tigers (*Panthera tigris*) and other large cats for almost 20 years (e.g., Karanth 1995; Karanth and Nichols 1998; Trolle and Kéry 2003; Maffei et al. 2004). These studies have relied on unique markings, such as stripe- or spot-patterns, to identify individuals and construct capture histories analogous to those generated in traditional mark–recapture livetrapping. However, this method is of limited utility, as many species do not typically feature natural markings that allow for the identification and enumeration of individuals.

Currently, methods for using cameras when individuals of the target species cannot be identified by unique markings can be broadly split into 2 approaches. The 1st approach is to use encounter or "hit" rates as an index of population density, which may in turn be converted to density following calibration with an independent estimate of density. This method was first proposed by Carbone et al. (2001) who used random walk computer simulations to show that hit rates could be used to estimate the density of tigers and their prey when individuals could not be identified because hit rates were strongly correlated with independent estimates of density. The second approach is to estimate density directly from hit rates and was first proposed by Rowcliffe et al. (2008), who developed a Random Encounter Model (hereafter, REM) in which density is directly calculated using a modified gas model that incorporates hit rates, average daily movement rates, and the detection area of the cameras. Rowcliffe et al. (2008) were able to estimate population densities of muntjac (*Muntiacus reevesi*), water deer (*Hydropotes inermis*), and red-necked wallabies (*Macropus rufogriseus*) accurately with their REM in an enclosed setting, but this approach performed poorly when applied to Harvey's duiker (*Cephalophus harveyi*) in the wild (Rovero and Marshall 2009), and it was concluded that hit rates as an index of density were a more appropriate application of camera trapping data for this species. Conversely, Zero et al. (2013) found that REM density estimates were comparable to line census density estimates for Grevy's zebra (*Equus grevyi*) in savannah habitat.

One question central to all approaches for handling camera trap data is how to quantify a hit. Rowcliffe et al. (2008) defined a hit as an encounter between an animal and the camera but recognized that multiple photos could be generated during a single encounter and recommended grouping photos suspected of being of the same encounter. Rovero and Marshall (2009) used a convention that we will here refer to as a hit window, and considered photos taken within 60 min of each other (within a 60-min hit window) not to be independent, and grouped them as a single hit. When Manzo et al. (2011) used a REM approach to assess European pine marten (*Martes martes*) densities in Italy, they utilized a 5-min delay setting on their cameras such that once a camera was triggered, it could not be triggered again until 5 min had elapsed. In these 3 cases, it is unclear if the hit window or delay setting used was the "best"; that is, if a different protocol for defining the hit would have had a significant impact on the density estimates obtained.

The object of this study was to determine if camera trap hit rates of *P. maniculatus* and *M. rutilus* could be calibrated with livetrapping density estimates, such that cameras can be used to estimate the population densities of these species during the summer (snow-free) months. We asked 2 questions. First, is there a hit window duration that maximizes the correlation between hit rate and livetrapping-based density estimates and minimizes the artifact of nonindependence of the same animal rapidly triggering the camera in close temporal succession? Second, given the "best" hit window, can we build a statistical model that allows us to use hit rates to obtain density estimates comparable in accuracy and precision to what we would obtain using livetrapping for these small rodents?

Materials and Methods

Focal species and study sites.—Both *Peromyscus* and *Myodes* fluctuate in population density in the Kluane Lake region, but for *Peromyscus*, these fluctuations have been irregular; this species made up almost half of the small rodents captured on livetrapping grids in the 1970s and 1980s before disappearing for 6 years in the early 1990s (Gilbert and Krebs 1981; Krebs and Wingate 1985; Krebs et al. 2010). Within the last 2 decades, densities have varied from year to year without any obvious cyclic pattern, with a maximum density of 5.38 animals/ha (Krebs et al. 2011). Conversely, *Myodes* exhibits 3–5 year population cycles, fluctuating in density from as low as 0 animals/ha to > 30 animals/ha (Boonstra and Krebs 2012). The 2 species also differ in their behavior; *Peromyscus* are strongly nocturnal (Gilbert et al. 1986), and females maintain nonoverlapping home ranges but males are very mobile (Galindo and Krebs 1987), while *Myodes* are active at all times of the day (Gilbert et al. 1986) and can exhibit spacing behavior in both sexes (Burns 1981). Both species typically do not feature distinguishing markings (e.g., stripes, spots, scars, etc.) that would allow for the identification and enumeration of individuals on film.

We conducted camera trapping and livetrapping on 3 small mammal trapping grids near Kluane Lake, Yukon (61°N; 138°W), during May–August 2010–2012. The trapping grids in the Kluane Lake area have been in operation since at least 1987, and the live traps are permanently left out at the trapping stations, hence the animals have longstanding familiarity with the traps. The forest in the Kluane region is dominated by white spruce (*Picea glauca*) with some balsam poplar (*Populus balsamifera*) and trembling aspen (*P. tremuloides*). Gray willow (*Salix glauca*) is the predominant shrub, followed by bog birch (*Betula glandulosa*), *Potentilla fruticosa*, and soapberry (*Shepherdia canadensis*). Abundant herbaceous species include *Lupinus arcticus*, *Anemone parviflora*, *Mertensia paniculata*, and *Achillea millefolium* (Turkington et al. 2002). The 3 Kluane grids are located in slightly different habitats; Chitty grid and J grid are located in open spruce forest, whereas Silver grid is located in denser old growth spruce forest with considerable deadfall.

We also conducted camera trapping and livetrapping on 4 grids near Mayo, Yukon (63°N; 136°W) in July 2012. Data were collected in Mayo in an attempt to maximize the range of densities at which *Myodes* and *Peromyscus* were trapped. At Mayo, the grids have been in operation since 2005; live traps on these grids are also left out permanently. The boreal forest in the Mayo region is dominated by white spruce, black spruce (*P. mariana*), and trembling aspen. Shrubs found in this area include willow and dwarf birch and ground cover species include kinnikinnick (*Arctostaphylos uva-ursi*), cranberries (*Vaccinium vitis-idaea*), blueberries (*Vaccinium* sp.), as well as various species of moss and lichen. B grid is located in an area that was burned in 1972 and is characterized by abundant deadfall, dense shrub cover and dense ground cover, while BS grid is located in open forest with minimal shrub cover and thick ground cover. GH grid is located in an area that was burned in 1990 and currently features abundant deadfall with some shrub cover and minimal ground cover. Finally, MB grid is located in open forest with some shrub cover and abundant ground cover.

Camera trapping.—Our general procedure was to conduct sessions on each grid, with each session consisting of 2 days of camera trapping, with 15–16 cameras, followed by 3 days of livetrapping. Our experimental unit was a trapping grid; hit rates for each session were calculated by pooling the camera trapping results (i.e., footage) from all of the cameras operating during the filming portion of that session (see below). We conducted 19 sessions on the Kluane grids over the course of 3 summers, whereas the Mayo grids were each visited only once in 2012.

Each of the 7 grids had 100 stations laid out in a 10 × 10 arrangement, with 15 m between stations. The Kluane grids had a single Longworth live trap (Longworth Scientific Instruments, Abingdon, England) at each station, and each trap was covered by a wooden board to protect it from the elements and placed inside a box or wire cage that allowed for access by mice and voles but not squirrels or larger animals. The Mayo grids had a single Longworth live trap at every other station (A1, B2, A3, B4, etc.), covered with a small metal plate as protection from the elements.

We placed cameras at random stations on the grids with the constraint that, within a summer, a given trapping station was not filmed twice. Additionally, cameras were not placed at adjacent trap stations during a filming session; therefore, cameras were always ≥ 30 m apart. At the selected trap stations, we placed a camera trap 75 cm from the front of the live trap and secured the camera trap to a wooden stake approximately 15–20 cm above ground level pointing toward the front of the live trap. We angled the camera downward using twigs or cones as wedges such that the entrance of the trap would appear in the upper half of the frame of the footage. We pushed or removed any obstructing vegetation out of the way to give camera traps a clear view of the live traps. Live traps were baited with oats and cotton bedding but locked open for the duration of the camera trapping portion of the session.

We used 34 camera traps, divided among the following models: 31 ScoutGuard Cameras (models SG550 and SG560; HCO Outdoor Products, Norcross, Georgia) and 3 Bushnell Trophy Cams (model 119455; Bushnell Outdoor Products, Overland Park, Kansas). According to the manufacturer's specifications, the camera trap models used were similar in performance specifications (e.g., trigger speed, detection distance, etc.) and all were equipped with a built-in passive infrared detector for detecting motion and an infrared lamp for filming at night. Meek et al. (2014a) reported that both of these models produce noise and illumination that can be detected by many mammals, but we did not observe any obvious instances where animals appeared disturbed by the cameras.

We conducted several nights of informal experiments with the cameras in controlled and field settings to assess the relative benefits of setting the cameras to take photographs or video. Using pairs of cameras, one set to take video and one set to take photographs, we determined that videos were optimal for detecting rodents; cameras set to take photographs often failed to obtain a useable photograph because the animals moved quickly, triggering the camera as they entered the trap or went behind it. For the sessions, cameras were set to record a 60-s video when triggered, and we set the delay option to the lowest possible setting for all cameras; this means that the cameras could be triggered continuously, with a delay of ≤ 1.2 s between videos for the ScoutGuards and a delay of ≤ 1 s for the Bushnells. We set camera motion sensitivity to high, except for the following sessions, in which sensitivity was set to normal: Chitty sessions 1 and 2, J sessions 1 and 2, and Silver sessions 2 and 3. At this time, cameras were often triggered by vegetation moving in the breeze, generating excessive amounts of uninformative footage that filled up memory cards before the end of the filming period. Experimenting with the cameras in controlled settings suggested that changing the sensitivity from high to normal reduced the amount of non-animal-induced footage but had a minimal effect on the amount of animal-induced footage obtained. Thus, the normal setting appeared optimal for these conditions.

Livetrapping.—Livetrapping occurred immediately after a grid was camera trapped and consisted of 3 days of livetrapping. We resupplied the live traps with cotton where needed, replenished the oats, and added apple slices to each trap upon setting the traps. Live traps were checked the morning and evening of the second trapping day, and the morning of the third trapping day, at which time we removed the oats and apple, locked the traps open, and left them in place. Captured animals were tagged using individually numbered fingerling fish tags (National Band and Tag Company, Newport, Kentucky), and their mass, sex, and reproductive status were recorded. All livetrapping was carried out under protocols approved by the University of British Columbia's Animal Care Committee and we followed the standard animal care principles of the American Society of Mammalogists (Sikes et al. 2011).

We calculated density estimates for each species for each trapping session using Efford's maximum-likelihood (ML) spatially explicit capture–recapture model, implemented in the program DENSITY 4.4 (Efford 2009). We followed Krebs et al. (2011) and Efford et al. (2009) and used the default parameters for DENSITY 4.4 for all estimates except buffer width; specifically, we used a Poisson distribution model and half-normal detection function, and full likelihood to fit the models. We used a 64 × 64-point integration mesh for the ML estimator, and we assumed populations were closed. We set the buffer width to 100 m as individual movements above 100 m are rare and simulations as well as our computations showed that density estimates are robust to larger buffer widths (Efford et al. 2009). When sample sizes were small (< 3 individuals), we used minimum number known alive (MNA) to estimate abundance and converted this to a density estimate by dividing by an average effective grid area of 3.43 ha (calculated from historical livetrapping). These 2 rodent species are highly trappable in this ecosystem.

Analyses.—All statistical analyses were done in R version 2.14.2 (R Development Core Team 2012, www.R-project.org). To address whether hit window has an effect on the correlation between hit rates and livetrapping-based density estimates, we calculated hit rates for the camera trapping portion of each session using different hit windows. The shortest hit window we used was 1 min; this is equivalent to treating all videos as independent hits. Applying a longer hit window, for example, 5 min, involved grouping videos as a single hit when they were obtained with the same camera, captured the same species, and were taken within 5 min of each other. We used hit windows of 5, 10, 30, 60, 90, 120, 150, 180, 210, 240, 720, and 1,440 min. Hit rates for *Myodes* and *Peromyscus* were calculated for each session as the total number of hits of the species obtained during the first 48 h of camera trapping divided by the total effort in camera-days (the number of 24-h periods each camera was in operation during that filming portion, summed together). When a camera's memory card filled in less than 48 h, we determined the amount of time that the camera was operational using the time stamp of the last video made by that camera.

Cameras that experienced lamp failure during night filming were excluded from hit rate calculations. In addition, 3 cameras operating in 2 sessions (2 from Chitty session 3 and 1 from Silver session 6) were omitted from the hit rate calculations for *Myodes* and subsequent analysis due to suspected hit rate overinflation. The number of videos these cameras obtained was high compared with the other cameras on the grid during their respective sessions, and the videos were in close succession (i.e., the camera was triggered continuously). The video footage was predominantly of a vole sitting near the entrance of the live trap, often in the same place, suggesting 1 individual was visiting the trap for an extended period of time. Counts and hit rates for *Myodes* reported in the results do not include data from these cameras. Omitted data comprised 1% of the total overall camera trapping effort.

Tundra voles (*Microtus oeconomus*) and meadow voles (*M. pennsylvanicus*) were occasionally captured during livetrapping and camera trapping at the Kluane grids, but low detection by both methods resulted in insufficient data to conduct an analysis (see "Results"). *Microtus* are primarily grassland voles, and all of the grids are located in forest habitat (see Boonstra et al. 2001 for an overview of the *Microtus* species potentially present on the Kluane grids). Further investigation into *Microtus* would require trapping in meadow habitat.

Pelt color was the primary feature used to distinguish between *Myodes* and *Microtus* in video footage obtained during the day, but the cameras we used employed an infrared lamp and filter to film at night, which results in black-and-white footage. As such, distinguishing between vole species filmed at night was difficult to do with confidence. For the majority of sessions in which no *Microtus* was identified in day-time videos, all night-time video footage of voles was assumed to be of *Myodes*. For the 2 sessions in which *Microtus* was observed in day-time video footage (J session 2 and Chitty session 2), the ratio of *Myodes*-to-*Microtus* day-time hits for that session was used to estimate the number of night-time hits that were of *Myodes* and *Microtus* (e.g., if 90% of the day-time vole hits were of *Myodes*, we assumed that 90% of the night-time vole hits were of *Myodes*). *Myodes* and *Microtus* have similar activity patterns (Webster and Brooks 1981; Gilbert et al. 1986; Halle 1995).

We used multiple linear regression to determine if livetrapping-based population density estimates could be predicted by hit rates for *Myodes* and *Peromyscus*. Two additional candidate variables—the week of the year during which livetrapping occurred and a weather rank variable based on the estimated amount of precipitation falling during the trapping portion of the session—and the full complement of interaction terms were included in the preliminary models. For Kluane grids, this was based on precipitation data recorded at the Burwash Landing and Haines Junction airports (Environment Canada); if the total precipitation for the 3 days of the livetrapping session averaged between the 2 stations was 0, the session was assigned a rank of 0; if between 0.1 and 10 mm, a rank of 1; and if > 10 mm, a rank of 2. For the Mayo grids, ranking was based on precipitation records for the Mayo airport (Environment Canada). Grid and year were included as random factors. Both trap-based density estimates and hit rates were square-root transformed to achieve linearity for both species. Backward stepwise model simplification was done using the stepAIC function of the MASS library in R (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 using a correlation matrix of included variables. Where multicollinearity between hit rate and another variable was found (correlation greater than 0.4), hit rate was retained in the model and the other variable removed. We also conducted forward stepwise model selection using the stepAIC function in MASS.

Excluding cameras that were operational for < 40 h had no effect on the identity of the parameters included in the final models for all hit windows for *Myodes* or *Peromyscus*, and no more than a 0.1% change in R^2 values for those models; therefore, cameras that were not operational for a full 48 h were retained in the analysis. Statistical significance of final models and model parameters was assessed using *F*-tests and *t*-tests, respectively, and the normality of residuals for all models was assessed using Shapiro–Wilks's tests with an α of 0.1 to account for small sample size.

We performed weighted regression analyses to determine if accounting for the variation in uncertainty in the livetrapping density estimates altered the correlation between hit rates and density estimates (see Supporting Information S1–S5 for details).

Results

Total camera trapping effort in our study was 582.5 camera-days. Mean effort for a single camera trapping session was

25.3 ± 3.1 (*SD*) camera-days and ranged from 17.6 to 29.5 camera-days (Table 1). Pooling across sites, we obtained a total of 1,165 videos of mice and voles; 669 of these were of *Myodes*, 468 were of *Peromyscus*, and 28 were of *Microtus*. *Myodes* was filmed on all grids, whereas *Peromyscus* was filmed on all grids at Kluane but only one in Mayo (MB; Table 1).

We recorded a maximum of 116 *Myodes* videos in a single session (24 camera-days of filming effort); when we convert this to a hit rate using the various hit windows, we obtain a hit rate ranging between 0.75 hits/camera-day using a 1,440-min hit window and 4.83 hits/camera-day using a 1-min hit window. The maximum number of *Peromyscus* videos we obtained in a single session was 127; converting this to a hit rate using the various hit windows results in a hit rate ranging from 0.78 hits/camera-day for a 1,440-min hit window to 5.82 hits/camera-day for a 1-min hit window. We recorded 12 videos of *Microtus* during Chitty session 2 and 16 videos during J session 2.

We captured a total of 217 individual *Myodes* in live traps over the course of this study. Estimated densities of *Myodes* ranged from 0.29 to 9.21 animals/ha (Table 1). We livetrapped 102 individual *Peromyscus*, and all but 5 were captured on J grid or Chitty grid (Table 1). Density estimates of livetrapped *Peromyscus* ranged from 0 to 5.90 animals/ha. Only 32 *Microtus* individuals were livetrapped, and densities were 0–2.77 animals/ha.

Forward and backward model simplification resulted in the same final model for each hit window for each species. Hit rate was the best predictor of livetrapping-based density for all hit windows for both *Myodes* and *Peromyscus*, and including week and weather as covariates, or grid or year as random effects, did not significantly improve the fit of any model for any hit window. The final model for each hit window for both species was therefore a simple linear regression of hit rate on density estimates derived from livetrapping.

R^2 values for *Peromyscus* varied only slightly from 0.81 to 0.84 over the range of hit windows, and the greatest R^2 value was observed using a 90-min hit window (Fig. 1). R^2 values for *Myodes* were somewhat more sensitive to the hit window and ranged from 0.48 to 0.59. For *Myodes*, increasing the duration of the hit window also improved model fit until the 90-min window; after which it declined (Fig. 1). The regressions for all of the hit windows for both species were statistically significant, but modeled estimates for the 90-min hit window were chosen as they had the highest R^2 values.

The regression model for the 90-min hit window was highly significant for both *Myodes* ($F_{1,21}$ = 29.7, P < 0.001, Fig. 2; Table 2) and *Peromyscus* ($F_{1,21}$ = 111.4, P < 0.001; Fig. 3;

Table 1.—Summary of the number of individuals trapped (or minimum number known alive, MNA), estimated density, filming effort, and video counts for northern red-backed voles (*Myodes*) and deer mice (*Peromyscus*) for each session. Densities are animals/ha, with 95% confidence limits shown in parentheses.

Session		MNA		Estimated density		Filming effort		Videos	
Grid	Date	*Myodes*	*Peromyscus*	*Myodes*	*Peromyscus*	Camera-days	Cameras	*Myodes*	*Peromyscus*
Chitty	10 Jun. 2010	4	3	0.36 (0.14, 0.97)	0.65 (0.17, 2.40)	23.0	13	5	14
	15 Jul. 2010	18	8	4.82 (2.89, 8.03)	2.72 (1.27, 5.84)	28[a]	14[a]	25[b]	13
	13 May 2011	1	5	0.29	1.26 (0.39, 4.08)	24.0	12	0	23
	23 Jul. 2011	15	19	3.18 (1.56, 6.48)	5.47 (3.32, 9.01)	26.0	13	15	109
	9 May 2012	8	8	0.86 (0.40, 1.88)	1.38 (0.49, 3.89)	20.0	11	6	15
	6 Aug. 2012	19	17	3.03 (1.23, 7.47)	5.9 (9.93, 3.51)	23.7	13	64	127
J	1 Jun. 2010	2	6	0.58	1.84 (0.79, 4.24)	26.0	13	2	18
	6 Jul. 2010	11	15	1.09 (0.57, 2.09)	4.35 (2.19, 8.64)	26.9	14	67[b]	34
	8 May 2011	10	5	1.77 (0.82, 3.83)	0.52 (0.21, 1.33)	26.0	13	35	17
	19 Jul 2011	18	12	5.81 (3.61, 9.34)	4.73 (2.54, 8.79)	28.0	14	24	63
	6 May 2012	16	3	3.27 (1.70, 6.29)	0.63 (0.10, 2.40)	24.0	12	20	1
	21 May 2012	18	2	2.57 (2.00, 3.28)	1.04 (0.20, 5.36)	28.0	14	92	9
	6 Aug. 2012	42	10	9.21 (6.46, 13.11)	3.12 (1.30, 7.46)	24.0	12	116	11
Silver	22 May 2010	7	0	0.87 (0.31, 2.47)	0.00	17.6	14	12	0
	20 Jun. 2010	3	1	0.79 (0.23, 2.68)	0.29	26.2	14	9	0
	29 Jul. 2010	4	0	0.87 (0.31, 2.47)	0.00	25.9	14	14	1
	1 Jun. 2011	5	0	1.09 (0.41, 2.86)	0.00	19.2	14	1	0
	27 Jul. 2011	27	3	7.87	0.87	28.0	14	91	5
	9 Jun. 2012	4	0	0.37 (0.14, 1.00)	0.00	24.9[c]	13[c]	11	0
B	16 Jul. 2012	9	0	0.97 (0.25, 3.78)	0.29	29.5	15	12	0
BS	16 Jul. 2012	3	0	1.73 (4.08, 0.73)	0.00	27.9	14	1	0
MB	12 Jul. 2012	5	1	1.32 (0.18, 9.78)	0.00	28.3	15	39	8
GH	12 Jul. 2012	6	0	1.89 (0.82, 4.34)	0.00	27.4	14	8	0
	Mean	11.1	5.1	2.37	1.52	25.2	13.4	27.5	20.3
	Total	217	102			582.5		669	468

[a]Videos from 2 cameras excluded from the *Myodes* counts shown due to suspected hit rate inflation (filming effort of 23.6 camera-days).

[b]Count consists of total number of day-time videos of *Myodes*, as well as the number of night-time videos estimated to be of *Myodes* using the day-time ratio of *Myodes*-to-*Microtus* videos.

[c]Videos from 1 camera excluded from the *Myodes* count due to suspected hit rate inflation (filming effort of 22.9 camera-days).

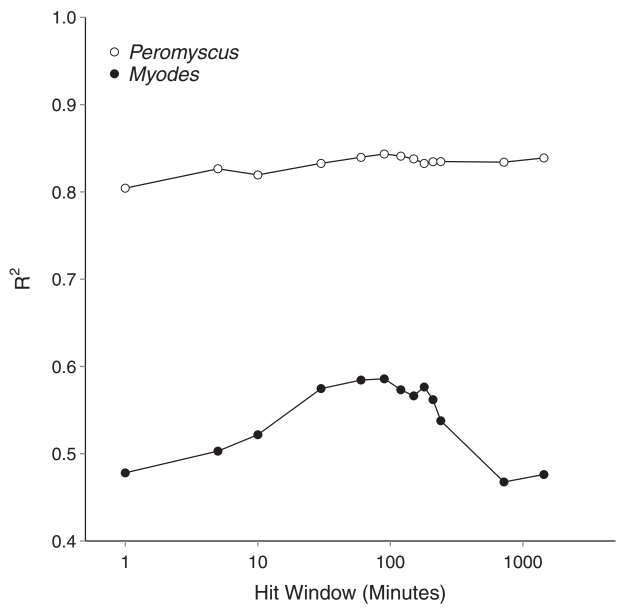

Fig. 1.—R^2 values for linear regressions between population density estimates obtained from livetrapping and camera trapping hit rates, calculated with different hit window lengths for deer mice (*Peromyscus maniculatus*) and northern red-backed voles (*Myodes rutilus*) sampled in Yukon, Canada, 2010–2012. Hit window lengths included: 1, 5, 10, 30, 60, 90, 120, 150, 180, 210, 240, 720, and 1,440 min and are presented on a log-scale.

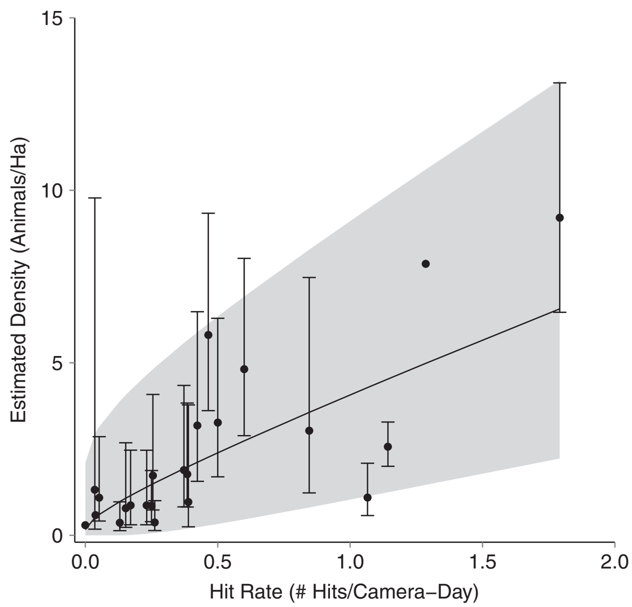

Fig. 2.—Relationship between camera trapping hit rates and density estimates obtained from livetrapping for northern red-backed voles (*Myodes rutilus*) using a 90-min hit window. Each point represents a 2-day filming session followed by a 3-day livetrapping session. Solid line indicates linear regression (R^2 = 0.59), gray band indicates 95% prediction intervals. Error bars are 95% *CI*s for density estimates.

Table 2). Slope estimates were highly significant for both *Myodes* and *Peromyscus* (t_{21} = 5.45, P < 0.001 and t_{21} = 10.55, P < 0.001, respectively), while intercept estimates were not significantly different from zero for either species (t_{21} = 2.01, P = 0.057 and t_{21} = 1.01, P = 0.325, for *Myodes* and *Peromyscus*, respectively).

Discussion

We have demonstrated that hit rates obtained from camera trapping are strongly correlated to density estimates based on traditional livetrapping for *P. maniculatus* and moderately correlated to those for *M. rutilu*s. Our data suggest that this correlation in *Myodes* is somewhat sensitive to hit window duration, whereas the correlation is relatively insensitive to hit window duration in *Peromyscus*. For both species, a 90-min hit window maximizes the correlation between hit rates from camera traps and density estimates from livetrapping.

We expected hit window to have an effect on the correlation between hit rates and density estimates based on livetrapping because we expected encounters with cameras and traps to be of variable length (if all encounters generated the same number of videos, then applying a hit window would affect all hit rates similarly and would not alter the correlation between hit rates and density estimates). As we used bait to attract animals to the cameras, we think encounter duration is likely to be influenced by behavioral processes like intraspecific spacing behavior, which has been observed in both species (Burns 1981; Wolff et al. 1983), and foraging behavior, which in mice and voles can involve multiple trade-offs including predator avoidance, interspecific competition, and resource availability (Anderson 1986; Lemaître et al. 2010). In addition, individuals inside the traps do not generate videos because the cameras cannot "see" them, which could also lead to variation in the number of videos generated by each encounter. With multiple possible sources of behavioral variation (spacing behavior, foraging behavior, and how long the individual chooses to be in a live trap that is locked open), we expected hit window duration to have a large impact on the correlation between hit rates and density estimates based on livetrapping data.

The results for *Myodes* support this expectation; goodness-of-fit of the relationship between hit rates and livetrapping-based density estimates was very sensitive to hit window duration (Fig. 1), with a 90-min hit window generating the highest correlation. Why the 90-min hit window is the "best" for this species is unclear; there are only 3 instances in which it appeared that a single individual was visiting the live trap for an extended period of time, and those were excluded from the analysis. One explanation is that individuals encountering live traps with cameras may be spending considerable amounts of time around the trap, but not necessarily within the camera's detection zone; the animals could be moving short distances away from traps, or entering the traps and disappearing from view. Caching the bait for later consumption could generate this pattern of video footage, and there were several instances in which voles were observed removing bait from the live trap without consuming it in front of the camera.

Conversely, hit window duration had little effect on the goodness-of-fit of the regression for *Peromyscus*; the 90-min hit window generated the strongest correlation, but all of the hit windows generated an R^2 of at least 0.8. One possible

Table 2.—Linear regressions to predict estimated densities from livetrapping and camera trapping hit rates for northern red-backed voles (*Myodes rutilus*) and deer mice (*Peromyscus maniculatus*). Hit rates were calculated using a 90-min hit window for both species, density is in animals/ha, and density and hit rate were square-root transformed to achieve linearity.

Species	Regression terms	Sample size	Mean squared error	Slope *SE*	R^2
Myodes	$\sqrt{\text{estimated density}} = 1.61\sqrt{\text{hit rate}} + 0.41$	23	0.10	0.30	0.59
Peromyscus	$\sqrt{\text{estimated density}} = 1.89\sqrt{\text{hit rate}} + 0.11$	23	0.19	0.18	0.84

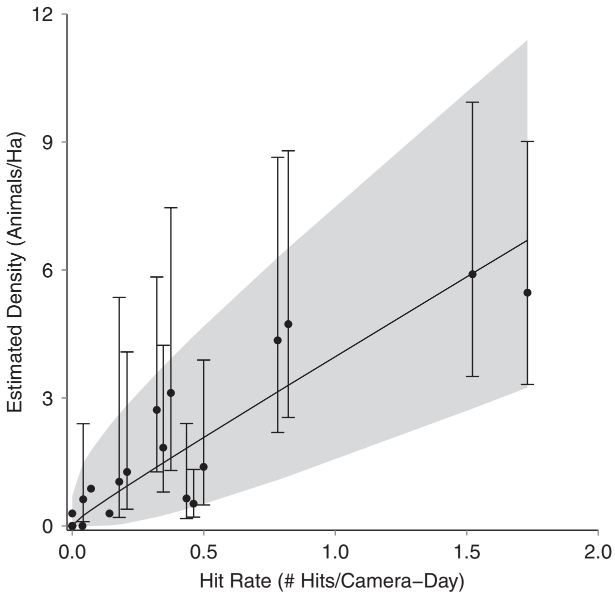

Fig. 3.—Relationship between camera trapping hit rates and density estimates obtained from livetrapping deer mice (*Peromyscus maniculatus*) using a 90-min hit window. Each point represents a 2-day filming session followed by a 3-day livetrapping session. Solid line indicates linear regression (R^2 = 0.84), gray band indicates 95% prediction intervals. Error bars are 95% *CI*s for density estimates.

explanation is that since *Peromyscus* are strictly nocturnal and summer nights at our study sites can be as short as 6 h in duration (Gilbert et al. 1986), there is little opportunity for variation in encounter duration because all individuals in the population have limited time budgets, and so trap visits are similarly constrained for all individuals. In addition, at low densities, we would have been less likely to place cameras near active burrows, which could have contributed to low visitation rates and lower variation in encounter duration.

We expected there to also be a strong correlation between hit rates and livetrapping-based density estimates for *Myodes* and *Peromyscus*, and our results for *Myodes* moderately supported this expectation. With the use of a 90-min hit window, hit rates account for almost 60% of the variation in *Myodes* density estimates obtained from livetrapping. There is considerable variability in the data, but all livetrapping density estimates fall within the 95% prediction intervals of the regression (Fig. 2).

Using the ratio of livetrapped *Myodes*-to-*Microtus* to estimate the amount of night-time vole video footage that was of *Myodes* improves the correlation between live trap-based density estimates and hit rates calculated using a 90-min hit window (R^2 increases from 0.59 to 0.61), but this improvement is small and suggests that misidentification of voles as *Myodes* when they were in fact *Microtus* is not a major concern, at least at these densities. Another possible explanation for the moderate correlation involves the hit window itself. The 90-min hit window is "best" when considering the entire data set but may be severely misrepresenting the number of encounters that actually occurred at the session or individual camera level, leading to a reduced correlation between hit rate and density. In general, the moderate correlation suggests that hit rates may be appropriate for estimating an approximate density for *Myodes* but would not be an appropriate method for obtaining precise density estimates without further refinements.

The correlation between hit rates and density estimates from livetrapping was higher for *Peromyscus*. Hit rates calculated using a 90-min hit window accounted for 84% of the variation in the *Peromyscus* density estimates. The variability in the *Peromyscus* data is less pronounced than in the *Myodes* data, and all livetrapping estimates fall within the 95% prediction intervals of the regression (Fig. 3). The strong correlation and overlap between model predictions and density estimates suggests that hit rates may be an appropriate method for obtaining precise density estimates for this species.

In terms of effort, camera trapping as employed here is not considerably better than livetrapping. A livetrapping session of 3 days, including prebaiting the traps beforehand, takes approximately 9 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. Importantly, however, the amount of time spent in the field is considerably less when camera trapping (setting up and retrieving the cameras typically took less than 2 person hours), and the time required to train someone to view and score footage is also less than that required for small mammal handling. Currently, both the ScoutGuard SG560 and the Longworth trap can be purchased for approximately 100 USD/unit, but since fewer cameras are required than traps, camera trapping is considerably less expensive. In summary, camera trapping and livetrapping as conducted here are similar in terms of effort, but camera trapping has lower equipment costs and requires less field work.

Given the promising results shown here and the lower equipment costs associated with camera trapping, we suggest several areas for future research that could increase the applicability of this method. First, determine if hit rates obtained from camera traps alone, without the inducement of bait or traps, are correlated to density. This would eliminate the costs associated with setting up and maintaining traps. In addition, it would also eliminate the problem of the trap itself preventing the camera from "seeing" the small mammal.

Second, determine the minimum number of cameras and filming effort required to obtain a strong correlation between hit rates and livetrapping-based density estimates and determine if stratification by habitat and camera trap spacing can influence this correlation.

Third, examine this method over a wider range of small mammal densities both locally and regionally. Vole densities shown here do not represent the entire range of possible densities in these Yukon locations. Historically, Kluane has had *Myodes* densities as high as 30 animals/ha (Krebs et al. 2011), whereas the highest density observed during this study was 9.2 animals/ha. Measuring the relationship between hit rate and density for the entire range of possible densities is necessary for this method to be more broadly applicable and is also necessary for determining if using weighted linear regression is appropriate (see Supporting Information S1–S5). Also, *Microtus* densities at Kluane can be much higher than those reported here (Krebs et al. 2010), and the applicability of this method when both genera are more abundant must be assessed, given that we are unable to reliably distinguish between *Myodes* and *Microtus* in night-time video footage.

Differences between trapping grids at Kluane and Mayo were assumed to be negligible in this investigation, but further work into measuring location effects is necessary for determining if the relationship between hit rate and density in 1 location can be applied to other locations with different habitats and community composition.

Finally, explore the effects of alternative camera settings. Determining if using the delay setting on the cameras would reduce the amount of video footage to view without compromising the correlation between hit rate and density would be useful, and of interest in this case because the hit windows were applied to the *Myodes* and *Peromyscus* data separately, and therefore the hit window is not analogous to the delay setting on the camera.

In conclusion, the results obtained in this study are encouraging because they indicate it may be possible to census small rodents with cameras, without the necessity of livetrapping, which is time-consuming and may result in stressing the animals. While we recognize that camera trapping will not replace livetrapping for studies that require data obtainable only from handling the animals, it may prove to be a useful means to monitor small mammal populations, particularly at broad spatial and temporal scales.

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Supporting Information

Supporting Information S1.—A brief description of the methods and results of weighting the regressions between livetrapping density estimates and hit rates for *Peromyscus maniculatus* and *Myodes rutilus* using the inverse of the standard errors of the livetrapping density estimates.

Supporting Information S2.—R^2 values for weighted and unweighted linear regressions between livetrapping-based population density estimates and hit rates calculated with different hit window lengths for deer mice (*Peromyscus*) and northern red-backed voles (*Myodes*), Kluane Lake and Mayo, 2010–2012.

Supporting Information S3.—The weighted and unweighted regressions between camera trap hit rates and livetrapping-based density estimates for deer mice (*Peromyscus maniculatus*) using a 90-min hit window.

Supporting Information S4.—The weighted and unweighted regressions between camera trap hit rates and livetrapping-based density estimates for northern red-backed voles (*Myodes rutilus*) using a 90-min hit window.

Supporting Information S5.—Weighted and unweighted linear regressions and their summary statistics for predicting livetrapping-based estimated densities from camera trap hit rates for northern red-backed voles (*Myodes rutilus*) and deer mice (*Peromyscus maniculatus*).

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