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

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. rutilis 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 white rubber bands, 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 live-trapping). 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 $\alpha$ 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 for 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*₁,₁₁ = 29.7, *P* < 0.001, Fig. 2; Table 2) and *Peromyscus* (*F*₁,₁₁ = 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.

<table>
<thead>
<tr>
<th>Session</th>
<th>MNA</th>
<th>Estimated density</th>
<th>Filming effort</th>
<th>Videos</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Myodes</td>
<td><em>Peromyscus</em></td>
<td>Myodes</td>
<td><em>Peromyscus</em></td>
</tr>
<tr>
<td>Chitty</td>
<td>10 Jun. 2010</td>
<td>4</td>
<td>3</td>
<td>0.36 (0.14, 0.97)</td>
</tr>
<tr>
<td></td>
<td>15 Jul. 2010</td>
<td>18</td>
<td>8</td>
<td>4.82 (2.89, 8.03)</td>
</tr>
<tr>
<td></td>
<td>13 May 2011</td>
<td>1</td>
<td>5</td>
<td>0.29</td>
</tr>
<tr>
<td></td>
<td>23 Jul. 2011</td>
<td>15</td>
<td>19</td>
<td>3.18 (1.56, 6.48)</td>
</tr>
<tr>
<td></td>
<td>9 May 2012</td>
<td>8</td>
<td>8</td>
<td>0.86 (0.40, 1.88)</td>
</tr>
<tr>
<td></td>
<td>6 Aug. 2012</td>
<td>19</td>
<td>17</td>
<td>3.03 (1.23, 7.47)</td>
</tr>
<tr>
<td>J</td>
<td>1 Jun. 2010</td>
<td>2</td>
<td>6</td>
<td>0.58</td>
</tr>
<tr>
<td></td>
<td>6 Jul. 2010</td>
<td>11</td>
<td>15</td>
<td>1.09 (0.57, 2.09)</td>
</tr>
<tr>
<td></td>
<td>8 May 2011</td>
<td>10</td>
<td>5</td>
<td>1.77 (0.82, 3.83)</td>
</tr>
<tr>
<td></td>
<td>19 Jul 2011</td>
<td>18</td>
<td>12</td>
<td>5.81 (3.61, 9.34)</td>
</tr>
<tr>
<td></td>
<td>6 May 2012</td>
<td>16</td>
<td>3</td>
<td>3.27 (1.70, 6.29)</td>
</tr>
<tr>
<td></td>
<td>21 May 2012</td>
<td>18</td>
<td>2</td>
<td>2.57 (2.00, 3.28)</td>
</tr>
<tr>
<td>Silver</td>
<td>22 May 2010</td>
<td>7</td>
<td>0</td>
<td>0.87 (0.31, 2.47)</td>
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<tr>
<td></td>
<td>20 Jun. 2010</td>
<td>3</td>
<td>1</td>
<td>0.79 (0.23, 2.68)</td>
</tr>
<tr>
<td></td>
<td>29 Jul. 2010</td>
<td>4</td>
<td>0</td>
<td>0.87 (0.31, 2.47)</td>
</tr>
<tr>
<td></td>
<td>1 Jun. 2011</td>
<td>5</td>
<td>0</td>
<td>1.09 (0.41, 2.86)</td>
</tr>
<tr>
<td></td>
<td>27 Jul. 2011</td>
<td>27</td>
<td>3</td>
<td>7.87</td>
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<tr>
<td></td>
<td>9 Jun. 2012</td>
<td>4</td>
<td>0</td>
<td>0.37 (0.14, 1.00)</td>
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<tr>
<td>B</td>
<td>16 Jul. 2012</td>
<td>9</td>
<td>0</td>
<td>0.97 (0.25, 3.78)</td>
</tr>
<tr>
<td>BS</td>
<td>16 Jul. 2012</td>
<td>3</td>
<td>0</td>
<td>1.73 (4.08, 0.73)</td>
</tr>
<tr>
<td>MB</td>
<td>12 Jul. 2012</td>
<td>5</td>
<td>1</td>
<td>1.32 (0.18, 9.78)</td>
</tr>
<tr>
<td>GH</td>
<td>12 Jul. 2012</td>
<td>6</td>
<td>0</td>
<td>1.89 (0.82, 4.34)</td>
</tr>
<tr>
<td>Mean</td>
<td>11.1</td>
<td>5.1</td>
<td>2.37</td>
<td>1.52</td>
</tr>
<tr>
<td>Total</td>
<td>217</td>
<td>102</td>
<td>582.5</td>
<td>669</td>
</tr>
</tbody>
</table>

1Videos from 2 cameras excluded from the *Myodes* counts shown due to suspected hit rate inflation (filming effort of 23.6 camera-days).
2Count 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.
3Videos from 1 camera excluded from the *Myodes* count due to suspected hit rate inflation (filming effort of 22.9 camera-days).
significant different from zero for either species (\(t_{21} = 5.45, P < 0.001\) 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 *Peromyscus maniculatus* and moderately correlated to those for *M. rutilus*. 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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Regression terms</th>
<th>Sample size</th>
<th>Mean squared error</th>
<th>Slope SE</th>
<th>( R^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Myodes</td>
<td>( \sqrt{\text{estimated density}} = 1.61 \sqrt{\text{hit rate}} + 0.41 )</td>
<td>23</td>
<td>0.10</td>
<td>0.30</td>
<td>0.59</td>
</tr>
<tr>
<td>Peromyscus</td>
<td>( \sqrt{\text{estimated density}} = 1.89 \sqrt{\text{hit rate}} + 0.11 )</td>
<td>23</td>
<td>0.19</td>
<td>0.18</td>
<td>0.84</td>
</tr>
</tbody>
</table>

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% CIs for density estimates.

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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.

**Acknowledgments**

We thank K. Broadley, L. Hofer, R. Johnson, A. Kenney, E. Lomax, L. Pavan, M. Perry, and N. Warren for their assistance in the field. Research funding was provided by the Natural Science and Engineering Research Council of Canada (CJK and RB), the Northern Scientific Training Program (PV, CJK), and Environment Yukon (TSJ). The facilities of the Kluane Lake Research Station of the Arctic Institute of North America were essential for this research; we thank S. Williams and L. Goodwin for their assistance.

**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 density estimates and hit rates for Peromyscus maniculatus and deer mice (Peromyscus maniculatus).

**Literature Cited**


Submitted 25 May 2015. Accepted 27 August 2015.

Associate Editor: Harald Beck