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Mitchell A. Parsons
Utah State University
5230 Old Main Hill
Logan, Utah, 84322-5230
(509) 679-8018
parsonsmitch953@gmail.com

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Evaluating Live Trapping and Camera-based Indices of Small Mammal Density

MITCHELL A. PARSONS[1,2], *School of Environmental and Forests Sciences, University of Washington, Box 352100, Seattle, WA 98195, USA*

ALISHIA E. ORLOFF[3], *School of Environmental and Forests Sciences, University of Washington, Box 352100, Seattle, WA 98195, USA*

LAURA R. PRUGH, *School of Environmental and Forests Sciences, University of Washington, Box 352100, Seattle, WA 98195, USA*

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[1] *Corresponding Author: email – parsonsmitch953@gmail.com*m

[2] *Current address: Utah State University Department of Wildland Resources, 5230 Old Main Hill, Logan, Utah, 84322-5230, USA*

[3] *Current address: Yale School of Forestry & Environmental Studies, 195 Prospect Street, New Haven, CT, 06511, USA*

ABSTRACT

Density estimates are integral to wildlife management, but they can be costly to obtain. Indices of density may provide efficient alternatives, but calibration is needed to ensure the indices accurately reflect density. We evaluated several indices of small mammal density using live trapping and motion-activated cameras in Washington's Cascade Mountains. We used linear regression to compare spatially-explicit capture recapture density estimates of mice, voles, and chipmunks to four indices. Two indices were based on live trapping (minimum number alive and number of captures per 100 trap nights) and two indices were based on photos from motion-activated cameras (proportion of cameras detecting a species and the number of independent detections). We evaluated how the accuracy of trap-based indices increased with trapping effort using subsets of the full dataset (n = 7 capture occasions per site). Most indices provided reliable indicators of small mammal density, and live trapping indices (R^2=0.64 – 0.98) outperformed camera-based indices (R^2=0.24 – 0.86). All indices performed better for more abundant species. The effort required to estimate each index varied, and indices that required more effort performed better. These findings should help managers, conservation practitioners, and researchers select small mammal monitoring methods that best fit their needs.

KEY WORDS abundance, camera trap, density, live trapping, *Microtus*, *Myodes*, *Neotamias*, *Peromyscus*, population monitoring, Washington.

Density estimates, which measure the number of individuals per unit area, are integral to monitoring the dynamics of animal populations. Long-term population data can help properly manage game species, identify species of conservation need, and understand ecological dynamics (Furnas et al. 2017; Pellerin et al. 2017). Density data can also identify populationlevel habitat relationships (Hernández-Sánchez et al. 2017) and facilitate evaluation of vulnerability to human disturbances (Holloway and Smith 2011). Beyond management and conservation of individual species, data on the density of species also provides information regarding conservation planning (Williams et al. 2014), ecosystem health (Rapport et al. 1998; Kiwia 2006), and prey availability for predators (Karanth et al. 2004).

Although density estimates are valuable for conservation and management, they are often difficult or expensive to obtain. A common alternative is to obtain indices of density, which are metrics that are proportional to density (Johnson 2008) that allow estimation of population trends in space and time (e.g. catch-per-unit-effort, detection rate; Thogmartin et al. 2007, Amar et al. 2010). Density indices are typically easier and less costly to obtain than actual density estimates, and indices may be sufficient to address many conservation and management decisions (O'Brien et al. 2003; Van De Kerk et al. 2018). To ensure density indices provide reliable information about population trends, they should be calibrated by comparing index values to estimates of actual density.

Here, we evaluate live trapping and camera-based indices of small mammal density. Small mammals are some of the most frequently enumerated species, likely due to their ease of capture, abundance in most habitats, and importance as prey, seed dispersers, and ecological indicators (Iriarte et al. 1989; Weir 2003; Pardini et al. 2005). Mark-recapture methods are well developed and frequently used for small mammals (Seber 1986), but indices, including captures per unit effort and minimum number of individuals alive are also commonly used as density indices (Krebs 1966; Shaner 2006; Wiewel et al. 2009). The accuracy of these indices has been evaluated in diverse systems, and both minimum number alive and captures per unit effort indices can provide precise indices of small mammal abundance (Hilborn et al. 1976; Graipel et al. 2014). Because of the ubiquity of these indices, they provide a valuable comparison for evaluating the efficacy of camera-based indices.

Even for estimating such indices, live trapping methods require intensive effort, and can have negative impacts on captured individuals (Delehanty and Boonstra 2009). Meanwhile, motion-triggered cameras are becoming a common tool in wildlife monitoring (Burton et al. 2015). Camera trapping has been used to estimate density of large and medium-sized mammals (Tobler et al. 2008; Rich et al. 2017), but using cameras to monitor small mammals is less common (Villette et al. 2016, 2017). Villette et al. (2016, 2017) evaluated the efficacy of camera-based indices of density for small mammals, squirrels, and hares in the boreal forest of the Yukon, Canada. The methods were reliable for all species ($R^2 = 0.41 – 0.90$), indicating that cameras may provide an alternative to live trapping small mammals. We aim to test these methods in a new system to further assess the effectiveness of camera-based density indices for small mammals and compare camera-based indices to live trapping indices.

We evaluated four indices of small mammal density against capture-recapture density estimates. We tested indices for three small mammal groups: mice (*Peromyscus keeni* Rhoads, 1894 and *P. maniculatus* Wagner, 1845), voles (*Microtus* spp. and *Myodes gapperi* Vigors, 1830), and chipmunks (*Neotamias townsendii* Bachman, 1839). We assessed two indices based on live trapping: the minimum number of individuals alive and captures per 100 trap nights (Hopkins and Kennedy 2004). For each of the live trapping indices, we evaluated whether the accuracy of the index increased with trapping effort after each of seven capture occasions. We also examined two camera-based indices: proportion of camera nights detecting the species and number of independent camera detections. This evaluation builds on previous work by providing additional calibration for camera indices in a new system, and comparing these methods to common live trapping indices.

MATERIALS AND METHODS

Study Area

The study area was the southern Cascade Mountains of Washington and included Gifford Pinchot National Forest (6,100 km^2), Mt. Rainier National Park (950 km^2), Elbe and Tahoma State forests (220 km^2) and surrounding private lands. This area is dominated by conifer forests ranging from young, intensively managed stands to old growth forests. The elevation of the study sites ranged from 403 to 1485 m with a mean of 977 m. The mean July and January temperatures were 25.8° and -1.5° C and average precipitation was 140 cm (67 cm snowfall) in the town of Packwood, Washington near the center of the study area (Western Regional Climate Center 2016; http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?wa6262).

Field Methods

We conducted small mammal trapping and camera trapping at 15 sites in the summers (June – September) of 2016 (6 sites) and 2017 (9 sites). We selected sites using a stratified random design to distribute sites among forest stands of different ages and land ownership (for details, see Parsons et al. 2020). At each site, we conducted mark-recapture surveys to estimate densities of small mammals. We established a 90-m x 90-m (0.81 ha) grid of 100 Sherman traps (LFA; 7.6 x 8.9 x 24.1 cm, H. B. Sherman Traps, Tallahassee, Florida, USA) with 10-m spacing for live captures of mice, voles, and chipmunks. The highest number of captures in one trapping occasion was 79 individuals, with most occasions having <50 captures suggesting no issues with trap saturation. We pre-baited traps at each site for three days prior to trapping (i.e. trap door locked open with bait inside). We baited traps with a combination of oats, seeds, mealworms (to reduce shrew mortality; Do et al. 2013), and polyester batting. We trapped each site for 3-4 consecutive nights after pre-baiting depending on recapture rates. We left traps open 24 hours per day and checked traps in the morning (0700) and evening (1800), for a total of seven occasions at most sites. At all sites, the first, third, fifth, and seventh occasions were morning trap checks and the second, fourth, and sixth occasions were evening trap checks. If no new animals were captured after the second morning capture occasion, we stopped trapping after the third morning capture occasion (5 occasions). We trapped one site with high recapture rates for 5 occasions and the remaining 14 sites for seven occasions. We recorded species, body mass, and sex of all captured mice, voles, and chipmunks, and marked each individual with a numbered ear tag prior to release (1005-1 Monel ear tag; National Band and Tag Company, Newport, Kentucky, USA). All animal handling procedures were approved by the University of Washington Institutional Animal Care and Use Committee (Protocol 4381-01) and were conducted under Washington Department of Fish and Wildlife Scientific Collection Permits 16-276 (2016) and 17-048 (2017).

Within each trapping grid, we set 16-20 cameras (Reconyx PC 900, Holmen, Wisconsin, USA (2016), Bushnell Aggressor No-Glow, Overland Park, Kansas, USA (2017)) located at randomly selected Sherman traps. We set cameras when Sherman traps were set for pre-baiting and we deployed cameras for 3-7 days at each site, resulting in a range of 60-140 trap nights per site. We placed cameras 10-20 cm off the ground and 1-2 m from Sherman traps facing the front or side of the trap so that animals entering/exiting traps were in view (Villette et al. 2016). We recognize that the number of cameras was much lower than the number of live traps. Our goal was to compare these indices as they would likely be implemented in a field setting. A grid of 100 live traps is a common grid size and 16-20 cameras is a feasible number for camera trapping.

Live Trapping Indices: Minimum Number Alive and Captures per 100 Trap Nights

To calculate the minimum number alive index, we summed the number of unique individuals of each species that we captured at each site, cumulatively after each capture occasion. Notably, this index still requires marking captured animals if more than one capture occasion is conducted. To calculate the captures per 100 trap nights index, we calculated the total number of captures of each species at each site, cumulatively after each capture event, and scaled to a common unit of captures per 100 trap nights.

For the minimum number alive and captures per 100 trap nights indices, we evaluated the index after each capture occasion (1 – 7) to evaluate how accuracy increased with increased trapping effort.

Camera Indices: Proportion Detected and Independent Detections

We used the program Timelapse2 (Greenberg and Godin 2015) to identify small mammal species in photos and extract date and time. For the proportion of cameras detecting a species, we calculated the proportion of camera trap nights where a species was detected as follows.

Because the majority of detections occurred at night, we calculated detections with trap nights beginning at noon each day so that each trap night included a continuous nocturnal period.

For the number of independent camera detections, we summed the number of photographs of each species at each site, scaled by the number of trap nights. We tested a range of times to define independence (0-30 minutes in 5-minute intervals, 30-300 minutes in 15-minute intervals, 300-420 minutes in 30-minute intervals), and selected the time interval for each species that resulted in the strongest Pearson’s correlation with density estimates. We increased the interval size because we saw large drops in correlation beyond 30 minutes, but wanted to examine much longer time intervals, as Villette et al. (2016, 2017) reported high correlations for most species with time intervals up to 240 minutes. Our use of "independent detections" does not imply statistical independence of the photographs, but separate visits to the camera where the individual was absent for at least 5 minutes. We used independent detections to remain consistent with previous camera trapping literature (Burton et al. 2015).

Statistical Analyses

We used secr 4.3.3 (Efford 2020) to estimate density and 95% confidence intervals of mice, voles, chipmunks, and all species combined at each site. For each species group, we ran a single model where detection probability (g0) was estimated separately for each site and the movement parameter (sigma) was estimated for each species but shared across sites. Because our goal was to compare density estimates to indices including minimum number alive, we allowed the detection parameter to vary by site. Sharing parameters among sites resulted in density estimates that were linearly related to minimum number alive (i.e. $R^2 = 1.00$). To facilitate model convergence without sharing parameters between sites, we used the null model and did not include a behavioral response to traps. Sites where no individuals of a species were captured were assumed to have abundance of zero. For sites with no recaptures ($n = 2$ sites for voles and 1 site for chipmunks), we used the minimum number alive as an estimate of abundance.

We evaluated each index using linear regression to compare index values to density estimates across the 15 sites. We square-root transformed density and all index values to achieve linearity and meet assumptions of linear regression (Villette et al. 2016). When testing the minimum number alive index, we excluded sites with no recaptures because minimum number alive was used as a density estimate in these situations. To address variability due to the small number of cameras, we used a non-parametric bootstrap approach to estimate parameter uncertainty. For each site, we sampled cameras with replacement to achieve the same number of cameras originally at the site. We then used the selected cameras to calculate the index for the site and then proceeded with the regression. We conducted 1000 iterations of this process. For regressions of camera indices, we report the mean and 95% confidence interval estimates of the intercept, slope, and R^2 of the regression. Plots of regressions for camera indices use the original data. Diagnostic plots of all regressions are available in the online supplementary information. All statistical analyses were performed in R 4.0.4.

RESULTS

Density Estimation

Across all 15 sites, we captured a total of 483 mice, 79 voles, and 82 chipmunks (Table 1). We captured mice at all 15 sites, while voles and chipmunks were both absent from two sites. Mice were the most abundant small mammal at 14 sites, with voles being most abundant at one site. Number of captures, minimum number alive, and density estimates for each species at each site are provided in Table 1. We documented 7 trapping-associated mortalities in 1759 captures of our target species (0.4%).

Live Trapping Indices

The minimum number alive (MNA) index provided the strongest relationship with density estimates, and the accuracy of this index increased with increasing trapping effort (Figure 1). R^2 values after one capture occasion ranged from 0.35 for chipmunks to 0.84 for mice. Accuracy for chipmunks increased substantially after the second capture occasion due to high captures during daytime (i.e., even-numbered occasions) for chipmunks. For all species, R^2 values continued to increase as additional captures occasions were added, and after seven captures sessions, the R^2 value for all species was >0.85 (Table 2).

The captures per 100 trap nights (100TN) index was related to small mammal density for all species as well, but R^2 values tended to be lower (range = 0.64 – 0.87) compared to MNA (range = 0.87 – 0.98). Similar to the MNA index, the reliability of this index generally increased with increasing trapping effort (Figure 2). Surprisingly however, the R^2 for all species combined was highest after one occasion and declined thereafter (Figure 2d). This index performed better for mice and voles than for chipmunks. (Figure 2).

Camera Indices

The proportion of camera trap nights where a species was detected was related to species density and performed better for mice and chipmunks than for voles. R^2 values ranged from 0.24 for voles to 0.67 for mice (Figure 3).

The number of independent detections was a superior index in comparison to the camera trap night index for all of the small mammal groups, with R^2 values ranging from 0.33 for voles to 0.86 for all species combined (Figure 4). For mice and chipmunks, the best time interval for defining independent detections was five minutes. For voles, the best time interval was 0 minutes (i.e., all photos were summed). For all species combined, the best time interval was 20 minutes (Figure 5). Although the time interval influenced the effectiveness of the independent detection index, correlations remained high for all species across a broad range of time intervals (Figure 5).

DISCUSSION

All tested indices were strongly related to small mammal density estimates obtained through live trapping. Live trapping indices outperformed camera-based indices, which was expected because live trapping indices were calculated from the same data used to estimate density in a reduced form and provide more information than data from camera traps. In particular, live trapping cannot detect the same individual multiple times within a trapping occasion, which can occur with camera traps. However, camera indices, particularly the number of independent detections, performed well, supporting the efficacy of using cameras to monitor small mammal density trends without the need for physical capture.

The two live trapping density indices were more strongly related to small mammal density than the camera indices. After seven trapping occasions, the estimated R^2 of the minimum number alive index (MNA) was >0.85 for all species. MNA has been calibrated in numerous systems, and is typically strongly related with small mammal abundance (Hilborn et al. 1976, Graipel et al. 2014). Hopkins and Kennedy (2004) used MNA to evaluate catch per unit effort as an index for small mammals, highlighting the strong association between MNA and small mammal density. However, MNA was also the most invasive and logistically demanding index we tested, as it still required live trapping, handling, and marking all captured individuals (except in the case of one capture occasion). Captures per 100 trap nights was also related to small mammal density, but to a lesser degree than MNA, similar to other studies (Wiewel et al. 2009). Unlike MNA and consistent with previous research, the accuracy of this index did not consistently increase with more capture occasions (Wiewel et al. 2009). This is likely because instead of adding additional individuals to the count of known individuals, each capture occasion provides a new data point that is averaged with previous capture occasions. Therefore, capture occasions that resulted in unusual capture patterns due to unknown factors could reduce the accuracy of this index no matter when they occurred. Our findings indicate that live trapping for even a single occasion can provide a useful index of total small mammal abundance, as was also found in Alaska (Sivy et al. 2018).

Few studies have evaluated how the accuracy of live trapping indices changes with increased trapping session length. Increasing trapping session length will increase cumulative capture probability of individuals, increasing the accuracy of the minimum number alive index (Hilborn et al. 1976). Although a full seven-occasion session of live trapping provided the strongest relationship between index and density in most cases, live trapping indices were strongly related to small mammal density after only a single occasion. For mice, the R^2 estimate for both minimum number alive and captures per 100 trap nights was higher after a single occasion than the R^2 estimate for either camera index. For voles and chipmunks, live trapping indices were more strongly related to density than camera-based indices after two occasions, excluding captures per 100 trap nights for chipmunks. Because chipmunks are diurnal, a single daytime trapping occasion may provide a similarly strong index for chipmunks as a single overnight trapping occasion did for mice. In systems with high capture probability, a single occasion of live trapping may provide a better index than camera surveys, while also allowing sampling of more sites due to fewer days spent sampling each location. However, we pre-baited traps at each site for 3 days prior to trapping, which likely increased capture probabilities, leading to strong relationships between live trapping indices and density with fewer trapping occasions. Hilborn et al. (1976) identified capture probability as an important factor influencing the accuracy of MNA as an index. Increasing capture probability through pre-baiting and use of appropriate equipment (Jung 2016) is key to live-trapping indices being effective with few occasions. In this study, higher capture probability of mice resulted in stronger relationships between indices and density than for voles or chipmunks.

Similar to Villette et al. (2016), the relationship between camera indices and density was stronger for mice than for voles in this study. This pattern may be due to higher density and/or detectability of mice relative to voles. While average mouse density was approximately 4 times higher than vole density, we captured 30 times more photos of mice, indicating that density alone did not account for low vole detections. Voles in this system prefer habitats with dense understories (Parsons et al. 2020), which may have reduced the likelihood of capturing them with cameras. This relatively poor performance highlights 2 possible limitations for camera indices: lower accuracy for rare species, and indices are dependent on detectability. Accuracy of density estimates, including indices, is affected by the amount and quality of data collected (Ngoprasert et al. 2019) and probability of detection (Hilborn et al. 1976). Species that are less common and/or that are rarely detected because of secretive behavior will be more difficult to accurately enumerate (Murphy et al. 2018).

The proportion detected index provided a significant relationship with density estimates while requiring the least intensive field effort and least intensive data processing. However, the performance of this index was notably poorer than the other 3 indices tested in this study and others (Pacheco et al. 2013; Graipel et al. 2014). Eriksson et al. (2019) used a variation of the proportion detected index to estimate relative abundance of marten prey species in Oregon where they calculated the proportion of cameras that detected a species over a seven-day period instead of the proportion of camera trap nights where a species was detected. With this method, Eriksson et al. (2019) experienced saturation of cameras (i.e. all cameras detected the species) by deer mice. They solved this issue by limiting their analysis to a two-day period for deer mice, but our results suggest that using the proportion of camera trap nights instead of number of cameras is also effective. We initially evaluated the proportion detected index as the proportion of cameras instead of the proportion of camera nights capturing photos of a given species, but we abandoned this metric due to similar camera saturation problems.

The number of independent detections of a species was more strongly related to density than the proportion detected index for all species. Mice and chipmunks in particular were frequently captured on camera, making this index especially reliable for these species. Because the small mammal community was dominated by mice, the independent detections index also proved reliable for all species combined. The relationship for voles was strongly influenced by one site with high vole density. Removal of this site resulted in a non-significant linear regression and R^2 value of 0.19, indicating that the number of independent detections of voles was not a reliable index at relatively low vole density in this system, contrary to the findings of Villette et al. (2016) from the Yukon. Low detection rates of voles due to secretive behaviors or their preference of dense understories may have limited the effectiveness of camera indices in this system.

Because cameras must be deployed in the presence of traps to calibrate camera-based indices, the relationship between photo rates and density could differ in studies without traps. Evaluating the relationship between camera detections rates and small mammal density without the presence of live traps is necessary for further evaluation of this method. One approach to test this would be to live trap an area initially to estimate density, remove the live traps, and subsequently set cameras in the same grid location. In the absence of traps, we recommend leaving a bait pile of similar size used in live trapping in front of cameras to attract small mammals. The absence of the trap may influence detection both by removing an object that may obscure animals, and by altering animal behavior (Villette et al. 2016). Trap removal may also influence the best time interval for determining independent detections, as animals may be more likely to spend more time in front a camera without a trap.

One limitation of the independent detections index is that it is difficult to select a time interval without conducting a calibration in other systems. While the time interval did influence the reliability of the index, correlations between number of detections and density was reasonably high (>0.6) across broad time intervals for the species we tested (Figure 5). This consistently good performance suggests that complete testing of time intervals may not be necessary for number of detections to be a useful index depending on the desired precision. Our results indicated that short time intervals to define independent events provided the most reliable index for mice, voles, and chipmunks; however, Villette et al. (2016) found that 90 minutes was the best time interval for voles and mice. These differences may be due to differences in density between the 2 studies. The mean density of voles and mice in our study area were 2 and 16 times higher respectively than voles and mice in Villette et al. (2016). Our results were similar to those of Villette et al. (2017), who found that 5- and 10-minute time intervals performed best for red squirrels (*Tamiasciurus hundsonicus* Erxleben, 1777) and snowshoe hares (*Lepus americanus* Erxleben 1777) respectively. Our data, combined with Villette et al. (2016, 2017) suggests that a short time interval such as 0, 5 or 10 minutes may provide a relatively robust index across species, densities, and systems. Further analysis of photographs to determine the average visit length of small mammals may also provide an indication of appropriate time intervals. However, comparison of camera-based indices to live trapping data is the most certain way to evaluate the effectiveness of these indices. With this in mind, the use of cameras to monitor small mammals may prove most effective for long-term monitoring projects. At the beginning of the project, camera-based indices can be calibrated against live trapping data. Cameras can then be used to monitor small mammal densities independent of live trapping, with occasional recalibration if the project continues for many years.

Our calibrations assume that our modeled small mammal densities are accurate. We believe this is a safe assumption, particularly for mice because of the high number of both captures and recaptures and high capture probability across all sites. Because of lower densities and capture probabilities, density estimates of voles and chipmunks have wider confidence intervals (Figure 3). Sherman traps are known to be less effective for voles than other small mammal traps (Jung 2016), and previous research with voles has suggested their densities may be underestimated when capture probability is low (Krebs 1966; Hilborn et al. 1976). By modeling detection probability individually for each site, we should have negated this bias. A higher than expected number of individuals that were never captured could also result in underestimated density (Krebs 1966). Camera indices may be less prone to behavioral responses to traps, but the inability to identify individuals prevents investigating these patterns.

Because of the difference in the best time interval and some field methods between this study and Villette et al. (2016), we are unable to meaningfully compare regression equations to estimate density from camera trapping rates. This indicates that while camera trapping rates can be effective for providing relative abundance information in diverse systems, using camera trapping rates to estimate density will require developing local equations. Similar to other indices, the local environment, animal densities, and specifics of sampling methods will result in different relationships between index and density in different sites (Prugh and Krebs 2004; Mills et al. 2005). For camera detection of small mammals, the time interval used to define independent detections will have a substantial impact on the equation to calculate density.

Both live capture indices outperformed camera-based indices in estimating density. However, camera-based indices are valuable due to their low time commitment in the field and less invasive nature (Villette et al. 2016). Seven occasions of live trapping required 22 person-hours on average; eight hours to set the grid and 14 hours to complete trap checks. Camera surveys required approximately four person-hours of field work (three hours setting grid, one hour taking down) and eight hours of photo processing per site, making the field time commitment substantially lower. Villette et al. (2016) found similar overall effort for live trapping and camera trapping surveys, but with a much lower field requirement for camera surveys. Regarding cost, 100 Sherman traps cost approximately $2500 while 20 Bushnell cameras cost approximately $2800 at the time of writing. Aside from effort and cost, camera indices may prove particularly useful for monitoring small mammals in designated wilderness areas, national parks, and other areas where research and monitoring protocols are required to exert minimal impact. Among the camera-based indices, calculating the number of independent detections requires no additional field data beyond the proportion detected index, and is therefore the preferred camera-based index of small mammal densities. Unlike live-trapping indices, camera indices do not allow collection of data on sex, reproductive status, and body mass. These data may be necessary or valuable in monitoring demographic trends in populations. Camera indices may prove valuable for broad population monitoring, but more intensive methods will be needed to acquire additional details about population structure when needed.

Our findings provide further evaluation of live trapping indices as robust proxies for small mammal densities (Graipel et al. 2014). Both minimum number alive and captures per 100 trap nights strongly related to density estimates, even after only one or two trapping occasions, providing a reliable index with lower effort than mark-recapture density estimation. However, due to the time requirements to set up small mammal trapping grids, live trapping indices based on one or two trapping occasions still required equal or more effort than camera indices. Our findings concur with those of Villette et al. (2016, 2017) in that cameras are an effective means to monitor small mammal populations with reduced field time requirements compared to live trapping. This project was conducted in different system with a different small mammal community and higher densities, suggesting that the effectiveness of cameras is widespread. Camera-based indices also provided a less invasive way to monitor small mammals, which can be essential when working in wilderness study areas or with endangered species. While live trapping density indices can provide more accurate information regarding small mammal density, camera-based methods can provide a lower effort approach to monitoring small mammal populations.

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COMPETING INTERESTS

The authors declare there are no competing interests.

AUTHOR CONTRIBUTIONS

MAP and LRP conceptualized the study and acquired funding, MAP led field data collection, MAP and AO conducted data analysis with input from LRP, AO and MAP wrote the original draft, MAP, AO, and LRP participated in review and editing of the manuscript.

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DATA AVAILABILITY

All data and code used in this manuscript are available at https://github.com/pars2997/Small-Mammal-Indices

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Table 1. Small mammal capture data summaries for mice (*Peromyscus keeni* Rhoads, 1894 and *P. maniculatus* Wagner, 1845), voles (*Microtus* spp. and *Myodes gapperi* Vigors, 1830), and chipmunks (*Neotamias townsendii* Bachman, 1839) at 15 sites in the South Cascades of Washington. If no confidence interval is given for density estimates, there were no recaptures of the species at that site, and minimum number alive was used as the abundance estimate. “Young”, “Mid”, and “Old” in site names refer to the average age of dominant trees at each location (Parsons et al. 2020). Data were collected from 15 sites in the southern Cascade Mountains of Washington, USA.

Site	Trapping occasions	Camera nights	Total captures			Minimum number alive			Density (95% CI, individuals/ha)		
			Mouse	Vole	Chip	Mouse	Vole	Chip	Mouse	Vole	Chipmunk
Young C	7	60	42	0	14	18	0	10	12.7 (7.8, 20.5)	0	5.4 (2.6, 11.2)
Young D	7	120	106	14	5	40	10	1	24.3 (17.7, 33.4)	9.9 (4.8, 20.3)	0.4 (0.1, 2.2)
Young E	7	100	85	27	7	21	13	4	11.2 (7.3, 17.2)	9.5 (5.4, 16.9)	2 (0.7, 5.8)
Young G	7	114	81	16	0	24	8	0	13.6 (9.1, 20.4)	7 (3.3, 14.7)	0
Mid C	7	100	47	4	0	16	3	0	10.5 (6.4, 17.2)	6.5 (1.7, 24.7)	0
Mid D	7	100	31	3	13	8	1	5	4.8 (2.4, 9.5)	2.5 (0.4, 15.3)	2 (0.8, 4.9)
Mid E	7	80	48	6	27	25	4	7	19.7 (12.9, 30)	5.7 (1.8, 18.3)	1.9 (0.9, 4)
Mid F	7	120	227	5	13	72	3	3	39.4 (31.1, 49.8)	5.2 (1.4, 18.7)	0.8 (0.3, 2.4)
Old A	7	100	52	8	16	18	2	5	10.8 (6.8, 17.2)	1.3 (0.4, 4.8)	1.7 (0.7, 4)
Old B	7	140	32	15	46	10	10	14	6.2 (3.3, 11.5)	8.9 (4.4, 17.9)	4 (2.2, 7.1)
Old C	5	100	15	1	5	5	1	3	5.5 (2.1, 14.4)	1	2.1 (0.6, 7.3)
Old D	7	95	152	0	37	56	0	11	32.3 (24.7, 42.2)	0	3.1 (1.6, 6)

Old E	7	80	89	30	1	39	22	1	25.9 (18.7, 35.8)	20.4 (12.6, 32.9)	1
Old F	7	90	162	2	43	54	1	16	30.9 (23.5, 40.5)	4.1 (0.6, 26.7)	3.5 (2, 6.5)
Old G	7	96	227	1	4	77	1	2	43.8 (34.8, 55)	1	1.3 (0.3, 5.7)
Mean	6.87	99.67	93.07	8.8	15.4	32.2	5.27	5.47	19.4	5.5	1.9

Table 2. Equations of linear models, R^2 values, and p-values for 4 indices of abundance for mice (*Peromyscus keeni* and *P. maniculatus*), voles (*Microtus* spp. and *Myodes gapperi*), and chipmunks (*Neotamias townsendii*). All data (density and index values) were square-root transformed prior to running regressions. Data were collected from 15 sites in the southern Cascade Mountains of Washington, USA.

Mouse	Intercept	95% CI	Slope	95% CI	R2	95% CI	p
Minimum number alive (7 occasions)	0.45	(0.08, 0.82)	0.70	(0.64, 0.77)	0.98		<0.001
Captures per 100 TN (7 occasions)	0.57	(-0.31, 1.45)	1.05	(0.81, 1.29)	0.87		<0.001
Independent detections	1.31	(1.02, 1.56)	1.58	(1.43, 1.75)	0.81	(0.74, 0.87)	
Proportion detected	-1.71	(-2.94, -0.53)	7.37	(6.00, 8.89)	0.67	(0.56, 0.78)	
Vole							
Minimum number alive (7 occasions)	0.46	(-0.02, 0.94)	0.85	(0.65, 1.05)	0.89		<0.001
Captures per 100 TN (7 occasions)	0.40	(-0.17, 0.96)	1.74	(1.23, 2.25)	0.81		<0.001
Independent detections	1.21	(1.00, 1.49)	1.09	(0.72, 1.49)	0.33	(0.12, 0.50)	
Proportion detected	1.13	(0.86, 1.51)	4.08	(2.36, 5.47)	0.24	(0.07, 0.44)	
Chipmunk							
Minimum number alive (7 occasions)	0.18	(-0.12, 0.48)	0.52	(0.39, 0.64)	0.87		<0.001
Captures per 100 TN (7 occasions)	0.42	(-0.02, 0.85)	0.65	(0.36, 0.94)	0.64		<0.001
Independent detections	0.12	(-0.04, 0.29)	2.02	(1.71, 2.35)	0.60	(0.48, 0.70)	
Proportion detected	0.05	(-0.24, 0.33)	2.68	(2.10, 3.26)	0.52	(0.35, 0.68)	
Total							
Minimum number alive (7 occasions)	0.84	(0.23, 1.45)	0.63	(0.54, 0.73)	0.94		<0.001

Captures per 100 TN (7 occasions)	1.27	(0.12, 2.42)	0.91	(0.63, 1.19)	0.79		<0.001
Independent detections	1.37	(0.98, 1.69)	2.08	(1.89, 2.32)	0.86	(0.79, 0.92)	
Proportion detected	-1.82	(-3.61, -0.16)	7.78	(5.87, 9.76)	0.65	(0.52, 0.78)	

FIGURE CAPTIONS

Figure Captions

Figure 1. Effect of the number of capture occasions on the R^2 value of regressions between the square-root transformed minimum number alive (MNA) index and square-root transformed density estimates of (a) mice (*Peromyscus keeni* and *P. maniculatus*), (b) voles (*Microtus* spp. and *Myodes gapperi*), (c) chipmunks (*Neotamias townsendii*), and (d) total small mammals. Data were collected from 15 sites in the southern Cascade Mountains of Washington, USA.

Figure 2. The relationship between the square-root transformed number of capture occasions and R^2 of the captures per 100 trap nights index (100TN) with square-root transformed estimated density of (a) mice (*Peromyscus keeni* and *P. maniculatus*), (b) voles (*Microtus* spp. and *Myodes gapperi*), (c) chipmunks (*Neotamias townsendii*), and (d) total small mammals. Data were collected from 15 sites in the southern Cascade Mountains of Washington, USA.

Figure 3. The relationship between the square-root transformed proportion of camera nights detecting a species and square-root transformed density estimates for (a) mice (*Peromyscus keeni* and *P. maniculatus*), (b) voles (*Microtus* spp. and *Myodes gapperi*), (c) chipmunks (*Neotamias

townsendii), and (d) total small mammals. Error bars represent the 95% confidence interval around density estimates. Values without error bars indicate sites without captures or recaptures where density was estimated as 0 (no captures) or the minimum number alive (no recaptures) Data were collected from 15 sites in the southern Cascade Mountains of Washington, USA.

Figure 4. Relationship between the square-root transformed number of independent detections and square-root transformed density for (a) mice (*Peromyscus keeni* and *P. maniculatus*), (b) voles (*Microtus* spp. and *Myodes gapperi*), (c) chipmunks (*Neotamias townsendii*), and (d) total small mammals. The time interval used to calculate independent detections was 5 minutes for mice, 0 minutes for voles (i.e., all photos were counted), 5 minutes for chipmunks, and 20 minutes for all species combined. Error bars represent the 95% confidence interval around density estimates. Values without error bars indicate sites without captures or recaptures where density was estimated as 0 (no captures) or the minimum number alive (no recaptures). Data were collected from 15 sites in the southern Cascade Mountains of Washington, USA.

Figure 5. Pearson’s correlation coefficients for species density and number of independent detections by cameras for (a) mice (*Peromyscus keeni* and *P. maniculatus*), (b) voles (*Microtus* spp. and *Myodes gapperi*), (c) chipmunks (*Neotamias townsendii*), and (d) total small mammals across 29 different time intervals to define independent detections. Data were collected from 15 sites in the southern Cascade Mountains of Washington, USA.

FIGURES

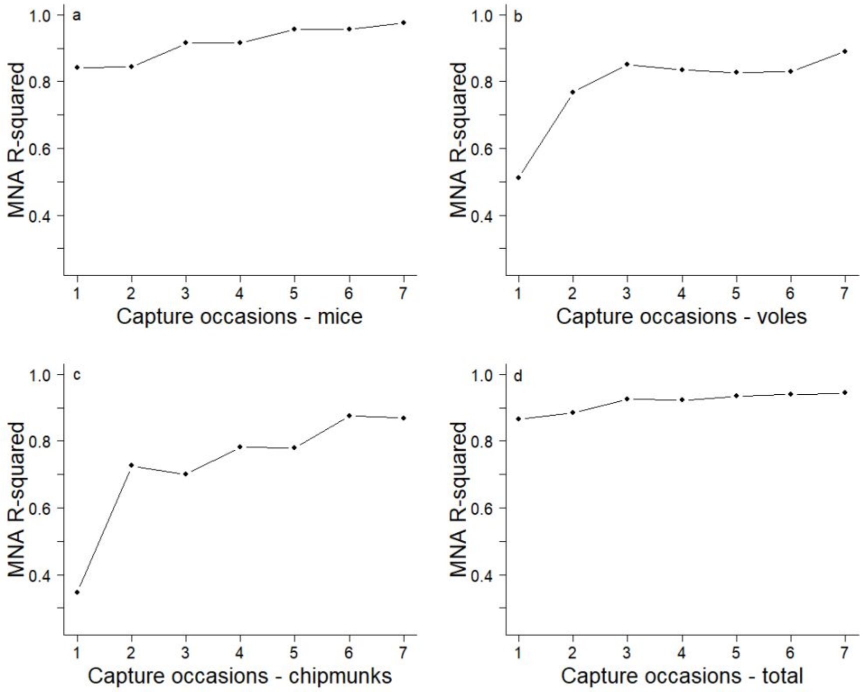
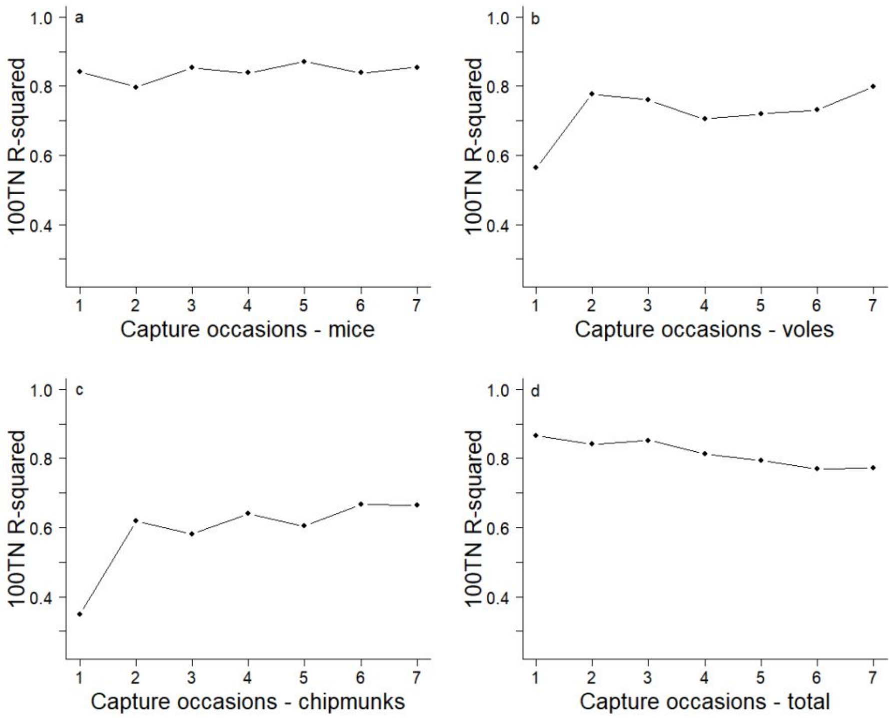


Figure 1.



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607 Figure 2.

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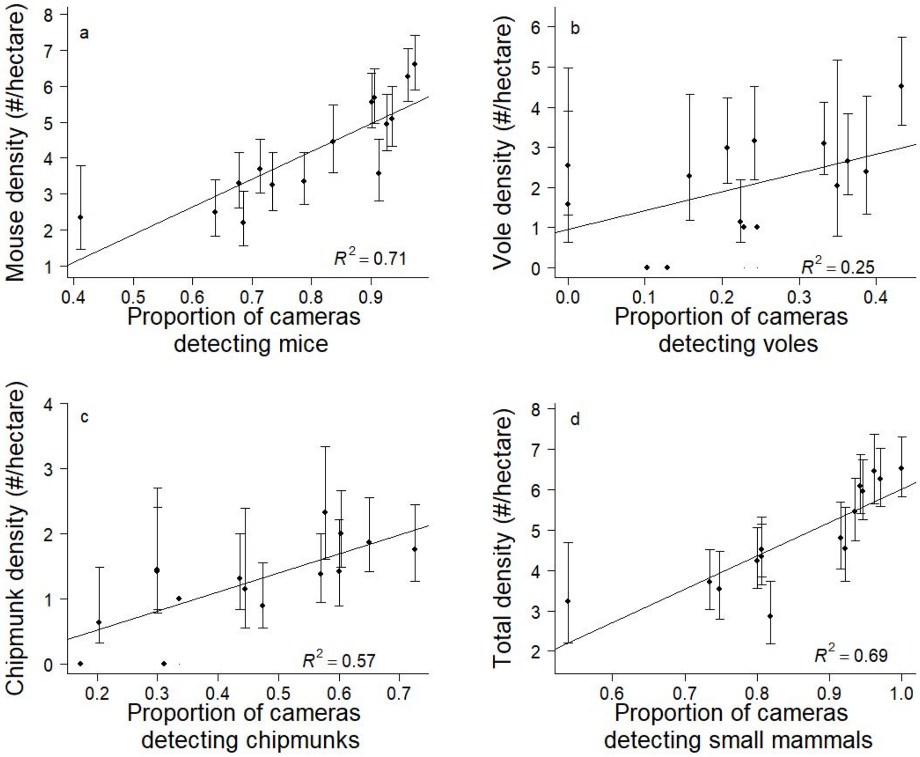
a
Mouse density (#/hectare)
Proportion of cameras detecting mice
$R^2 = 0.71$
b
Vole density (#/hectare)
Proportion of cameras detecting voles
$R^2 = 0.25$
c
Chipmunk density (#/hectare)
Proportion of cameras detecting chipmunks
$R^2 = 0.57$
d
Total density (#/hectare)
Proportion of cameras detecting small mammals
$R^2 = 0.69$

Figure 3.

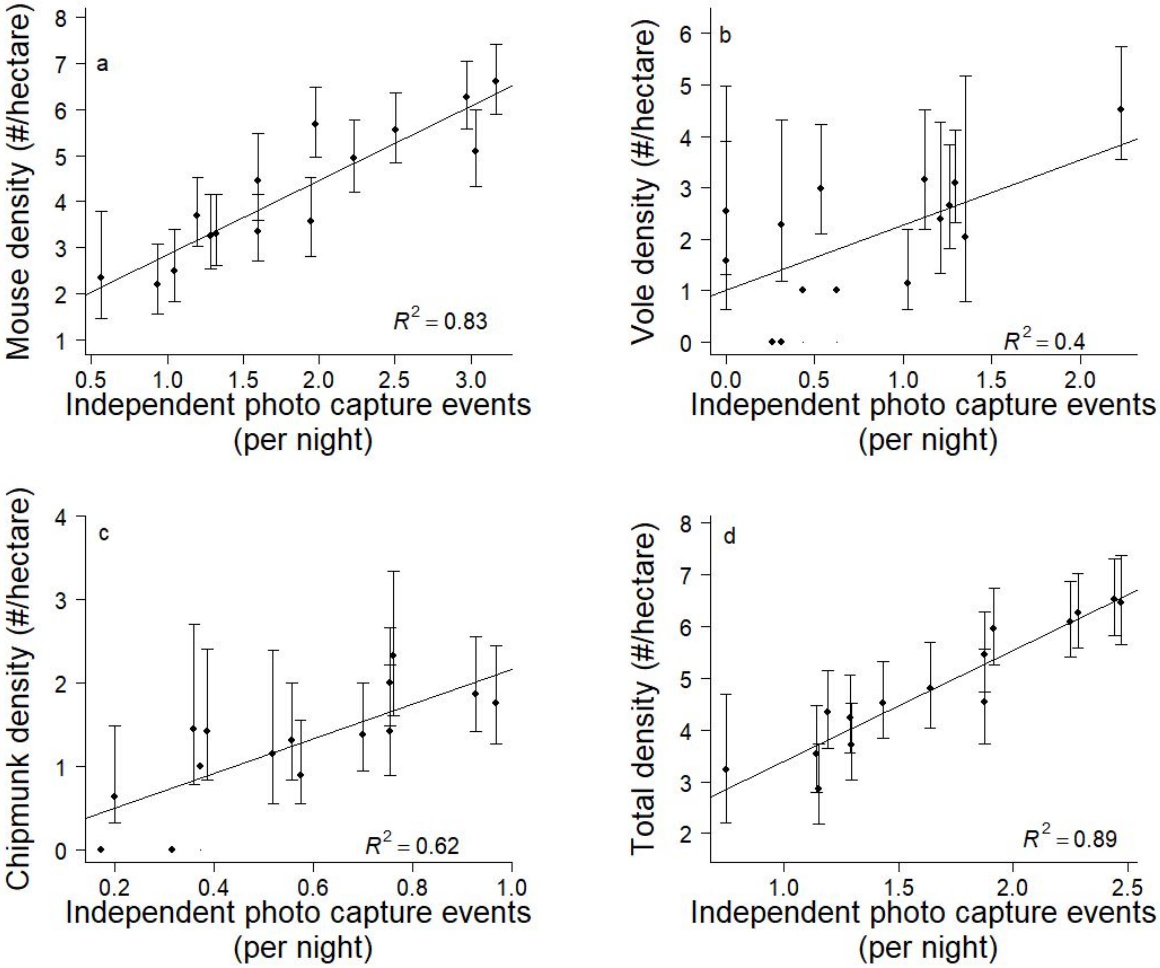
a
Mouse density (#/hectare)
8
7
6
5
4
3
2
1
0.5
1.0
1.5
2.0
2.5
3.0
$R^2 = 0.83$
Independent photo capture events (per night)
b
Vole density (#/hectare)
6
5
4
3
2
1
0
0.0
0.5
1.0
1.5
2.0
$R^2 = 0.4$
Independent photo capture events (per night)
c
Chipmunk density (#/hectare)
4
3
2
1
0
0.2
0.4
0.6
0.8
1.0
$R^2 = 0.62$
Independent photo capture events (per night)
d
Total density (#/hectare)
8
7
6
5
4
3
2
1.0
1.5
2.0
2.5
$R^2 = 0.89$
Independent photo capture events (per night)

Figure 4.

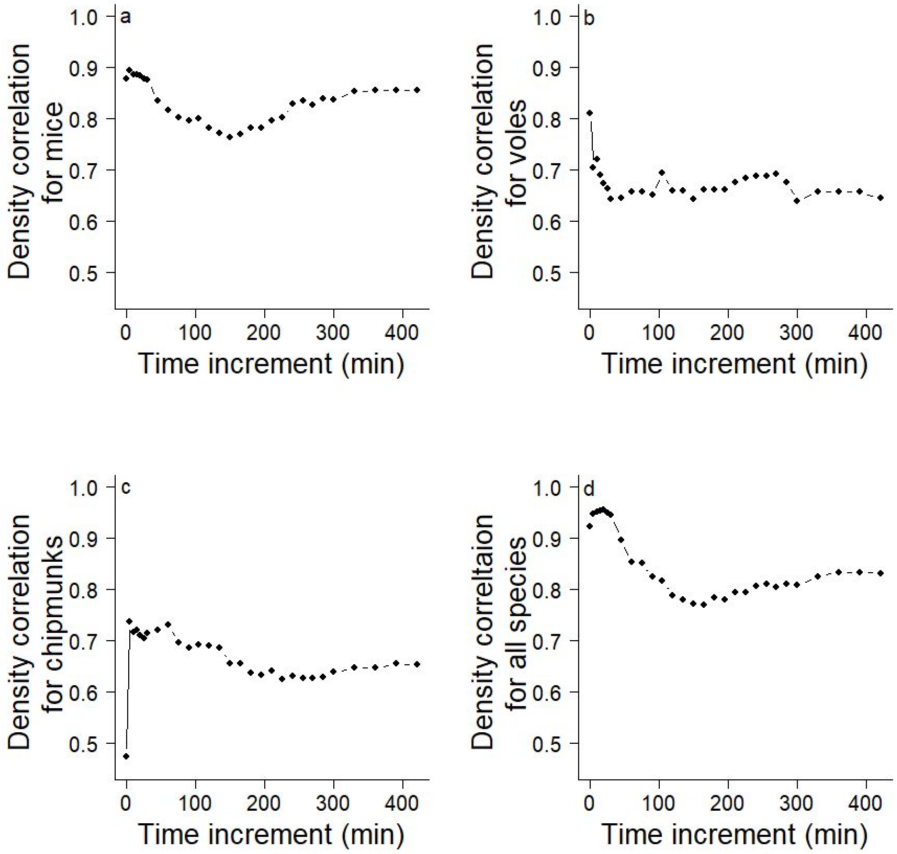
a
Density correlation for mice
b
Density correlation for voles
c
Density correlation for chipmunks
d
Density correltaion for all species
1.0
0.9
0.8
0.7
0.6
0.5
0
100
200
300
400
Time increment (min)

Figure 5.