

Predator-prey interactions in the canopy

Mark Linnell¹ and Damon Lesmeister¹

¹USDA Forest Service Pacific Northwest Research Station

May 5, 2020

Abstract

Small mammal abundances are frequently limited by resource availability but predators can exert strong lethal (direct mortality) and non-lethal limitations (e.g. depressed site-level activity). Artificially increasing resource availability for small mammals provides a unique opportunity to examine predator-prey interactions. We monitored the 3-year response of arboreal rodents and their predators at nest platforms ($n = 598$; 23 young forest sites), using annual inspections and remote cameras ($n = 168$). One year after adding nest platforms we found a 2.9 to 9.2-fold increase in red tree vole (*Arborimus longicaudus*) use at the site-level, but little use by potential predators. Predator use of nest platforms began in year two and increased in year three of the study. Most potential nest predators were positively correlated with tree vole presence at nest platforms but effect size and direction varied with temporal grain considered (e.g. hour vs day time-bin widths). Flying squirrels (*Glaucomys humboldtensis*) were positively correlated with disturbances caused by digging birds. Using a Cormack-Jolly-Seber model and encounter histories produced from visual re-captures of marked tree voles, we estimated apparent annual survival to be 0.099 ± 0.057 ($x \pm 1$ SE) for females and 0.005 ± 0.014 for males. Weasels (*Mustela* spp.), an active seeking predator, preyed upon tree voles most frequently with 10% of weasel detections resulting in mortality of a tree vole ($n = 8$) whereas owls, an ambush predator, did not prey upon tree voles at nest platforms even though they were detected at similar frequencies as weasels. Weasels also exerted potential non-lethal effects and we observed a >10-fold reduction in the number of tree vole detections per week after weasel detection. Our evidence indicates that predators exert direct and indirect effects on tree vole populations with active seeking predators being the most important predators at nest sites.

Introduction

Lack of resources, including availability of nest substrates and food, can limit abundances of small mammals and birds (Aitken & Martin, 2012; Berthier, Leippert, Fumagalli, & Arlettaz, 2012; Hanski, Hansson, & Henttonen, 1991). In turn, predators are frequently limited by prey availability and increases in abundance of small mammals, at least locally, can support increased predator numbers albeit temporally lagged behind abundances of their prey (Hanski et al., 1991). Artificially increasing resources, including structural habitat (e.g. nest boxes), can provide a unique opportunity to examine intrinsic increases in abundances of the targeted population but also potential responses of the broader vertebrate community, including predators (Aitken & Martin, 2012; Cockle & Martin, 2015; Dunn, 1977). Yet, studies of wild small mammal (<1 kg) population response to increases in structural habitat and the potential responses of predators and competitors remains relatively scarce (Newton, 1994).

Predators can reduce abundances of their prey directly through predation (lethal) and indirectly by inducing non-lethal behavioral constraints to foraging, resting, and reproduction (Preisser, Bolnick, & Benard, 2005). Prey can exhibit differential responses to predator foraging mode, including active avoidance of locations where active seeking predators (e.g. weasels, *Mustela* spp.; (King & Powell, 2007) have visited or relying on indirect cues, such as overhead cover and light intensity to select areas with high overhead cover to reduce risk while foraging from sedentary ambush predators such as most forest owls (Jaksić & Carothers, 1985; Jędrzejewski & Jędrzejewska, 1990; Jędrzejewski, Rychlik, & Jędrzejewska, 1993; Kotler, Brown, & Hasson,

1991). Prey vulnerability to predators exhibiting different foraging modes may thus vary depending on where encounters occur, whether at prey resting or foraging sites.

The timing and extent of biological phenomena and the statistical models used to interpret can be sensitive to the period in which observations are made (Steenweg, Hebblewhite, Whittington, Lukacs, & McKelvey, 2018). Continuous monitoring, such as remote camera or video devices, enables varying the temporal grain of observation (e.g., time-bin width of 1-hour vs. 1-day), providing insights into statistical sensitivity but also potentially to observed biological phenomenon. The decision to bin continuous data to a coarser temporal grain is often arbitrary or based on properties of statistical models rather than biological phenomena (Sollmann, 2018).

In 2015, Linnell et al. (2018) initiated a study examining the response of arboreal rodents (red tree vole, *Arborimus longicaudus* ; Humboldt flying squirrel, *Glaucomys oregonensis* ; Douglas' squirrel, *Tamiasciurus douglasii*) to an increase in nest substrates in young forests (<80 years old), a resource hypothesized to be limiting there as compared to old forests ([?]80 years old). They observed a 5.8-fold increase (95% confidence interval(*CI*) : 2.9, 9.2) in plot-level occupancy of the main target population (red tree voles, henceforth: tree voles), a small arboreal rodent that builds nests and forages exclusively in the live-tree canopy, and that was not likely to be limited by food as their diet primarily consists of conifer needles, which are readily available in conifer forests. Tree voles are important prey for predators that exhibit different foraging modes, including forest owls (*Strix occidentalis caurina*, *Strix varia*, *Aegolius acadicus*) and weasels, and have low annual survival of 0.15 (95% *CI* : 0.06, 0.31), due primarily to high predation rates (Forsman, Anthony, & Zabel, 2004; Forsman & Maser, 1970; Swingle, Forsman, & Anthony, 2010; Wiens, Anthony, & Forsman, 2014) .

Herein we describe predation and non-lethal avoidance of the suite of nest predators and competitors of arboreal rodents, in particular tree voles, during monitoring of artificial nest substrates (henceforth, nest platforms) for three years. We describe the indirect and direct short (i.e. ~1 week) and long term effects (12-weeks) of four taxa that are documented predators of tree voles (weasels, owls) or that may exhibit competition but represent low predation risk (flying squirrels, probing or digging birds) on patterns of nest occupancy by tree voles as observed by remote cameras placed directly above nest platforms (Graham & Mires, 2005; Swingle et al., 2010). We predicted that weasels and forest owls would have an immediate lethal effects (mortality) and cause longer term non-lethal avoidance of nest platforms. Interactions between Humboldt flying squirrels (henceforth, flying squirrels) and tree voles, as estimated from nest platform occupancy, are likely to be more subtle involving weak correlations although have the potential to influence nest occupancy if those interactions occur frequently.

Materials and Methods

Study area

We conducted this study on federal forest lands in the eastern portion of the central Oregon Coast Range (44°30'0"N 123°30'0"W; Fig. 1). Vegetation consisted primarily of Douglas-fir (*Psuedotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) forests typically growing on steep terrain with numerous and deeply incised drainages. The climate was cool and wet during winter (i.e., wet season; November 1 – March 31) with occasional sub-freezing temperatures and snow, and warm and dry in the summer (i.e., dry season; April 1 – October 31). Forest age was highly correlated with management history, fire, and land ownership. Old forests (>80 years old) were located primarily on federal lands in relatively small patches in a matrix of young forests (<80 years old) and non-forest (Kennedy & Spies, 2004; Linnell, Davis, Lesmeister, & Swingle, 2017; Wimberly & Ohmann, 2004). Young forests (22 – 44 years old) in this study were typical of the region and were established as plantations, which resulted in stands dominated by Douglas-fir trees with straight-boles, simple branches, few cavities, and highly interconnected live crowns.

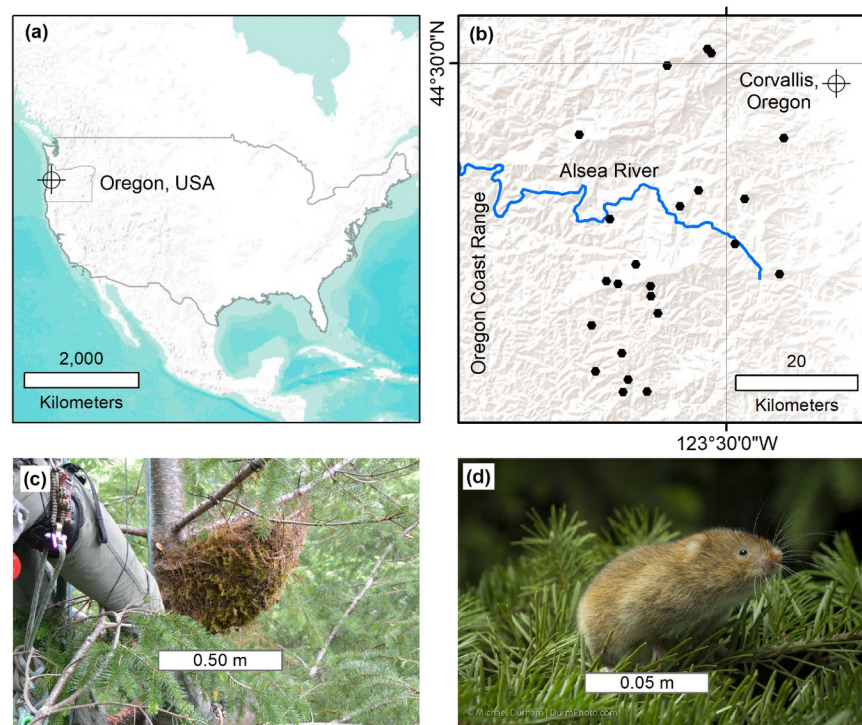


Figure 1 . The scale at which the study was conducted: (a, b) the study area was located on the eastern edge of the central Coast Range in western Oregon, USA, at approximately 44°30'0"N 123°30'0"W, c) we placed 2 nest platforms per ha at 23 randomly located young-forest sites. Nest platforms were designed to provide nesting substrates for our primary target species, the red tree vole (d; photo courtesy of Michael Durham).

Site selection and monitoring of nest platforms

See Linnell et al. (2018) for detailed description of sites used in this study. Briefly, we added nest platforms to 23 randomly selected young forest sites (17 in 2015, six in 2016) that were located adjacent to old forests that contained sign of tree vole presence. At each site, we randomly selected two plots per hectare and constructed 1 nest platform in the tree at plot center within the live canopy (live limbs vertically above and below). To construct a nest platform, we stretched a length of hexagonal wire mesh (2.54 cm openings) between two or three branches to form an open basket and placed ~8 liters of conifer branch tips and moss within the basket.

We used two sources of data: annual nest platform inspections ($n = 1640$) that occurred each summer 2016 – 2018, and photographic data from nest platforms monitored with a remote camera ($n = 168$) June 2015 – October 2018. Each nest platform was inspected annually for diagnostic sign of nesting activity by arboreal rodents, including discarded resin ducts, fecal pellets, and conifer branch tips for tree voles and moss formed into a distinctive nest chamber for flying squirrels (Lesmeister & Swingle, 2017).

At nest platforms with remote cameras we used devices with infra-red LED flash with a 0.2 second trigger speed (Reconyx Hyperfire, Holmen, Wisconsin or Bushnell Aggressor, Overland Park, MI). We deployed remote cameras at a random selection of ~10% (2015) or ~20% (2016) of nest platforms ($n = 96$). To ensure we had a sufficient sample of monitored tree vole nests, we placed cameras at an additional 72 nest platforms containing a tree vole nest identified during an annual inspection in 2016. Remote cameras were mounted 0.6 – 1.0 m above the platforms and faced down such that the entire nest platform and some adjacent branches were within the field of view of the camera sensor and included in each image. We set each camera to record

photos when triggered by motion with a five minute (2015 – 2016) or one-minute (2016 – 2018) quiet period. We tagged each photo with species identity, age class of tree voles (juvenile, adult), and activity of birds (e.g. digging and upturning nest material). We tracked photo tagging and estimated a rate of 2616 photos per hour (95% confidence interval [CI]: 2406, 2826; $n = 175$ sessions). Using this rate, we estimated that tagging the 852,000 photos in our data set required 326 hours (95% CI: 301, 354).

Analysis

Observations of spatial and temporal activity patterns can potentially provide insights into predator-prey relationships as animals perceive their environment through time and space (Hut, Kronfeld-Schor, van der Vinne, & De la Iglesia, 2012). Because species interactions are often complex and difficult to identify we used photographic data to examine temporal overlap at nest platforms among tree voles and four other taxa that were potential predators. We classified these potential nest predators as flying squirrels, owls, weasels, or probing/digging birds. For each nest predator we created detection/non-detection encounter histories by binning data at 1-hour, 1-day, or 1-week time bin-widths, creating logistic regression models at each bin-width that represented predator-prey temporal overlap. We also constructed monthly encounter histories (1-month bin-width) to quantify multi-annual trends of activity at nest platforms.

Predator-prey temporal overlap models

We fit nine models to examine correlations with tree vole detections as the dependent variable (three time-bin widths x three time lags (described below)) and six models using flying squirrels. In each model, tree vole (or flying squirrel) encounter histories (detection (1) or non-detection (0)) comprised the dependent binomially distributed variable and each other species' detections were independent variables. At time lag $t0$ (unlagged), we examined whether nest predator presence was correlated with tree vole presence. Tree voles used nest platforms intensively with a high number of detections per day (Linnell et al., 2018), therefore we interpreted positive correlations as representing potential attraction of the nest predator to the nest while tree voles were present.

To examine hypotheses of lagged effects of predator presence on tree vole presence ($t + 1$, $t + 12$), we used predator detection in the previous time step as the independent variables in our $t + 1$ and $t + 12$ models. For example, a weasel detected on occasion three in a $t0$ encounter history of five occasions (00100) would result in a $t + 1$ of 00010. Negative correlations of $t + 1$ were thus interpreted as immediate and potentially direct outcomes of the nest predator's visit to the tree vole nest platform in the previous time step. To examine a potential longer-term, up to 12-week, lag in tree vole response to predator visit at nest site we developed an independent variable for any previous detection of a predator during the encounter history. For example, a predator detected during time three of a 15 occasion encounter history with a $t0$ of (001000000000000) would result in 000111111111111 for model $t + 12$. Tree vole models included time lags of $t0$, $t + 1$, $t + 12$, and flying squirrel models time lags of $t0$ and $t + 1$.

We made predictions of positive (+), negative (-), or neutral interactions (=) with the number of symbols indicating the predicted strength of correlation. We predicted that weasels and owls would be attracted to nests with tree voles present ($t0$; ++), tree vole detections immediately following a predator detection would be negatively correlated ($t + 1$; -) but those correlations would weaken through time ($t + 12$; -). We hypothesized that flying squirrels would be weakly attracted to tree voles at $t0$ (+) as they potentially use the same nests and that those effects would remain weak through time at $t + 1$ (+) and $t + 12$ (+). We predicted that birds digging would be weakly positively correlated with tree vole detections at $t0$ (+) as they would be targeting insects in decaying organic materials prevalent at tree vole nests but that co-occurrence would be incidental with no effect through time at $t + 1$ (=) and $t + 12$ (=). For flying squirrels as the dependent variable, we predicted moderate negative correlations of owls and weasels as we expected these predators to have stronger correlations with flying squirrels at $t + 1$ (-) and neutral (=) with regards to birds digging.

We used generalized linear mixed models with a logistic link function for our analyses. To account for spatial and temporal dependence of observations, we modeled individual nest platforms and the next coarser bin-

width (e.g. 1-week bin-width for 1-day bin-width encounter histories) as random effects. We represented *a priori* hypotheses as fixed effect independent variables (R package MCMCglmm; (Hadfield, 2010; R Core Team, 2018)). We used uniform and multivariate normal priors for fixed and random effects parameters and used the inverse-Wishart distribution for variance components of priors. We used four Markov chains of 200,000 with a burn-in period of 100,000, and set the thin to 0.02. To assess convergence, we visually evaluated chains and estimated the Gelman-Rubin convergence diagnostic in the coda package in R (Brooks & Gelman, 1998; Gelman et al., 2014; Plummer, Best, Cowles, & Vines, 2006; R Core Team, 2018). We used values of convergence diagnostics for parameters with < 1.1 indicating chain convergence. We reported means and 95% credible intervals (*CrI*) of the posterior distributions, and interpreted log odds coefficients as probability of presence. In addition, we transform some model output to odds ratios for ease of interpretation.

Lethal and non-lethal effects of predators and temporal trends in activity

We summarized direct cause-specific mortalities of tree voles by recording when a dead tree vole was observed in the presence of a predator on the nest platform. We interpreted these events as the strongest causal evidence of direct mortality of tree voles by a specific nest predator. To assess the potential response of nest predators to increases in tree voles in year 1, we assessed trends in seasonal and multi-annual detections of species at monitored nest platforms. We presented trend results as a multi-annual graph of monthly occupancy (proportion of monitored nest platforms occupied in a given month) and interpreted seasonal and annual peaks in detections for each taxa.

To examine non-lethal effects of nest predators, in addition to the previous predator detection analysis of detection/non-detection data, we summarized an index of tree vole activity at nest platforms (count of # detections per week) 12-weeks before and 12-weeks after a predator was detected and compared this among our three nest predators. We excluded zeros (weeks in which no tree vole was detected at a given nest platform) to avoid zero-inflating our count data.

Predators can adjust their temporal activity patterns to coincide with those of their main prey (Forsman, Anthony, Meslow, & Zabel, 2004). To examine whether temporal activity of predators coincided with those of their prey we created two density plots: 1) diel patterns of tree voles, flying squirrels, owls, weasels, and digging birds, and 2) diel patterns depicting high and low likelihood of predation (for details on assignment of low versus high likelihood, see Appendix S1) of tree voles by weasels.

Apparent survival of tree voles

We estimated annual apparent-survival for tree voles using a Cormack-Jolly-Seber model implemented in R package RMark (Laake & Rexstad, 2008; White & Burnham, 1999). During annual nest platform checks we attempted to capture any tree voles that were present and marked tree voles by clipping the tips of their dorsal fur, making a high contrast mark readily identifiable using remote camera photographs. We then resighted those individuals and analyzed 1-day bin-width encounter histories of marked tree voles that began on the date of capture. Capture and handling methods were approved by the U.S. Forest Service Institutional Animal Care and Use permit #2016-009 and Oregon Department of Fish and Wildlife Scientific Taking Permit 041-18.

Because tree voles molt, growing their fur at unknown intervals and we had only one capture occasion per year, we right-censored encounter histories to a survey period such that we minimized the uncertainty that animals were likely to leave the sample due to their mark fading while also retaining most of the data. To estimate the longevity of marks we reviewed sequential photographs of marked female tree voles ($n = 40$) for which we observed their unique marking fading to become indistinguishable from an unmarked vole. We estimated that 20% of marks became indistinguishable at 63-days or fewer although some lasted longer as we estimated marks faded at a median of 88 days and a mean of 83.4 ± 28.7 days ($n = 20$). We used 63-days to estimate apparent survival to minimize underestimates of survival due to mark-loss. To assess sensitivity of our survival models to encounter history length, we present survival estimates using encounter histories of 35-days to 84-days.

As tree voles were only marked in the summer months (June – August), our inferences were limited to June – October. To provide an estimate of annual survival comparable to previous studies (Swingle et al., 2010), however, we assumed that if survival and predation risk was constant year-round, extrapolating our 1-day survival rate to a 1-year period (365 days) would provide a valid comparison. To assess the assumption that predation was consistent year-round in our study, we summarized our qualitative assessment of weasel predation for each month (Fig. S1a). We pooled data across years but provided separate estimates for males and females. To estimate the variance of average annual survival, we temporally rescaled our data using the delta method (Powell, 2007).

Apparent survival can underestimate actual survival compared to known-fate estimates as it is impossible to distinguish emigration from mortality within the model. We presented data on observations of known fates of marked tree voles, including observations of mortality due to predators and emigration when a marked tree vole was observed at a different nest platform than the capture location. In 2017 we applied passive integrated transmitters to tree voles and recaptured tree voles in 2018 to provide further information on apparent survival based on the rate of recapture of these transmitters in live tree voles.

Results

We monitored 168 nest platforms using remote cameras for 670 ± 264 days ($x \pm 1$ standard deviation [SD]); 28 cameras monitored nest platforms for three years, 79 monitored for two years, and 61 for one year of the study. We monitored $34\% \pm 13\%$ of nest platforms at sites ($n = 14$) in which we estimated encounter histories of marked tree voles and cameras were placed at a density of approximately one camera per 1.5 ha at those sites.

Predator-prey temporal overlap models

For models of $t0$ (no lag) with 1-day and 1-week bin-width encounter histories, detections of weasels (Fig. 2a), flying squirrels (Fig. 2b), owls (Fig. 2c), and birds (Fig. 2d) were all positively correlated with tree voles. We observed consistent negative correlations among dependent and independent variables for all models with 1-hour bin-width encounter histories (Fig. 2). Tree vole detections were consistently negatively correlated with weasels in $t + 1$ and $t + 12$ models (Fig. 2a). Tree vole detections were weakly positively correlated with flying squirrels and birds digging one time-lag after these predators were detected ($t + 1$; Fig. 2). Interpreting odds ratios, we observed a nearly ten-fold decrease in odds of detecting a tree vole one time lag after a weasel was detected ($t + 1$), from approximately 2 : 1 at $t0$ (odds ratio = 2.1 (1.2, 3.7; 95% CrI)) to approximately 1 : 5 (odds ratio = 0.19 (0.09, 0.41)) one time-lag after a weasel was detected ($t + 1$; days), and odds of detecting a tree vole remained low 0.16 (0.13, 0.21) when modelling time steps to day 12 ($t + 12$, days).

Flying squirrels were weakly but consistently positively correlated with birds digging (except for hour) across bin-widths and time-lags (Fig. 2g). One-hour bin-width showed extreme negative correlations across models except for the $t0$ model for owls which slightly overlapped 0 (Fig. 2e, f, g).

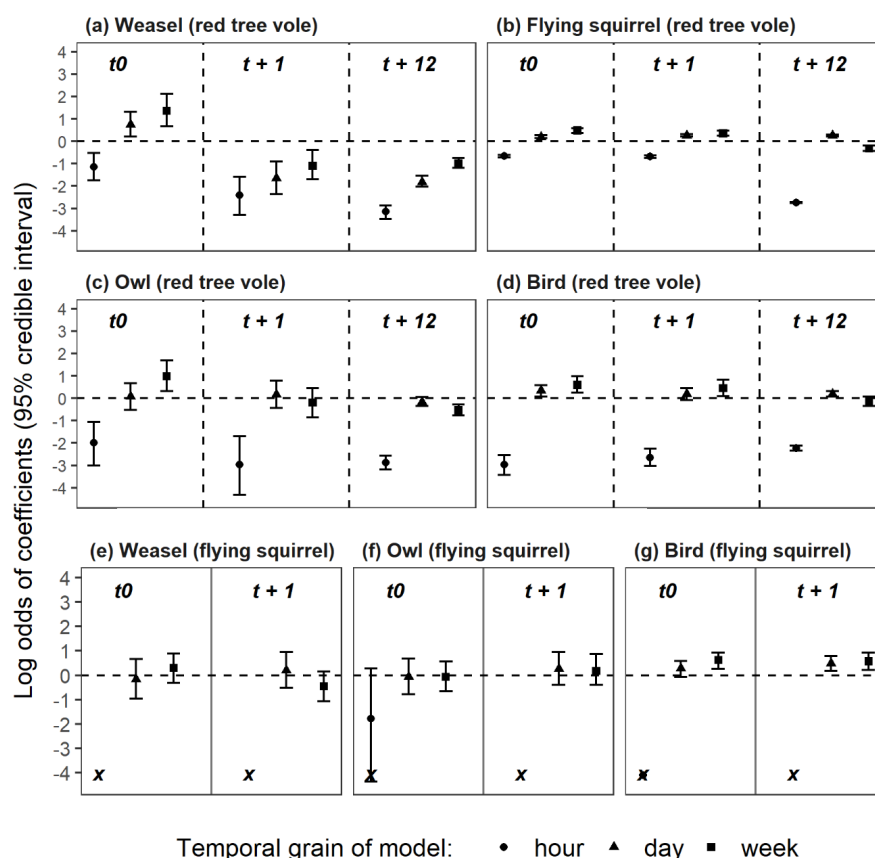


Figure 2. Logistic regression model results of predator-prey temporal overlap at nest platforms of four potential nest predators modeled as independent variables: Weasel, Flying squirrel, Owl, Bird: and two potential prey species as dependent variables (red tree vole, flying squirrel; shown in parentheses). Each model contains predators, two random effects, and is a unique combination of three temporal grains (bin-widths) and three time-lags (red tree voles; panels a, b, c, d) or three bin-widths and two time-lags (flying squirrels; panels e, f, g). The x in flying squirrel models indicates negative values less than four with hour as the bin-width.

Lethal and non-lethal effects of predators and temporal trends in activity

We observed 12 mortalities of tree voles at nest platforms, of which seven were attributed to short-tailed weasels (*M. erminea*), one to a long-tailed weasel (*M. frenata*), two to flying squirrels, one to a small owl (northern saw-whet owl; *Aegolius acadicus*), and one to a Steller's jay (*Cyanocitta stelleri*; Table 1). Of the 12 mortalities, eight were adult tree voles and four were juveniles. In addition, we observed one flying squirrel mortality which we determined was a young animal during an annual climbing inspection, and one case where a barred owl (*Strix varia*) used the nest platform as a perch to consume a brush rabbit (*Sylvilagus bachmanni*).

Table 1. Summary of temporal patterns at nest platforms. Summary of different species or groups detected at 168 nest platforms monitored by remote cameras for up to 177 weeks (670 ± 264 days; $x \pm SD$) at 23 young forest sites in the central Oregon Coast Range, Oregon, USA. Italics indicate species that represent a subset of a taxonomic group. Data represent weekly detections (# of detections per week) during the sampling period in which each nest platform was monitored ($n = 15,510$ monitoring-weeks). Predation rate is the proportion of detections resulting in an observed mortality of a red tree vole attributable to a given nest predator.

Species	Detection rate	# of detections	Detections per week ^a	# sites observed	Predation rate
Tree vole	0.3703	5744	80.1 ± 107.4	23	n/a
Flying squirrel	0.4458	6915	5.5 ± 10.8	23	0.0003
Birds digging	0.0172	267	31.3 ± 44.6	16	0.0037
Owl	0.0063	99	3.3 ± 5.0	19	0.0103
<i>Small owl</i> ^b	0.0036	56	2.7 ± 3.1	16	0.0179
<i>Barred owl</i>	0.0028	43	3.7 ± 6.7	15	0.0000
Weasel	0.0052	82	3.5 ± 3.8	18	0.1000
<i>Short-tailed weasel</i>	0.0029	45	4.0 ± 4.5	14	0.1556
<i>Long-tailed weasel</i>	0.0024	37	2.5 ± 1.7	11	0.0270
Raptor (<i>Accipiter sp.</i>)	0.0020	31	1.8 ± 1.2	13	0.0000

^aData includes only weeks in which a species or group was detected such that no 0 values were included. Mean $\pm$ 1 standard deviation.

^b Northern saw-whet owl ($n = 20$), Western screech owl ($n = 9$), Northern pygmy owl ($n = 9$), Unidentified small owl ($n = 17$)

Tree vole activity (i.e., the number of detections per week at nest platforms with detections) the week following detection of weasels decreased dramatically compared to weeks prior to weasel detection (Fig. 3a). With detections of other potential nest predators, tree vole activity was constant 12 weeks before and after a detection with lower variance for flying squirrels which were detected much more frequently than birds digging or owls (Fig. 3).

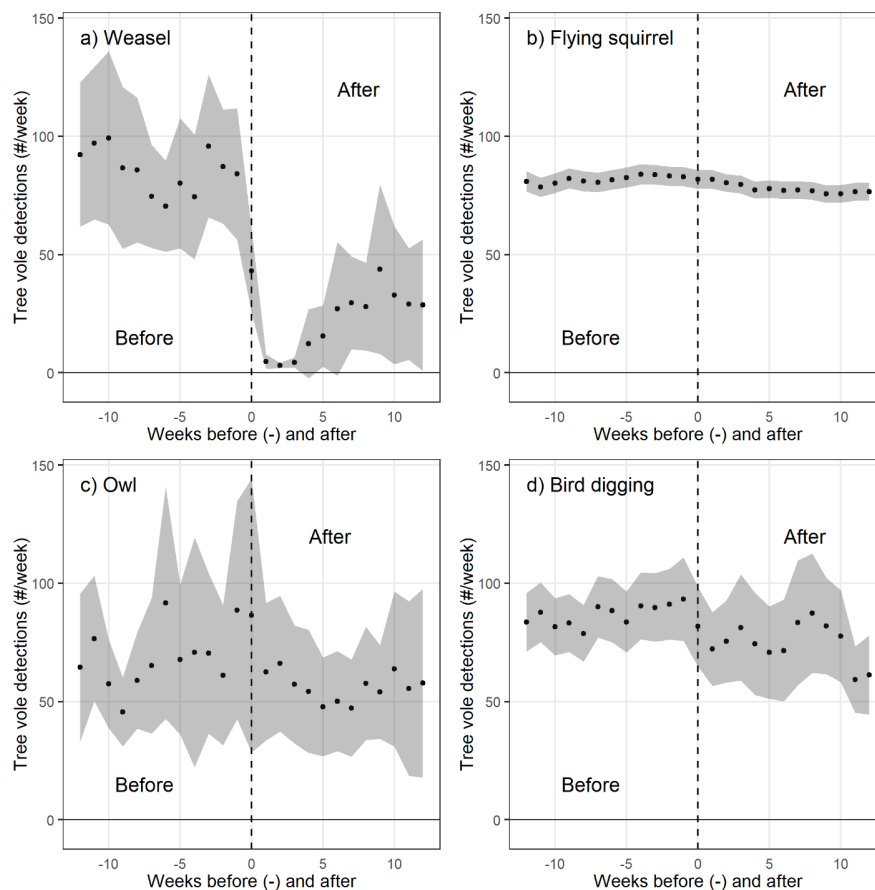


Figure 3. Index of tree vole activity at nest platforms before and after predator detections in young forests of the central Coast Range, Oregon, USA. Each black dot represents mean number of detections of tree voles per week (gray shading is 95% CI) and plots are centered on the detection of a nest predator (vertical dashed line) and includes detections 12 weeks before and after predator detection. We defined bird digging as an event whereby a bird turned over nest material at the nest for >3 minutes.

Patterns of use of nest platforms varied by species. For example, the mean number of detections per week was higher for tree voles and birds digging than flying squirrels, weasels, owls, or raptors. We found a higher weekly detection rate (# of detections per week) for tree voles and flying squirrels compared to other species or groups (Table 1). Tree voles and flying squirrels were detected at all 23 sites, weasels at 18, birds digging at 16, and owls at 19.

Diel activity periods broadly overlapped among tree voles, flying squirrels, owls and weasels with tree voles peaking in the middle of the night and flying squirrels in the nocturnal period before midnight (Fig. 4a). Small owls and weasels showed weak positive trends in activity near dawn with barred owls arrhythmic but these species or groups had much smaller sample sizes and should be cautiously interpreted (Fig. 4a, Table 1). Digging birds were active at nest platforms during the day (Fig. 4a). Although weasels were detected throughout the diel period, they had a higher likelihood of preying upon a tree vole in the early morning (Fig. 4b).

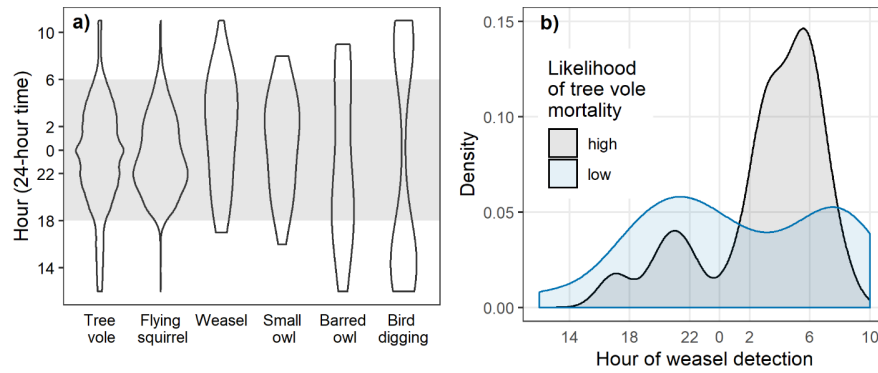


Figure 4. Diel activity patterns of tree voles and nest predators. Density plots (a) showing the hours in which six species or groups were detected (using hour as the bin-width such that only one detection per hour is included) at nest platforms in young trees, central Coast Range, Oregon, USA. Shading indicates average nocturnal period in the study area. Panel b shows weasel density plot split into weasel detections whereby we assigned a high and low likelihood of a tree vole mortality after a weasel was detected.

We observed a relatively strong pattern of birds digging late in wet seasons (February – April) of 2016 and 2017, but weaker trends for other species or groups (Fig. 5). Tree voles were detected on most nest platforms with some reduction in use during the dry season, but presence of juveniles was also highest during this season in 2016 and 2017 (Fig. 5). During most months flying squirrels were detected on most platforms with lower number of platforms with a detection during February of 2016 and 2018 (Fig. 5). Weasels were not detected at nest platforms until summer of 2016 and proportion of platforms with detections remained low until the wet season in late 2017 to early 2018, which was also a peak of birds digging detections (Fig. 5).

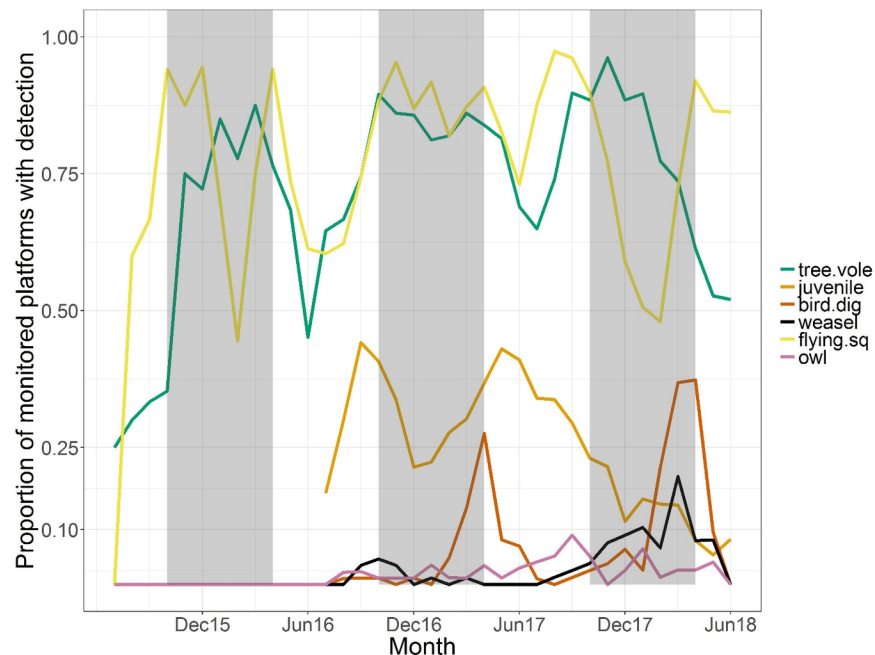


Figure 5 . Monthly patterns of nest platforms use (proportion of nest platforms with detections) by several vertebrate species in young forests in the central Coast Range, Oregon. We separated detections of tree

voles by age class (adult: tree.vole and juvenile). We defined bird.dig as an event whereby a bird turned over nest material at the nest for >3 minutes. Vertical gray boxes indicate the wet season in western Oregon (November 1– April 1). We observed strong seasonal patterns of birds digging and noted an increase in late wet season 2018 coinciding with an increase in weasel (*Mustela erminea* or *M. frenata*) detections. Note: tree vole age classes were only assessed for photos later than June 2016 and we truncated the data to reflect this.

Apparent survival of tree voles

Mean daily apparent survival rate (DSR) for female tree voles was 0.995 ($SE = 0.00176$; $n = 34$) and 0.983 for male tree voles ($SE = 0.00849$; $n = 7$) using a 63-days sampling period. Estimated annual apparent survival was 0.099 (95% $CI : -0.027, 0.226$) for females and 0.005 (95% $CI : -0.023, 0.033$) for males, and although 95% confidence intervals overlapped substantially was overall higher for females. Daily survival was sensitive to the length of the monitoring period with a gradual decline in estimated survival in periods longer than 56-days (Fig 6a). Presence of a weasel at a nest platform decreased daily survival of tree voles throughout the marking period (Fig. 6b). We observed two mortalities of marked tree voles, at 25 and 47 days after capture; both were attributed to a short-tailed weasel. Nine of 34 females (26%) and four of seven (57%) males were observed at two nest platform with mean distances moved of 138.2 ± 68.7 m and 84.5 ± 36.4 m from initial to subsequent nest platform, respectively; none were observed at >2 nest platforms.

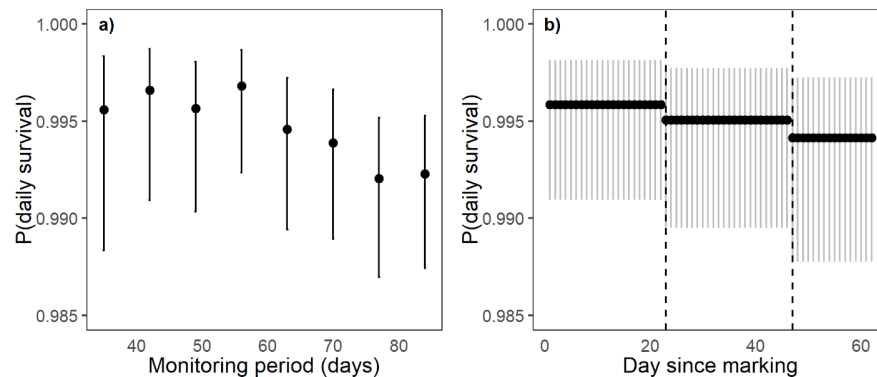


Figure 6. Sensitivity of survival estimates to length of monitoring period (a) and daily probability of nest survival when a weasel was detected (b). The dashed line in b indicates the first day at which a weasel was detected at a platform inhabited by a marked tree vole in young forests of the central Coast Range, Oregon, USA.

Discussion

Our study identified strong direct and indirect effects of active, seeking predators (weasels) on arboreal rodent presence, activity, and survival at nest platforms. Arboreal rodents, primarily tree voles, were killed most frequently by weasels and their activity several weeks post weasel-detection remained depressed. Secondary nest predators, thrushes and jays, probed and dug out nests in apparent pursuit of invertebrates in discarded and decaying nest materials of tree voles, and were positively correlated with flying squirrel presence, perhaps indicating that flying squirrels were attracted to nest disturbances (Forsman & Swingle, 2007).

Predator foraging mode can strongly influence the timing and location where prey are killed. In our study, weasels (i.e., active, seeking predator) were the strongest nest predators whereas owls and flying squirrels exhibited comparatively weak effects at prey nest sites. Owls were detected at similar rates as weasels but may simply be ineffective nest predators, unable to reliably enter or drive tree voles from their nests. Our inferences were limited to nest platforms in young forests and did not extend to foraging tree voles or to the old forests in which strong relationships between tree voles and one of their main predators, the northern spotted owl (*Strix occidentalis caurina*), have been established (Forsman, Anthony, Meslow, et al., 2004).

Nonetheless, our results provide evidence that tree voles face strong pressure from weasels at nests and owls while tree voles are foraging (Forsman, 1974; Swingle et al., 2010).

Although foraging mode may have differed, diel activity patterns of predators broadly overlapped those of tree voles except for diurnally active digging birds. Weasels can be active throughout the day (Linnell, Epps, Forsman, & Zielinski, 2017) but appeared to be more effective at capturing tree voles in the morning hours (Fig. 3b), a pattern similar to least weasels (*M. nivalis nivalis*) which were more active at sunset but captured most *Microtus* field voles in the morning (Sundell, Norrdahl, Korpimäki, & Hanski, 2000). Determining if this reflects a temporal vulnerability of prey will require additional studies, including where and how weasels use cues to locate arboreal prey.

Weasels can cue into rodent scent when hunting, and scent can accumulate at or near small rodent nests and is hypothesized to increase predation risk (Sharpe & Millar, 1990; Ylönen, Sundell, Tiilikainen, Eccard, & Horne, 2003). Female tree voles may be especially at risk of nest-site mortality because they have high fidelity (typically only one nest used per month) to nests that they invest substantial effort into building, resulting in extensive structures (0.06 m³) (Swingle 2005; Sharpe and Millar 1990). Large, old tree vole nests typically contain multiple tunnels and chambers within layers of soil, providing shelter and escape routes from predators (Maser, 1966). The relative tradeoffs of long-term habitation with predation risk from predators cuing into accumulated scent remains unknown but the higher visitation rates by weasels after year three in our study indicates a response of these predators to prolonged tree vole occupancy of nests. Whether this was due to a functional response to environmental cues such as scent or to numerical response of the predators is unknown, but indicates predation risk can limit long-term population growth of tree voles regardless of an increase in resource availability (i.e., new nests).

Homogeneity of nest platform placement could have provided a visual cue to avian nest predators (Santisteban, Sieving, & Avery, 2002) although vertical placement within the live tree canopy was broadly representative of natural nest substrates found in young forests (Linnell et al., 2018; Swingle, 2005). In contrast, older forests have much higher heterogeneity in tree height and natural substrates for tree vole nests vary in type (Lesmeister & Swingle, 2017), location within the canopy, and may be more numerous (Swingle, 2005). Moreover, higher nests in a more heterogenous environment may disperse scent, decoupling cues from terrestrial predators. These characteristics of tree vole nests in old forest—more numerous nest substrates, varied height, size, and substrate—may make those nests more difficult to locate for predators using visual or olfactory cues.

Predators can effectively reduce resource availability for prey through non-lethal avoidance and non-lethal effects can be of higher magnitude than direct consumption, an effect closely tied to prey population densities (Preisser et al., 2005). In the case of weasels in our study, we observed potentially lethal effects followed by reduction of activity (a non-lethal effect) by tree voles for up to several weeks post weasel detection. Most weasel detections occurred towards the end of our study, limiting our inferences with regards to longer-term non-lethal effects of weasel presence on tree vole nest platform occupancy. But given the limited nest substrate availability in young forests, removal of even several productive nest substrates through predation followed by non-lethal avoidance could cause a substantial limit on tree vole populations. Continued monitoring of nest platforms to assess long-term lethal and non-lethal effects could provide a measure of the effect nest predators have on limiting tree vole populations in young forests.

The relative degree of specialization of predators can determine their functional response to numerical increases in their prey (Sundell et al., 2000). Least weasels, similar-sized to short-tailed weasels in our study, show a type II functional response to higher densities of field voles (rapid initial increased predation rate with prey density) in boreal ecosystems with a lower diversity of prey available (Sundell et al., 2000). In temperate forests weasels have access to a higher diversity of prey but specialization depends on sex and age of weasels with adult females typically the most specialized (King & Powell, 2007). Weasels seem unlikely to exhibit a type II functional response to tree voles, particularly because tree voles do not reach sufficiently high densities to elicit such a response and functional response of weasels may be more similar to a generalist predator (type III) than a specialist (type II) with regards to tree voles (Sundell et al. 2000).

We observed a marked difference in model strength and direction at our finest temporal grain size (1-hour bin-width) compared to coarser bin-widths (1-day and 1-week), which could dramatically affect interpretation of the observed species interactions. Weasels clearly exhibited the strongest indirect (reduction in tree vole activity) and direct (predation) effects on tree voles but in models using 1-hour bin-widths these effects were indistinguishable from other species and the direction of the relationship was negative, opposite that of models with coarser bin-widths. Using multiple bin-widths provided additional insights into predator-prey interactions. For example, the lack of positive correlations of weasels and tree voles at 1-hour bin-widths indicates that weasels were unlikely to have visually cued into tree vole activity as they did not overlap directly the exact hours in which tree voles were detected even though our sampling schedule (1 photo per minute) should have been more than adequate to detect such overlap. For the predator-prey interactions that we observed in our study, temporal grain sizes appeared to have strong effects in interpretation of model output particularly at the finest temporal grain.

Our models were likely inadequate at detecting weak non-lethal interactions occurring over longer time periods, such as potential interference competition between flying squirrels and tree voles. Flying squirrels were ubiquitous but weak lethal predators of tree voles at nests killing them at a rate of 0.03% ($n = 2$ observed mortalities) compared to the 10% ($n = 8$ observed mortalities) predation rate of weasels (Table 1). Nonetheless, the observed weak decrease in tree vole activity up to several weeks after detection of a flying squirrel (Fig. 3b) providing circumstantial evidence that flying squirrels exhibit competition with tree voles, albeit weak and potentially lagged and further evidence would be needed to corroborate this observation.

Our technique of artificial marks and visual recaptures using multiple remote cameras at each site appeared to function well for females, but this technique may have been less effective for males which have lower nest fidelity (and conversely, higher local emigration rates; Swingle 2005). Furthermore, our hair clipping technique was effective, but limited the temporal extent of visual recaptures as fur grew back, obscuring our marks. This technique, narrowly applied to monitoring nests of high nest fidelity animals such as female tree voles, may provide accurate estimates of apparent survival as emigration is expected to be relatively low and observations of nest predators can corroborate the fate of marked individuals.

Tree voles responded with strong population growth in 2016 1-year after addition of nest platforms (Linnell et al., 2018). Herein we demonstrated that predator activity increased over a 3-year monitoring period and had strong direct effects on tree voles at nest platforms. The success or failure of nest-box and nest platform to increase prey population size may ultimately depend on longer term predator-prey dynamics inherent to the cover types in which artificial nest substrates are placed (Sonerud, 1985). Our evidence indicates that predators, particularly weasels, can exert strong acute effects on tree vole activity at nests in young forests. Determining whether predators in young forests represent a substantial limit to tree vole populations as compared to old forests per se, will require additional monitoring, ideally of naturally occurring nest substrates or nest platforms (or both) in old forests.

Data availability statement

Data will be made available at the Dryad Digital Repository.

References

- Aitken, K. E. H., & Martin, K. (2012). Experimental test of nest-site limitation in mature mixed forests of central British Columbia, Canada. *The Journal of Wildlife Management* , 76 (3), 557–565. <https://doi.org/doi:10.1002/jwmg.286>
- Berthier, K., Leippert, F., Fumagalli, L., & Arlettaz, R. (2012). Massive nest-box supplementation boosts fecundity, survival and even immigration without altering mating and reproductive behaviour in a rapidly recovered bird population. *PLoS ONE* , 7 (4), e36028. <https://doi.org/10.1371/journal.pone.0036028>
- Brooks, S. P., & Gelman, A. (1998). General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics* , 7 (4), 434–455. <https://doi.org/10.1080/10618600.1998.10474787>

- Cockle, K. L., & Martin, K. (2015). Temporal dynamics of a commensal network of cavity-nesting vertebrates: increased diversity during an insect outbreak. *Ecology* , 96 (4), 1093–1104. <https://doi.org/doi:10.1890/14-1256.1>
- Dunn, E. (1977). Predation by weasels (*Mustela nivalis*) on breeding tits (*Parus* Spp.) in relation to the density of tits and rodents. *Journal of Animal Ecology* , 46 (2), 633–652. <https://doi.org/10.2307/3835>
- Forsman, E. D. (1974). *A preliminary investigation of the spotted owl in Oregon* . <https://doi.org/http://localhost/files/pv63g313j>
- Forsman, E. D., Anthony, R. G., Meslow, E. C., & Zabel, C. J. (2004). Diets and foraging behavior of northern spotted owls in Oregon. *Journal of Raptor Research* , 38 (3), 214–230.
- Forsman, E. D., Anthony, R. G., & Zabel, C. J. (2004). Distribution and abundance of red tree voles in Oregon based on occurrence in pellets of northern spotted owls. *Northwest Science* , 78 (4), 294–302.
- Forsman, E. D., & Maser, C. (1970). Saw-whet owl preys on red tree mice. *The Murrelet* , 51 (1), 10. Retrieved from <http://www.jstor.org/stable/3534259>
- Forsman, E. D., & Swingle, J. K. (2007). Use of arboreal nests of tree voles (*Arborimus* spp.) by amphibians. *Herpetological Conservation and Biology* , 2 , 113–118.
- Gelman, A., Carlin, J. B., Stern, H. S., Dunson, D. B., Vehtari, A., & Rubin, D. B. (2014). *Bayesian data analysis* (Vol. 2). Boca Raton, Florida: CRC press.
- Graham, S. A., & Mires, G. W. (2005). Predation on red tree voles by owls and diurnal raptors. *Northwestern Naturalist* , 86 (1), 3.
- Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software* , 33 (2), 1–22. Retrieved from <http://econpapers.repec.org/RePEc:jss:jstsof:v:033:i02>
- Hanski, I., Hansson, L., & Henttonen, H. (1991). Specialist predators, generalist predators, and the microtine rodent cycle. *Journal of Animal Ecology* , 60 (1), 353–367. <https://doi.org/10.2307/5465>
- Hut, R. A., Kronfeld-Schor, N., van der Vinne, V., & De la Iglesia, H. (2012). In search of a temporal niche: Environmental factors. In A. Kalsbeek, M. Merrow, T. Roenneberg, & R. G. Foster (Eds.), *Progress in Brain Research* (Vol. 199, pp. 281–304). <https://doi.org/https://doi.org/10.1016/B978-0-444-59427-3.00017-4>
- Jaksić, F. M., & Carothers, J. H. (1985). Ecological, morphological, and bioenergetic correlates of hunting mode in hawks and owls. *Ornis Scandinavica* , 16 (3), 165–172. <https://doi.org/10.2307/3676627>
- Jędrzejewski, W., & Jędrzejewska, B. (1990). Effect of a predator's visit on the spatial distribution of bank voles: experiments with weasels. *Canadian Journal of Zoology* , 68 (4), 660–666. <https://doi.org/10.1139/z90-096>
- Jędrzejewski, W., Rychlik, L., & Jędrzejewska, B. (1993). Responses of bank voles to odours of seven species of predators: experimental data and their relevance to natural predator-vole relationships. *Oikos* , 68 (2), 251–257. <https://doi.org/10.2307/3544837>
- Kennedy, R. S. H., & Spies, T. A. (2004). Forest cover changes in the Oregon Coast Range from 1939 to 1993. *Forest Ecology and Management* , 200 (1–3), 129–147. <https://doi.org/http://dx.doi.org/10.1016/j.foreco.2003.12.022>
- King, C. M., & Powell, R. A. (2007). *The natural history of weasels and stoats: ecology, behavior, and management* . Oxford University Press.
- Kotler, B. P., Brown, J. S., & Hasson, O. (1991). Factors affecting gerbil foraging behavior and rates of owl predation. *Ecology* , 72 (6), 2249–2260. <https://doi.org/doi:10.2307/1941575>

Laake, J., & Rexstad, E. (2008). RMark—an alternative approach to building linear models in MARK, (Appendix C). In E. Cooch & G. C. White (Eds.), *Program MARK: A Gentle Introduction* (pp. C1–C111). < [www.phidot.org/software/mark/docs/ book/](http://www.phidot.org/software/mark/docs/book/) >.

Lesmeister, D. B., & Swingle, J. K. (2017). *Field guide to red tree vole nests*. Portland, OR: Pacific Northwest Research Station.

Linnell, M. A., Davis, R. J., Lesmeister, D. B., & Swingle, J. K. (2017). Conservation and relative habitat suitability for an arboreal mammal associated with old forest. *Forest Ecology and Management*, 402, 1–11. <https://doi.org/https://doi.org/10.1016/j.foreco.2017.07.004>

Linnell, M. A., Epps, C. W., Forsman, E. D., & Zielinski, W. J. (2017). Survival and predation of weasels (*Mustela erminea*, *Mustela frenata*) in North America. *Northwest Science*, 91 (1), 15–26. <https://doi.org/10.3955/046.091.0104>

Linnell, M. A., Lesmeister, D. B., Bailey, J. D., Forsman, E. D., & Swingle, J. K. (2018). Response of arboreal rodents to increased availability of nest substrates in young forests. *Journal of Mammalogy*, 99 (5), 1174–1182. <https://doi.org/10.1093/jmammal/gyy111>

Maser, C. (1966). Life histories and ecology of *Phenacomys albipes*, *Phenacomys longicaudus*, *Phenacomys silvicola*. In *MSc Thesis, Oregon State University*. Corvallis, United States: MSc Thesis, Oregon State Univ.

Newton, I. (1994). Experiments on the limitation of bird breeding densities: a review. *Ibis*, 136 (4), 397–411.

Plummer, M., Best, N., Cowles, K., & Vines, K. (2006). CODA: convergence diagnosis and output analysis for MCMC. *R News*, 6, 7–11.

Powell, L. A. (2007). Approximating variance of demographic parameters using the delta method: a reference for avian biologists. *The Condor*, 109 (4), 949–954. [https://doi.org/10.1650/0010-5422\(2007\)109\[949:avodpu\]2.0.co;2](https://doi.org/10.1650/0010-5422(2007)109[949:avodpu]2.0.co;2)

Preisser, E. L., Bolnick, D. I., & Benard, M. F. (2005). Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology*, 86 (2), 501–509. <https://doi.org/10.1890/04-0719>

R Core Team. (2018). *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Santisteban, L., Sieving, K. E., & Avery, M. L. (2002). Use of sensory cues by fish crows *Corvus ossifragus* preying on artificial bird nests. *Journal of Avian Biology*, 33 (3), 245–252. <https://doi.org/10.1034/j.1600-048X.2002.330306.x>

Sharpe, S. T., & Millar, J. S. (1990). Relocation of nest sites by female deer mice, *Peromyscus maniculatus borealis*. *Canadian Journal of Zoology*, 68 (11), 2364–2367. <https://doi.org/10.1139/z90-328>

Sollmann, R. (2018). A gentle introduction to camera-trap data analysis. *African Journal of Ecology*, 56 (4), 740–749. <https://doi.org/10.1111/aje.12557>

Sonerud, G. A. (1985). Nest hole shift in Tengmalm's owl *Aegolius funereus* as defence against nest predation involving long-term memory in the predator. *Journal of Animal Ecology*, 54 (1), 179–192. <https://doi.org/10.2307/4629>

Steenweg, R., Hebblewhite, M., Whittington, J., Lukacs, P., & McKelvey, K. (2018). Sampling scales define occupancy and underlying occupancy–abundance relationships in animals. *Ecology*, 99 (1), 172–183. <https://doi.org/10.1002/ecy.2054>

Sundell, J., Norrdahl, K., Korpimäki, E., & Hanski, I. (2000). Functional response of the least weasel, *Mustela nivalis nivalis*. *Oikos*, 90 (3), 501–508. <https://doi.org/10.1034/j.1600-0706.2000.900308.x>

- Swingle, J. K. (2005). Daily activity patterns, survival, and movements of red tree voles (*Arborimus longicaudus*) in western Oregon. In *MSc Thesis, Oregon State University*. Corvallis, United States: MSc Thesis, Oregon State Univ.
- Swingle, J. K., Forsman, E. D., & Anthony, R. G. (2010). Survival, mortality, and predators of the red tree vole (*Arborimus longicaudus*). *Northwest Science*, 84, 255–265.
- White, G. C., & Burnham, K. P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study*, 46, S120–S139.
- Wiens, J. D., Anthony, R. G., & Forsman, E. D. (2014). Competitive interactions and resource partitioning between northern spotted owls and barred owls in western Oregon. *Wildlife Monographs*, 185 (1), 1–50. <https://doi.org/10.1002/wmon.1009>
- Wimberly, M. C., & Ohmann, J. L. (2004). A multi-scale assessment of human and environmental constraints on forest land cover change on the Oregon (USA) Coast Range. *Landscape Ecology*, 19 (6), 631–646. <https://doi.org/10.1023/B:LAND.0000042904.42355.f3>
- Ylönen, H., Sundell, J., Tiilikainen, R., Eccard, J. A., & Horne, T. (2003). Weasels' (*Mustela nivalis nivalis*) preference for olfactory cues of the vole (*Clethrionomys glareolus*). *Ecology*, 84 (6), 1447–1452. [https://doi.org/10.1890/0012-9658\(2003\)084\[1447:WMNNPF\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[1447:WMNNPF]2.0.CO;2)