



Response of arboreal rodents to increased availability of nest substrates in young forests

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Many forest-dependent animals require complex branch and bole structural features as substrates for nesting, and these features may take decades or centuries to develop. In young forests, lack of suitable nest substrates may limit occurrence and abundance of arboreal rodents. To test this hypothesis, we measured the response of arboreal rodents to installation of 429 artificial nest platforms at 17 young forest sites in the Coast Range of Oregon, United States. We compared the percentage of 100-m² plots at sites containing nests before and after installation of nest platforms, and examined 5 a priori hypotheses of spatial patterns of use using logistic regression. One year after installation, we observed a 5.8-fold increase (95% CI = 2.4–9.2) in plots containing nests of red tree voles (*Arborimus longicaudus*) and a 2.9-fold increase (95% CI = 1.3–4.4) of tree squirrels (*Glaucomys oregonensis*, *Tamiasciurus douglasii*). In addition, we captured 37 adult red tree voles (30 females, 7 males). Presence of conspecific nests < 75 m away increased the odds of use by red tree voles but not by tree squirrels. Our results support the hypothesis that lack of suitable nest substrates limits occurrence of red tree voles in young forests, but results were ambiguous for tree squirrels. Increasing the availability of nest substrates via installation of nest platforms may increase abundance of red tree voles in young forests. However, we do not know if this will allow red tree voles to persist in young forests that are subjected to repeated commercial thinning and clear-cut harvesting.

Key words: *Arborimus longicaudus*, conspecific attraction, Douglas' squirrel, Humboldt's flying squirrel, nest box, nest platform, red tree vole, tree structural complexity

At the landscape scale, configuration and composition of forests can influence the movements and occurrence of forest-dependent vertebrates, especially species with low dispersal capabilities (Prugh et al. 2008; Forsman et al. 2016; Linnell et al. 2017). At very fine scales, complex branch and bole structural features of trees, such as cavities, forked boles, and broken tops, provide substrates for nest building for many arboreal rodents and birds. The scarcity of suitable arboreal nest substrates can limit species occurrence, survival, and reproductive success (Berthier et al. 2012). Structural complexity in trees, including development of multiple complex tree structural features, often takes decades or centuries to develop and is more common in large, old trees compared to young trees (Banks et al. 2013; Lindenmayer et al. 2017a). Many contemporary

forests lack complex tree structural features because old trees are missing from these forests due to timber harvest and limited recruitment (Franklin et al. 2002; Lindenmayer et al. 2017a).

Ecological treatments to mitigate loss of forests containing abundant complex structural features are often only possible at fine spatial and temporal scales because broader restoration or conservation of forested landscapes depends on social and economic decisions requiring decades or centuries to implement (Lindenmayer et al. 2017b). For example, nest boxes are a fine-scale treatment used to mitigate loss of natural cavities but may be effective for less than a decade (Lindenmayer et al. 2009). Nonetheless, nest boxes have been used to experimentally determine if lack of nesting substrates limits occurrence, density, or population dynamics of cavity-obligate species (Newton

1994; Juškaitis 2006; Berthier et al. 2012; Lindenmayer et al. 2017b). Use of nest boxes by target species depends on whether the design meets attributes provided by natural cavities, including entrance size, physical dimensions, microclimatic temperature mediation, and placement within the landscape (Beyer and Goldingay 2006; Le Roux et al. 2016).

Arboreal rodents that forage and nest exclusively in trees may be particularly sensitive to scarcity of suitable substrates for nesting because typically they have low vagility, thus are dependent on local availability of arboreal nest substrates (Jackson 2000; Swingle 2005; Clavel et al. 2011). The red tree vole (*Arborimus longicaudus*; hereafter, tree vole) is an arboreal rodent endemic to mesic coniferous forests in western Oregon and northwestern California. Tree voles are solitary, occur at low densities, have limited dispersal capabilities, and nest in the forest canopy feeding exclusively on needles and twigs of conifers (Howell 1926; Maser 1966; Forsman et al. 2009; Swingle and Forsman 2009). Tree voles use a variety of arboreal substrates for nesting including abandoned nests of other arboreal species and are closely associated with old forests (> 80 years old) where complex structural features of trees are most abundant (Spies and Franklin 1991; Swingle 2005; Forsman et al. 2016). Occurrence of tree voles in young forests (20–80 years old) appears to be strongly influenced by landscape context, especially proximity to old forests (Linnell et al. 2017), and local availability of arboreal nest substrates to support the establishment of spatially aggregated populations (Howell 1926; Swingle 2005).

Compared to tree voles, Humboldt's flying squirrels (*Glaucomys oregonensis*; hereafter, flying squirrels) and Douglas' squirrels (*Tamiasciurus douglasii*) tend to be more general in their arboreal habits and are more widely distributed in forests of the Pacific Northwest (Steele 1999; Arbogast et al. 2017). These tree squirrels use multiple nests, breed once per year, are highly vagile, can disperse up to several kilometers, and forage and nest both in trees and on the ground (Maser et al. 1985; Carey et al. 1997; Ritchie et al. 2009). Flying squirrels are associated with characteristics of old forests, including availability of trees containing cavities used for nesting. The lack of food resources and cavities for nesting has been hypothesized to limit densities of flying squirrels and Douglas' squirrels, especially in young forests (Carey 1995; Ransome and Sullivan 2004).

We conducted a before-and-after treatment experiment to examine spatial and temporal response by arboreal rodents to the installation of artificial nest substrates (henceforth, nest platforms) in young forests. At the site level, we predicted that addition of nest platforms in trees would increase occurrence and abundance of arboreal rodents, particularly tree voles. Second, we predicted that use of nest platforms would be higher near edges adjacent to old forests because old forests would be the primary source of immigrating arboreal rodents that would use nest platforms. Third, we predicted that presence of conspecifics nearby would increase nest platform occupancy due to conspecific attraction, social cues, or limited dispersal capabilities (Swingle 2005; Fisher et al. 2009). Finally, we predicted

that due to higher mobility, tree squirrels would arrive at nest platforms first, but that tree voles would use nest platforms for longer durations because of their high nest fidelity (Forsman et al. 2009; Swingle and Forsman 2009).

MATERIALS AND METHODS

Study area.—The study was conducted on federal lands managed by the U.S. Bureau of Land Management and U.S. Forest Service in the central Coast Range of Oregon (44°20'N, 123°35'W; Fig. 1). The study area was within the southern portion of the distinct population segment where the tree vole is a candidate for listing under the U.S. Endangered Species Act (USDI 2011). Vegetation in the study area consisted primarily of forests of Douglas-fir (*Psuedotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) growing on steep terrain with numerous deeply incised stream drainages. The climate was cool and wet in winter, and warm and dry in summer (Franklin and Dyrness 1973). Within the distinct population segment, timber harvesting and fire during the 20th century had reduced old forest extent by > 80%, resulting in the landscape being comprised of small patches of old forest in a matrix of young forest and nonforest (Kennedy and Spies 2004; Wimberly and Ohmann 2004; Linnell et al. 2017). Most forest loss occurred in the northern portion of the distinct population segment of tree voles. Young even-aged forests, which dominated much of the landscape, were managed at high tree densities during the first 30–40 years of regeneration. This produced trees with straight boles, simple branches, few cavities, and multiple interconnected live limbs between adjacent trees.

Site selection.—We randomly selected young forest sites (20–80 years old) that 1) originated from plantings of native conifers (primarily Douglas-fir) on old clear-cuts, 2) had not been commercially thinned, and 3) were located adjacent to old forests > 20 ha in extent. Young forest sites that met our criteria were identified in ArcGIS (Environmental Systems Research Institute, Redlands, California) using a combination of light detection and ranging (lidar) data and stand management data from the Forest Service and Bureau of Land Management (Linnell et al. 2017).

Nest platform installation and nest surveys.—Prior to nest platform installation at each site, we assumed tree voles were present in the area if we found a tree vole nest within 200 m of the site during a 2-h time-constrained search. Sites in which we did not find tree vole nests during the time-constrained nest search ($n = 1$) were excluded from our sample. We used Geospatial Modeling Environment (Beyer 2012) to randomly generate 2 spatial points per hectare within each young forest site. To ensure that points were well distributed, they were spaced ≥ 50 m from the nearest adjacent point. Using handheld GPS units, we navigated to each spatial point and selected the nearest Douglas-fir tree for nest platform installation. These trees became the center of our 5.6-m radius (100 m²) survey plots. While installing nest platforms, we visually searched for arboreal nests in trees within the plot. We climbed trees to examine all nests within the plot and searched for diagnostic

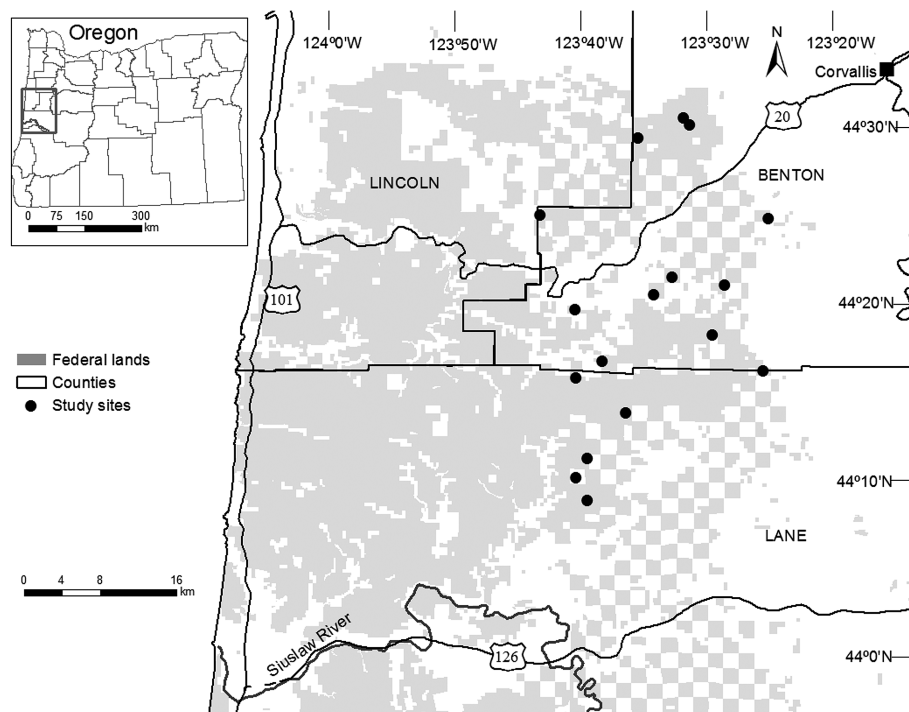


Fig. 1.—Location of 17 young forest sites (22–44 years old) where 429 artificial nest platforms were installed in 2015 in the central Coast Range of Oregon (44°20'N, 123°35'W).

nest materials to identify species that previously had occupied the nest. Tree vole nest material consisting of cuttings from conifer branch tips, resin ducts, fecal pellets, and debarked twigs was easily distinguished from the large sticks, moss, and shredded bark used by Douglas' and flying squirrels as nest material (Maser 1966; Swingle 2005). We used presence or absence of nest materials within plots as a Bernoulli distributed covariate "prior presence" in subsequent modeling. We also estimated the number of complex branch and bole structural features within each plot that potentially could provide nest substrates, including broken tops, secondary leaders, densely spaced branch whorls, dwarf mistletoe brooms (*Arceuthobium* sp.), and forked trunks (Swingle 2005).

In the live crown of the tree at plot center, we installed a nest substrate that consisted of a piece of galvanized mesh poultry netting with 2.54-cm hexagonal openings. The poultry mesh platform was suspended between 2–3 live limbs, formed into a basket, and attached with vinyl cable ties with 1 side of the platform against the trunk of the tree. The openings in the mesh were large enough for tree voles to move through but small enough to retain nest material. We added approximately 8 liters of loosely packed moss and fresh conifer branch tips that were 10–20 cm long on top of the wire mesh. We assumed that added material would provide initial cover for arboreal rodents and substrate for addition of nest materials. The final nest platform measured approximately 50 × 50 × 40 cm (length × width × depth). Heights of trees and nest platforms were measured with a laser hypsometer (Laser Technology, Englewood, Colorado).

Surveys 1 year after installation.—We returned to survey for arboreal rodent nests in trees within our plots 11–12 months after nest platforms were installed and examined nest material

to determine which species used each nest platform. Flying squirrel nests typically consisted of a mound of moss with an interior chamber and were usually distinct from Douglas' squirrel nests, but not all were, so we combined all tree squirrel nests for most analyses but report estimated species use in Table 1. We used *t*-tests to compare nest volume (length × width × depth) between male and female tree voles and between tree voles and tree squirrels.

We attempted to capture tree voles from nests containing fresh resin ducts or branch tips by gently probing nests with a stiff wire until the tree vole left the nest and was captured by the tree climber or by a ground crew (Swingle et al. 2004). We classified tree voles as adult, subadult, or juvenile based on mass and pelage color (Swingle 2005). We determined sex of tree voles based on anogenital distance. Males were classified as scrotal or nonscrotal and females as lactating or nonlactating (Swingle 2005). All animal capture and handling methods were approved by the U.S. Forest Service Institutional Animal Care and Use permit #2016-009, and conformed to guidelines of the American Society of Mammalogists (Sikes et al. 2016).

Models and statistical analysis: site and plot levels.—At the site level, we used paired *t*-tests to compare differences in the mean percentage of plots per site with arboreal rodent sign before and after installation of nest platforms. Using the plot as the unit of replication, we evaluated 5 a priori hypotheses of patterns of nest platform use using 1 model for tree voles and 1 model for tree squirrels. Each model contained 5 covariates representing fixed effects that we predicted would be either negatively associated with presence (distance from old forest, presence of heterospecifics within a 75-m radius) or positively associated with presence (mean vegetation height within 10 m,

Table 1.—Mean percentage of artificial nest platforms used as nests by different mammal species in 17 young forest sites in the central Coast Range of Oregon within 1 year after installation of platforms. The average number of artificial nest platforms per site was 25 ± 6 ($\bar{X} \pm SD$) and age of young stands ranged from 22 to 44 years.

Species	$\bar{X} \pm SD$	Range
Arboreal rodent ^a	46 ± 20	19–85
Red tree vole	30 ± 23	0–83
Occupied red tree vole	12 ± 11	0–44
Tree squirrel ^b	16 ± 14	0–54
Humboldt's flying squirrel	8 ± 9	0–33
Douglas' squirrel	1 ± 2	0–5
Wasps or hornets	12 ± 7	0–26

^a Red tree vole (*Arborimus longicaudus*), Humboldt's flying squirrel (*Glaucomys oregonensis*), and Douglas' squirrel (*Tamiasciurus douglasii*).

^b Humboldt's flying squirrel and Douglas' squirrel.

presence of conspecifics within 75-m radius, and prior presence of natural nests within survey plots). We used 75 m as the focal radius because it represented a relevant spatial and behavioral scale within our sites for our focal species: maximum observed natal dispersal distance for tree voles (75 m, $n = 6$ —Swingle 2005) and average movements between successive daily telemetry locations for flying squirrels (71 m; range = 0 to > 600 m, $n = 39$ —Martin and Anthony 1999). For tree voles, we interpreted presence of conspecific use of nest platforms as likely to represent a population-level process of clustering of multiple individuals to form spatial aggregations. For tree squirrels, clustering of conspecific nests within the 75-m buffer potentially represented an individual using multiple nests within a home range.

Each model was fitted as a generalized linear mixed model with a logistic link function. Response was modeled using a Bernoulli distribution with a binary response (presence or absence of nest material of tree voles or tree squirrels at the nest platform). A priori hypotheses were represented as fixed effects and site as a random effect to account for spatial dependence of nest platforms at the site level (R package MCMCglmm—Hadfield 2010; R Core Team 2018).

To standardize and scale binary covariates prior to running models, we divided the continuous covariate “distance from old forest” by 2 SDs (Gelman 2008). We set noninformative and multivariate normal priors for fixed effects parameters and used the inverse-Wishart distribution for variance components of priors. We ran 4 Markov chains of 200,000 with a burn-in period of 100,000 after setting the thin to 0.02. We assessed convergence by visually evaluating chains and estimating the Gelman–Rubin convergence diagnostic in the coda package in R (Brooks and Gelman 1998; Plummer et al. 2006; Gelman et al. 2014; R Core Team 2018). All convergence diagnostic values for parameters were < 1.1, indicating chain convergence. We interpreted log odds coefficients as probability of presence for confirmatory hypothesis testing and reported means and 95% credible intervals of the posterior distributions.

Remote camera data.—We monitored 10% ($n = 42$) of the nest platforms with passive infrared cameras (Reconyx

Hyperfire, Holmen, Wisconsin) installed 0.6–1.0 m above the tops of nest platforms. When triggered, cameras were set to record photos with a 5-min quiet period between photos. We interpreted estimates from camera data as minimum estimates. We used photographic data to estimate days to first detection at the nest platform after installation, total number of days used, and the number of detections per day for each species. We further estimated the minimum number of young observed over time, scaled to previously reported data on tree vole gestation and juvenile development (Forsman et al. 2009). Juvenile tree voles easily were distinguishable from adults by their small size and gray pelage. We summarized the camera data using box plots with 95% confidence intervals (CIs). We report mean ± 1 SD and range for summary statistics.

RESULTS

In 2015, we installed 429 nest platforms (1 per plot) at 17 young forest sites that were 22–44 years old. We installed an average of 25 ± 6 nest platforms per site (range = 14–36). Average height of nest platform trees and nest platforms was 23 ± 5 m and 16 ± 4 m, respectively. Average distance from nest platforms to the nearest old forest edge was 95 ± 57 m (range = 14–277 m). Within 137 (32%) of the 429 plots a single tree had some type of complex branch or bole structural features, and 38 plots (9%) had ≥ 2 such features (range = 2–3). During nest platform installation, we located 17 tree vole and 24 tree squirrel nests in the plots, which were all old unoccupied nests and represented 5 ± 4 (%) and 6 ± 5 (%), respectively, of the plots per site (Fig. 2).

Approximately 1 year after installation (11–12 months), we examined 414 of 429 nest platforms for use by arboreal rodents. Fifteen nest platforms were not examined thoroughly and were excluded from the analysis because they were occupied by wasps or hornets (Vespididae, $n = 14$) or had poison oak ($n = 1$; *Toxicodendron diversilobum*) encircling the bole. One year after installation, the mean percentage of nest platforms used by tree voles per site was 30% (range = 0–83%), representing a 5.8-fold (95% CI = 2.4–9.2) increase over the site-level percentage of natural nests within plots in 2015 (paired t -test; $t_{16} = 4.7$, $P < 0.01$; Fig. 2). We found squirrel sign in 16% (range = 0–54%) of the nest platforms, which represented a 2.9-fold (95% CI = 1.3–4.4) increase compared to 2015 (paired t -test; $t_{16} = 2.8$, $P = 0.01$).

Occupied tree vole nests and captures.—In 2016, the mean percentage of nest platforms per site occupied by tree voles was 12 ± 11 (%) (range = 0–44%). From the 46 occupied nest platforms, we captured 37 adult tree voles (30 females and 7 males). Most adult females (66%) had young in the nest or were lactating. In contrast, none of the male tree voles had scrotal testes. We also captured 5 subadults (2 females, 3 males) and 6 juveniles. One plot had a natural nest that was occupied by an adult female tree vole adjacent to a nest platform that had been used by a tree vole but was not occupied.

Volume of nests in which we captured adult tree voles was greater for females (48.2 ± 30.5 liters, $n = 30$) than for males

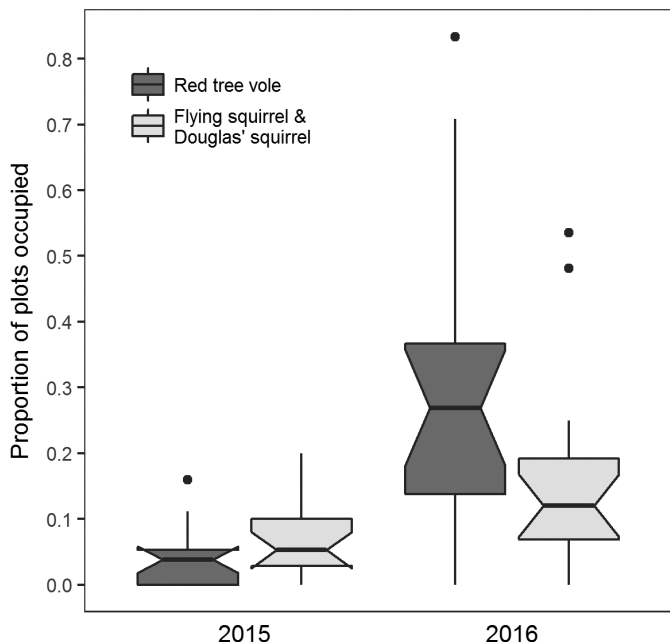


Fig. 2.—Box plots showing the change in site-level use before (2015) and 1 year after (2016) installation of artificial nest platforms for arboreal rodents at 17 young forest sites in the central Coast Range of Oregon (44°20'N, 123°35'W). Each site averaged 25 ± 6 artificial nest platforms. Medians are the horizontal bars, notches indicate 95% CIs of the medians, the boxes represent interquartile ranges, whiskers are 1.5 interquartile ranges beyond the boxes, and dots represent extreme data points > 1.5 interquartile range beyond the boxes.

(18.8 ± 13.1 liters, $n = 7$; 95% CI of difference of means = 13.9–44.8 liters). Most of the nest platforms occupied by female tree voles ($n = 21$) contained a soil-like material from decomposing nest material, indicating that these nests were occupied for long periods of time. Mean volume of nests was greater for tree voles (28.3 ± 28.6 liters, $n = 94$) than for tree squirrels (7.1 ± 8.0 liters, $n = 84$; 95% CI of difference of means = 15.1–27.3 liters).

Logistic regression model results.—Probability of presence of tree voles was higher with conspecific presence or sign at a nearby nest platform or when a natural tree vole nest had been detected within the plot during nest platform installation. We found little evidence that use of nest platforms by tree voles was influenced by distance from old forest, tree height, or heterospecific presence (Squirrel 75 m) at nearby nest platforms as all 95% credible intervals overlapped 0 (Fig. 3).

Probability of presence of tree squirrels was negatively associated with tree height, suggesting that use of nest platforms by tree squirrels was associated with smaller, younger trees. Credible intervals of 3 other covariates minimally overlapped 0 and probability of presence was positively correlated with distance from old forest or conspecific presence, and negatively correlated with if a natural nest of a tree squirrel had been detected during installation of nest platforms (Fig. 3).

Remote camera data.—We monitored 42 nest platforms by use of remote cameras for 340 ± 30 days. We detected 5 species of arboreal or scansorial rodents, including tree voles, flying squirrels, Douglas' squirrels, Townsend's chipmunks (*Tamias*

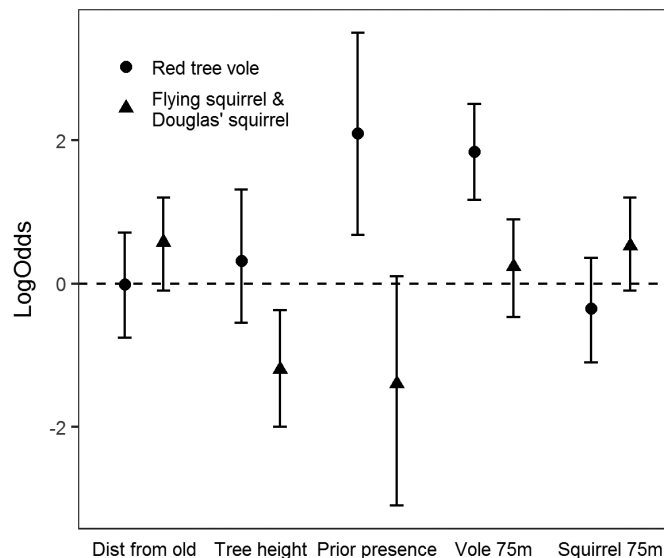


Fig. 3.—Log odds ratios with 95% credible intervals for use of artificial nest platforms by arboreal rodents in 17 young forest sites in the central Coast Range of Oregon (44°20'N, 123°35'W) in 2015–2016. We fitted 1 logistic regression model with all covariates for red tree voles (*Arborimus longicaudus*) and 1 model for tree squirrels (Humboldt's flying squirrel, *Glaucomys oregonensis* and Douglas' squirrel, *Tamiasciurus douglasii*). Covariates on the x-axis were distance from old forest (Dist from old), mean tree height within a 10-m radius, presence of natural tree vole or squirrel nests in the 5.6-m plots prior to installation of nest platforms (Prior presence), and concurrent presence of conspecific or heterospecific nest material located in nest platforms < 75 m (Vole 75 m; Squirrel 75 m).

townsendii), and North American deer mice (*Peromyscus maniculatus*). Flying squirrels were detected at all 42 nest platforms, Douglas' squirrels at 88%, and tree voles at 57%.

Tree voles used nest platforms throughout the year, whereas flying squirrels exhibited seasonal low use in winter. No Douglas' squirrels were detected in January or February (Fig. 4). At 7 nest platforms where we did not find tree vole nest material, photographic data indicated that tree voles were detected an average of 5.4 ± 6.8 days that occurred primarily on nonconsecutive days, indicating tree voles did not settle and added little nest material if any. We located tree squirrel nest material at 3 nest platforms monitored by cameras, indicating that tree squirrels infrequently built discernible nests on nest platforms but were ubiquitous at our study sites.

Of 24 monitored nest platforms where tree voles were detected by cameras, 17 also had tree vole nest material detected by the tree climber. At those 17 nest platforms, the average days to first detection was 66 ± 45 days and mean number of days that tree voles were detected was 120 ± 72 (Fig. 5). We had photographic evidence that tree voles at 5 nest platforms produced at least 1 litter during the 1-year monitoring period. Flying squirrels and Douglas' squirrels were detected on fewer days than tree voles, and flying squirrels were detected on more days than Douglas' squirrels (Fig. 5). On days that they were detected, the average detections per day was 3.7 ± 2.4 for tree voles, 1.3 ± 0.3 for flying squirrels, and 1.3 ± 0.4 for Douglas' squirrels.

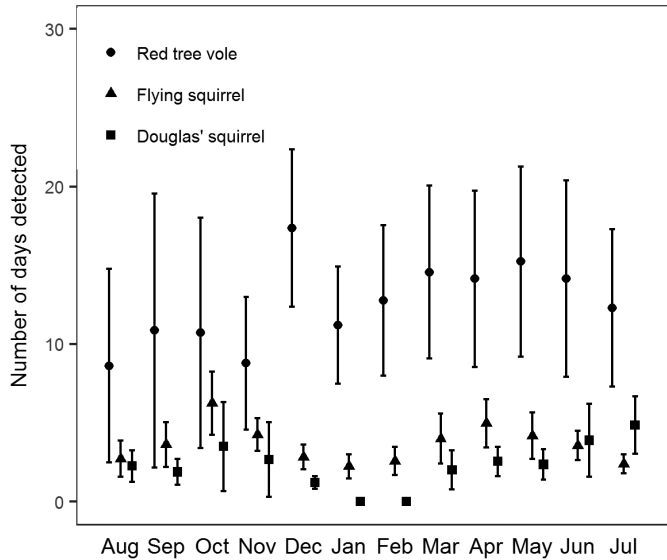


Fig. 4.—Mean and 95% CIs of number of daily detections summarized by month for red tree voles (*Arborimus longicaudus*), Humboldt's flying squirrels (*Glaucomys oregonensis*), and Douglas' squirrels (*Tamiasciurus douglasii*) at 42 artificial nest platforms monitored using remote cameras in the central Coast Range of Oregon (44°20'N, 123°35'W) in 2015–2016.

DISCUSSION

Scarcity of suitable arboreal nest substrates can limit occurrence of vertebrates in areas that otherwise may be suitable at the landscape and local scales (Berthier et al. 2012). After we installed nest platforms, site-level nesting activity of tree voles increased 2.4–9.2 times. This rapid population increase was similar to that of a small scansorial rodent after the addition of nest boxes (Morris et al. 1990; Juškaitis 2005). We observed a weaker response for tree squirrels that generally was consistent with the hypothesis that factors other than availability of suitable substrates for nesting were likely to limit these species in most circumstances (Brady et al. 2000; Ransome and Sullivan 2004; Priol et al. 2014).

The presence of conspecifics can inform settlement by dispersing individuals, particularly at low densities, by providing cues about habitat quality and this can lead to the formation of spatial aggregations (Fisher et al. 2009; Le Galliard et al. 2012; Brommer et al. 2017). Howell (1926) suggested that spatial aggregations of tree voles formed as a result of gradual dispersal over an area. In our study, we suspect that most nest platforms were colonized by dispersing individuals as tree voles were rare or absent at sites prior to installation of nest platforms. We concluded that the positive associations between tree vole occupancy and presence of conspecifics, either prior to installation or in nearby nest platforms after installation, were evidence that settlement was positively influenced by conspecifics (Fig. 3). Moreover, this process may occur over several generations of tree voles whereby short-distance dispersal (i.e., < 75 m) followed by settlement nearby by offspring of initial dispersers forms spatial aggregations in areas of low density, such as in our study. Fisher et al. (2009) observed similar

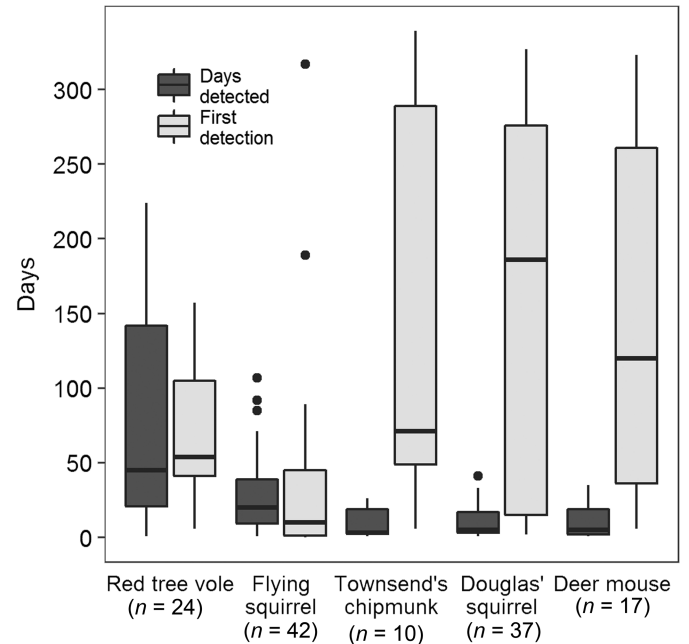


Fig. 5.—Box plots illustrating species-specific occupancy patterns of 42 artificial nest platforms monitored with passive infrared cameras in the central Coast Range of Oregon (44°20'N, 123°35'W) during July 2015–September 2016. Light gray boxes indicate number of days to first detection and dark boxes indicate the number of days each species was detected at nests after the first detection. The data were collected continuously for an average of 340 ± 30 days and the number of nests where a species was detected is in parentheses under species name. Medians are the horizontal bars, the boxes represent interquartile ranges, whiskers are 1.5 interquartile ranges beyond the boxes, and dots represent extreme data points > 1.5 interquartile range beyond the boxes.

results for translocated juvenile water voles (*Arvicola terrestris*) as odds of settlement at release sites with low densities were greater if conspecifics were present. Understanding the process of multigenerational dispersal through young forests, and the role of conspecifics in providing genetic and demographic connectivity between patches of old forest, is a pressing research need within the distinct population segment of tree voles in the Oregon Coast Range, where the average distance between old forest patches (3.4 ± 4.7 km—Linnell et al. 2017) greatly exceeds dispersal distances of tree voles. Direct tests to assess the role of conspecifics in settlement, similar to Fisher et al. (2009), could be achieved through experimental installation of nest platforms and translocating individuals to areas with high and low densities of tree voles.

Some arvicoline voles exhibit skewed sex ratios at low population densities (Myllymäki 1977; Lambin 1994; Aars et al. 1995). We observed a highly skewed adult sex ratio of 4.6 females to 1.0 males at nest platforms. Forsman et al. (2016) reported that the female to male sex ratio of adult tree voles captured by tree climbers was 2.2 to 1.0 ($n = 793$) in young and old forests and 1.0 to 1.1 in a sample collected by loggers in old forests ($n = 109$). Given that both sexes of tree voles require arboreal nests (Swingle 2005), we present 3 alternative,

but not mutually exclusive hypotheses regarding the disparity of adult sex ratios: 1) the population has an even sex ratio but females were detected more frequently in our study because females exhibit strong selection for large nest substrates such as our nest platforms, 2) our observed female-biased sex ratio is a true reflection of the population and this ratio is driven by lower survival of adult and subadult males because they are exposed to higher rates of predation as they disperse or seek out reproductive females (Swingle et al. 2010), or 3) the population is female-biased, but the underlying cause is that females immigrate and settle in areas sooner than males at low densities (Myllymäki 1977; Lambin 1994; Aars et al. 1995). We suggest that the magnitude of female bias we observed likely was driven by female selection of nest platforms but that female-biased immigration and low male survival may have contributed to the general pattern of female-biased sex ratios.

Tree voles are morphologically and ecologically adapted to an arboreal life and appear adept at nest building on a variety of arboreal substrates compared to obligate cavity-nesting species (Maser 1966). For secondary obligate cavity-nesting species, nesting niche is often narrowly defined (Martin et al. 2004) and efficacy of nest boxes depends on the design closely matching natural cavity dimensions of the target species (Goldingay and Stevens 2009). In contrast to obligate cavity-nesting species (Le Roux et al. 2016), tree voles are capable of substantial nest construction and will use preexisting nest material, such as the conifer tips and moss we incorporated into nest platforms, which may provide protection from some predators and adverse weather conditions, potentially increasing survival upon initial occupancy. The ability to build and alter nests with a variety of nest substrates, and the comparatively high fecundity and short-generation times of tree voles compared to cavity-nesting mammals evaluated in other studies, likely contributed to the strong response of tree voles in our study compared to the weak response frequently observed in nest box studies of obligate cavity nesters (Lindenmayer et al. 2017b).

Scarcity of resources or other factors can limit populations year-round or seasonally (Fretwell 1972). Because tree voles reproduce and use arboreal nests throughout the year and rarely nest on the ground (Maser 1966; Thompson and Diller 2002), year-round use of nest platforms was consistent with the hypothesis that suitable nest substrates were a limiting resource. In contrast, tree squirrels were detected with cameras at most nest platforms much of the year but detections were substantially less frequent during winter (Fig. 4). Similarly, other studies found that use of nest boxes by flying squirrels (*G. oregonensis*; *G. sabrinus*; *G. volans*) was higher in the breeding season compared to the nonbreeding season (Brady et al. 2000; Carey 2002). Even though flying squirrels frequently use nest boxes, other researchers have concluded that scarcity of food (Ransome and Sullivan 2004) or ubiquity of natural nest substrates (Brady et al. 2000) likely limit population enhancement and individual fitness dynamics attributed to installation of nest boxes (Priol et al. 2014). In our study, nest platforms apparently provided a seasonal resource for flying squirrels but our data were likely insufficient to evaluate population dynamics

because flying squirrels have shown increased use of nest boxes over multiple years (Carey 2002). Seasonality of resource use may have contributed to the relatively lower use of nest platforms by flying squirrels. For tree voles, suitable nest substrates in young forests are likely a limiting resource throughout the year.

Spatial patterns of resource use and scarcity can vary based on animal movement patterns, and we observed distinct spatial and temporal patterns of use of nest platforms by tree squirrels compared to that of tree voles. The relatively shorter time to first detection and ubiquity of flying squirrels at nest platforms based on photographic data likely was due to greater movement of flying squirrels, whose daily movement distances greatly exceed those of tree voles, who spend most of their time within a few meters of their nests (Swingle 2005). We observed a positive association between tree squirrel occupancy and distance from old forest (Fig. 3). Higher mobility may mean that tree squirrels perceive scarcity differently than tree voles, and require multiple arboreal nests within a home range. If old trees at edges provide sufficient arboreal nest substrates, they may have mitigated scarcity in young forests near edges, whereas further from edges, tree squirrels had fewer options within their home ranges, necessitating use of nest platforms. Although we predicted a negative association between platform use and distance from old forest for tree voles, we found no relationship. Placing nest platforms at distances greater than our average of 95 m from old forest edges would provide an opportunity to examine the potential for landscape-scale connectivity by simultaneously examining limits on dispersal capabilities and lack of nest substrates in young forests.

Nest platforms provide an opportunity to examine additional hypotheses for limitations on arboreal rodents. For example, commercial thinning harvest that removes stand basal area is a common practice that reduces canopy cover and isolates individual trees in temperate coniferous forests within the range of the tree vole (Bailey and Tappeiner 1998). Such change may reduce arboreal resources at fine (nest substrates) and local scales (interconnecting branches between trees) resulting in lower densities of flying squirrels (Manning et al. 2012) and tree voles (Wilson and Forsman 2013; Forsman et al. 2016). Installation of nest platforms to provide abundant nest substrates may allow for examination of alternative hypotheses for limitations on arboreal rodents, such as the elimination of interconnecting branches between trees that occurs during commercial thinning.

Development of complex branch and bole structural features in young forests (Bailey and Tappeiner 1998) can influence the occurrence of arboreal rodents that construct arboreal nests. Tree vole occurrence in young forests (Forsman et al. 2016) provides encouragement that young forests may constitute low-contrast matrix and provide demographic and gene flow between more stable populations in old forests (Linnell et al. 2017). If silvicultural practices can broadly increase recruitment of structurally complex young trees with broken tops, forked trunks, dwarf mistletoe brooms, and densely spaced branch whorls, then young forests may provide the nest substrates that tree voles and other arboreal rodents require (Swingle and

Forsman 2009). Processes that produce structural complexity, however, may simply require time (Spies and Franklin 1991), necessitating retention and recruitment of old, structurally complex trees. Manual installation of surrogates such as nest platforms likely will be limited to small spatial areas of special concern for maintaining and linking populations.

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