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Spatiotemporal dynamics in vital rates of Humboldt's flying squirrels and Townsend's chipmunks in a late-successional forest

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Knowledge of the spatiotemporal variability of abundance and vital rates is essential to the conservation of wildlife populations. In Pacific Northwest forests, previous small mammal research has focused on estimating abundance; few studies have focused on vital rates. We used robust design temporal symmetry models and live-trapping data collected 2011–2016 at nine sites to estimate apparent annual survival, population growth rate, and recruitment of Humboldt's flying squirrels (*Glaucomys oregonensis*) and Townsend's chipmunks (*Neotamias townsendii*) in a late-successional forest of the Cascade Mountains of Oregon, United States. We also estimated the proportional contribution of apparent annual survival and recruitment to population growth rate. Covariates previously associated with abundance were also associated with vital rates for Townsend's chipmunks, but less so for Humboldt's flying squirrels. Apparent annual survival was nearly constant (range = 0.47 to 0.51) among years and sites for Humboldt's flying squirrels but was consistently lower and more variable among years for Townsend's chipmunks (range = 0.13 to 0.31). Recruitment was variable among years for both species. Apparent annual survival generally contributed more than recruitment to the population growth rate of Humboldt's flying squirrels. For Townsend's chipmunks, recruitment consistently contributed more than apparent annual survival to population growth rate. These findings suggest that life history strategies differed for these co-occurring species. This study demonstrates substantial temporal variation in vital rates and some differences in abundance and vital rate habitat associations, suggesting that habitat suitability inferences based on short time series or variation in abundance could be misleading.

Key words: H. J. Andrews Experimental Forest, live trapping, mark-recapture, multispecies, proportional contribution, robust design, spatiotemporal variation, temporal symmetry model, tree squirrel, vital rates

Conservation of wildlife populations can be improved with understanding of spatiotemporal variation of population attributes (abundance or density) and vital rates (survival, population growth, recruitment). Previous research has explored the associations among variable population attributes and spatiotemporal covariates (e.g., Coppeto et al. 2006; Fauteux et al. 2012). However, estimates of abundance, density, or count indices can be poor indicators of habitat associations, especially when detection probability or habitat quality are variable (Van Horne 1983; Todd and Rothermel 2006). Thus, corroboration of abundance associations through the consideration of vital rate associations (Williams et al. 2002; Cushman 2006) and consideration of potentially misleading inference in short-term studies is important, especially in populations that exhibit strong temporal variation in population attributes or vital rates.

Much of the previous small mammal research in the Pacific Northwest, United States has focused on the effects of forest management practices on population attributes, especially for important prey species of northern spotted owls (*Strix occidentalis caurina*) such as northern flying squirrels (*Glaucomys sabrinus*; see studies reviewed in Holloway and Smith 2011), Humboldt's flying squirrels (*G. oregonensis*), and bushy-tailed woodrats (*Neotoma cinerea*; Carey et al. 1992; Carey et al. 1999b). Many of these studies focus on

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abundance, but several have estimated vital rates of flying squirrels. For example, Ransome and Sullivan (2002) estimated survival and recruitment of flying squirrels in managed western hemlock (*Tsuga heterophylla*) forests using Jolly–Seber estimates and enumerative proportional methods, Lehmkuhl et al. (2006) estimated annual survival and recruitment in a dry ponderosa pine (*Pinus ponderosa*) forest east of the Cascades Mountains in the state of Washington using Pradel models, and Smith (2012) estimated recruitment in western hemlock and Sitka spruce (*Picea sitchensis*) forests on two Southeast Alaskan islands using enumerative measures. We know of no studies that focused on the vital rates of Townsend's chipmunks (*Neotamias townsendii*), excepting that of Sullivan et al. (1983) estimating apparent annual survival of chipmunks. This research has been important in understanding the effects of forest management on small mammals (Klenner and Sullivan 2009; Manning et al. 2012), the differences in small mammal abundance between managed and old forests (Ransome and Sullivan 2003; Coppeto et al. 2006; Holloway and Smith 2011; Sullivan et al. 2017), and the potential bottom up effects of variation in small mammal abundance on northern spotted owls (Ward et al. 1998; Wiens et al. 2014; Holm et al. 2016). However, little is known about natural spatial or temporal variation of population attributes or vital rates within late-successional forests.

In this study, we examine population attributes and habitat associations of Humboldt's flying squirrels and Townsend's chipmunks in a late-successional forest of the Cascade Mountains in Oregon. Humboldt's flying squirrels and Townsend's chipmunks occur sympatrically across a broad range of forested habitat throughout western Oregon. Both species are important components of the avian and mammalian preybase (Fryxell et al. 1999; Bull 2000; Forsman et al. 2001; Rosenberg et al. 2003). Humboldt's flying squirrels are larger and heavier than Townsend's chipmunks (Aubry et al. 1991), but both species have broadly similar diets that consist largely of hypogeous fungi (Maser et al. 1978; North et al. 1997; Carey et al. 1999a), lichens, berries, and seeds (Bowers and Dooley, Jr 1993; Hayes et al. 1995). Yet, some studies have presented evidence for niche partitioning of food resources within these general categories (Maser and Maser 1988; Lehmkuhl et al. 2004). For example, Maser et al. (1978) reported that northern flying squirrels and Townsend's chipmunks both had high occurrences of hypogeous fungi in their digestive tracts, but *Gauteria* spp. and *Leucogaster* spp. were more common in the feces of northern flying squirrels than in those of Townsend's chipmunks (Maser et al. 1985; Maser and Maser 1988). High densities of Humboldt's flying squirrels have been associated with structurally rich understories and high volumes of coarse woody debris (Carey et al. 1999a; Smith 2007). Townsend's chipmunks select similar, structurally rich habitat with high volumes of coarse woody debris and shrub cover (Waldien et al. 2006), and are sensitive to ground disturbance (Wilk et al. 2015). Both species' abundances are associated positively with productive food-rich forests (Aubry et al. 1991), negatively with winter severity (Lehmkuhl et al. 2004), and both occur more abundantly in old forests relative to young forests (Rosenberg and Anthony 1993; Holloway and Smith 2011).

Interspecific interactions among small mammals in the Pacific Northwest remain understudied. However, dietary breadth (Maser et al. 1978; Maser and Maser 1988; Lehmkuhl et al. 2004), activity patterns (Carey 1995), hibernation strategies (Levesque and Tattersall 2010; Olson et al. 2017), and dominant associated predators (Maser 1981; Reynolds and Meslow 1984; Forsman et al. 2001, 2004) appear to vary by species. Despite some resource competition hypotheses (Carey 1995; Weigl 2007), few studies have found significant effects of competition (Smith 2012; Smith and Fox 2017). Thus, we expected life history strategies to differ for Humboldt's flying squirrels and Townsend's chipmunks, and that those differences would be reflected in species-specific abundances or vital rate associations.

Here, we estimate the vital rates (apparent annual survival, recruitment rate, and population growth rate) of Humboldt's flying squirrels and Townsend's chipmunks using 6 years of live-trapping data recorded on nine trapping sites at the H. J. Andrews Experimental Forest in the Oregon Cascade Mountains. Spatio-temporal drivers of Humboldt's flying squirrel and Townsend's chipmunk abundances in this study area were previously characterized by Weldy et al. (2019). From 2011 to 2016, fall abundance estimates of both species were spatially and temporally variable. Mean fall abundance of Humboldt's flying squirrels was negatively associated with elevation but positively associated with berry-producing plant cover and minimum winter temperature during the previous winter. Mean fall abundance of Townsend's chipmunks was positively associated with elevation, canopy openness, and minimum winter temperature during the previous winter, and negatively associated with berry-producing plant cover (Weldy et al. 2019).

In this study, we pursued three primary objectives: 1) to develop estimates of apparent annual survival, recruitment rate, and population growth rate; 2) to evaluate the effects of abundance-associated covariates on apparent annual survival and recruitment (Table 1); and 3) to evaluate whether habitat quality inferences based on variability of abundance correspond with those based on vital rates. We hypothesized that previously identified abundance-associated covariates would be associated with the vital rate contributing most to population growth rate. For Humboldt's flying squirrels, we predicted that the vital rate contributing most to population growth rate would be associated with berry-producing plant cover (Smith et al. 2004; Smith 2007; Weldy et al. 2019). For Townsend's chipmunks, we predicted that the vital rate contributing most to population growth rate would be associated with elevation or canopy openness because of the hypothesized correlations between those variables and cone productivity (Carey 1991; Weldy et al. 2019). We also developed species-specific hypotheses about the potential direction of effect in parameter and covariation associations (Table 2). We predicted that capture and recapture probabilities would be temporally variable (year, Julian date, season, trapping day) and would be influenced by trap availability (effort,

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Table 1.—Description of variables considered in models of recapture probability (*c*), capture probability (*p*), apparent survival (*φ*), and recruitment (*f*) for Humboldt's flying squirrels (HFS) and Townsend's chipmunks (TC) using 2011–2016 mark-recapture data recorded in the H. J. Andrews Experimental Forest, near Blue River, Oregon.

Covariate	Description	Range
Elevation	Average site elevation, estimated using lidar data.	683–1,244 m
Canopy	Percentage of canopy openness measured from lidar data as the number of 1 × 1 m pixel with canopy height <10 m in proportion to the number of pixels with height >10 m.	9–38%
Shrub	Mean percentage cover of all woody shrubs between 0.5 m and 1.5 m in height, measured on the ground.	10.3–58.3%
Berry	Mean percentage cover of berry-producing plants, measured on the ground.	12.1–51.2%
Year	A year specific effect for each trapping occasion from 2011 to 2016.	2011–2016
JDate	Julian date; trend from the first to the last day of the project across the 6 years of data collection.	11,269–16,323
Effort	Trap type specific trapping effort (i.e., trap nights), adjusted for stuck and sprung traps.	945–1,499
Season	Within-season linear trend from the first to the last day of the trapping season.	1–36
Trapping	Trapping trend is a linear trend from the first to the last day of trapping session. The trend is the same across all sites and describes a protocol related effect independent of seasonality.	1–12 days
Min. temp.	Minimum daily mean temperature during previous winter.[a]	−13 to −3.9°C
TC captured	Number of TC captures per trapping session.	189–941
TC abundance	TC abundance estimated by Weldy et al. (2019).	25.1–172.8
HFS abundance	HFS abundance estimated by Weldy et al. (2019).	5.7–62.5

[a]Winter was defined as October 1 through April 1.

Table 2.—A priori predictions of variable effects in models of recapture probability (*c*), capture probability (*p*), apparent survival (*φ*), and recruitment (*f*) for Humboldt's flying squirrels (HFS) and Townsend's chipmunks (TC). Habitat covariates were measured once during the summer of 2016 at 18 standardized trap stations per study site in the H. J. Andrews Experimental Forest, near Blue River, Oregon. Plus (+) indicates a positive prediction, minus (−) indicates a negative prediction, and empty box indicates no prediction made. Apostrophes (') indicate covariates where predictions matched observations, and asterisks (*) indicate covariates where predictions did not match observations. See Table 1 for variable descriptions.

	Expected results							
	HFS				TC			
Covariate	*p*	*c*	*φ*	*f*	*p*	*c*	*φ*	*f*
Elevation	−	+'	−*	+'	−	+*	−	+
Canopy	−	−	−	+	+	−	−	+'
Shrub	+	+			+'	+		
Berry			+	+			+	+
Year								
JDate	+	+			+	+		
Effort	+	+			+	+		
Season	−	+			+	+		
Trapping	−	+			−'	+*		
Min. temp.			+	+'			+*	+'
TC captured	−	−						
TC abundance			−	−			−	−
HFS abundance			−	−			/	/

count of captured Townsend's chipmunks), elevation, and habitat features related to predation exposure (canopy openness, shrub cover). We predicted that apparent annual survial and recruitment rate would be influenced by elevation, winter temperatures (minimum winter temperature), density dependence, interspecific interactions, and habitat features related to food availability (berry producing plant cover) and predation exposure (canopy openness). We note that northern flying squirrels in the Pacific Northwest west of the Cascades were recently described as a separate species, the Humboldt's flying squirrel (Arbogast et al. 2017); thus, we assume that previous studies conducted on northern flying squirrels in this region pertain to Humboldt's flying squirrels.

Materials and Methods

Study area and trapping sites.—Our study took place during September–November 2011–2016 in the H. J. Andrews Experimental Forest (hereafter HJA) on the west slope of the Cascade Range, 19.6 km east of Blue River, Oregon, United States (44°N, 112°W; Fig. 1). The HJA is part of the Willamette National Forest and is administered by Oregon State University, Willamette National Forest, and the USDA Forest Service Pacific Northwest Research Station.

We were primarily interested in estimating small mammal vital rates in a late-successional forest. We randomly generated 1,000 10-ha sites within late-successional forests across the HJA using the Geospatial Modelling Environment (Beyer 2012). We then classified each site into three elevation ranges (500–799 m, 800–999 m, 1,000–1,500 m) and three canopy openness classes (0–15%, 15–30%, 30–40%; Table 1). We chose these elevation and canopy openness classes because they resulted in relatively even representation of each class across the HJA. Elevation at the HJA ranges from 410 to 1,630 m and canopy openness within late-successional forests at the HJA rarely exceeds 45% at the scale of our study. We then selected nine sites to fit each category resulting from a cross of the three elevation and three canopy openness classes. The average inter-site distance was 2,963 m (range = 1,078–5,940 m). All sites were in a relatively undisturbed late-successional forest (>400 years old) dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock, and Pacific silver fir (*Abies amabilis*—Franklin et al. 1990; Cissel et al. 1999; Schulze and Lienkaemper 2015). Overstory trees were typically >81 cm in diameter at breast height (Schulze and Lienkaemper 2015). Understory characteristics varied among sites and ranged from open to dense with shrubs. Common understory vegetation consisted of blackberry, raspberry, salmonberry (*Rubus* spp.), common snowberry

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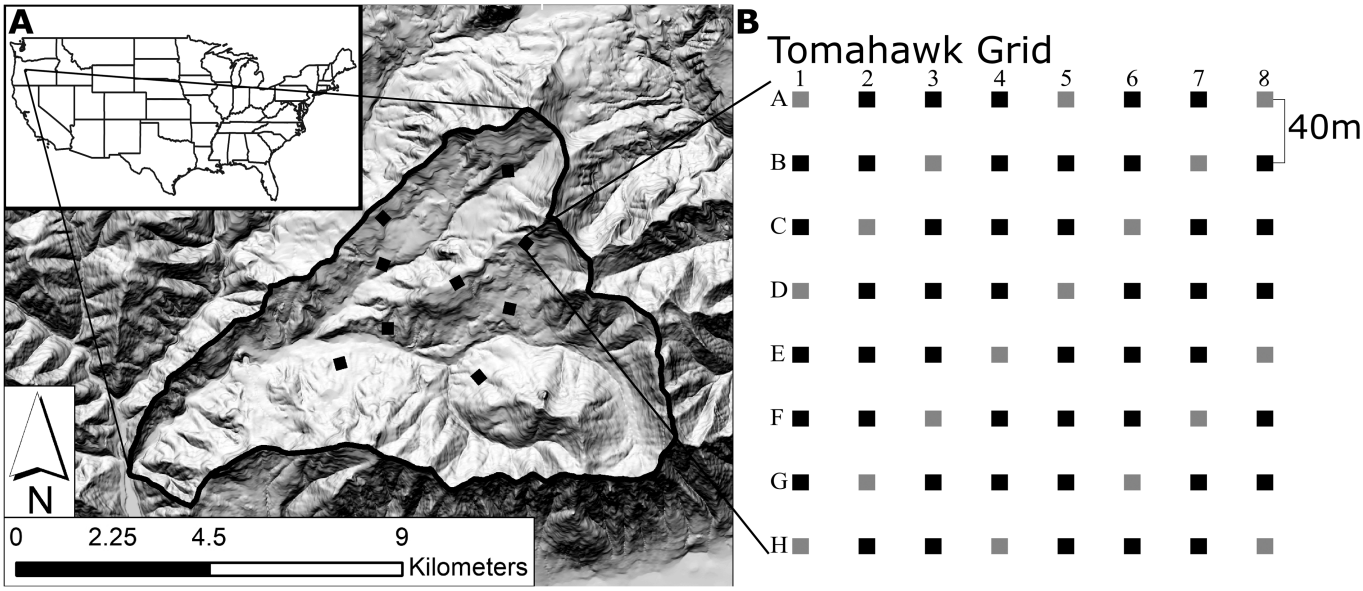

Fig. 1.—(A) Location of 9 late-successional forest plots (dark squares) where we sampled small mammal populations on the H. J. Andrews Experimental Forest, in western Oregon, 2011–2016. (B) Each sampling site consisted of 64 Tomahawk trapping stations arranged in an 8 × 8 array with 40 m inter-trap distances. We sampled vegetation once during the summer of 2016 on 18 (light gray) of the 64 Tomahawk trapping stations in each site.

(*Symphoricarpos mollis*), deer fern (*Blechnum spicant*), huckleberry (*Vaccinium* spp.), Oregon grape (*Mahonia aquifolium*), oxalis (*Oxalis* spp.), salal (*Gaultheria shallon*), sword fern (*Polystichum munitum*), and vine maple (*Acer circinatum*). Annual precipitation primarily occurred during the winter and consisted of rain at low elevations (<1,000 m) and snow at high elevations (>1,000 m—Swanson and Jones 2002). Average daily temperature during trapping was 9.3 ± 0.55°C (± *SE*), and the average daily rainfall was 6.4 ± 0.40 mm (±*SE*—Daly and McKee 2016).

Live trapping.—Our protocols were approved by Oregon State University's IACUC (ACUP #4191 2011–2013; #4590 2014–2016) and were in accordance with the standard animal care principles of the American Society of Mammalogists (Sikes et al. 2016). On each of the nine selected sites, we established 64 trap stations arranged in an 8 × 8 array (7.84 ha) with 40 m (corrected for slope) between traps. We placed 2 Tomahawk Model 201 live traps (Tomahawk Live Trap, WI, United States) at each trap station (128 total Tomahawk traps per site) within 5 m of the trap station center, with 1 trap attached to a suitable tree bole (~1.5 m from the ground) and the other trap placed on the ground (Risch and Brady 1996). We placed both traps on the ground if there was no suitable tree bole within 5 m of the trap station center. We placed traps near habitat features, such as fallen logs, to increase the probability of small mammals encountering traps (Carey et al. 1991). Across the 6 years of the study, this protocol resulted in placement of both traps on the ground at 10.5% (*SE* = 0.7%; 95% *CI* = 8.92% to 12.03%) of the trap stations on average. Trap stations with double ground-trap placements were less variable among years than among sites, but the rank ordered count of stations per site with double ground-trap placement was similar among years with some exceptions (see Supplementary Data SD1). Our highest elevation and highest canopy openness site had the most trap stations with double ground-trap placements during 4 of the 6 years of the study. Sites with higher canopy openness tended to have more trap stations with double ground-trap placements.

We established the site trapping order at the onset of the study and repeated it each following year. We prioritized trapping higher elevation sites, to reduce the impact of decreasing fall temperatures and snow on the survival of captured animals. Each year of the study we live-trapped each site for three consecutive weeks during the fall. A trapping week consisted of four trap nights, with traps checked once per day. We marked each animal with a unique ear tag and recorded individual body weight, reproductive condition, species, and sex. To reduce trapping related mortalities, we placed each trap in a waxed cardboard carton and supplied each with a dry, cotton-stuffed nest box. We pre-baited each trap once, 12 days before the trapping session, with a mixture of peanut butter, molasses, oats, and sunflower seeds (Carey et al. 1991). We then used the same bait mixture during the trapping session.

Development of covariates.—We used two covariates to characterize understory characteristics (Berry, Shrub), and two covariates to characterize forest stand characteristics (Canopy, Elevation; Table 1). Using ArcGIS version 10.3.1 (ESRI 2014) and light detection and ranging (lidar) data collected in 2008, we estimated average site elevation and canopy openness (Spies 2016). Average site-level canopy openness was the number of pixels per site with low height returns (<10 m) in proportion to the number of pixels with high height returns (>10 m). During the summer of 2016, one observer visually estimated

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the percentage of ground covered by shrubs and berry-producing plants, to the nearest 5%, at 18 circular (diameter = 2 m) habitat sampling stations per site. Habitat sampling stations were centered on Tomahawk trapping stations and arranged on each site with three habitat sampling stations along each edge and two habitat sampling stations along each interior row (Fig. 1). Shrub cover was a site-level average percentage of ground covered by woody shrubs <1.5 m tall at each habitat sampling station. Similarly, the percentage cover of berry-producing plants was a site-level average sum of *Rubus* spp., huckleberry (*Vaccinium* spp.), salal (*Gaultheria shallon*), and Oregon grape (*Mahonia aquifolium*) cover at each habitat sampling station. The total percentage cover of berry-producing plants could exceed 100%, due to layering of plants within a habitat sampling station. Weldy et al. (2019) tested for differences among sites in understory characteristics using a Bonferroni multiple test corrected separate means model. In this study, we considered only understory characteristics that were significantly different among sites after Bonferroni correction and important predictors of abundance from that analysis.

We used two covariates to characterize annual change (Min. Temp., Year), three covariates to characterize within season and multiseason trends (Julian date, Season, Trapping), and four covariates to characterize site-specific temporal patterns (Effort, TC [Townsend's chipmunk] Captured, TC Abundance, HFS [Humboldt's flying squirrel] Abundance; Table 1—Weldy et al. 2019). We used minimum daily air temperature measurements recorded by the HJA Central Meteorological Station, which was just east of the project's center at an elevation of 1,020 m (Daly and McKee 2016). For the covariates of interest, we assumed that this location was representative of the study sites. Julian date was included to describe a linear trend within and across years. A linear trend from the first to last day of the fall trapping season was included to describe potential variation affected by seasonal weather changes from late summer through fall. We employed a linear trend from the first to last day of trapping a site to describe potential behavioral changes related to trapping, as well as four spatiotemporal covariates that captured site-specific temporal patterns (Table 1). Variation in site and year-specific trap availability was characterized using effort and number of chipmunk captures. The effort covariate described the site- and year-specific adjusted trapping effort. The number of chipmunk captures covariate described the remaining trap availability for the nocturnal Humboldt's flying squirrel after the diurnal Townsend's chipmunks had first access to newly opened traps (Table 1). Finally, we included site- and year-specific estimates of Humboldt's flying squirrel and Townsend's chipmunk abundance (Weldy et al. 2019) to characterize potential direct density-dependence and competition effects.

Analysis.—We used robust design temporal symmetry models implemented in Program MARK to estimate recapture probability (c), capture probability (p), apparent annual survival (φ), recruitment rate (f), and population growth rate (λ), of the target species during six primary trapping periods on nine sites (Pradel 1996; White and Burnham 1999). Each primary trapping period included 12 daily secondary periods for Humboldt's flying squirrels, but only eight daily secondary periods for Townsend's chipmunks, because chipmunks were released without processing during the third week of live-trapping due to high capture rates. The robust design temporal symmetry models assume population closure during the primary trapping periods and estimate p and c using a Huggins closed population capture–recapture model (Huggins 1989, 1991). Between primary trapping occasions, populations are assumed to be open, and the temporal symmetry model estimates φ and f across these intervals (Pradel 1996). Temporal symmetry models derive realized λ from two linearly related components: φ, which reflected both individual annual survival between the fall primary trapping periods and site fidelity; and f, the per capita number of animals added to the population between primary fall trapping periods, which reflected juvenile survival, adult immigration, juvenile emigration, and the number of births. We chose a model parameterization that included φ and f in the model likelihood, which allows direct modeling of these parameters with covariates, but λ cannot be modeled directly with covariates (Nichols 2016). Our data satisfied both of the primary model assumptions of constant survey effort and constant sampled area during each sampling period. We discarded both the first and last estimates of f and λ estimates, because they can be unreliable or confounded (Hines and Nichols 2002).

We used a sequential modeling strategy to develop and select the most supported models. We made a priori predictions for each covariate effect (Table 2). The data were insufficient to accommodate interactions, so we considered only 1- and 2-factor additive models for each parameter. Each model structure was further limited to 1 spatial and 1 temporal covariate. We began by considering behavioral responses to trapping (e.g., trap happiness and trap shyness) for each of the target species using models with variable structures for p and c, which could provide evidence for changes in average behavior after first capture. Then, we modeled c while maintaining a time-varying p model structure. Next, we modeled p using the best c model structure identified in the second step. Per-capita λ, φ, and f are linearly related, and linear constraints placed on either of the two modeled parameters would have affected the estimation of the other parameter, which would have biased parameter inference (Nichols 2016). Thus, we modeled φ while holding f to a time-varying model structure and both p and c to the most supported structure. Similarly, we modeled f while holding φ to a time-varying model structure and both p and c to the most supported structure. We estimated model-averaged φ and f by averaging the parameter of interest over the parameter-specific candidate model set. We derived λ by model averaging over a combined model set, which contained all models used to estimate φ and f.

For model selection and covariate inference, we used Akaike's Information Criterion, corrected for small sample sizes (AIC_c), and AIC_c weights (w) to select the most-supported model in

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each sequential modeling step (Burnham and Anderson 2002). We selected the model with the lowest AIC_c and highest *w* as our best-supported model (Burnham and Anderson 2002). However, models within two AIC_c units of the top-ranking model were considered competitive (Stanley and Burnham 1998). In addition, we used the relative change in AIC_c (ΔAIC_c) to evaluate models relative to the top-ranking model. We used the degree to which 95% confidence intervals (hereafter *CI*) for the slope coefficients overlapped 0 to evaluate the strength of evidence for specific effects (e.g., Forsman et al. 2011; Dugger et al. 2016). We considered covariates with 95% *CIs* that did not overlap zero to be strongly supported, covariates in competitive models with ≤ 10% of the 95% *CIs* overlapping zero to be weakly supported, and covariates with > 10% of the 95% *CIs* overlapping zero not to be supported.

Proportional contributions to population growth rate.—We calculated site- and year-specific φ and *f* proportional contributions to annual λ by dividing each site- and year-specific vital rate estimate by the corresponding λ estimate (Nichols et al. 2000). We also averaged proportional contributions of φ and *f* across sites and years, where rates > 0.50 demonstrated a higher relative contribution.

Results

From 2011 to 2016, we captured 1,076 individual Humboldt's flying squirrels and 3,464 individual Townsend's chipmunks during 62,217 adjusted trap nights. Yearly site-specific detection probability adjusted estimates of abundance ranged from 5.7 to 62.5 for Humboldt's flying squirrels and 25.1 to 172.8 for Townsend's chipmunks (see Supplementary Data SD2). We detected individual adult Humboldt's flying squirrels and Townsend's chipmunks that were captured during 2011 and 2016, and thus were at least 6 years old.

Behavioral response models for both species accounted for 100% of the cumulative model weight, and the highest-ranking model without a behavioral effect was ranked substantially lower than the top-ranking model (Humboldt's flying squirrel ΔAIC_c = 174.75; Townsend's chipmunks ΔAIC_c = 2,431.58; see Supplementary Data SD3). Humboldt's flying squirrels were more likely to be recaptured on high elevation sites ($\beta_{Elevation}$: 0.47, 95% *CI* = 0.15 to 0.80), whereas Townsend's chipmunks were less likely to be recaptured on high elevation sites ($\beta_{Elevation}$: −0.95, 95% *CI* = −1.13 to −0.77; Table 3). Recapture probability (*c*) for Townsend's chipmunks decreased during the trapping session ($\beta_{Trapping}$: −0.16, 95% *CI* = −0.18 to −0.15). On low elevation sites, Humboldt's flying squirrel *c* (0.23, 95% *CI* = 0.22 to 0.24) and *p* (0.25, 95% *CI* = 0.21 to 0.30) were similar and 95% *CIs* overlapped completely; however, on high elevation sites, *c* (0.27, 95% *CI* = 0.25 to 0.29) was higher than *p* (0.20, 95% *CI* = 0.16 to 0.25) despite slight overlap of 95% *CIs* (see Supplementary Data SD4 and SD5). For Townsend's chipmunks, *c* was substantially higher than *p* on all sites. For example, on low elevation sites in 2016 *c* was 0.77 (95% *CI* = 0.75 to 0.78) and *p* was 0.21 (95% *CI* = 0.18 to 0.23).

Humboldt's flying squirrel *p* was most strongly associated with year-specific effects and elevation, whereas *p* for Townsend's chipmunks was most strongly associated with the trapping session day and shrub cover (Table 4). Humboldt's flying squirrel *p* varied yearly, but only the negative effect of 2011 was strongly supported (β_{2011}: −2.61, 95% *CI* = −2.90 to −2.32). Townsend's chipmunk *p* was positively associated with shrub cover (β_{Shrub}: 0.016, 95% *CI* = 0.01 to 0.02) and negatively associated with the day of the trapping session ($\beta_{Trapping}$: −0.22, 95% *CI* = −0.25 to −0.19).

Model-averaged φ for Humboldt's flying squirrels ranged from 0.47 (95% *CI* = 0.43 to 0.51) to 0.51 (95% *CI* = 0.45 to 0.57) and was nearly constant among years and sites (Fig. 2; see Supplementary Data SD6). For Humboldt's flying squirrels, φ on high elevation sites appeared slightly higher than for those on low elevation sites ($\beta_{Elevation}$: 0.54, 95% *CI* = −0.07 to 1.16), but 5.6% of the 95% *CI* overlapped zero and models including the

Table 3.—Top ranking models used to estimate recapture probability (*c*) of Humboldt's flying squirrels (HFS) and Townsend's chipmunks (TC) in late-successional forests in the H. J. Andrews Experimental Forest, 2011–2016. Column headings indicate change in Akaike's Information Criterion adjusted for sample size from the top-ranking model (ΔAIC_c), Akaike weight (ω), and the number of parameters (*k*). See Table 1 for variable descriptions.

Species	Model[a]	ΔAIC_c	ω	*k*	Deviance
HFS	TC captured + Elevation	0.00	0.97	25	18,722.92
	TC captured	6.80	0.03	24	18,731.74
	Year	13.44	0.00	28	18,730.29
	Null	34.38	0.00	23	18,761.34
TC	Trapping + Elevation	0.00	1.00	25	19,238.61
	Trapping + Canopy	69.77	0.00	25	19,308.39
	Null	556.88	0.00	23	19,799.51

[a]Other parameters held constant as: φ(t) *f*(t) *p*(YR*T).

Table 4.—Top ranking models used to estimate capture probability (*p*) of Humboldt's flying squirrels (HFS) and Townsend's chipmunks (TC) in late-successional forests in the H. J. Andrews Experimental Forest, 2011–2016. Column headings indicate change in Akaike's Information Criterion adjusted for sample size from the top-ranking model (ΔAIC_c), Akaike weight (ω), and the number of parameters (*k*). See Table 1 for variable descriptions.

Species	Model	ΔAIC_c	ω	*k*	Deviance
HFS[a]	Year + Elevation	0.00	0.70	20	18,783.46
	Year + Canopy	2.55	0.20	20	18,786.01
	Year	4.61	0.07	19	18,790.08
	Year + Shrub	6.56	0.03	20	18,790.02
	JDate + Canopy	117.06	0.00	16	18,908.59
	Null	212.02	0.00	14	19,007.57
TC[b]	Trapping + Shrub	0.00	1.00	16	19,319.75
	Trapping + Elevation	21.06	0.00	16	19,340.81
	Null	242.14	0.00	14	19,565.90

[a]Model structure for initial recapture probability (*c*) for Humboldt's flying squirrels was held to the top-ranking model structure from Table 3: φ(t) f(t) *c*(Chipmunk + Elevation).

[b]Model structure for initial recapture probability (*c*) for Townsend's Chipmunks was held to the top-ranking model structure from Table 3: φ(t) *f*(t) *c*(Trapping + Elevation).

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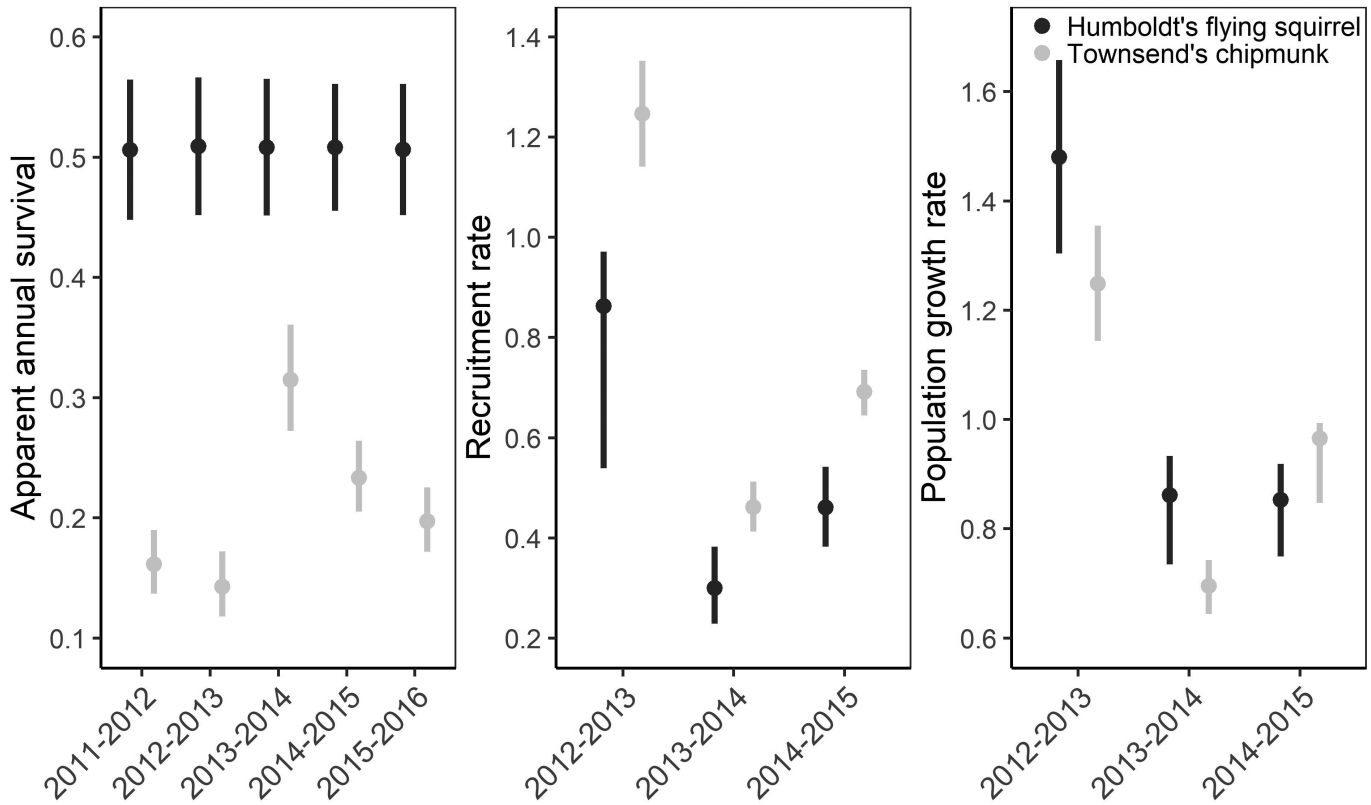

Fig. 2.—Model averaged apparent annual survival (φ), recruitment rate (f), and population growth rate (λ) of Humboldt's flying squirrels and Townsend's chipmunks, 2011–2016 in the H. J. Andrews Experimental Forest in Oregon. Estimates were nearly indistinguishable among grids by visual inspection, thus we present estimates from 1 site with elevation 890–920 m and canopy openness 15–30%.

Table 5.—Top ranking models used to estimate apparent survival (φ) of Humboldt's flying squirrels (HFS) and Townsend's chipmunks (TC) in late-successional forests in the H. J. Andrews Experimental Forest, 2011–2016. Column headings indicate change in Akaike's Information Criterion adjusted for sample size from the top-ranking model (ΔAIC_c), Akaike weight (ω), and the number of parameters (k). See Table 1 for variable descriptions.

Species	Model	ΔAIC_c	ω	k	Deviance
HFS[a]	Elevation	0.00	0.25	17	18,804.38
	TC abundance	0.47	0.20	17	18,803.91
	Null	0.89	0.16	16	18,806.81
TC[b]	Min. temp. + Canopy	0.00	0.34	14	19,502.87
	Min. temp.	0.31	0.29	13	19,505.18
	Min. temp. + Elevation	0.59	0.25	14	19,503.45
	Min. temp. + Berry	1.94	0.13	14	19,504.81
	HFS abundance	51.23	0.00	13	19,556.10
	Null	54.24	0.00	12	19,561.11

[a]Model structure used to estimate apparent annual survival (φ) was held constant as: f(t) p(Year + Elevation) c(Trapping + Elevation).
[b]Model structure used to estimate apparent annual survival (φ) was held constant as: f(t) p(Trapping + Shrub) c(Trapping + Elevation).

elevation covariate were weakly supported (w = 0.35; Table 5). Townsend's chipmunk φ ranged from 0.13 (95% CI = 0.11 to 0.16) to 0.31 (95% CI = 0.27 to 0.36; see Supplementary Data SD6). There was a 2.2-fold increase in φ of Townsend's chipmunks on all sites from the 2012–2013 interval to the 2013–2014 interval when abundance was increasing, and φ was highest during the 2013–2014 interval when abundance was at its peak (Fig. 2). In addition to year-specific effects, relatively warm winters ($\beta_{\text{Min. Temp.}}$: −0.11, 95% CI = −0.14 to −0.08) were associated with lower Townsend's chipmunk φ (Table 5).

Model-averaged f ranged from 0.23 (95% CI = 0.18 to 0.29) to 0.86 (95% CI = 0.54 to 0.97) for Humboldt's flying squirrels and 0.45 (95% CI = 0.40 to 0.50) to 1.25 (95% CI = 1.14 to 1.35) for Townsend's chipmunks (see Supplementary Data SD7). Both species experienced a > 2.5-fold decrease (Humboldt's flying squirrel: 2.78-fold; Townsend's chipmunk: 3.74-fold) in f on all sites from the 2012–2013 interval to the 2013–2014 interval. This decrease was then followed by a slight increase in f for both species on most sites during the 2014–2015 interval when abundance was decreasing (Fig. 2). Relatively high minimum winter temperatures were positively associated with higher f for both Humboldt's flying squirrel ($\beta_{\text{Min. Temp.}}$: 0.12, 95% CI = 0.08 to 0.16) and Townsend's chipmunks ($\beta_{\text{Min. Temp.}}$: 0.11, 95% CI = 0.09 to 0.13; Table 6). High elevation ($\beta_{\text{Elevation}}$: 0.57, 95% CI = 0.11 to 1.02) sites were associated with higher Humboldt's flying squirrel f (Table 6). Open canopy forests (β_{Canopy}: 0.24, 95% CI = −0.04 to 0.52) were positively associated with Townsend's chipmunk f, but the effect was weak (7.1% of the 95% CI overlapped zero; Table 6).

Humboldt's flying squirrel and Townsend's chipmunk λ estimates were highest on all sites during the 2012–2013 interval, when abundance was increasing, but then decreased during the 2013–2014 and 2014–2015 intervals when abundance

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Table 6.—Top ranking models used to estimate recruitment (*f*) for Humboldt's flying squirrels (HFS) and Townsend's chipmunks (TC) in late-successional forests in the H. J. Andrews Experimental Forest, 2011–2016. Column headings indicate change in Akaike's Information Criterion adjusted for sample size from the top-ranking model (ΔAIC_c), Akaike weight (ω), and the number of parameters (*k*). See Table 1 for variable descriptions.

Species	Model	ΔAIC_c	ω	*k*	Deviance
HFS[a]	Min. temp. + Berry	0.00	0.53	18	18,819.22
	Min. temp. + Elevation	0.51	0.41	18	18,819.73
	Min. temp.	4.42	0.06	17	18,825.66
	Berry	38.94	0.00	17	18,860.18
	Null	42.42	0.00	16	28,514.25
TC[b]	Min. temp. + Canopy	0.00	0.47	14	19,379.25
	Min. temp.	0.87	0.30	13	19,382.12
	Min. temp. + Berry	2.82	0.11	14	19,382.07
	Min. temp. + Elevation	2.87	0.11	14	19,382.12
	TC abundance	162.54	0.00	13	19,543.79
	Null	167.87	0.00	12	19,551.12

[a]Model structure used to estimate apparent annual survival (*f*) was held constant as: φ(t) *p*(Year + Elevation) *c*(Trapping + Elevation).
[b]Model structure used to estimate apparent annual survival (*f*) was held constant as: φ(t) *p*(Trapping + Shrub) *c*(Trapping + Elevation).

was decreasing (Fig. 2). Humboldt's flying squirrel λ ranged from 0.82 (95% *CI* = 0.73 to 0.88) to 1.48 (95% *CI* = 1.30 to 1.66; Fig. 2) and Townsend's chipmunks λ ranged from 0.68 (95% *CI* = 0.63 to 0.73) to 1.25 (95% *CI* = 1.14 to 1.35; see Supplementary Data SD8). Mean proportional vital rate contributions indicated that φ contributed (0.50 ± 0.02 *SE*) more to Humboldt's flying squirrel λ than *f* (0.49 ± 0.02 *SE*), but the effects were similar in size. Conversely, mean proportional vital rate contributions indicated that *f* (0.79 ± 0.03 *SE*) contributed more to the λ of Townsend's chipmunks than mean φ (0.21 ± 0.03 *SE*) in all years. For Humboldt's flying squirrels, the proportional contribution of φ and *f* varied among years, with φ contributing more to λ, and *f* contributing more during 2012–2013.

Discussion

We observed variable patterns of vital rates among co-occurring Humboldt's flying squirrels and Townsend's chipmunks in a late-successional forest of the Oregon Cascades. From 2011 to 2016, apparent annual survival of Humboldt's flying squirrels was nearly constant among years and sites, with only slight spatial variability. In contrast, the apparent annual survival of Townsend's chipmunks was spatially and temporally variable, and during each interval, was lower than that of Humboldt's flying squirrels. Recruitment of both species was highly variable among years, but only slightly variable among sites. Our results generally support previous studies showing evidence that Humboldt's flying squirrel demography did not strongly vary over space, but was potentially more variable over time (Rosenberg and Anthony 1992; Lehmkuhl et al. 2006). Our findings highlight the importance of studies designed to assess the temporal variability of small mammal demographics.

Temporal variation was greater than spatial variation for most vital rate estimates, except for apparent annual survival of Humboldt's flying squirrels. Our estimates of Humboldt's flying squirrel recruitment rate show more variability among years than previous estimates (Lehmkuhl et al. 2006). We suggest this temporal variability may be more important than previously thought, especially in the assessment of habitat quality. We observed a 2-fold increase in the apparent annual survival of Townsend's chipmunks, a 3-fold decrease in recruitment of Humboldt's flying squirrels and Townsend's chipmunks, and population growth rates were much higher during 2012–2013 interval than during 2013–2014 or 2014–2015 intervals. Because of this, single estimates from different years of this study could have resulted in different classifications of habitat suitability.

Previous estimates of Humboldt's flying squirrel apparent annual survival ranged from 0.32 to 0.68 (Ransome and Sullivan 2002; Gomez 2005; Lehmkuhl et al. 2006). Our estimates were intermediate to these, but less variable among years and sites. We did not estimate age-specific apparent survival, which may have lowered our overall apparent annual survival estimates. High mortality of young Humboldt's flying squirrels, caused by a range of conditions such as variable age-specific predation rates or winter sensitivity, could lower the estimate of overall survival (Carey 2000). Sullivan et al. (1983) reported high Townsend's chipmunk minimum survival rates that ranged from 0.73 to 0.88 for adult males on control sites and 0.74 to 0.91 for adult females on control sites. Those estimates are not comparable to our study because our estimates cover much longer intervals than the 14- and 21-day intervals used by Sullivan et al. (1983). However, our estimates were within the range of estimated apparent survival for yellow-pine chipmunks (*Neotamias amoenus*) in the Rocky Mountains, United States (Schulte-Hostedde et al. 2002).

With the exception of 1 year with high recruitment (2012–2013), our estimates of Humboldt's flying squirrel recruitment were similar to estimates reported by Lehmkuhl et al. (2006) in dry forests dominated by ponderosa pine, Douglas-fir, and grand fir (*A. grandis*). Similarly, our estimates of Humboldt's flying squirrel recruitment were comparable to recruitment estimates derived using juvenile to adult ratios (Rosenberg and Anthony 1992; Smith and Nichols 2003). Differences between our study and previous studies may have been methodological in part, but our study highlights the potential for strong temporal variation in annual recruitment of Humboldt's flying squirrels. We are unaware of any studies that estimated Townsend's chipmunk recruitment.

Humboldt's flying squirrels have evolved K-selected strategies in stable environments with stable food and nest resources (Wilson and Bossert 1971; Villa et al. 1999; Smith 2007), and in less suitable environments population densities and vital rates decrease (Smith and Nichols 2003; Smith and Person 2007). Previous studies in other late-successional forests of the Pacific Northwest described them as K-selected (Villa et al. 1999; Smith 2007); based on our study in a late-successional Oregon Cascade forest, we likewise propose that Humboldt's

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flying squirrels are K-selected and that they experience these forests as relatively stable environments where low mortality rates contribute to high abundances. Our estimates of apparent survival are only slightly less than proportional estimates of survival (that do not account for detection probability) presented by Villa et al. (1999) for Humboldt's flying squirrels in the Oregon Coast Range, which they described as K-selected. In addition, for Humboldt's flying squirrels in our study, apparent annual survival had a higher proportional contribution to population growth rate than recruitment rate, which likewise supports the K-selected classification.

Townsend's chipmunks are much less studied, and we are unaware of any previous studies exploring life history selection strategies. Our apparent annual survival estimates for Townsend's chipmunks were 1.5–3-fold lower than our estimates for Humboldt's flying squirrel apparent annual survival during all intervals, more variable among years, and population growth rates were primarily driven by recruitment. Thus we propose that Townsend's chipmunks were moderately r-selected on our study sites, and have evolved periods of high population growth rate in response to changes in these forests. We remain uncertain about the primary driver(s) of these periods of growth for Townsend's chipmunks. However, low apparent annual survival rates coupled with high recruitment rates, and conversely, high apparent annual survival rates coupled with low recruitment rates, suggest future research should consider potential for age-specific variation in apparent annual survival of Townsend's chipmunks and its associations with previous winter conditions.

Recruitment of both species decreased following relatively cold winter temperatures, but the biological mechanism is unclear. Cold winters might induce individual-level physiological responses which may reduce fecundity of reproductive adults, in turn lowering spring reproduction (Murie et al. 1980; Rödel et al. 2005). Alternatively, population-level ecological responses to lower food availability might reduce spring reproduction or juvenile survival (Stephens et al. 2018). However, relatively colder winter temperatures affected the apparent annual survival of Humboldt's flying squirrels and Townsend's chipmunks differently. Contrary to prediction, the apparent annual survival of Townsend's chipmunks increased when minimum winter temperatures were lower, whereas minimum winter temperatures did not appear to affect the apparent annual survival of Humboldt's flying squirrels. We suggest two possible explanations. Townsend's chipmunks can enter torpor during the winter (Levesque and Tattersall 2010), while Humboldt's flying squirrels practice social thermoregulation and do not enter true winter torpor (Olson et al. 2017). During particularly cold winters, Townsend's chipmunks might be more likely to enter torpor, which in turn could lower winter mortality. Alternatively, due to higher litter sizes, female Townsend's chipmunks likely have lower energetic costs per offspring relative to Humboldt's flying squirrels, but individual female Townsend's chipmunks might bear higher cumulative annual energetic costs of reproducing. During severe winters both species might abort litters resulting in lowered recruitment, in turn, early litter termination might increase female Townsend's chipmunk apparent survival by reducing the annual energetic costs of reproduction.

Links between abundance-associated covariates and vital processes were clear for Townsend's chipmunks, but less clear for Humboldt's flying squirrels. Our results support the inference of Weldy et al. (2019) that abundance for Townsend's chipmunks was associated with canopy openness, because canopy openness likewise was associated with both recruitment and mean abundance in our study, and recruitment contributed more to population growth relative to apparent annual survival rate during all years. The vital rate contributions to population growth rate were more variable for Humboldt's flying squirrels than for Townsend's chipmunks. Apparent annual survival contributed more to Humboldt's flying squirrel population growth rate than recruitment during most years, but the top-ranking apparent annual survival model included elevation, which was not strongly associated with abundance (Weldy et al. 2019). However, elevation was negatively correlated with berry-producing plant cover, which was an abundance-associated covariate (Weldy et al. 2019). During the 2012–2013 interval, just prior to peak abundance, recruitment contributed more than apparent annual survival to Humboldt's flying squirrel population growth rate, and berry-producing plant cover, which was an abundance-associated covariate, was in the top-ranking model for Humboldt's flying squirrel recruitment (Weldy et al. 2019). Thus, for Humboldt's flying squirrels, our results only support the abundance-associated inference during the 1 interval when recruitment contributed more to population growth rate. Previous studies have highlighted potential biases that might affect habitat quality inferences based on spatial or temporal variation of abundance (Armstrong 2005; Todd and Rothermel 2006). We suggest that in addition to these concerns, habitat quality inferences based on variation among abundances or vital rates might also be influenced by life history characteristics.

Our results highlight some similarities and differences in the life-history strategies of two co-occurring small mammals and help clarify the links among abundance-associated habitat features and the vital processes of the species (Weldy et al. 2019). We emphasize the importance of temporal variation in vital rate estimation and highlight the importance of long-term data in addressing key knowledge gaps, such as the patterns of covariation of co-occurring small mammal abundance and the relative contributions of vital rates to changes in abundance.

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Hutton, P. C. Kannor, B. E. Kerfoot, T. J. Mayer, H. M. Oswald, S. M. Pack, D. C. Tange, S. E. Ward, and J. M. Winiarski. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official U.S. Department of Agriculture or U.S. Government determination or policy. The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Government of any product or service.

Supplementary Data

Supplementary Data SD1.—Site- and year-specific trap placement rates for traps placed on the ground and traps attached to tree boles during a live-trapping project targeting Humboldt's flying squirrels (*Glaucomys oregonensis*) and Townsend's chipmunks (*Neotamias townsendii*) in 9 late-successional forest plots in the H. J. Andrews Experimental Forest in western Oregon, 2011–2016. Column headings indicate site characteristics, the year, the count of traps placed on the ground, and the count of traps attached to tree boles.

Supplementary Data SD2.—Abundance estimates for Humboldt's flying squirrel (HFS) and Townsend's chipmunk (TC) on 9 late-successional forest plots (7.84 ha) within the H. J Andrews Experimental Forest, near Blue River, OR. Estimates were derived with Huggins closed population models in a study conducted by Weldy et al. (2019).

Supplementary Data SD3.—Model selection results used to characterize behavioral effects between recapture probability (c) and capture probability (p) for Humboldt's flying squirrels (HFS) and Townsend's chipmunks (TC) in 9 late-successional forest plots in the H. J. Andrews Experimental Forest in western Oregon, 2011–2016. Column headings indicate change in Akaike's Information Criterion adjusted for sample size from the top-ranking model (ΔAIC_c), Akaike weight (ω), and the number of parameters (k).

Supplementary Data SD4.—Estimates of recapture probability (c) for Humboldt's flying squirrels (HFS) and Townsend's chipmunks (TC) captured in 9 late-successional forest plots in the H. J. Andrews Experimental Forest in western Oregon, 2011–2016. Column headings indicate site characteristics, year, trapping day (Day), the estimated interval and 95% confidence interval (LCL: Lower Confidence Limit and UCL: Upper Confidence Limit).

Supplementary Data SD5.—Estimates of capture probability (p) for Humboldt's flying squirrels (HFS) and Townsend's chipmunks (TC) captured in 9 late-successional forest plots in the H. J. Andrews Experimental Forest in western Oregon, 2011–2016. Column headings indicate site characteristics, year, trapping day (Day), the estimated interval and 95% confidence interval (LCL: Lower Confidence Limit and UCL: Upper Confidence Limit).

Supplementary Data SD6.—Estimates of apparent annual survival (φ) for Humboldt's flying squirrels (HFS) and Townsend's chipmunks (TC) captured in 9 late-successional forest plots in the H. J. Andrews Experimental Forest in western Oregon, 2011–2016. Column headings indicate site characteristics, the estimated interval and 95% confidence interval (LCL: Lower Confidence Limit and UCL: Upper Confidence Limit).

Supplementary Data SD7.—Estimates of recruitment (f) for Humboldt's flying squirrels (*Glaucomys oregonensis*) and Townsend's chipmunks (*Neotamias townsendii*) captured in 9 late-successional forest plots in the H. J. Andrews Experimental Forest in western Oregon, 2011–2016. Column headings indicate site characteristics, the estimated interval and 95% confidence interval (LCL: Lower Confidence Limit and UCL: Upper Confidence Limit).

Supplementary Data SD8.—Model averaged estimates of population growth for Humboldt's flying squirrels (*Glaucomys oregonensis*) and Townsend's chipmunks (*Neotamias townsendii*) captured in 9 late-successional forest plots in the H. J. Andrews Experimental Forest in western Oregon, 2011–2016. Column headings indicate site characteristics, the estimated interval and 95% confidence interval (LCL: Lower Confidence Limit and UCL: Upper Confidence Limit).

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