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1 Title: Emigration Effects on Estimates of Age- and Sex-specific Survival of Small Mammals

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6 Abstract

- 7 1. Age- and sex-specific survival estimates are crucial to understanding important life-
8 history characteristics and variation in these estimates can be a key driver of population
9 dynamics. When estimating survival using Cormack–Jolly–Seber (CJS) models and
10 capture–recapture data, emigration is typically assumed to have a negligible effect on
11 estimates such that apparent survival is indistinguishable from true survival.
12 Consequently, especially for populations or age classes with high dispersal rates,
13 apparent survival estimates are often biased low and temporal patterns in survival might
14 be masked when site fidelity varies temporally.
- 15 2. We used 9 years of annual mark-recapture data to estimate age-, sex-, and time-specific
16 apparent survival of Humboldt’s flying squirrels (*Glaucomys oregonensis*) and
17 Townsend’s chipmunks (*Neotamias townsendii*). For Humboldt’s flying squirrels, these
18 estimates support a small body of research investigating potential variation of survival
19 among age and sex classes, but age- and sex-specific survival has not been evaluated for

20 Townsend's chipmunks. We also quantified the effects of age- and sex-specific
21 emigration on confounded estimates of apparent survival.

22 3. Our estimates of juvenile flying squirrel survival were high relative to other small
23 mammal species and estimates for both species were variable among years. We found
24 survival differed moderately among age and sex classes for Humboldt's flying squirrels,
25 but little among age and sex classes for Townsend's chipmunks, and that the degree to
26 which emigration confounded apparent survival estimates varied substantially among
27 years. Without correcting for emigration, apparent survival estimates were lower and
28 temporal variation was obscured, particularly for male Humboldt's flying squirrels and
29 female Townsend's chipmunks.

30 4. Our results demonstrate that emigration can influence commonly used estimates of
31 apparent survival. Unadjusted estimates confounded the interpretation of differences in
32 survival between age and sex classes and masked potential temporal patterns in survival
33 because the magnitude of adjustment varied among years. We conclude that apparent
34 survival estimators are robust during some time periods; however, when emigration rates
35 vary in time the effects of emigration should be carefully considered and accounted for,
36 especially in comparative studies and those with policy and conservation implications.

37 Keywords

38 Apparent survival, emigration, immigration, Sciuridae, site-fidelity, vital rates

39 1| Introduction

40 Variation in survival rates can be a key driver of population dynamics (Cole, 1954), and
41 thus is vital for the study of population demography and life history (Franklin et al., 1996).

42 Within a population, the relative survival of juveniles and adults (Charlesworth, 1994) or males
43 and females (Promislow, 1992) can help inform which factors are important to population
44 dynamics and how populations will change through time (Morrison & Hik, 2007). In mammals,
45 adult and juvenile survival are often correlated, although juvenile survival is usually lower and
46 more variable (Promislow & Harvey, 1990). This variation is thought to be regulated by juvenile
47 life history characteristics such as natal dispersal (Rödel et al., 2015), or increased sensitivity to
48 limited food (Jackson et al., 2001), thermoregulatory stress (Rödel et al., 2004), and predation
49 (Garrett & Franklin, 1988). Similarly, there is a long-standing belief that males exhibit lower
50 survival rates than females (Vinogradov, 1998) because of exposure to higher costs of dispersal
51 associated with locating and competing for mates (Promislow, 2003). Despite their importance in
52 understanding the relative influence of survival on population dynamics, age-, sex-, and time-
53 specific estimates of survival are unavailable for many small mammal species because obtaining
54 suitable data is challenging.

55 One common method for estimating survival is the Cormack–Jolly–Seber (CJS) model,
56 which jointly estimates apparent survival and recapture probabilities (Cormack, 1964; Jolly,
57 1965; Seber, 1965). Apparent survival estimates from capture-recapture data and CJS models are
58 commonly interpreted as estimates of survival; however, the estimated parameter is the product
59 of true survival and site-fidelity (Lebreton et al., 1992) because individual survival is
60 indistinguishable from permanent emigration. If emigration is permanent or non-random, CJS
61 survival probability estimates will be biased low (Schaub et al., 2004) and the magnitude of bias
62 can be large (e.g., Cooper et al., 2008; Horton & Letcher, 2008). A number of approaches have
63 been suggested to deal with this bias. For example, a multistate approach allows for separation of
64 movement and survival probabilities (Brownie et al., 1993), the robust design approach (Pollock

65 et al., 1990) can account for temporary emigration, and data integrations can allow joint
66 estimation of true survival and site fidelity (e.g., Burnham, 1993). More recently, Gilroy et al.
67 (2012) and Schaub and Royle (2014) developed CJS model extensions that adjusted estimates of
68 apparent survival with those of site fidelity. In some cases, estimates of apparent survival will
69 suffice for conservation or management. However, when little is known about species-specific
70 variation in survival (age or sex variation) or patterns of dispersal, inferences based on apparent
71 survival estimates could mask important spatial or temporal variation in true survival.

72 Forest-adapted small mammals are important to forest heath as prey species and dispersal
73 agents of hypogeous fungi and spermatophyte seeds (Trappe et al., 2009); yet, few papers have
74 estimated movement rates (emigration, immigration, or site-fidelity) for these species, and thus
75 unbiased estimates of survival are rare or non-existent. We focused our analyses on two small
76 mammal species, Humboldt's flying squirrels (*Glaucomys oregonensis*; hereafter flying squirrel)
77 and Townsend's chipmunks (*Neotamias townsendii*; hereafter chipmunk). Flying squirrels have
78 been characterized as a potentially K-selected species, with survival that is higher than similar-
79 sized mammals (Smith, 2007; Villa et al., 1999) and varies little across time (Lehmkuhl et al.,
80 2006). However, other demographic characteristics such as abundance (Weldy et al. 2019), sex
81 ratio (Rosenberg & Anthony, 1992), and recruitment (Weldy et al. 2020) vary substantially
82 across time. Much less is known about chipmunk demography, but they have been characterized
83 as an r-selected species with population growth rates primarily driven by recruitment and
84 generally lower survival which can exhibit substantial temporal variation (Weldy et al., 2020).
85 Little is known about variation in survival among age or sex classes for either species, but
86 differential juvenile mortality rates (Forsman et al., 2004) or sex-specific effects could cause
87 negative biases in apparent survival estimates.

88 Our objectives for this study were to estimate age-, sex-, and time-specific annual
89 survival and recapture probability for flying squirrels and chipmunks captured in old forests
90 during a relatively undisturbed 9-year period. We used mark-recapture data and two estimators to
91 quantify sensitivity of survival estimates to variation in movement probabilities: 1) a CJS
92 estimator which jointly estimates apparent survival and recapture probability, and 2) an
93 integrated modelling approach to estimate immigration rates, which we used to derive site-
94 fidelity rates and emigration-adjusted survival. We hypothesized that survival would vary among
95 age and sex classes and that differences in apparent survival among age and sex classes was
96 confounded by variation in emigration rates. For juveniles of both species, we predicted lower
97 survival probabilities and higher immigration rates relative to subadults and adults, but that
98 adjusting apparent survival for emigration would reduce differences in survival among age-
99 classes (Dobson, 1982). We also predicted that males of both species would have lower survival
100 and higher immigration rates relative to females because male mammals typically disperse more
101 frequently and farther, and have higher predation risk and resource acquisition costs (Lemaître et
102 al., 2020).

103 2| Materials and Methods

104 2.1 | Study Area:

105 We collected field data annually during September–November 2011–2019 on nine sites
106 in the H. J. Andrews Experimental Forest on the west slope of the Cascade Mountains in Oregon,
107 United States (44°14' N, 122°10' W). The study sites were all located in a late-successional
108 forest (> 400 years) dominated by large Douglas-fir (*Pseudotsuga menziesii*), western hemlock
109 (*Tsuga heterophylla*), and Pacific silver fir (*Abies amabilis*; Schulze & Lienkaemper, 2015).

110 Understory characteristics on the study sites ranged from open understories to dense shrubs and
111 common understory vegetation included black berry, raspberry, and salmonberry (*Rubus* spp.),
112 common snowberry (*Symphoricarpos albus*), deer fern (*Blechnum spicant*), huckleberry
113 (*Vaccinium* spp.), Oregon grape (*Mahonia aquifolium*), oxalis (*Oxalis* spp.), salal (*Gaultheria*
114 *shallon*), sword fern (*Polystichum munitum*), and vine maple (*Acer circinatum*).

115 Weather on the study sites was typically warm and dry from May–September, and cool
116 and wet from October–April when approximately 80% of the annual precipitation occurs.
117 Annual precipitation primarily consists of rain at elevations < 1,000 m and snow at elevations \geq
118 1,000 m (Bierlmaier & McKee, 1989). At 605 m, 30-year (1981–2010) averages were 1,955.8
119 mm of precipitation, 4.3° C minimum temperature, and 15.6° C maximum temperature (PRISM
120 Climate Group, 2004). Monthly temperature and precipitation varied seasonally and inter-
121 annually during the period of our study (Figure S1).

122 2.2 | Data Collection

123 The nine study sites (7.84 ha each) were randomly selected across gradients of elevation
124 (range = 683–1,244 m) and canopy openness (range = 0–40%). The average distance among sites
125 was 2,963 m (range = 1,078–5,940 m). As described by Weldy et al. (2020), at each site we
126 established and conducted live-trapping at 64 stations, each with two traps, arranged in an 8 × 8
127 array with 40 m between stations. For each animal, we recorded age, body mass (g), reproductive
128 condition, species, and sex (Villa et al. 1991; Gashwiler, 1976). Live-trapping protocols were
129 approved by the Oregon State University’s Institutional Animal Care and Use Committee
130 (ACUP #4191 2011–2013; #4590 2014–2016; #4959 2017–2019) and were consistent with the
131 American Society of Mammalogists guidelines for the use of wild mammals in research and
132 education (Sikes et al., 2016).

133 2.3 | Analytical Methods

134 We estimated apparent annual survival (φ) and recapture probability (p) for flying
135 squirrels and chipmunks using mark-recapture data and CJS models (Cormack, 1964; Jolly,
136 1965; Seber, 1965) in a state-space formulation (Gimenez et al., 2007), with an additional sub
137 model to estimate immigration rates (I). This hierarchical model consists of two state processes
138 and one observation process. The first state process, φ (the probability of surviving and
139 remaining in the study area), was linked with the observation processes p (the capture probability
140 of a marked individual; Lebreton et al., 1992). The second state process, I , was independent from
141 the φ process and the p process and was used to derive site-fidelity rates (r) and emigration-
142 adjusted survival estimates ($\varphi_{\text{adjusted}}$).

143 For the φ process, we first defined a latent variable $z_{i,t}$ as the true state of individual i at
144 time t , where a value of 1 indicated i was alive at t and a value of 0 indicated i was dead at t . We
145 also defined a vector f , where f_i was the first capture occasion for individual i . We modelled the
146 probability that i was alive at $t+1$, conditional on first capture and being alive at t , as a Bernoulli
147 trial where the success probability is the product of $\varphi_{a,s,t}$ and $z_{i,t}$

$$z_{i,f_i} = 1$$

148
$$z_{i,t+1} | z_{i,t} \sim \text{Bernoulli}(z_{i,t} * \varphi_{a,s,t}).$$

149 We modelled variation in φ as a logit-linear function of an age-specific (a) intercept for i at t ,
150 where ages ranged 1–3 (juvenile, subadult, adult) for flying squirrels and 1–2 (juvenile, adult) for
151 chipmunks, and an additive age- and sex-specific (s) effect, where the effect of sex differed by
152 age, the sex variable was defined as 0 for males and 1 for females, and we included a zero-
153 centered age-, sex-, and time-specific random effect with standard deviation $\sigma_{a,s,t}$.

154

$$\text{logit}(\varphi_{a,s,t}) = \beta_{age_i} + \beta_{sex} * Sex_i + \epsilon_{a_i,s_i,t}$$

$$\epsilon_{a,s,t} \sim Normal(0, \sigma_{a,s,t}^2)$$

155 We used a standard observation process for capture-recapture data $y_{i,t}$, where recaptures
156 at each occasion from the second to the last trapping occasion were modelled as Bernoulli trials
157 with success probability $p_{i,t}$. To determine the most supported model structure for the
158 observation process we considered nine logit-linear model structures (seven univariate, two
159 bivariate) for both species to account for variation in p (Table 1).

$$y_{i,t} | z_{i,t} \sim Bernoulli(z_{i,t} * p_{i,t})$$

160 We used Poisson regression to estimate age-, sex-, and time-specific immigration rates
161 ($I_{a,s,t}$) during t from $t = 2$ to the number of occasions. The response variable ($Imm_{a,s,t}$) was the
162 age-, sex-, and time-specific counts of captured unmarked individuals.

$$Imm_{a,s,t} \sim Poisson(C_{a,s,t} * I_{a,s,t})$$

163 We modelled variation in $I_{a,s,t}$ as a log-linear function of an age-specific effect, a sex-specific
164 effect, and a zero-centered normally distributed time-specific random effect with standard
165 deviation σ_t .

$$\log(I_{a,s,t}) = \beta_{age} + \beta_{sex} + \alpha_t$$

$$\alpha_t \sim Normal(0, \sigma_t^2)$$

166 We assumed that age- and sex-specific emigration at t was equal to $I_{a,s,t+1}$, and that age- and sex-
167 specific $r_{a,s,t}$ was the complement to emigration (i.e., $r_{a,s,t} = 1 - \text{emigration}_{a,s,t}$). These
168 assumptions were reasonable on the study sites, which were randomly placed within a large,
169 continuous, old late-successional forest. We then derived estimates of emigration-adjusted
170 survival ($\varphi_{\text{adjusted}}$), defined as:

$$171 \varphi_{\text{adjusted } a,s,t} = \frac{\varphi_{a,s,t}}{r_{a,s,t}}$$

172 For the observation process, we used the Watanabe-Akaike information criterion (WAIC;
173 Watanabe, 2010) to select the most supported model structure for p (Hooten & Hobbs, 2015;
174 Vehtari et al., 2017). We considered the model with the smallest WAIC value and highest model
175 support weight (ω) the most supported model. We used the relative change in WAIC (Δ WAIC)
176 to evaluate models relative to the top-ranking model, and because the estimate of WAIC is
177 sensitive to the sample distribution, we estimated the 95% credible interval (CI) for the
178 difference in WAIC from the top-ranking model. We assessed the meaningfulness of a difference
179 between two models based on the degree to which the 95% CI for the difference did or did not
180 overlap zero.

181 We evaluated goodness-of-fit for the CJS model using a posterior predictive check
182 approach (Gelman et al., 2013) to estimate a Bayesian p -value (Meng, 1994). The data are binary
183 and standard fit statistics are uninformative about model fit. Thus, a Bayesian p -value was
184 derived as the proportion of times that Chi-squared test statistics (Pearson, 1900) calculated for
185 simulated datasets were higher than chi-squared test statistics for an aggregation of the observed
186 datasets (i.e., individual row sums; Royle et al., 2014). Perfect agreement between the observed
187 and simulated datasets occurs when the Bayesian p -value equals 0.5.

188 We conducted all analyses using R version 3.6.1 (R Core Team, 2020). The models were
189 fitted using JAGS software version 4.3.0 (Plummer, 2003) through the R2jags package version
190 0.6-1 (Su & Yajima, 2009). We used diffuse priors for all parameters and evaluated prior
191 sensitivity using two sets of priors. During model selection steps, each model was estimated with
192 three independent chains of 5,000 iterations following a burn-in period of 2,000 iterations. For
193 inference, the top-ranking models for flying squirrels and chipmunks were estimated with three
194 independent 50,000 iteration chains each following a burn-in period of 50,000 iterations. We

195 assessed model convergence by visual examination of trace plots and computed the Brooks–
196 Gelman–Rubin convergence diagnostic (\hat{R} ; Brooks & Gelman, 1998). We described the posterior
197 distributions for each parameter by their mean and 95% CI and assessed the strength of
198 individual effects or the magnitude of difference between estimates based on the degree to which
199 the 95% CI for the estimate did or did not overlap zero.

200 3| Results

201 We live-trapped 117,432 trap nights and captured 1,403 individual flying squirrels (692
202 females, 711 males) and 4,394 individual chipmunks (1,825 females, 2,569 males). Of these, we
203 estimated ϕ for the 1,272 flying squirrels and 3,873 chipmunks that were captured before the
204 final trapping occasion. Average site- and year-specific individual captures were 28.7 (range =
205 4–57) flying squirrels and 69.1 (range = 19–165) chipmunks. Site- and year-specific (2012–
206 2019) counts of unmarked individuals ranged 0–12 for flying squirrels and 3–54 for chipmunks.

207 The most supported model of p for flying squirrel included the additive effects of a mean
208 intercept and an individual-level random effect (Table 2; Table S1). Mean p of flying squirrels
209 was 0.66 (95% CI: 0.51–0.73), but individual estimates varied substantially ($\sigma_{\text{mH}} = 4.26$, 95%
210 CI: 3.19–4.96), ranged 0.25 (95% CI: 0.02–0.69) to 0.96 (95% CI: 0.76–0.99), and had a bi-
211 modal posterior density with a dominant peak at approximately 0.45 and a smaller secondary
212 peak at 0.81 (Figure 1). The most supported model of p for chipmunk included the additive
213 effects of a mean intercept, a permanent behavioral trap response, and an individual-level
214 random effect (Table 2; Table S1). Mean p of chipmunks was 0.37 (95% CI: 0.01–0.94), and the
215 probability of recapture of individuals after encountering traps was 0.77 (95% CI: 0.74–0.80).
216 Individual p of chipmunks varied substantially ($\sigma_{\text{mH}} = 4.19$, 95% CI: 2.9–4.96), ranged 0.21

217 (95% CI: 0.01–0.62) to 0.93 (95% CI: 0.61–0.99), and also had a bi-modal posterior density with
218 a dominant peak at approximately 0.50 and a much smaller secondary peak at 0.83 (Figure 1).

219 Immigration rates varied among years for flying squirrels ($\sigma_t = 2.88$, 95% CI: 1.76–4.59),
220 but less so for chipmunks ($\sigma_t = 1.41$, 95% CI: 0.83–2.55), and the species-specific pattern of
221 temporal variation was similar for both sexes. Flying squirrel immigration rates for females and
222 males were low (≤ 0.11) for both age-classes during six of eight study occasions (2013–2016,
223 2018, 2019), but were much higher (~ 0.22) for females and males of both age classes in 2012
224 and 2017 (Table S2). Similarly, chipmunk immigration rates were relatively low during six of
225 eight study occasions (2012, 2014–2018), and were much higher for females and males during
226 two occasions (2013, 2019; Table S2). Chipmunk immigration rates were higher relative to
227 flying squirrel immigration rates during all occasions. We observed weak evidence that
228 immigration rates of subadult and adult flying squirrels were lower than for juveniles, with <
229 10% of the coefficient 95% CI overlapping zero ($\beta_{\text{Age}} = -0.13$, 95% CI: -0.28–0.02). Female
230 flying squirrels ($\beta_{\text{Sex}} = -0.21$, 95% CI: -0.36– -0.06) and chipmunks ($\beta_{\text{Sex}} = -0.33$, 95% CI: -0.41–
231 -0.25) had lower immigration rates than males of those species respectively.

232 For flying squirrels, ϕ estimates varied among age, year, and sex ($\sigma_{a,s,t} = 0.73$, 95% CI:
233 0.46–1.06). For female flying squirrels, ϕ ranged 0.31 (95% CI: 0.12–0.55) to 0.71 (95% CI:
234 0.49–0.90) for juveniles, 0.43 (95% CI: 0.27–0.60) to 0.83 (95% CI: 0.69–0.94) for subadults,
235 and 0.43 (95% CI: 0.32–0.55) to 0.84 (95% CI: 0.69–0.95) for adults (Figure 2). For male flying
236 squirrels, ϕ ranged 0.29 (95% CI: 0.11–0.53) to 0.50 (95% CI: 0.29–0.73) for juveniles, 0.39
237 (95% CI: 0.19–0.61) to 0.70 (95% CI: 0.54–0.85) for subadults, and 0.37 (95% CI: 0.26–0.49) to
238 0.80 (95% CI: 0.61–0.94) for adults. Pairwise differences in ϕ and ϕ_{adjusted} among flying squirrel
239 age and sex classes were generally small and the 95% CIs for the pairwise differences broadly

240 overlapped zero. We found weak evidence that female juvenile ϕ was lower relative to female
241 subadult ϕ ($\phi_{female\ juvenile} - \phi_{female\ subadult} = -0.19$, 95% CI: -0.41–0.03) and male
242 juvenile ϕ was lower relative to both male subadult ϕ ($\phi_{male\ juvenile} - \phi_{male\ subadult} =$
243 -0.20 , 95% CI: -0.40–0.02) and male adult ϕ ($\phi_{male\ juvenile} - \phi_{male\ adult} = -0.18$, 95% CI: -
244 0.37–0.02). The rank order of ϕ among age classes was more variable among years for female
245 flying squirrel's relative to males, with all age classes represented as the minimum and
246 maximum of the within-year estimates at least once during eight years (Figure 2). For male
247 flying squirrels, juvenile ϕ was lowest among within-year estimates during all eight years, with
248 the maximum of within-year estimates alternating between the subadult (maximum 5 of 8 years)
249 and adult (maximum 3 of 8 years) age classes (Figure 2). Emigration adjustments varied
250 temporally, ranged 0.01 (95% CI: 0.00–0.02) to 0.18 (95% CI: 0.10–0.27), and were substantial
251 during the 2011–2012 and 2016–2017 intervals (Figure 3). The magnitude of differences in
252 adjustments among age and sex classes were small (Table S3).

253 For chipmunks, annual ϕ varied among years, but differed much less among age and sex
254 relative to flying squirrels ($\sigma_{a,s,t} = 0.69$, 95% CI: 0.39–0.1.13). Annual ϕ ranged 0.13 (95% CI:
255 0.03–0.32) to 0.25 (95% CI: 0.09–0.50) for juvenile females and ranged 0.09 (95% CI: 0.02–
256 0.19) to 0.38 (95% CI: 0.30–0.46) for adult females (Figure 2). For males, annual ϕ ranged 0.11
257 (95% CI: 0.03–0.26) to 0.30 (95% CI: 0.13–0.55) for juveniles and 0.07 (95% CI: 0.02–0.16) to
258 0.31 (95% CI: 0.26–0.37) for adults (Figure 2). Pairwise differences in ϕ and $\phi_{adjusted}$ among
259 each chipmunk sex and age class were small and the 95% CI for each difference broadly
260 overlapped zero. For both sexes, the rank order of juvenile ϕ was lower than adult survival
261 during most years (female: 7 of 8 years, male: 6 of 8 years). Emigration adjustments ranged 0.03
262 (95% CI: 0.01–0.07) to 0.33 (95% CI: 0.24–0.43), varied temporally for both sexes, and were

263 substantial during the 2012–2013 interval (Figure 3). Emigration adjustments were larger in
264 magnitude for males relative to females during all years (Table S3).

265 Covariate posterior distributions were similar for both sets of priors (Table 3, Figure S2).
266 Visual inspection of trace plots and estimates of the Brooks–Gelman–Rubin convergence
267 diagnostic indicated convergence was obtained for all monitored parameter estimates ($\hat{R} < 1.03$).
268 Bayesian p-values estimated from the posterior predictive checks were 0.53 for flying squirrels
269 and 0.44 for chipmunks, indicating adequate fit for all models and suggesting that both candidate
270 models generated data consistent with the observed data.

271 4| Discussion

272 Our analysis provided estimates of age-, sex-, and time-specific apparent annual survival
273 and emigration-adjusted survival for two small mammal species captured in a late successional
274 forest 2011–2019, and reinforces the need to adjust for emigration in estimates of apparent
275 survival. Here we also present analytical methods to parse confounded survival and movement
276 probabilities to reduce bias in empirical apparent annual survival estimates relative to
277 emigration-adjusted survival. By reducing bias associated with emigration, we revealed that
278 juvenile flying squirrel survival may be much higher than expected as our estimates are among
279 the highest observed for any small mammal species (Table S4; Kraus et al., 2005). Indeed, our
280 emigration-adjusted survival for juvenile flying squirrels exceeded reported adult apparent
281 annual survival estimates for many other species (Schaub & Vaterlaus-Schelegel, 2001),
282 including adult chipmunks in our study. Our approach also uncovered temporal variation in
283 apparent survival biases that are likely applicable to a wide range of species and ecosystems.

284 Our findings were consistent with previous studies that demonstrated sometimes-
285 substantial negative biases of apparent survival relative to true survival, due to confounding

286 among survival and emigration probabilities (Lebreton et al., 1992; Schaub & Royle, 2014).
287 Beyond that widely-recognized phenomenon (e.g., Schaub et al., 2004; Schaub & Royle, 2014),
288 we demonstrated that levels of bias in apparent survival can vary substantially over time due to
289 temporal variation in site-fidelity rates. For both species examined here, the bias induced by
290 confounding of emigration and survival probabilities was not consistent among years. In general,
291 we observed consistent agreement between apparent survival and adjusted survival estimates for
292 both species, sexes, and all age-classes. However, during some years, the bias for one or more
293 age- and sex-specific classes was >1 order of magnitude larger than the bias in other years, and
294 during those years, inferences for temporal variation in apparent survival and adjusted survival
295 differed. For example, our estimates of apparent annual survival for juvenile and subadult male
296 flying squirrels during 2016–2017 and 2017–2018 are similar, whereas mean emigration-
297 adjusted survival is much higher during 2016–2017 relative to 2017–2018. This is concerning for
298 unadjusted apparent survival estimates, especially for short-term studies that cannot differentiate
299 between years when apparent survival is a suitable estimator for survival and years when
300 movement probabilities are important and influential confounders. Moreover, differences in
301 survival probabilities or movement behavior among age or sex classes could further confound
302 estimation of either quantity individually (Schaub & Royle, 2014).

303 For flying squirrels, our estimates of adult apparent annual survival and adjusted survival
304 were intermediate to previously-reported estimates that ranged 0.32–0.68 (Gomez, 2005;
305 Lehmkuhl et al., 2006; Ransome & Sullivan, 2002), including those reported by Weldy et al.
306 (2020) for data collected on these sites 2011–2016. In that analysis, temporal variation in
307 apparent annual survival was not supported by model selection criteria, consistent with the
308 findings of Lehmkuhl et al. (2006). But, in this analysis, we focused on estimates of age- and

309 sex-specific survival and estimated substantial temporal variation in apparent annual survival,
310 especially for the juvenile and subadult age-classes. In the expanded time series of mark-
311 recapture data used here, our estimates of apparent annual survival during 2012–2016 were
312 similar to those reported by Weldy et al. (2020) and showed little temporal variation, especially
313 for the adult age class. However, during 2016–2019, we observed a peak and subsequent decline
314 in apparent survival and emigration-adjusted survival. For chipmunks, our estimates of apparent
315 annual survival and adjusted survival were similar to conspecifics and congenics (Schulte-
316 Hostedde et al., 2002; Weldy et al., 2020). But we found less evidence for temporal variation in
317 apparent annual survival, and temporal variation in adjusted survival did not match previously
318 reported patterns (Weldy et al. 2020).

319 Consistent with our hypotheses, juvenile flying squirrel survival was lower relative to
320 subadults or adults, and male survival was lower relative to females for all three age classes, but
321 the magnitude of that difference diminished with age. We also expected lower survival in
322 juvenile chipmunks, but we found little difference in age- or sex-specific survival. For both
323 species, however, temporal variation of survival within age and sex classes was larger than
324 variation among age and sex classes, highlighting the importance of long-term studies to
325 understand variation of demographic traits.

326 The importance of estimating age-specific survival while correcting for emigration is
327 demonstrated by contrasting findings of this study with those of previous research in this system.
328 Weldy et al. (2020) observed a negative association between apparent annual survival and
329 recruitment rate for chipmunks, where low apparent survival was coupled with high recruitment
330 and low recruitment was coupled with high survival. If age-specific survival were a primary
331 driver of this observation, we expected to observe relatively stable survival of adult chipmunks

332 while juvenile survival varied. Instead, we conclude that the low survival estimates coupled with
333 high recruitment were associated with individual movement. Recruitment was large because
334 individuals moved into study populations, while survival was low because marked individuals
335 left those populations.

336 Immigration rates of flying squirrels were generally low, except in 2012 and 2017 when
337 estimated immigration rates were more than 2-fold higher. For chipmunks, in comparison,
338 immigration rates were more variable and much higher overall. For example, the lowest
339 estimates of chipmunk immigration rates were nearly equivalent to the two peak flying squirrel
340 immigration estimates. Taken together, these estimates demonstrate different temporal patterns
341 of immigration, and consequently temporal variation in the influence of emigration on estimates
342 of apparent survival. During most years, immigration is likely an unimportant driver of flying
343 squirrel population dynamics, whereas it is likely consistently influential to chipmunk population
344 dynamics.

345 We were concerned that age- or sex-specific variation in site-fidelity rates would bias
346 inferences about differences in survival. We chose to use a sub-model extension to the CJS
347 model framework that estimated age-, sex-, and time-specific immigration probabilities, which
348 we used to derive estimates of site-fidelity rates and adjusted survival. This approach is similar to
349 others that integrate data to estimate adjusted survival (Abadi et al., 2010), which typically
350 parameterize immigration as a Poisson-distributed rate or count (Schaub & Fletcher, 2015). Early
351 integrated analyses suggested that one crucial assumption of integrated models is that the
352 datasets to be integrated are independent (Besbeas et al., 2002; Schaub & Abadi, 2011); violation
353 of that assumption is thought to result in overestimates of precision (Lebreton et al., 1992).

354 However, Weegman et al. (2020) found no effects on parameter bias or precision from integrated
355 population models fit to simulated data with complete overlap.

356 Employing the emigration correction on survival estimates by our method requires
357 carefully considering whether source or sink habitats exist within the study area. Our
358 immigration sub-model extension was contingent on the assumption that emigration rates at time
359 t are equivalent to immigration rates at time $t+1$ and that the site-fidelity rates were complement
360 to emigration rates. This is equivalent to the assumption that our study species are moving
361 through the study system randomly in an even flow within a year. We felt that this assumption
362 was met on our study-sites, which were randomly placed within a large, continuous, old late-
363 successional forest where site edges did not reflect biological edges. Further, Carey (1995)
364 suggested that there was no evidence that the densities of flying squirrels and chipmunks were
365 misleading indicators of habitat suitability, and Weldy et al. (2019) found no evidence for
366 marginal or sink habitat on our study sites. Presence of sink habitats would have indicated that
367 individuals were more likely to emigrate from or immigrate to specific sites. In that case,
368 apparent annual survival estimates would be biased low, and violation of our random and even
369 movement adjustment assumption would have caused our adjustment to apparent annual survival
370 to overcompensate for the negative biases caused by movement on some sites.

371 Our study demonstrates a novel approach to gaining insight into links between movement
372 and survival for two species of small mammals. The study of small mammal movement ecology
373 often lags behind that of larger species, leading to knowledge gaps such as how movement of
374 small mammals influences ecosystem health through the dispersal of hypogeous fungi spores and
375 plant seeds (Trappe et al., 2009). However, while our methods are appropriate given the
376 homogenous nature of our study area, the necessary assumptions might not hold in other systems

377 with more fragmentation, variable habitat quality, or potential for source-sink dynamics among
378 sites. Future studies could continue to explore the movement ecology of small mammals by
379 incorporating study designs suitable for directly estimating movement parameters (i.e., multistate
380 mark-recapture or telemetry) and evaluating the effects of spatiotemporal predictors on
381 movement probabilities, or by linking temporal variation of movement rates to studies of
382 population cycling (e.g., Fryxell et al., 1998; Weldy et al., 2019).

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399 Author Contributions:

400 MW conceived the ideas, collected data, led manuscript writing, designed methodology and
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402 approval for publication.

403 Data Availability Statement

404 Data used to estimate apparent annual survival and immigration for flying squirrels and
405 chipmunks are available from figshare: https://figshare.com/projects/Small_Mammal_Age-Specific_Survival/119784. R and JAGS code to recreate the analyses and figures is available on
406 GitHub https://github.com/MJWeldy/SM_MAMM_AGE_SURVIVAL.

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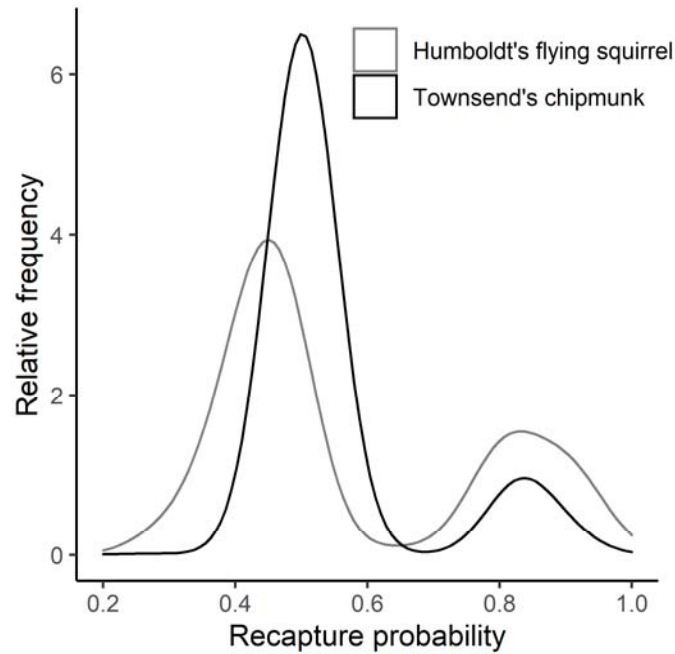
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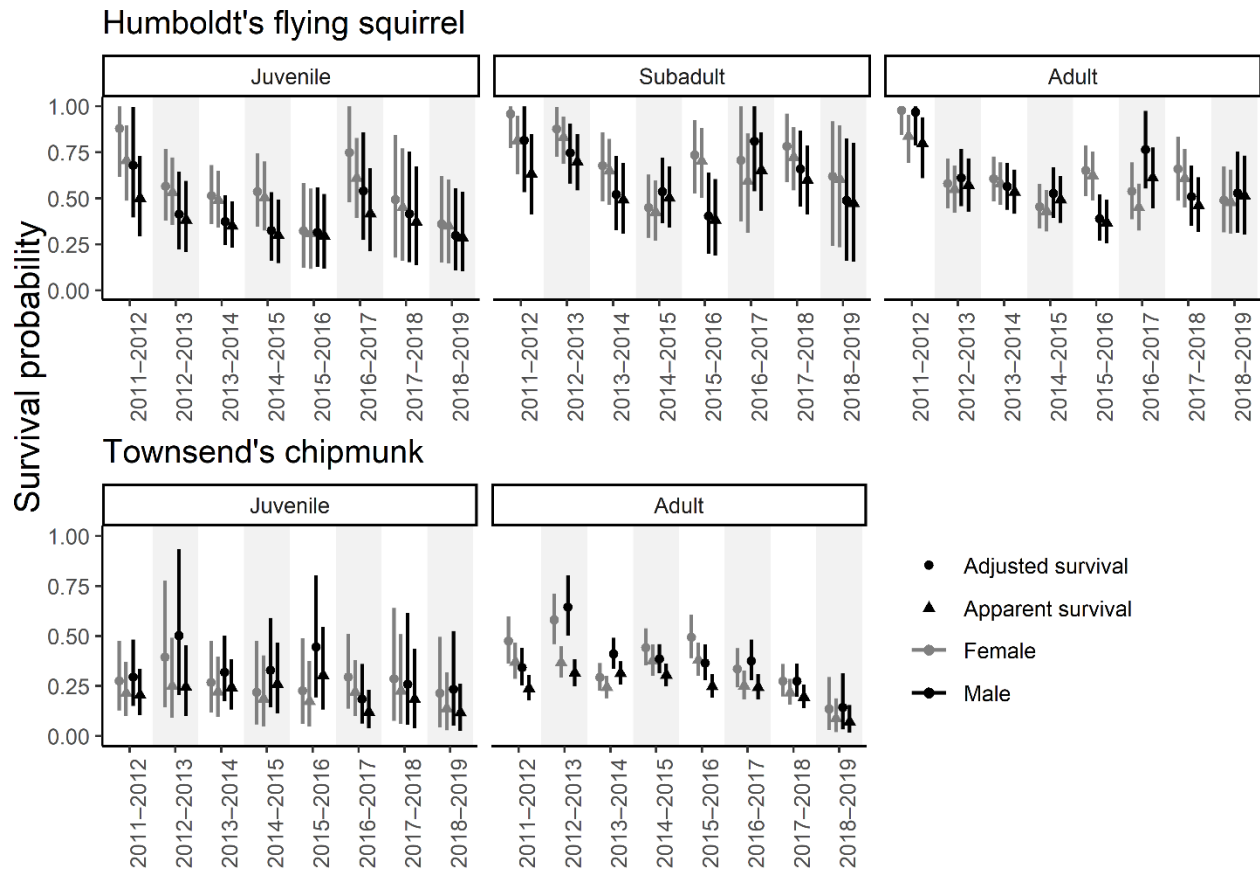
633 Figures:

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635

636 FIGURE 1 Relative frequencies of individual recapture probabilities for Humboldt's flying
637 squirrels (*Glaucomys oregonensis*) and Townsend's chipmunks (*Neotamias townsendii*)
638 estimated from models including an individual level random effect describing the observation
639 process. The bimodal density plots are displayed with a gaussian kernel using a smoothing
640 bandwidth of 0.05.



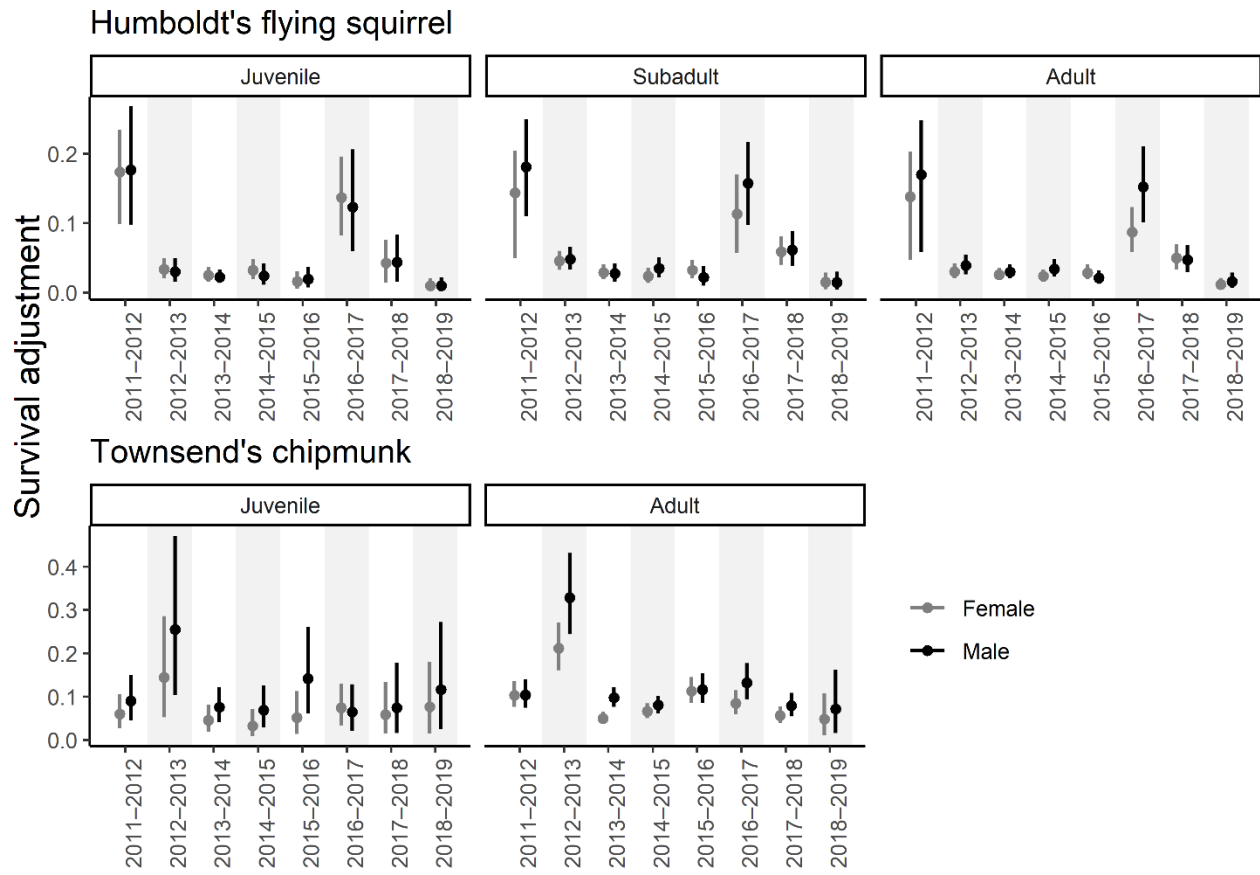
641

642 FIGURE 2 Estimates (mean and 95% credible interval) of annual apparent survival (φ ,

643 triangles) and adjusted survival ($\varphi_{\text{adjusted}}$, circles) for female (grey) and male (black) Humboldt's

644 flying squirrels (*Glaucomys oregonensis*) and Townsend's chipmunks (*Neotamias townsendii*),

645 2011–2019, in the H. J. Andrews Experimental Forest in Oregon.



646

647 FIGURE 3 Age- and sex-specific apparent survival emigration-adjustment

648 ($\Delta_{survival\ adjustment} = \varphi_{adjusted} - \varphi$) estimates (mean and 95% credible intervals) for

649 Humboldt's flying squirrels (*Glaucomys oregonensis*) and Townsend's chipmunks (*Neotamias*

650 *townsendii*) captured 2011–2019 on the H. J. Andrews Experimental Forest in Oregon.

651 Tables:

652 TABLE 1 Description of variables considered in Cormack–Jolly–Seber models of recapture
653 probability (p) for Humboldt’s flying squirrels (*Glaucomys oregonensis*) and Townsend’s
654 chipmunks (*Neotamias townsendii*) fitted using mark-recapture data, 2011–2019, recorded in the
655 H. J. Andrews Experimental Forest, near Blue River, Oregon.

Model ^a	Description
Null	Constant effect.
s	Site specific variation.
b	Permanent behavioral effect indicating captures after first capture.
t	A year-specific fixed-effect for each trapping occasion from 2011 to 2019.
T	Trend from the first to the last trapping occasion 2011 to 2019.
tRE	Temporal effects 2011–2019 treated as a normally distributed random effect with a mean of 0 and standard deviation σ_t .
mH	Individual-level normally distributed random effect with a mean of 0 and standard deviation σ_{mH} .
b + tRE	Additive model including a behavioral effect and

normally distributed random effect with a mean
of 0 and standard deviation σ_t .

b + mH Additive model including a behavioral effect and
normally distributed random effect with a mean
of 0 and standard deviation σ_{mH} .

656 ^a Model structure for apparent annual survival for both species was held to the model structure of
657 primary research interest: age-, sex-, and time-specific apparent survival.

658 TABLE 2 Top three ranking models used to estimate recapture probability (p) of Humboldt’s
 659 flying squirrels (*Glaucomys oregonensis*; HFS) and Townsend’s chipmunks (*Neotamias*
 660 *townsendii*; TC) on nine late-successional forest sites in the H. J. Andrews Experimental Forest,
 661 2011–2019. Column headings indicate the species, recapture probability model structure, the
 662 relative change in Watanabe–Akaike information criterion (Δ WAIC) from the top-ranking
 663 model, the lower 95% credible level for the relative change (Lower), the upper 95% credible
 664 interval for the relative change (Upper), and the model support weight (ω).

Species	Model ^a	Δ WAIC	Δ WAIC 95% CI		ω
			Lower	Upper	
HFS	mH	0	NA	NA	1
	s	32	12.195	51.805	0
	b + tRE	48.43	26.907	69.953	0
	Null	469.83	451.498	488.162	0
TC	b + mH	0	NA	NA	1
	mH	91.24	71.168	111.312	0
	b + tRE	449.28	428.737	469.823	0
	Null	658.99	640.594	677.386	0

665 ^a Model structures are defined in Table 1.

666 TABLE 3 Time-invariant age- and sex-specific estimates of mean apparent annual survival (ϕ ;
 667 real scale) and associated 95% credible intervals (lower: 2.5%, upper: 97.5%) for Humboldt’s
 668 flying squirrels (*Glaucomys oregonensis*; HFS) and Townsend’s chipmunks (*Neotamias*
 669 *townsendii*; TC) captured 2011–2019 on the H. J. Andrews Experimental Forest in Oregon.
 670 Super columns ‘Prior 1’ and ‘Prior 2’ refer to estimates obtained using two covariate prior sets,
 671 strong differences would indicate model sensitivity to prior selection. Age and sex categories
 672 include juvenile (J), subadult (SA), adult (A), male (M), and female (F).

Species	Age	Sex	Prior 1			Prior 2		
			Mean	Lower	Upper	Mean	Lower	Upper
HFS	J	M	0.366	0.232	0.518	0.301	0.190	0.438
	SA	M	0.561	0.404	0.709	0.488	0.350	0.637
	A	M	0.550	0.418	0.685	0.518	0.400	0.645
	J	F	0.622	0.404	0.805	0.618	0.429	0.786
	SA	F	0.625	0.407	0.813	0.621	0.432	0.788
	A	F	0.530	0.344	0.711	0.532	0.365	0.694
TC	J	M	0.203	0.110	0.325	0.257	0.135	0.416
	A	M	0.239	0.154	0.344	0.281	0.176	0.403
	J	F	0.486	0.261	0.711	0.494	0.252	0.737

A F 0.545 0.361 0.712 0.548 0.346 0.733

673 Supporting Information for “Emigration effects on estimates of age- and sex-specific survival of
674 small mammals” – Weldy et al.

675 Figure S1: Average monthly temperatures and cumulative monthly precipitation

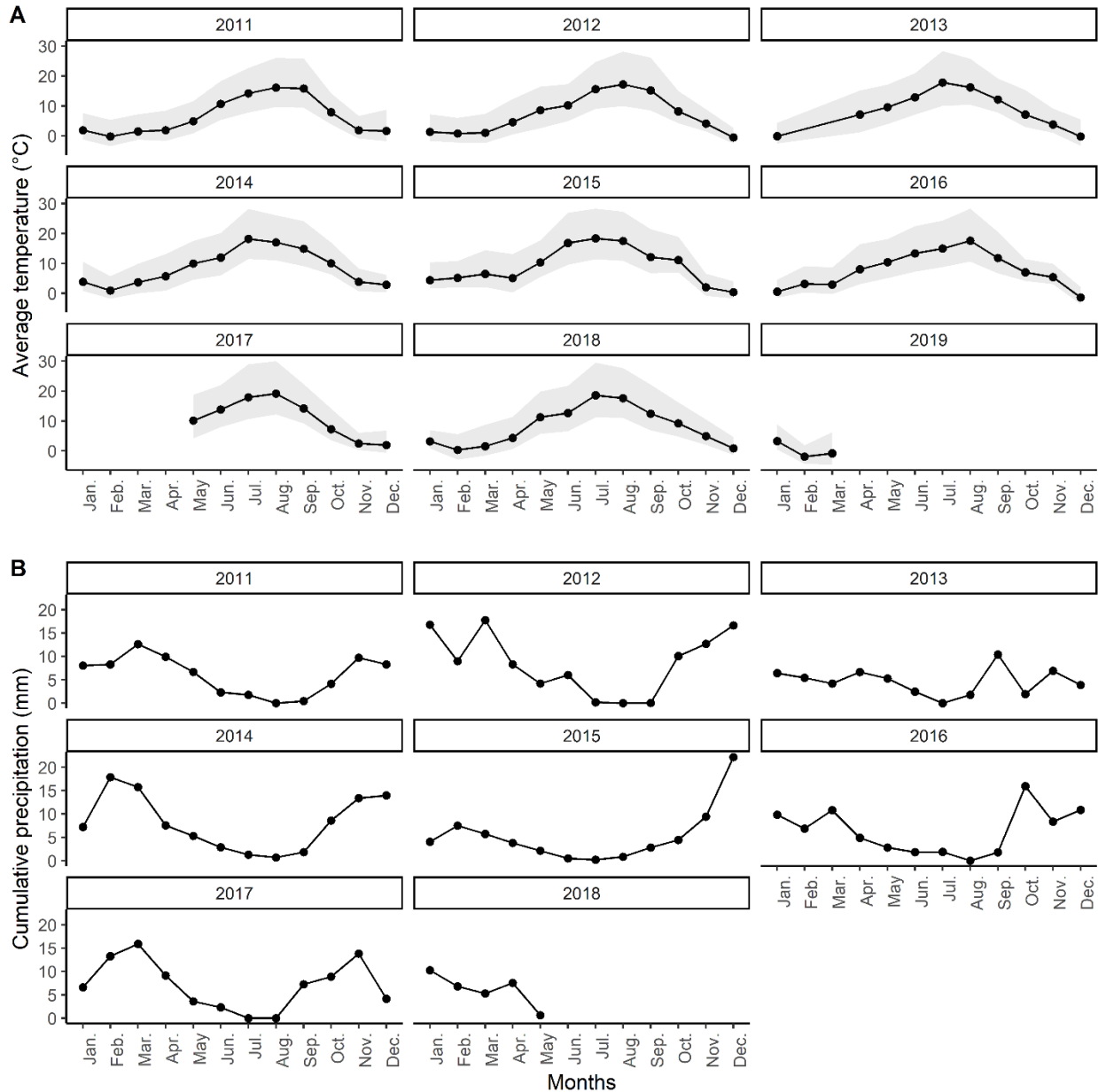
676 Figure S2: Prior sensitivity plot for uninformative prior sets 1 and 2 used to estimate apparent
677 annual survival, recapture probability, and immigration rates

678 Table S1: Full model selection results used to estimate recapture.

679 Table S2: Age- and sex-specific estimates of immigration rates

680 Table S3: Age- and sex-specific apparent survival emigration-adjustment estimates

681 Table S4: Ratios of adult to juvenile survival, including apparent annual survival (ϕ) and
682 adjusted annual survival



683

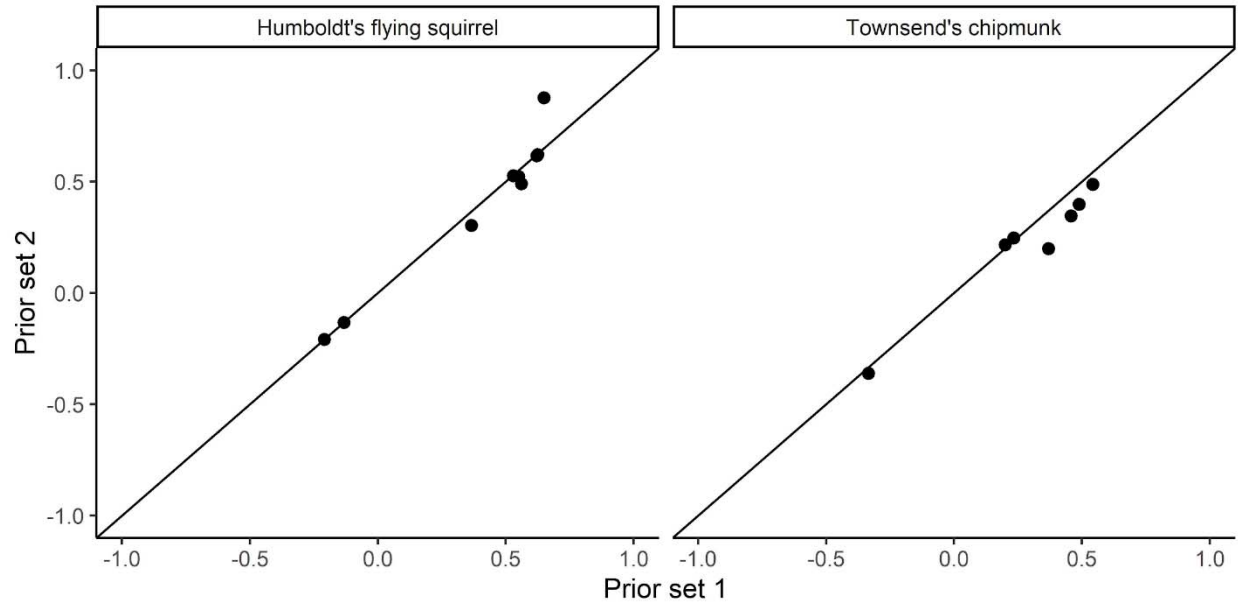
684 FIGURE S1 A) Average monthly temperatures (°C; April 2011 to March 2019) and B)

685 cumulative monthly precipitation (mm; April 2011 to September 2018) recorded at the central

686 meteorological station (1,020 m) weather station in the H. J. Andrews Experimental Forest. The

687 grey color band around average monthly temperature values indicates the range (minimum to

688 maximum) of temperatures recorded within the month.



689

690 FIGURE S2 Prior sensitivity plot for uninformative prior sets 1 and 2 used to estimate apparent
691 annual survival, recapture probability, and immigration rates of Humboldt's flying squirrels
692 (*Glaucomys oregonensis*) and Townsend's chipmunks (*Neotamias townsendii*) captured during
693 2011–2019 in the H. J. Andrews Experimental Forest in Oregon.

694 TABLE S1 Model selection results used to estimate recapture probability (p) of Humboldt's
 695 flying squirrels (*Glaucomys oregonensis*; HFS) and Townsend's chipmunks (*Neotamias*
 696 *townsendii*; TC) on nine late-successional forest sites in the H. J. Andrews Experimental Forest
 697 2011–2019. Column headings indicate the species, recapture probability models structure, the relative
 698 change in Watanabe–Akaike information criterion (Δ WAIC) from the top-ranking model, the lower 95%
 699 credible level for the relative change (Lower), the upper 95% credible interval for the relative change
 700 (Upper), and the model support weight (ω).

Species	Model ^a	Δ WAIC	Δ WAIC 95% CI		ω
			Lower	Upper	
HFS	mH	0	NA	NA	1
	s	32.00	12.195	51.805	0
	b + tRE	48.43	26.907	69.953	0
	b + mH	55.53	33.985	77.075	0
	tRE	57.77	53.497	62.043	0
	T	108.49	89.870	127.110	0
	b	250.18	232.500	267.860	0
	t	413.72	395.333	432.107	0
	Null	469.83	451.498	488.162	0
TC	b + mH	0	NA	NA	1
	mH	91.24	71.168	111.312	0
	b + tRE	449.28	428.737	469.823	0
	b	509.36	490.014	528.706	0
	tRE	510.88	508.085	513.675	0
	s	592.63	575.126	610.134	0

Null	658.99	640.594	677.386	0
t	666.00	648.158	683.842	0
T	683.62	666.198	701.042	0

701 ^a Model structures are defined in Table 1.

702 TABLE S2 Age- and sex-specific estimates of immigration rates and associated 95% credible
 703 intervals (lower: 2.5%, upper: 97.5%) for Humboldt’s flying squirrels (*Glaucomys oregonensis*;
 704 HFS) and Townsend’s chipmunks (*Neotamias townsendii*; TC) captured 2011–2019 on the H. J.
 705 Andrews Experimental Forest in Oregon. Age and sex categories include juvenile (J), subadult
 706 (SA), adult (A), male (M), and female (F).

Species	Sex	Age	Year	Mean	95% CI	
					Lower	Upper
HFS	F	J	2012	0.21	0.17	0.26
			2013	0.06	0.05	0.08
			2014	0.05	0.04	0.06
			2015	0.06	0.05	0.08
			2016	0.05	0.04	0.07
			2017	0.18	0.15	0.22
			2018	0.09	0.07	0.11
			2019	0.03	0.02	0.04
			A	2012	0.19	0.15
	2013	0.05		0.04	0.07	
	2014	0.04		0.03	0.05	
	2015	0.05		0.04	0.07	
	2016	0.04		0.03	0.06	
	2017	0.16		0.13	0.20	
	2018	0.08		0.06	0.09	
	2019	0.02		0.01	0.04	

	M	J	2012	0.26	0.21	0.31
			2013	0.07	0.06	0.09
			2014	0.06	0.05	0.08
			2015	0.07	0.06	0.09
			2016	0.06	0.04	0.08
			2017	0.23	0.19	0.27
			2018	0.11	0.08	0.13
			2019	0.03	0.02	0.05
		A	2012	0.23	0.19	0.28
			2013	0.06	0.05	0.08
			2014	0.05	0.04	0.07
			2015	0.06	0.05	0.08
			2016	0.05	0.04	0.07
			2017	0.20	0.16	0.24
			2018	0.09	0.07	0.12
			2019	0.03	0.02	0.05
TC	F	A	2012	0.22	0.19	0.24
			2013	0.36	0.33	0.40
			2014	0.17	0.15	0.19
			2015	0.15	0.13	0.17
			2016	0.23	0.20	0.26
			2017	0.25	0.22	0.28
			2018	0.21	0.18	0.23
			2019	0.35	0.30	0.42

M	2012	0.30	0.27	0.34
	2013	0.51	0.46	0.56
	2014	0.24	0.21	0.26
	2015	0.21	0.18	0.24
	2016	0.32	0.28	0.36
	2017	0.35	0.31	0.39
	2018	0.29	0.25	0.32
	2019	0.49	0.42	0.58

707

708 TABLE S3 Age- and sex-specific apparent survival emigration-adjustment estimates and
 709 associated 95% credible intervals (lower: 2.5%, upper: 97.5%) for Humboldt’s flying squirrels
 710 (*Glaucomys oregonensis*; HFS) and Townsend’s chipmunks (*Neotamias townsendii*; TC)
 711 captured 2011–2019 on the H. J. Andrews Experimental Forest in Oregon. Age and sex
 712 categories include juvenile (J), subadult (SA), adult (A), male (M), and female (F).

Species	Sex	Age	Interval	Mean	95% CI	
					Lower	Upper
HFS	F	J	2011–2012	0.17	0.10	0.23
			2012–2013	0.03	0.02	0.05
			2013–2014	0.03	0.02	0.04
			2014–2015	0.03	0.02	0.05
			2015–2016	0.02	0.01	0.03
			2016–2017	0.14	0.08	0.20
			2017–2018	0.04	0.01	0.08
			2018–2019	0.01	0.00	0.02
			SA	2011–2012	0.14	0.05
	2012–2013	0.05		0.03	0.06	
	2013–2014	0.03		0.02	0.04	
	2014–2015	0.02		0.01	0.04	
	2015–2016	0.03		0.02	0.05	
	2016–2017	0.11		0.06	0.17	
	2017–2018	0.06		0.04	0.08	
	2018–2019	0.02		0.00	0.03	

	A	2011–2012	0.14	0.05	0.20	
		2012–2013	0.03	0.02	0.04	
		2013–2014	0.03	0.02	0.04	
		2014–2015	0.02	0.02	0.03	
		2015–2016	0.03	0.02	0.04	
		2016–2017	0.09	0.06	0.12	
		2017–2018	0.05	0.03	0.07	
		2018–2019	0.01	0.01	0.02	
	M	J	2011–2012	0.18	0.10	0.27
			2012–2013	0.03	0.02	0.05
			2013–2014	0.02	0.01	0.03
			2014–2015	0.02	0.01	0.04
			2015–2016	0.02	0.01	0.04
			2016–2017	0.12	0.06	0.21
			2017–2018	0.04	0.02	0.08
			2018–2019	0.01	0.00	0.02
		SA	2011–2012	0.18	0.11	0.25
			2012–2013	0.05	0.03	0.07
			2013–2014	0.03	0.02	0.04
			2014–2015	0.03	0.02	0.05
			2015–2016	0.02	0.01	0.04
			2016–2017	0.16	0.10	0.22
			2017–2018	0.06	0.04	0.09
			2018–2019	0.01	0.00	0.03

		A	2011–2012	0.17	0.06	0.25
			2012–2013	0.04	0.03	0.05
			2013–2014	0.03	0.02	0.04
			2014–2015	0.03	0.02	0.05
			2015–2016	0.02	0.01	0.03
			2016–2017	0.15	0.10	0.21
			2017–2018	0.05	0.03	0.07
			2018–2019	0.02	0.01	0.03
TC	F	J	2011–2012	0.06	0.03	0.11
			2012–2013	0.14	0.05	0.29
			2013–2014	0.05	0.02	0.08
			2014–2015	0.03	0.01	0.07
			2015–2016	0.05	0.01	0.11
			2016–2017	0.07	0.03	0.13
			2017–2018	0.06	0.02	0.13
			2018–2019	0.08	0.02	0.18
		A	2011–2012	0.10	0.08	0.13
			2012–2013	0.21	0.16	0.27
			2013–2014	0.05	0.04	0.06
			2014–2015	0.07	0.05	0.08
			2015–2016	0.11	0.08	0.15
			2016–2017	0.08	0.06	0.11
			2017–2018	0.06	0.04	0.08
			2018–2019	0.05	0.01	0.11

M	J	2011–2012	0.09	0.04	0.15
		2012–2013	0.25	0.10	0.47
		2013–2014	0.08	0.04	0.12
		2014–2015	0.07	0.03	0.12
		2015–2016	0.14	0.06	0.26
		2016–2017	0.06	0.02	0.13
		2017–2018	0.07	0.02	0.18
		2018–2019	0.12	0.02	0.27
	A	2011–2012	0.10	0.07	0.14
		2012–2013	0.33	0.24	0.43
		2013–2014	0.10	0.08	0.12
		2014–2015	0.08	0.06	0.10
		2015–2016	0.12	0.09	0.15
		2016–2017	0.13	0.09	0.18
		2017–2018	0.08	0.05	0.11
		2018–2019	0.07	0.02	0.16

714 TABLE S4 Ratios of adult to juvenile survival, including apparent annual survival (ϕ) and
 715 adjusted annual survival (ϕ_{adjusted}), for male (M) and female (F) Humboldt’s flying squirrels
 716 (*Glaucomys oregonensis*; HFS) and Townsend’s chipmunks (*Neotamias townsendii*; TC)
 717 captured during 2011–2019 on the H. J. Andrews Experimental Forest in Oregon.

Species	Estimate	Sex	Mean	Min	Max
HFS	ϕ	F	1.22	0.74	2.02
		M	1.49	1.24	1.78
	ϕ_{adjusted}	F	1.19	0.72	2.01
		M	1.46	1.22	1.78
TC	ϕ	F	1.40	0.62	2.18
		M	1.18	0.61	2.02
	ϕ_{adjusted}	F	1.40	0.62	2.18
		M	1.18	0.61	2.03

718