Annual survival of Allegheny woodrats in a nonequilibrium metapopulation

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Many declining populations of the imperiled Allegheny woodrat (Neotoma magister) function as nonequilibrium metapopulations in which rates of subpopulation extirpation exceed recolonization. Quantifying and maximizing survival rates thus becomes critical for the conservation of these spatially structured populations. We used encounter histories of individually marked woodrats from subpopulations in Indiana, monitored annually from 2005 to 2013, to 1) estimate apparent annual survival rates while accounting for imperfect detection, 2) evaluate differences in apparent survival between unaugmented subpopulations and subpopulations reestablished or restored through translocation efforts, and 3) describe the effect of genetic diversity on survival. From Cormack–Jolly–Seber models developed in a Bayesian framework, apparent survival was greater for adults than for juveniles, greater for females than males, and there was a modest negative effect of density dependence. Although heterozygosity rates at 11 microsatellites increased among reinforced subpopulations following translocations, we observed no effect of heterozygosity on apparent survival. However, after translocations, average apparent survival was approximately 14% greater among recipient subpopulations than remnant subpopulations. This suggests that viability of recipient subpopulations was limited by low connectivity and the absence of genetic benefits conveyed by immigration or the potential for patches to be recolonized following local extinction. Under conditions of reduced connectivity, translocation among subpopulations to replicate natural gene flow may be appropriate to facilitate the long-term persistence of this and perhaps other nonequilibrium metapopulations.

Key words: Allegheny woodrat, apparent survival, Cormack–Jolly–Seber, genetic rescue, heterozygosity, inbreeding, mark-recapture, metapopulation, Neotoma magister

In a metapopulation context, the dynamics of individual subpopulations reflect the cumulative effects of local demographic processes, such as births and deaths, and connectivity among subpopulations, through immigration and emigration (Harrison and Taylor 1997). Small subpopulations are susceptible to extinction; thus, connectivity is critical for the recolonization of vacant habitat patches. Similarly, immigration into extant subpopulations can significantly impact genetic and demographic processes. Connectivity within metapopulations, however, may be disrupted by increasing demographic pressure (e.g., reduced survival due to predation, parasitism, or disease) or changes in landscape composition (e.g., loss of habitat patches or increased matrix viscosity—Fahrig and Merriam 1994; Fischer and Lindenmayer 2007; Govindan and Swihart 2012). Under such circumstances, spatially structured systems can take on the attributes of a nonequilibrium metapopulation in which rates of recolonization are insufficient to offset rates of subpopulation extirpation (Hanski and Simberloff 1997;
Further, with reduced dispersal among extant subpopulations, remnant subpopulations become susceptible to the loss of genetic diversity through drift, the onset of inbreeding effects, and associated decreases in fitness (Saccheri et al. 1998). As connectivity declines, the persistence of metapopulations becomes increasingly dependent upon demographic processes occurring within individual subpopulations (Brown and Kodric-Brown 1977). Thus, understanding and maximizing, if possible, birth and survival rates within individual subpopulations becomes critical for the conservation of spatially structured systems until connectivity within metapopulations can be restored.

Populations of Allegheny woodrats (*Neotoma magister*) are readily described as metapopulations given that local distributions are restricted to patches of rocky habitat (e.g., caves, rock fissures, boulder piles) dispersed throughout the deciduous forests of the eastern United States (Castleberry et al. 2002, 2006). Within habitat patches, woodrats depend upon interstices within rocky structures for the establishment of dens, which they defend from conspecifics (Peles and Wright 2008). Given the territorial social structure of woodrats, disjunct habitat patches support a limited number of individuals with adjacent subpopulations connected through dispersal (Castleberry et al. 2002). Rare dispersal among patches generally follows a pattern of isolation by distance in which subpopulations separated by > 3 km demonstrate little connectivity (Castleberry et al. 2002). Given that suitable den sites are an abiotically fixed resource within habitat patches, it is likely that woodrats demonstrate patterns of saturation dispersal with dispersal rates increasing as the availability of den sites within a patch decreases (Smyser et al. 2012a). With small population sizes and limited dispersal capacity, woodrat subpopulations are highly susceptible to disruptions in connectivity and the concomitant loss of diversity through genetic drift.

Recent and rapid range-wide declines in abundance and increasing habitat vacancy suggest that many Allegheny woodrat populations may exhibit characteristics of nonequilibrium metapopulations (LoGiudice 2006, 2008; Smyser et al. 2012b). Woodrat declines have been attributed to the synergistic interaction of reduced hard mast availability associated with the functional extirpation of the American chestnut (*Castanea dentata*) and declining oak (*Quercus* spp.) abundance, increased mortality associated with *Baylisascaris procyonis* infection, and habitat fragmentation and associated increases in predation pressure from great-horned owls (*Bubo virginianus*) and mammalian mesopredators (LoGiudice 2006, 2008; Smyser et al. 2012b). These extrinsic pressures have immediate consequences for within-subpopulation demographic processes but also impact patterns of connectivity at the metapopulation scale. Amid mounting demographic pressures and concomitant decreases in connectivity, translocation within nonequilibrium metapopulations can be used to reestablish stepping stone subpopulations or restore genetic diversity within isolated subpopulations (Westemeier et al. 1998; Madsen et al. 1999; Johnson et al. 2010; Whiteley et al. 2015).

Our goal was to use long-term capture–recapture data from subpopulations within a nonequilibrium metapopulation of Allegheny woodrats in Indiana, collected from 2005 to 2013, to describe apparent survival rates over time and across space, while explicitly accounting for imperfect detection. Our analysis included subpopulations that were either reestablished or reinforced through translocations during the monitoring period. This allowed us to evaluate whether recipient subpopulations were limited by either low survival imposed by poor habitat quality or low connectivity without the genetic augmentation or recolonization effects conveyed with immigration. Further, evaluating survival across a range of heterozygosity values as a result of the reinforcement of isolated, inbred subpopulations allowed us to test for a genetic rescue elicited through translocation and to specifically evaluate the efficacy of translocation in the recovery of nonequilibrium metapopulations of small-bodied prey species.

**Materials and Methods**

**Study area.**—Our study was conducted along a discontinuous line of cliffs adjacent to the Ohio River in southern Indiana (Fig. 1). Extensive efforts to describe the distribution of Allegheny woodrats in Indiana during the 1980s and 1990s documented 16 extant subpopulations spanning 76 river km, with the most distal subpopulations separated by 41 linear km (Cudmore 1983; Johnson 2002). Of the 16 subpopulations identified, 10 became locally extinct between 1982 and 2005. Similar to patterns observed throughout the Allegheny woodrat’s range, local declines have been attributed to *B. procyonis*-related mortality, reduced diversity of mast-producing species, and habitat fragmentation and concomitant loss of genetic diversity through drift (Smyser et al. 2012b).

**Fig. 1.**—Distribution of Allegheny woodrat (*Neotoma magister*) subpopulations monitored in southern Indiana, United States from 2005 to 2013. Sites include remnant subpopulations (SH2, CF, SHCSF, PIN), reinforced subpopulations (BPB, RHR), and reintroduced subpopulations (TL, NAR). BPB = Bulls Point Bluff; CF = Cold Friday; NAR = Narrows; PIN = Pinnacle Point; RHR = Rabbit Hash Ridge; SH2 = Shelterhouse 2; SHCSF = South Harrison-Crawford State Forest Bluff; TL = Tobacco Landing.
extirpation has left many of the remnant subpopulations genetically isolated, with nearest-neighbor distances that exceeded the dispersal capacity of the species (Castleberry et al. 2002; Smyser and Rhodes 2008; Smyser et al. 2012a). However, translocation of 68 woodrats from Kentucky and Tennessee into Indiana between 2007 and 2008 served to reestablish 2 previously extirpated subpopulations (Tobacco Landing [TL] and Narrows [NAR]) and reinforced 2 numerically diminished and genetically depauperate subpopulations (Bull’s Point Bluff [BPB] and Rabbit Hash Ridge [RHR]; Fig. 1) that were approaching extinction (detailed in Smyser et al. 2013).

From 2005 through 2013, we used standard livetrapping protocols to annually monitor all 8 known extant woodrat subpopulations throughout Indiana. These included the 4 recipient subpopulations described above (TL, NAR, BPB, and RHR) as well as unaugmented remnant subpopulations (Shelter House 2 [SH2, monitored from time of natural recolonization via immigration in 2006–2013], Cold Friday [CF], South Harrison-Crawford State Forest Bluff [SHCSF], and Pinnacle Point [PIN; from discovery in 2011–2013]; Fig. 1). Within each subpopulation, we conducted a single 2-night trapping session once per year between June and November, with the timing selected to avoid disturbance during the peak of the breeding season (Mengak et al. 2008). We saturated known woodrat activity areas (e.g., den sites [rock fissures, boulder piles, and caves], thoroughfares [undercut rock ledges], and latrines) with live traps (Model #102, Tomahawk Live Trap, Hazelhurst, Wisconsin) baited with fresh, sliced apples. By using a consistent number of traps within sites across years and by placing traps within specific microsites (den sites, thoroughfares, and active or historic latrines) mapped throughout habitat patches, the minimum number of unique individuals known to be alive served as an index of subpopulation abundance (Table 1). Upon initial capture each year, woodrats were weighed and classified as young-of-the-year or adults based on weight and pelage characteristics (Mengak et al. 2008). We marked woodrats with uniquely numbered ear tags (Monel #1, National Band and Tag Company, Newport, Kentucky) and collected a 2-mm biopsy punch from each ear for DNA analysis. We genotyped all captured individuals at 11 microsatellite loci developed for Allegheny woodrats (Nma01, 02, 04, 05, 06, 08, 10, 11, 12, 14, and 15) using established single locus amplification protocols (Castleberry et al. 2000; Smyser et al. 2012a). Similarly, for woodrats that lost both tags between successive encounters, we remarked animals, collected a 2nd genetic sample, and confirmed the individual’s identity by genotype. All trapping and handling methods conformed to Purdue University Animal Care and Use Committee policies (Protocol 1201000596) and guidelines provided by the American Society of Mammalogists (Sikes et al. 2011).

Statistical analysis.—We used extensions of Cormack–Jolly–Seber models (Lebreton et al. 1992; Gimenez et al. 2007) to estimate detection probabilities and apparent survival rates for Allegheny woodrats. Our primary focus was to evaluate sources of variation in survival rates, but to do so it is important to also account for possible variations in detection probability.

Table 1—Minimum number of Allegheny woodrats (Neotoma magister) known to be alive (number of adults used for estimation of density-dependent effects presented in parentheses) based on encounters during 2 nights of live trapping efforts among 8 subpopulations that comprise a nonequilibrium metapopulation in southern Indiana, United States. BPB = Bulls Point Bluff, CF = Cold Friday, NAR = Narrows, PIN = Pinnacle Point, RHR = Rabbit Hash Ridge; SH2 = Shelterhouse 2; SHCSF = South Harrison-Crawford State Forest Bluff.

<table>
<thead>
<tr>
<th>Subpopulation</th>
<th>2009</th>
<th>2010</th>
<th>2011</th>
<th>2012</th>
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<td>19</td>
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<tr>
<td>NAR</td>
<td>12</td>
<td>10</td>
<td>9</td>
<td>7</td>
<td>6</td>
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<td>34</td>
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<td>25</td>
<td>23</td>
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<tr>
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<td>8</td>
<td>6</td>
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<td>CF</td>
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<td>8</td>
<td>7</td>
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<tr>
<td>SHCSF</td>
<td>23</td>
<td>21</td>
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<td>16</td>
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<tr>
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<td>19</td>
<td>16</td>
<td>15</td>
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<td>12</td>
</tr>
<tr>
<td>Total</td>
<td>81</td>
<td>72</td>
<td>63</td>
<td>55</td>
<td>50</td>
</tr>
</tbody>
</table>

| Subpopulations unmanipulated through translocation included SH2, CF, SHCSF, and PIN. |
(Kéry and Schmidt 2008; Chen et al. 2013; Kellner and Swihart 2014). Male mammals are typically more likely to disperse than females (Greenwood 1980), and male woodrats often are located at the periphery of habitat patches (Peles and Wright 2008). Hence, we evaluated the effect of sex on detection probability. Additionally, sites differed in habitat configuration, which may influence temporary movement of individuals out of the trapping area. Given that such temporary emigration manifests as reduced detection probability (Kendall and Nichols 1995), we also evaluated whether detection probability varied by site.

For apparent survival rates, we evaluated the following sources of variation:

1. **Age.** We evaluated several possible age parameterizations (Supplementary Data SD1 for details on all age structures). The simplest age parameterization included only a juvenile and an adult age class. More complex parameterizations included up to 4 age classes for known-aged individuals (first captured as young-of-the-year) and up to 3 age classes for unknown-aged individuals (first captured as unknown-age adults with time-since-marking representing minimum ages). In a subset of models, we constrained survival rates for the terminal age classes of known-aged and unknown-aged individuals to be equal to one another because the oldest unknown-aged individuals must be at least as old as the oldest known-age class. We also included models where survival differed between unknown-age and known-age individuals, but with a parallel pattern on the logit scale (i.e., survival differed only by an additive offset parameter).

2. **Sex.** We investigated differences in apparent survival rates between males and females because annual recapture rates uncorrected for detection bias have been shown to be lower for males than females (Wood 2008).

3. **Site.** Spatial variation in survival probability is likely within rodent metapopulations and can have important demographic consequences (Ozgul et al. 2006). We modeled site as a fixed effect because our 8 sites (Fig. 1) represent all known woodrat subpopulations in Indiana and site-specific variation was of direct interest.

4. **Year.** Annual stochasticity in resources likely is a substantial source of variation in survival rates, particularly for juveniles (Ozgul et al. 2006). We modeled years as mean-zero random effects, common across all sites and ages.

5. **Population size (dd).** Given likely patterns of saturation dispersal in which individuals disperse if all suitable den sites are occupied, we expected lower apparent survival rates at higher population densities. To evaluate the effect of density dependence, we modeled survival as a function of a density covariate calculated as the ratio of the number of adults captured at a given site in a given year relative to the maximum number of adults ever observed at that site during population monitoring efforts conducted during 1991–2013 (Table 1). Note that similar values for dd among different sites do not imply the same abundance, but rather similar density-dependent pressures relative to the maximum local density.

6. **Juvenile weight (wt; measured for apparent 1st year survival for individuals captured as juveniles).** We predicted that juvenile weight would be positively correlated with apparent survival given that 1) larger woodrats are likely to be older and may have passed through selective filters (i.e., encounters with predators, natal dispersal, den site establishment); thus, their survival rates would more closely reflect those of adult woodrats; or 2) larger woodrats were in better body condition and had greater energy reserves for over-winter survival. However, weight also was correlated with date as juveniles captured later in the season were often heavier. Consequently, those captured late in the trapping season, which were generally heavier, were at risk for a shorter period than those captured earlier in the season, which were generally lighter. To mitigate potential bias introduced by capture date, we calculated a wt covariate for analysis of apparent survival.

7. **Heterozygosity (het).** Given the potential fitness consequences within isolated woodrat populations associated with a loss of genetic diversity and the concomitant onset of inbreeding depression (Smyser et al. 2012a), we used heterozygosity rate across 11 microsatellite loci as an individual covariate in our analyses. We centered the het covariate by subtracting average heterozygosity, so that individuals for which genotypic data were missing (6 individuals were not genotyped, 1 individual was missing data at 1 locus) could be assigned a value of zero to minimize the influence of missing data on coefficient estimates (Lebreton et al. 1992).

8. **Survival interval length (int).** The trapping interval between years varied from 8 months to 15 months and differed among sites. Ignoring this variation could falsely lead to estimated differences in annual survival. We defined the int covariate as deviation in trapping interval from 12 months.

Bayesian Markov Chain Monte Carlo (MCMC) methods are well suited for modeling random effects in survival analyses, and the resulting posterior distributions of estimates are intuitively interpretable and useful for parameterizing population models (Link and Barker 2009; Kéry and Schaub 2012). However, model selection is computationally difficult to implement with Bayesian methods (Link and Barker 2009), and we wanted to evaluate the relative support for competing models that included different covariate effects on survival and detection. Therefore, we first fitted models in a maximum likelihood framework and used Akaike information criterion corrected for finite sample sizes (AICc) to evaluate support for the effects of the different covariates (Supplementary Data SD2–SD5). We then selected biologically interesting models, supported by AICc, as a basis for fitting models by MCMC.

In a Bayesian MCMC context, we fitted 2 models that represented biologically interesting and well-supported models (similar to model XIV in Supplementary Data SD5), to estimate sex-specific detection probability and effects on apparent survival of age (3 known-age classes and 2 unknown-age classes with an offset for unknown age), sex, site, and year (as}
a random effect), while accounting for the length of the survival interval (int). We also included the covariates het, wt, and dd (for model 2 below). The 2 survival models were:

\[
\logit(\phi_{i,t,j}) = \beta_0 + \beta_{\text{wt}} \times \text{int}_{i,t,j} + \phi_{i,t,j} + \beta_{\text{het}} \text{wt}_{i,t,j} + \epsilon_i
\]

(1)

\[
\logit(\phi_{i,t,j}) = \beta_0 + \beta_{\text{wt}} \times \text{int}_{i,t,j} + \phi_{i,t,j} + \beta_{\text{het}} \text{wt}_{i,t,j} + \beta_{\text{dd}} \times \text{dd}_{i,t,j} + \epsilon_i
\]

(2)

where \(\phi_{i,t,j}\) denotes apparent survival of individual \(i\), at site \(j\), from year \(t\) to \(t+1\) and \(\epsilon_i \sim N(0,\sigma_i)\) denotes 8 random year effects with SD \(\sigma\). Although we made inference largely based on model 2, we included model 1 so that we could evaluate how much the inclusion of the density covariate reduced \(\sigma\).

To assess model fit, we used posterior predictive checks to evaluate how well models could predict features of the observed data set (Gelman et al. 2004; Chambert et al. 2013; Table 2). For each set of joint posterior values, we generated a capture–recapture dataset with the same number of new individuals encountered per site and per year as in the original dataset. We used the mean and SD of site- and year-specific return rates (i.e., the proportion of individuals encountered in year \(t\) that were re-encountered in year \(t+1\)) as the metrics to compare the similarity between actual and simulated datasets. The model performs well when about half of the metrics calculated from the simulated datasets are larger and half are smaller than the metrics calculated from the observed data. We calculated the mean and SD for the observed data set, and then defined a fit statistic (Bayesian \(P\)) as the proportion of values calculated from the simulated data that exceeded the value calculated from the observed data. Gelman et al. (2004) suggested a “reasonable” range of 0.05–0.95 for \(P\), where values outside this range clearly indicate poor fit.

To evaluate the effect of translocation, we used posterior distributions from model 2 to derive and compare mean adult apparent survival rates for both males and females between remnant (SH2, CF, and SHCSF) and recipient subpopulations (BPB, RHR, TL, and NAR) for the period after translocations (2007–2013). Holding dd constant at 0.5, we derived posterior values for mean survival across all years for all recipient sites and then subtracted these values from similarly derived values for remnant sites. We calculated the proportion of the resulting posterior distribution that was negative and considered this proportion as the probability that survival was greater at recipient than at remnant sites, independent of density-dependent effects. We excluded PIN from this portion of the analysis because the subpopulation was only monitored for a limited number of years (2011–2013) during this period.

We used JAGS (Plummer 2003) executed through the R2jags package (Su and Yajima 2015) for program R (R Core Team 2015) to generate posterior distributions of survival estimates and estimate the effect sizes of various covariates. For all coefficient parameters, we used \(\beta \sim N(0, \sigma^2 = 10)\) priors, and for SD of the random year effect, we used a \(\sigma \sim U(0,10)\) prior. For each model, we saved 1,000 samples from each of 3 Markov chains of length 50,000, after a burn-in of 1,000 iterations and a thinning rate of 50.

**Results**

Across all subpopulations and years, we captured 634 (310 male, 324 female) woodrats, encountered over 918 occasions (Table 1). Three hundred eighty-eight individuals were captured as young-of-the-year and thus were of known age, and 246 were of unknown age. One hundred ninety-eight individuals were recaptured \(\geq 1\) time, and the maximum number of recaptures was 5 (1 individual).

For all estimated parameters, the Gelman–Rubin \(\hat{\text{R}}\) values < 1.01 indicated adequate convergence on posterior distributions (Gelman et al. 2004). Posterior predictive checks also indicated that both models predicted the mean recapture rates and their SD reasonably well (Bayesian \(P = 0.23–0.36\) for \(\bar{X}\) and 0.38–0.45 for SD; Table 2). Coefficient estimates were similar between models 1 and 2.

Based on estimates derived from model 2, detection probabilities were greater for females (posterior mean = 0.94, 95% credible interval [CrI] = 0.87–0.98) than for males (posterior mean = 0.76, 95% CrI = 0.62–0.88; Table 3). Apparent annual survival was lowest in the 1st year of life, highest in the 2nd year of life, and dropped slightly thereafter (Fig. 2a). For example, apparent survival of juvenile females at an example site (TL) and year (2007) was 0.49 (estimate is mean of the posterior distribution; 95% CrI = 0.34–0.63). For age 1 and age 2+ females, respectively, the estimated apparent survival rates were 0.64 (95% CrI = 0.47–0.79) and 0.57 (95% CrI = 0.39–0.72). Apparent survival rates for known-age individuals were greater than those for unknown-age individuals (Fig. 2a). Apparent survival rates were greatest at PIN and TL, and lowest at CF.
and NAR (Fig. 2b), were greater for females than males, and generally decreased over the timeframe of the study (Fig. 2c).

As predicted, the effect of juvenile weight (wt) on apparent survival was positive with predicted survival increasing nearly 2-fold (Fig. 2d) over the range of residual weights observed. For example, at TL, the annual survival rate for juvenile females was 0.33 (95% CrI = 0.16–0.53) for an individual 111 g smaller than expected, given the time of year it was captured versus 0.60 (95% CrI = 0.40–0.77) for an individual 88 g heavier than expected. The 95% CrI for $\beta_{\text{het}}$ included zero ($X = 0.63$, $SD = 0.35$, 95% CrI = −0.04 to 1.35), but 97% of the posterior values for $\beta_{\text{het}}$ were positive.

The effect of population size ($dd$) was negative, with most (96.0%) of the posterior mass for $\beta_{\text{dd}}$ ($X = −0.76$, $SD = 0.44$) less than zero (model 2, Supplementary Data SD6(h)), indicating negative density dependence in survival. For example, predicted apparent survival averaged over all sites and years for adult females was 0.53 (95% CrI = 0.42–0.62) when $dd = 0.2$ and only 0.40 (95% CrI = 0.32–0.50) when $dd = 0.9$. Given that $dd$ varied annually (although not completely synchronously across sites), population density also was able to explain a small portion of variation in the random year effects. When $\beta_{\text{dd}}$ was added to model 1, the posterior mean $SD (\overline{\sigma})$ of the random year effects were reduced by 25%, from 0.52 to 0.40 (Supplementary Data SD6(h)).

The effect of increasing $het$ had a slight but uncertain positive effect on survival ($\beta_{\text{het}} = 0.028$, $SD = 0.037$), with 78% of the posterior estimates for $\beta_{\text{het}}$ greater than zero. For example, predicted survival for a juvenile female at an example site (TL) and year (2007) was 0.45 (95% CrI = 0.28–0.63) for a completely homozygous individual versus 0.52 (95% CrI = 0.36–0.69) for a completely heterozygous individual.

Following translocation, mean adult survival rates among recipient subpopulations were approximately 14% greater than among remnant subpopulations when compared at fixed levels of density dependence ($dd = 0.5$; Fig. 3). Mean adult female survival among recipient subpopulations (2007–2013) was 0.47 (95% CrI = 0.39–0.56) versus 0.42 (95% CrI = 0.34–0.50) among remnant subpopulations. For males, mean survival was 0.42 (95% CrI = 0.33–0.52) among recipient subpopulations and 0.37 (95% CrI = 0.29–0.45) among remnant subpopulations. For both males and females, the posterior probability that survival was greater for recipient than remnant subpopulation was > 0.91.

### Table 3.

Bayesian posterior means and 95% credible limits for logit-link coefficients describing apparent annual survival ($\phi$) and detection probability ($p$) of Allegheny woodrats (*Neotoma magister*) in 2005–2012 among 8 subpopulations in southern Indiana, United States. BPB = Bulls Point Bluff; CF = Cold Friday; NAR = Narrows; PIN = Pinnacle Point; RHR = Rabbit Hash Ridge; SH2 = Shelterhouse 2; SHCSF = South Harrison-Crawford State Forest Bluff; TL = Tobacco Landing; LCrL = lower credible limit; UCrL = upper credible limit.

<table>
<thead>
<tr>
<th>Parameter used to model logit ($\phi$) or detection ($p$)</th>
<th>$\overline{X}$</th>
<th>LCrL</th>
<th>UCrL</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\phi$: intercept (reference is age 0 females at site TL)</td>
<td>0.354</td>
<td>−0.387</td>
<td>1.065</td>
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<tr>
<td>$\phi$: offset for age 1</td>
<td>0.642</td>
<td>0.190</td>
<td>1.101</td>
</tr>
<tr>
<td>$\phi$: offset for age 2+</td>
<td>0.338</td>
<td>−0.179</td>
<td>0.857</td>
</tr>
<tr>
<td>$\phi$: offset for unknown ages</td>
<td>−0.369</td>
<td>−0.808</td>
<td>0.069</td>
</tr>
<tr>
<td>$\phi$: effect size of heterozygosity</td>
<td>0.028</td>
<td>−0.042</td>
<td>0.098</td>
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<tr>
<td>$\phi$: offset for survival interval deviation</td>
<td>−0.195</td>
<td>−0.328</td>
<td>−0.074</td>
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<table>
<thead>
<tr>
<th>Parameter used to model logit ($\phi$) or detection ($p$)</th>
<th>$\overline{X}$</th>
<th>LCrL</th>
<th>UCrL</th>
</tr>
</thead>
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<tr>
<td>$\phi$: offset for males</td>
<td>−0.220</td>
<td>−0.558</td>
<td>0.140</td>
</tr>
<tr>
<td>$\phi$: offset for site SH2</td>
<td>−0.620</td>
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</tr>
<tr>
<td>$\phi$: offset for site RHR</td>
<td>−0.489</td>
<td>−1.048</td>
<td>0.078</td>
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<td>$\phi$: offset for site BPB</td>
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<td>−0.770</td>
<td>0.310</td>
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<td>$\phi$: offset for site NAR</td>
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</tr>
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<td>$\phi$: offset for site CF</td>
<td>−0.696</td>
<td>−1.296</td>
<td>−0.096</td>
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<td>$\phi$: offset for site SHCSF</td>
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<td>−0.947</td>
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<td>$\phi$: offset for site PIN</td>
<td>0.191</td>
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<td>$\phi$: offset for site June weight</td>
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<tr>
<td>$\phi$: random effect for year 2005</td>
<td>0.004</td>
<td>−0.612</td>
<td>0.570</td>
</tr>
<tr>
<td>$\phi$: random effect for year 2006</td>
<td>0.295</td>
<td>−0.140</td>
<td>0.913</td>
</tr>
<tr>
<td>$\phi$: random effect for year 2007</td>
<td>−0.091</td>
<td>−0.626</td>
<td>0.389</td>
</tr>
<tr>
<td>$\phi$: random effect for year 2008</td>
<td>0.455</td>
<td>−0.070</td>
<td>1.259</td>
</tr>
<tr>
<td>$\phi$: random effect for year 2009</td>
<td>−0.075</td>
<td>−0.566</td>
<td>0.360</td>
</tr>
<tr>
<td>$\phi$: random effect for year 2010</td>
<td>−0.106</td>
<td>−0.670</td>
<td>0.348</td>
</tr>
<tr>
<td>$\phi$: random effect for year 2011</td>
<td>−0.214</td>
<td>−0.773</td>
<td>0.211</td>
</tr>
<tr>
<td>$\phi$: random effect for year 2012</td>
<td>−0.224</td>
<td>−0.806</td>
<td>0.272</td>
</tr>
<tr>
<td>$\phi$: sd of random year effects</td>
<td>0.386</td>
<td>0.055</td>
<td>0.933</td>
</tr>
</tbody>
</table>

| $p$: intercept (reference is females) | 2.854 | 1.891 | 4.118 |
| $p$: offset for males | −1.672 | −3.011 | −0.483 |

### Discussion

Our work provides one of the most comprehensive analyses of Allegheny woodrat apparent survival rates conducted to date and contributes to understanding the life history of this imperiled species. Despite previous descriptions of the Indiana woodrat system as a nonequilibrium metapopulation (Smyser et al. 2012a), our estimates of apparent annual survival rates generally exceed those published for other populations. Summarizing available published and unpublished results, Wood (2008) reported survival rates of 10–25% and 26–61% for juvenile males and females, respectively. In contrast, we observed mean apparent survival rates across all sites and years of 32% and 36% for juvenile males and females, respectively. Similarly, adult survival rates observed in this study were higher than those published previously (overall adult male apparent survival of 38% versus 22% in West Virginia, and 45% versus 38% for 1-year-old adults and 39% versus 25% for 2-year-old adults in Pennsylvania; overall adult female apparent survival of 43% versus 33% in West Virginia, and 51% versus 26% and 44% versus 17% for 1- and 2-year-old adults in Pennsylvania—Wood 2008).

Although we used standard annual monitoring protocols for Allegheny woodrats (Mengak et al. 2008), disparities in estimates of apparent survival may have been attributable, in part, to differences in methodological approaches. First, our survival estimates explicitly accounted for imperfect detection. Under standard monitoring protocols, managers place live traps within or immediately adjacent to suitable den sites and observe very high capture and recapture rates across successive nights of trapping (Castleberry et al. 2014). Therefore, managers often
do not consider detection bias when reporting results from woodrat monitoring efforts. Our estimates of detection probability (0.76 for males and 0.94 for females) suggest that naive survival estimates that do not account for imperfect detection are likely to be negatively biased, and the bias may be substantial, particularly for males. For example, our overall male survival estimate was 0.38, but a naive estimate that fails to consider nondetection would be approximately $0.38 \times 0.76 = 0.29$. Second, by monitoring all known woodrat subpopulations within the state, we were able to minimize the bias in apparent survival attributable to emigration. In the rare cases in which woodrats successfully dispersed between subpopulations (1 of 189 woodrats captured multiple times was encountered in > 1 site), we were able to continue the individual’s encounter history rather than falsely assuming the individual had died. While we recognize the possibility that unknown subpopulations may exist within the metapopulation, we believe the bias in survival estimates attributable to successful immigration into these unknown subpopulations would be minimal given the extensive efforts to describe the distribution of woodrats within Indiana (Cudmore 1983; Johnson 2002) and ongoing efforts by the Indiana Department of Natural Resources to evaluate suitable habitat for the presence of active woodrat populations. The negative bias in apparent survival associated with emigration may be higher in other populations for which survival estimates have been published (Wood 2008), as the spatial proximity of habitat patches within these landscapes would promote connectivity, in contrast to the isolation of habitat patches in Indiana (Smyser et al. 2012a).

Despite the recovery of genetic diversity observed among recipient subpopulations following reinforcement, we did not find a strong relationship between heterozygosity and apparent survival (Smyser et al. 2013). Among other species, reinforcement has elicited a strong rebound in measures of fitness (Westemeier et al. 1998; Madsen et al. 1999; Johnson et al. 2010); however, it is possible that apparent survival of woodrats is not affected by levels of heterozygosity. We believe the lack of observed association is more likely attributable to mitigating factors. Identifying the consequences of inbreeding depression requires large sample sizes across a broad range of levels of inbreeding (Keller and Waller 2002; Groombridge et al. 2012; Keller et al. 2012). Although we observed a broad range of individual heterozygosity rates over the course of the study, individuals of very low heterozygosity (those most likely to express the cost of inbreeding depression) were underrepresented as a consequence of the reinforcements and subsequent
admixture that occurred early in the study period (Smyser et al. 2013). Further, the most severe effects of inbreeding depression are expected to be revealed in prezygotic, zygotic, embryonic, or fetal stages, rather than in reduced rates of juvenile and adult survival (Lacy et al. 1996; Keller and Waller 2002). With the live trap methods implemented in this study, we were only able to detect juvenile woodrats once they were moving freely and able to leave their natal nest (approximately 21 days postpartum—Alligood et al. 2008; Smyser and Swihart 2014). Individuals with the most severe genetic defects may have perished before reaching this developmental milestone and, thus, were unavailable for sampling. Although we observed no effect of heterozygosity on survival, the numeric recovery of reinforced subpopulations (Table 1) suggests translocations and concomitant increases in heterozygosity may have had positive effects on other local demographic processes (i.e., birth rates). Efforts are ongoing to evaluate the relationship between genetic diversity and reproductive success within this system.

Collectively, the modestly higher survival rates observed among recipient subpopulations accompanied by a positive numeric response following translocation (Table 1) demonstrate that the viability of recipient subpopulations was not limited by low survival imposed by poor habitat quality. Rather, these subpopulations appear to have been limited by a history of isolation and the absence of the beneficial effects conveyed by immigration associated with the recolonization of vacant patches or genetic augmentation of extant populations. Contemporary levels of connectivity appear to be inadequate for recolonization rates to balance extirpations rates or for gene flow to replace the diversity lost through drift (Smyser et al. 2012a). Therefore, the proactive use of translocation among subpopulations to replicate natural gene flow may be appropriate to facilitate the long-term persistence of this and perhaps other metapopulations.

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SUPPLEMENTARY DATA

Supplementary Data SD1.—Description of different parameterizations to model age influences on apparent survival of Allegheny woodrats (Neotoma magister) based on live trap population monitoring conducted among all known subpopulation in Indiana, United States, 2005–2013.

Supplementary Data SD2.—Maximum likelihood estimation and model selection for Cormack–Jolly–Seber models of apparent annual survival of Allegheny woodrats (Neotoma magister) for subpopulations in southern Indiana, United States, monitored 2005–2013 with mark-recapture livetrapping.

Supplementary Data SD3.—Cormack–Jolly–Seber model selection results to assess support for the influence of sex and subpopulation (site) on detection probability for Allegheny
woodrats (Neotoma magister) monitored with live trap mark-recaptured methods among all known subpopulations in Indiana, United States, 2005–2013.

**Supplementary Data SD4.**—Cormack–Jolly–Seber model selection results to assess support for 11 age different parameterizations for modeling apparent survival among Allegheny woodrats (Neotoma magister) monitored across all known subpopulations in Indiana, United States, from 2005 to 2013.

**Supplementary Data SD5.**—Cormack–Jolly–Seber model selection results to assess the influence of sex, subpopulation (site), and temporally dynamic covariates (year, dd, int) on apparent annual survival probability of Allegheny woodrats (Neotoma magister) monitored among all known subpopulations in Indiana, United States, 2005–2013.

**Supplementary Data SD6.**—Posterior distributions of effect sizes and comparable maximum likelihood estimates with 95% confidence intervals derived from Cormack–Jolly–Seber models of apparent annual survival of Allegheny woodrats (Neotoma magister) for all subpopulations in Indiana, United States, 2005–2013.

**LITERATURE CITED**


