

Are declines of an endangered mammal predation-driven, and can a captive-breeding and release program aid their recovery?

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Keywords

Key Largo woodrat; capture–mark–recapture analysis; predation; Pradel's model; survival; recruitment; release; captive breeding.

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Abstract

Declines of imperiled small mammals are often attributed to predation without investigating the relative influence of survival and reproductive parameters on population growth. Accordingly, declines in the endangered Key Largo woodrat *Neotoma floridana smalli* (KLWR) population have been attributed to predation by feral cats *Felis catus*, Burmese pythons *Python molurus bivittatus* and raccoons *Procyon lotor*. We estimated survival, recruitment and realized population growth rates from four capture–mark–recapture studies to determine if the pattern of demographic variation was consistent with predation as the primary cause of KLWR declines. Additionally, we evaluated the KLWR captive-breeding and release program by comparing survival of captive-born and released KLWRs to wild-born KLWRs. The realized population growth rate of wild-born KLWRs had a strong pattern of covariation with recruitment; covariation between the realized population growth rate and apparent survival was negligible. Consistent with demographic theory, our results suggest that KLWR population dynamics were driven primarily by variation in recruitment, and that periodic reductions in recruitment led to population declines. We found that the survival curve and the first month (S_1) and first 3-month (S_{1-3}) survival estimates for the wild-born KLWRs [$S_1 = 0.929$ (0.890–0.968); $S_{1-3} = 0.942$ (0.919–0.965)] were considerably higher ($\chi^2 = 33.9$, 1 d.f., $P < 0.001$) than released KLWRs [$S_1 = 0.521$ (0.442–0.600); $S_{1-3} = 0.561$ (0.493–0.629)]. Low survival rates from predation limited the success of the captive-breeding and release program. This study illustrates the importance of pre-release conditioning of captive-bred animals and the importance of considering reproductive parameters in conjunction with survival estimates to understand the drivers of population decline.

Introduction

Demographic insights are critical for understanding the causes of imperiled species' declines and devising management actions to help mitigate them (Skalski, Ryding & Millsaugh, 2005; Reid *et al.*, 2008). However, discerning demographic drivers of population dynamics necessitates simultaneous consideration of survival and recruitment rates; failure to do so can result in incorrect or misleading conclusions about population declines (Pradel *et al.*, 1997). For example, declines in small mammal populations are often attributed to predators (Rave & Holler, 1992; Sinclair

et al., 1998; Forsy & Humphrey, 1999), but observations of predation and survival are rarely examined in conjunction with reproductive parameters. Demographic theories predict that reproductive parameters, not survival, should have a greater influence on population growth rates of small mammals, which are typically characterized by early maturity and high reproductive rates (Cole, 1954; Oli & Dobson, 2003). Additionally, there is empirical evidence to suggest that variability in rodent populations, including endangered species, can be attributed to variation in recruitment patterns (Lima & Jaksic, 1999; Reed & Slade, 2008; Schorr, 2012).

One management strategy that is commonly used to prevent the extinction of endangered species is a captive-breeding and release program (CBRP; Snyder *et al.*, 2002). For CBRP to be successful, released animals have to survive long enough to reproduce in their native habitats (Jule, Leaver & Lea, 2008; Aaltonen *et al.*, 2009). Accordingly, population declines and subsequent CBRP cannot be evaluated without a proper and complete understanding of population demography.

Declines in the endangered Key Largo woodrat *Neotoma floridana smalli* (KLWR) population since the 1970s have been attributed to the loss and alteration of their habitat (McCleery *et al.*, 2006) and competition with non-native black rats *Rattus rattus* (Hersh, 1981; Humphrey, 1992). More recently, there appears to be a growing consensus among researchers and managers that predation by feral cats *Felis catus*, Burmese pythons *Python molurus bivittatus* and raccoons *Procyon lotor* are primarily responsible for KLWR population declines (Greene *et al.*, 2007; Winchester, Castleberry & Mengak, 2009; Alligood *et al.*, 2011; Potts *et al.*, 2012). Despite these assertions, there is little empirical and no demographic evidence that predators are limiting the KLWR population (Winchester *et al.*, 2009). Understanding demography of endangered species can be notoriously difficult given their inherently small population size and regulatory constraints. Accordingly, demographic information on the KLWR has been sparse or missing (McCleery *et al.*, 2005), and the mechanisms underlying this species' population dynamics remain unknown.

The components of realized growth, survival and recruitment are often affected by different environmental factors. The pattern of covariation between population growth and its components can help identify the primary demographic driver of population dynamics, which, in turn, can lead to the determination of environmental factor(s) responsible for population declines. For example, strong covariation between population growth and survival rates of post-juvenile KLWRs might be consistent with the hypothesis that predation is the primary cause of KLWR population declines (hereafter, 'predation hypothesis'), whereas strong covariation between population growth and recruitment is likely consistent with an alternative hypothesis that the KLWR population growth is driven by variable reproduction. Thus, an understanding of the relative importance of survival and reproductive parameters to population growth rate is essential in understanding the cause(s) of KLWR population decline.

In an attempt to bolster the wild population of KLWR and to safeguard against possible extinction, two captive-breeding colonies were established at Lowry Park Zoo and Disney's Animal Kingdom in 2002 and 2005, respectively (Alligood *et al.*, 2011). Both of these facilities successfully bred and reared KLWRs that were released into the wild during 2010–2012. The success of the CBRP was dependent on survival of released individuals; however, estimates of survival of released KLWRs remain unknown.

Our goals for this study were to (1) provide estimates of survival, recruitment and realized population growth rates for the KLWR population; (2) determine if estimates of, and

covariation among, demographic parameters were consistent with the predation hypothesis; (3) determine the success of the KLWR CBRP by comparing survival of captive-born versus wild-born KLWRs. Under the predation hypothesis, we expected the realized population growth rate to co-vary more strongly with survival than recruitment rates because predation primarily affects survival rates. Additionally, because Burmese pythons have only recently invaded the island (Greene *et al.*, 2007), and raccoon and feral cats also appear to be a more recent problem (McCleery *et al.*, 2005; Winchester *et al.*, 2009; Potts *et al.*, 2012), we predicted that survival rates would be lower during more recent study periods. Finally, we expected survival of released captive-born KLWRs to be lower than wild-born KLWRs due to exposure of captive-born individuals to novel risks in the environment (Seddon, Armstrong & Maloney, 2007).

Materials and methods

Study area

The KLWR population is isolated in *c.* 972 ha of tropical hardwood hammock on the northern one-third of the island of Key Largo, located off the south-eastern tip of peninsular Florida (McCleery *et al.*, 2006; Fig. 1). The hardwood hammock habitats of Key Largo are unique, with a high diversity of mast-producing trees and shrubs of West Indian origin (Karim & Main, 2009). The climate of Key Largo is subtropical, exhibiting marked wet and dry seasons. Rainfall patterns are variable, but the region averages 1179 mm of rainfall annually, most occurring from May through September (Bancroft, Bowman & Sawicki, 2000). All the trapping and most releases of KLWRs occurred on Key Largo; however, some KLWRs were released in the hardwood hammocks of Palo Alto Key, north of Key Largo (Fig. 1).

Capture–mark–recapture data and analysis

We used four capture–mark–recapture (CMR) datasets collected for over 12 years (1995–2007) by different research teams, using differing trapping methodologies and trapping intervals. A brief description of the studies follows.

The United States Fish and Wildlife Service (USFWS) initiated CMR studies in 1995 and 2000. Both studies used similar protocols, trapping for four nights on the same four grids (USFWS, unpublished data). The grids consisted of 144 traps spaced 15 m apart in a 12 × 12 configuration (3.24 ha). The grids were trapped approximately every 2 months from July 1995 to early June 1996, and from July 2000 to late May 2001.

Researchers from the University of Georgia conducted a CMR study in 2005 on 40 grids with nine trapping sites (two traps per site) spaced 25 m apart in 3 × 3 configuration (0.56 ha) (Winchester *et al.*, 2009). Each grid was trapped for four nights every 3 months, for a total of three sessions, from May 2005 to November 2005. The University of Georgia conducted another CMR study in 2007 on 34 grids with a 7 × 7 configuration and traps spaced 10 m apart (0.36 ha; Greene,

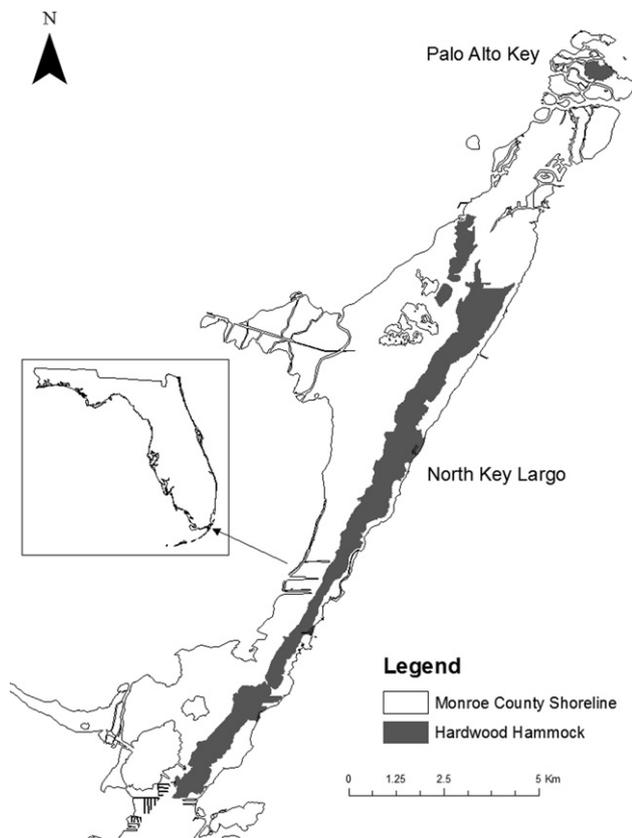


Figure 1 Extent of Key Largo woodrat *Neotoma floridana smalli* habitat in the tropical hardwood hammocks of northern Key Largo and Palo Alto Key, Monroe County, FL.

Mengak & Castleberry, 2013). These grids were trapped every 4 months, for four nights, from March 2007 to December 2007.

Because of differences in trapping protocols and capture intervals (CIs), it was not possible to analyze all datasets together. Instead, we analyzed the data in three sets; 1995/1996 and 2000/2001 combined, 2005, and 2007. We used a Pradel's temporal symmetry modeling framework for estimating and modeling capture probabilities (P), realized population growth rate (λ), and its components, apparent survival (Φ) and recruitment rates (f) (Pradel, 1996; Hines & Nichols, 2002). Additionally, we used the seniority parameter (γ), the probability an animal in the population was present in the population the previous period (month), to quantify the proportional contribution of f and Φ to λ (Hines & Nichols, 2002).

For the 1995 and 2001 datasets, we evaluated models accounting for the influence of sex, CI and study period on P , Φ and λ . We tested the same models for 2005 and 2007 datasets, excluding the no longer relevant study period model.

We developed models for program MARK version 6.1 (White & Burnham, 1999) using R version 2.12.2 (R Development Core Team, 2011) package RMark 2.0.1

(Laake & Rextad, 2008). We used a sequential approach to model selection, starting with the parameterization of Pradel's model that estimated Φ and λ . First, we fixed model structure for Φ and λ to CI {i.e. [$\Phi(CI) \lambda(CI)$]} and allowed capture probability (P) to be affected by CI, sex, study period (1995–1996/2000–2001 dataset only) and their additive effects. Next, we fixed model structure for λ to CI and P to the model identified as the most parsimonious in the preceding analysis and tested for the effects of aforementioned covariates (and their additive effects) on Φ . Finally, we fixed model structure for P and Φ to the model identified as the most parsimonious in preceding analysis and tested for the effect of the same covariates (and their additive effects) on λ . For the analysis of f and γ we used alternative parameterization of Pradel's model (Hines & Nichols, 2002), fixing model structure for P and Φ to the model identified in the analysis of λ (parameterization described above) and tested for the effect of CI, sex and for 1995–1996/2000–2001 dataset, study period and their additive effects on f or γ .

We used an information-theoretic approach using Akaike's information criterion corrected for small sample size (AICc) for model comparison and statistical inference (Burnham & Anderson, 2002). Models with a difference in AICc ($\Delta AICc$) < 2 were considered to have similar empirical support; models $2 \leq \Delta AICc \leq 4$ were considerably less supported by data, and those with $4 \leq \Delta AICc$ were an unlikely representation of the data (Burnham & Anderson, 2002). The model with the lowest AICc value was considered the most parsimonious. We reported estimates of parameters and confidence intervals as monthly rates and reported annual population growth rates (λ^{12} , monthly rate raised to the 12th power).

Known-fate data and analysis

We utilized records from KLWR captive-breeding programs at Disney's Animal Kingdom and Lowry Park Zoo in Tampa, Florida to estimate survival of captive KLWRs (captive groups) for comparison with captive-bred and released KLWR and wild-born KLWR (USFWS, unpublished data). We acquired records on 58 individuals at Disney and 33 individuals at Lowry Park from April 2002 to December 2011. Animals were checked daily and records indicated date of entry to the zoo (birth or loan) and date of exit (mortality, transfer or release).

Adult KLWRs were taken from the captive-breeding facilities and released into a man-made nest structure surrounded by a cage (release group). Thirteen KLWR were released on Key Largo in February of 2010, and 12 more were released there from December 2010 to February 2011. An additional 15 KLWRs were released on Palo Alto Key in December 2011. Each KLWR was fitted with a radio-tag and located at least every other day using hand-held telemetry equipment for up to 4 months.

We used telemetry data from two studies to estimate true survival of wild-adult KLWRs (wild-born group). Both studies live-trapped KLWRs on Key Largo, attached radio-tags to adults, released the animals at the place of capture and radio-tracked them until their radios failed or the woodrats

Table 1 Model comparison for capture probability (P), survival (Φ) and population growth rates (λ) of Key Largo woodrats *Neotoma floridana smalli*, evaluating for the effect of capture interval (CI), sex and study period (SP)

Study period	Models	K	AICc	Δ AICc	Weight	
1995–1996/2000–2001	Capture probability (P)					
	$\Phi(\text{CI}) P(\cdot) \lambda(\text{CI})$	11	365.462	0.000	0.583	
	$\Phi(\text{CI}) P(\text{sex}) \lambda(\text{CI})$	12	367.733	2.271	0.187	
	$\Phi(\text{CI}) P(\text{SP}) \lambda(\text{CI})$	12	367.990	2.527	0.165	
	$\Phi(\text{CI}) P(\text{sex} + \text{SP}) \lambda(\text{CI})$	13	369.988	4.526	0.061	
	$\Phi(\text{CI}) P(\text{SP} + \text{CI}) \lambda(\text{CI})$	17	377.381	11.919	0.002	
	$\Phi(\text{CI}) P(\text{CI}) \lambda(\text{CI})$	16	377.833	12.371	0.001	
	$\Phi(\text{CI}) P(\text{sex} + \text{CI}) \lambda(\text{CI})$	17	379.788	14.326	0.000	
	$\Phi(\text{CI}) P(\text{sex} + \text{SP} + \text{CI}) \lambda(\text{CI})$	18	380.263	14.801	0.000	
	Survival rate (Φ)					
	$\Phi(\cdot) P(\cdot) \lambda(\text{CI})$	7	359.057	0.000	0.463	
	$\Phi(\text{SP}) P(\cdot) \lambda(\text{CI})$	8	360.564	1.507	0.218	
	$\Phi(\text{sex}) P(\cdot) \lambda(\text{CI})$	8	360.844	1.786	0.189	
	$\Phi(\text{sex} + \text{SP}) P(\cdot) \lambda(\text{CI})$	9	362.246	3.189	0.094	
	$\Phi(\text{CI}) P(\cdot) \lambda(\text{CI})$	11	365.462	6.405	0.019	
	$\Phi(\text{SP} + \text{CI}) P(\cdot) \lambda(\text{CI})$	12	367.124	8.066	0.008	
	$\Phi(\text{sex} + \text{CI}) P(\cdot) \lambda(\text{CI})$	12	367.627	8.570	0.006	
	$\Phi(\text{sex} + \text{SP} + \text{CI}) P(\cdot) \lambda(\text{CI})$	13	369.251	10.194	0.003	
	Population growth rate (λ)					
	$\Phi(\cdot) P(\cdot) \lambda(\text{CI})$	7	359.057	0.000	0.399	
	$\Phi(\cdot) P(\cdot) \lambda(\text{sex} + \text{CI})$	8	360.888	1.831	0.160	
	$\Phi(\cdot) P(\cdot) \lambda(\text{SP} + \text{CI})$	8	360.945	1.888	0.155	
	$\Phi(\cdot) P(\cdot) \lambda(\cdot)$	3	361.626	2.569	0.110	
	$\Phi(\cdot) P(\cdot) \lambda(\text{sex} + \text{SP} + \text{CI})$	9	362.744	3.687	0.063	
	$\Phi(\cdot) P(\cdot) \lambda(\text{sex})$	4	363.041	3.983	0.054	
	$\Phi(\cdot) P(\cdot) \lambda(\text{SP})$	4	363.696	4.639	0.039	
	$\Phi(\cdot) P(\cdot) \lambda(\text{sex} + \text{SP})$	5	365.137	6.080	0.019	
	2005	Capture probability (P)				
		$\Phi(\text{CI}) P(\cdot) \lambda(\text{CI})$	5	177.120	0.000	0.662
		$\Phi(\text{CI}) P(\text{sex}) \lambda(\text{CI})$	6	179.292	2.172	0.224
		$\Phi(\text{CI}) P(\text{CI}) \lambda(\text{CI})$	7	181.844	4.724	0.062
		$\Phi(\text{CI}) P(\text{sex} + \text{CI}) \lambda(\text{CI})$	8	182.212	5.092	0.052
		Survival rate (Φ)				
$\Phi(\cdot) P(\cdot) \lambda(\text{CI})$		4	175.541	0.000	0.490	
$\Phi(\text{CI}) P(\cdot) \lambda(\text{CI})$		5	177.120	1.579	0.223	
$\Phi(\text{sex}) P(\cdot) \lambda(\text{CI})$		5	177.264	1.723	0.207	
$\Phi(\text{sex} + \text{CI}) P(\cdot) \lambda(\text{CI})$		6	179.159	3.618	0.080	
Population growth rate						
$\Phi(\cdot) P(\cdot) \lambda(\cdot)$		3	173.370	0.000	0.552	
$\Phi(\cdot) P(\cdot) \lambda(\text{sex})$		4	175.417	2.047	0.198	
$\Phi(\cdot) P(\cdot) \lambda(\text{CI})$		4	175.541	2.170	0.186	
$\Phi(\cdot) P(\cdot) \lambda(\text{sex} + \text{CI})$		5	177.684	4.313	0.064	
2007	Capture probability (P)					
	$\Phi(\text{CI}) P(\cdot) \lambda(\text{CI})$	5	177.160	0.000	0.652	
	$\Phi(\text{CI}) P(\text{sex}) \lambda(\text{CI})$	6	179.036	1.876	0.255	
	$\Phi(\text{CI}) P(\text{CI}) \lambda(\text{CI})$	7	182.059	4.899	0.056	
	$\Phi(\text{CI}) P(\text{sex} + \text{CI}) \lambda(\text{CI})$	8	182.906	5.745	0.037	
	Survival rate (Φ)					
	$\Phi(\cdot) P(\cdot) \lambda(\text{CI})$	4	175.102	0.000	0.493	
	$\Phi(\text{sex}) P(\cdot) \lambda(\text{CI})$	5	176.431	1.329	0.253	
	$\Phi(\text{CI}) P(\cdot) \lambda(\text{CI})$	5	177.160	2.058	0.176	
	$\Phi(\text{sex} + \text{CI}) P(\cdot) \lambda(\text{CI})$	6	178.796	3.694	0.078	
	Population growth rate					
	$\Phi(\cdot) P(\cdot) \lambda(\cdot)$	3	173.250	0.000	0.406	
	$\Phi(\cdot) P(\cdot) \lambda(\text{sex})$	4	173.708	0.457	0.323	
	$\Phi(\cdot) P(\cdot) \lambda(\text{CI})$	4	175.102	1.851	0.161	
	$\Phi(\cdot) P(\cdot) \lambda(\text{sex} + \text{CI})$	5	175.847	2.596	0.111	

Results are presented separately for three datasets (1995–1996/2000–2001, 2005 and 2007). The table includes the number of parameters (K), Akaike's information criterion corrected for small sample size (AICc), difference in AICc (Δ AICc) and model weights. The most parsimonious model for each analysis is highlighted in bold.

died. Nineteen KLWRs were captured and radio-tracked at least three times a week from March to December 2002 (McCleery *et al.*, 2005), and 39 KLWRs were tracked two to five times a week from June 2005 to February 2006 (Winchester, 2007).

We used the nonparametric Kaplan–Meier estimator to estimate survival by group (wild-born, released or captive), sex and release location (Kaplan & Meier, 1958; Kleinbaum & Klein, 2005). We used a log-rank test to compare survival curves between the captive-bred and wild-born KLWRs, and between wild-born and released groups. Additionally, we used the log-rank test to test for the effect of sex on survival of all three groups. We estimated survival rates by averaging survival (S_i) for the first month and for first 3 months (S_{1-3}). All analyses were performed using the survival package (Therneau & Lumley, 2011) for R version 2.12.2 (R Development Core Team, 2011).

Results

CMR data

There were 43 (M = 26, F = 17, recaptures = 128), 14 (M = 9, F = 5, recaptures = 32), 46 (M = 23, F = 23, recaptures = 171) and 55 individual KLWRs (M = 34, F = 21, recaptures = 96) captured during the 1995–1996, 2000–2001, 2005 and 2007 studies, respectively. For all datasets, we used $P(\cdot)$ model for subsequent analyses because it was the most parsimonious model across all datasets, and it had fewer parameters than other competing models (Table 1).

The constant parameter model $\Phi(\cdot)$ was also the most parsimonious for all datasets and used for subsequent analyses (Table 1). Based on this model, monthly estimates of Φ were as follows: 1995–1996/2000–2001, 0.822 (0.744–0.880); 2005, 0.879 (0.786–0.935); and 2007, 0.859 (0.693–0.943). Model

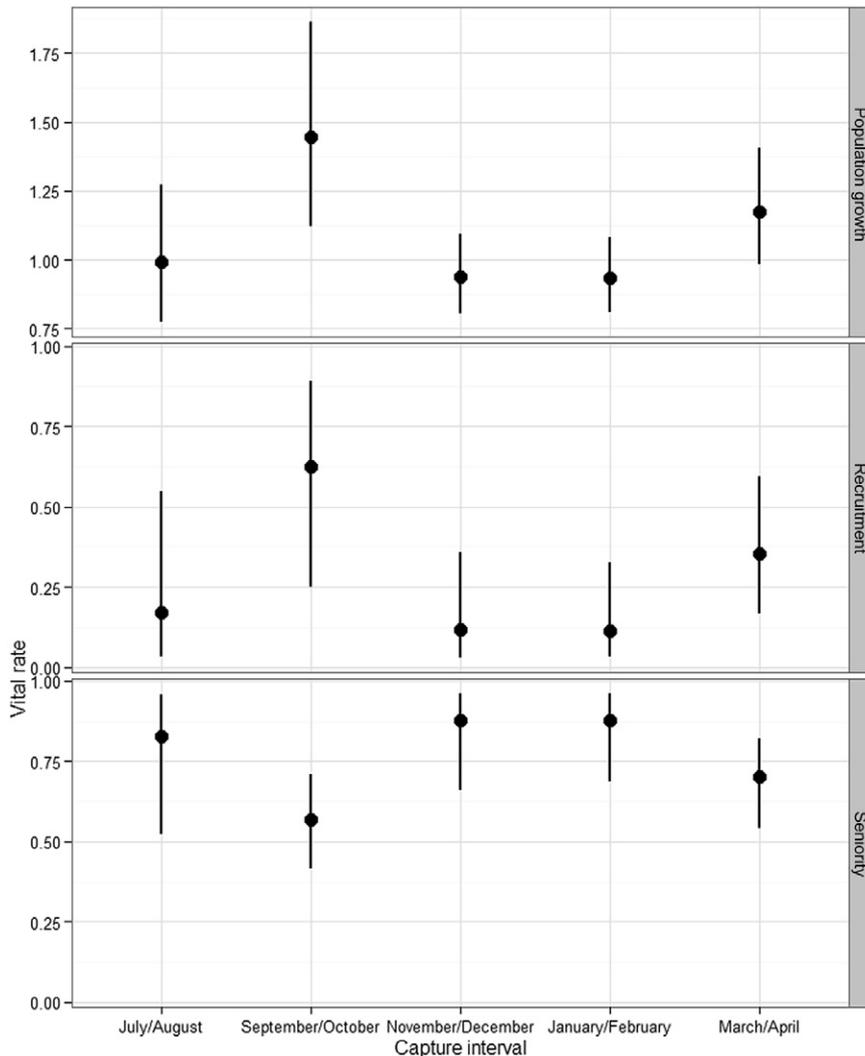


Figure 2 Estimates and 95% capture intervals (CI) of monthly realized population growth, recruitment and seniority for the Key Largo woodrat *Neotoma floridana smalli* for each trapping interval from July 1995 to June 1996 and July 2000 to May 2001.

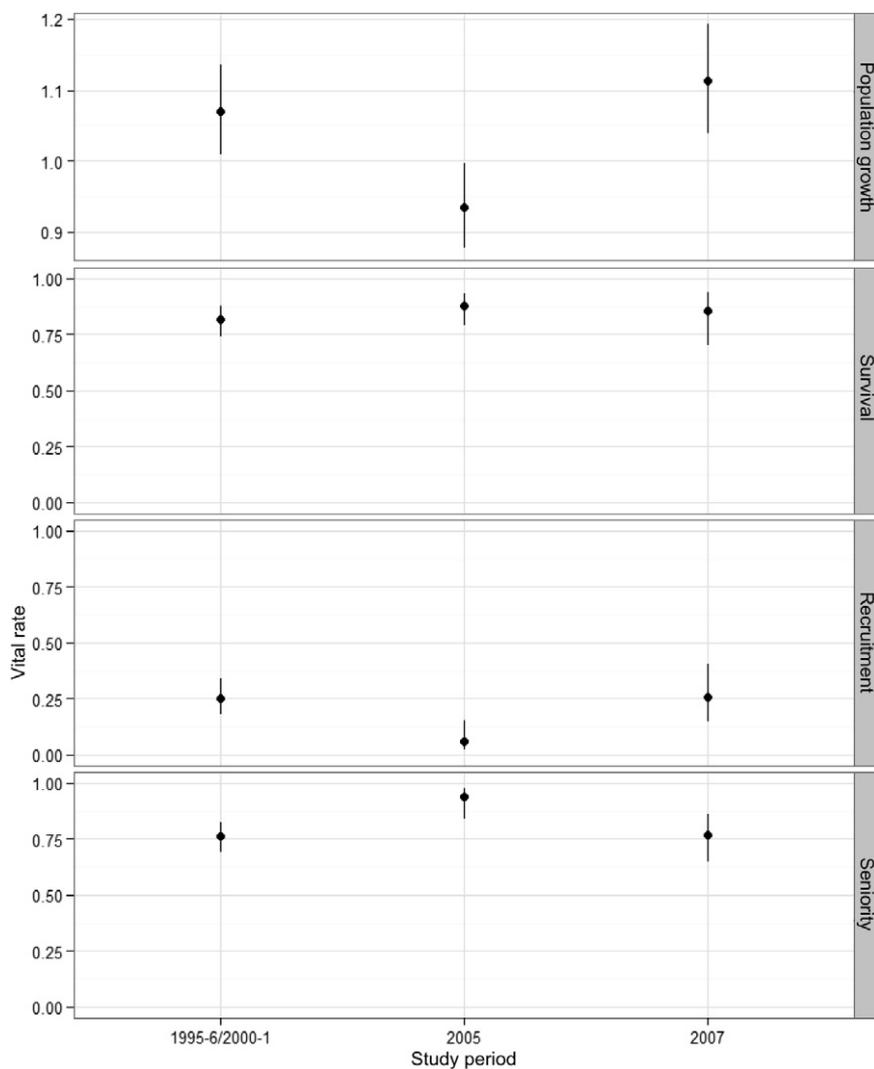


Figure 3 Estimates and 95% capture intervals (CI) of realized population growth, recruitment, survival and seniority for the Key Largo woodrat *Neotoma floridana smalli* from July 1995 to June 1996 and July 2000 to May 2001, May 2005 to November 2005, and March 2007 to December 2007.

structure for other well-supported models varied among datasets. For 1995–1996/2000–2001 dataset, models with sex and study-period effects also received substantial support (Table 1), providing some evidence for sex- and time-specific (CI and study period) variation in survival.

Model selection for λ differed between 1995–1996/2000–2001 and the other datasets, with temporal (CI) variation in λ as the most parsimonious (Table 1). Based on this model, λ was greater than 1.0 during two CIs (Fig. 2); September/October [$\lambda = 1.444$ (1.121–1.862)] and March/April [$\lambda = 1.175$ (0.982–1.405)]. The models, including an additive effect of sex and study period along with CI, also received substantial support. For 2005 and 2007 datasets, the models with constant growth rate were the most parsimonious. Based on these models, monthly realized population growth rates were 0.935 [(0.877–0.997), annual growth $\lambda^{12} = 0.446$] and 1.113 [(1.038–1.193), $\lambda^{12} = 3.613$] for the 2005 and 2007 datasets, respectively. Models with sex and CI effects on λ also received substantial support; however, in both cases, the addition of an

extra parameter did not improve model parsimony (Table 1). Overall, the population grew during 1995–1996/2000–2001 [$\lambda = 1.070$ (1.008–1.136), $\lambda^{12} = 2.252$] and 2007 but declined during 2005 (Fig. 3).

Model selection results for f or γ were identical to λ for all datasets (Table 2). Increases in f across the study periods corresponded with increases in λ (Fig. 3). Average monthly f was high in 1995–1996/2000–2001 [0.253 (0.181–0.341)] and 2007 [0.255 (0.149–0.403)] and greatly reduced in 2005 [0.057 (0.02–0.154); Fig. 3]. The proportional contribution of f and Φ to λ , as measured by γ , was similar for 1995–1996/2000–2001 [0.764 (0.689–0.825)] and 2007 [0.770 (0.644–0.861)] when λ was increasing, but γ increased during 2005 [0.939 (0.839–0.978)] when λ was decreasing [0.935 (0.877–0.997)].

Examining parameter estimates from the best models graphically, there was seasonal and annual covariation between f and λ , with both increasing and decreasing together (Figs 2 and 3). This suggests a strong influence of f on λ . Similarly, f covaried with changes in γ and appeared to con-

Table 2 Model comparison for recruitment rates (f) of Key Largo woodrats *Neotoma floridana smalli*, evaluating the effect of capture interval (CI), sex and study period (SP)

	Model	K	AICc	Δ AICc	weight
1995–1996/2000–2001	f (CI)	7	359.057	0.000	0.400
	f (sex + CI)	8	360.621	1.564	0.183
	f (SP + CI)	8	361.241	2.184	0.134
	f (.)	3	361.626	2.569	0.111
	f (sex + SP + CI)	9	362.856	3.798	0.060
	f (sex)	4	363.041	3.983	0.055
	f (SP)	4	363.696	4.639	0.039
	f (sex + SP)	5	365.157	6.100	0.019
2005	f (.)	3	173.370	0.000	0.524
	f (sex)	4	175.416	2.046	0.188
	f (CI)	4	175.541	2.170	0.177
	f (sex + CI)	5	176.481	3.111	0.111
2007	f (.)	3	173.250	0.000	0.400
	f (sex)	3	173.708	0.457	0.318
	f (CI)	4	175.102	1.851	0.158
	f (sex + CI)	5	175.600	2.350	0.123

Results are presented separately for three datasets (1995–1996/2000–2001, 2005 and 2007). For these analyses, model structures for probability (P) and survival (Φ) were fixed to that identified as most parsimonious in Table 1 for the respective datasets. The table includes the number of parameters (K), Akaike's information criterion corrected for small sample size (AICc), difference in AICc (Δ AICc) and model weights. The most parsimonious model for each analysis is highlighted in bold.

tribute more to changes in γ than in Φ , which varied little annually and was constant across seasons (Figs 2 and 3).

True survival

There were 91 captive KLWRs housed in the Lowry Park Zoo and Disney's Animal Kingdom for an average of 885 days. A total of 35 fatalities were recorded over the 9-year period. Additionally, 58 wild-born adult KLWRs were radio-tracked for an average of 80 days over a 15-month period, with 10 known fatalities. The released group consisted of 40 adult KLWRs radio-tracked for an average of 49 days, with 33 known fatalities. All but one KLWR mortality for both wild-born and released groups were believed to be caused by predation.

The survival curve was higher ($\chi^2 = 7.1$, 1 d.f., $P = 0.008$) for captive KLWRs [$S_1 = 0.978$ (0.963–0.993); $S_{1-3} = 0.988$; (0.982–0.994)] than for wild-born KLWRs [$S_1 = 0.929$ (0.890–0.968); $S_{1-3} = 0.942$ (0.919–0.965)] (Fig. 4). There was no difference in survival between the sexes for either groups (captive: $\chi^2 = 2.0$, 1 d.f., $P = 0.160$; wild-born: $\chi^2 = 0.10$, 1 d.f., $P = 0.815$) and between release sites ($\chi^2 = 1.4$, 1 d.f., $P = 0.235$). Finally, survival for the wild-born KLWRs was higher ($\chi^2 = 33.9$, 1 d.f., $P = 0.001$) than the released group [$S_1 = 0.521$ (0.442–0.600); $S_{1-3} = 0.561$ (0.493–0.629)]; there was no evidence that survival differed between sexes ($\chi^2 = 1.50$, 1 d.f., $P = 0.222$).

Discussion

Our results suggest that the KLWR population has not been consistently declining over the last several decades; in fact, it

was growing during three of the four time periods examined from 1995 to 2007, with annual growth rates $>25\%$. However, the data used in this study were likely biased toward years of relatively high KLWR populations. We know of at least one instance in 2002 when KLWR trapping efforts were suspended because no KLWRs were captured. Some of the trapping data might have also been biased toward periods of recruitment in the late spring and early fall, potentially biasing estimates of λ and the contribution of f to λ . However, the 2005 trapping effort (May–November) was the most likely to be skewed toward periods of recruitment, yet our analysis suggested dramatic population declines during that time, with annual declines approaching 55%.

Our analysis clearly shows that KLWR population fluctuated from 1995 to 2007, but our data and analysis were not designed to make inferences about overall changes in population abundance during that time period. Rodents are well known for their rapid population fluctuations (Taylor & Green, 1976; Elias, Witham & Hunter, 2004), and we found evidence for substantial fluctuations in realized population KLWR growth rate, which make the population more vulnerable to extinction (McCleery *et al.*, 2005). In concordance with other studies on KLWRs, we also found that the population fluctuated seasonally with peaks in recruitment from August to November (Hersh, 1981; Sasso & Gaines, 2002).

The consistent and strong seasonal and annual covariation between f and λ , with both increasing and decreasing together (Figs 2 and 3), coupled with no apparent covariation between Φ on λ , suggests that KLWR population was driven primarily by variation in recruitment. The strong covariation between f and λ was not consistent with the predation hypothesis, which

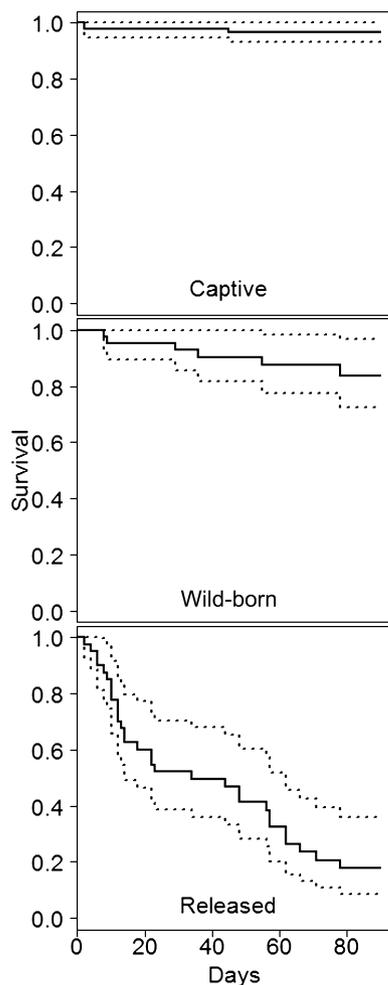


Figure 4 Comparison of Kaplan–Meier survival curves and 95% capture intervals (CI) from captive [Lowry Park Zoo ($n = 33$), Disney Animal Kingdom ($n = 58$)], wild-born [2002 ($n = 19$), 2007 ($n = 39$)], and captive-bred Key Largo woodrat *Neotoma floridana smalli* that were released in Key Largo ($n = 25$) and Palo Alto Key ($n = 15$), FL.

postulates that reduced survival rates of post-juvenile KLWRs due to predation by pythons, cats or raccoons were limiting the population. Survival varied little over the four study periods; in fact, Φ was the lowest in 1995–1996/2000–2001 before feral cats and pythons were perceived to be a major problem (Hersh, 1981; Humphrey, 1992; Sasso & Gaines, 2002).

It appears more likely that periodic reduction in recruitment due to reduced reproduction may have led to population declines. Research on Allegheny woodrats *Neotoma magister* and other rodents has shown a strong relationship among food availability (Selås, 1997; Elias *et al.*, 2004; Marcello, Wilder & Meikle, 2008), weather patterns and recruitment (Taylor & Green, 1976; Clotfelter *et al.*, 2007; Wood, 2008). In areas with distinct wet and dry season like Key Largo, reproductive rates of rodents have been linked to the onset and intensity of rainfall during the wet season (Leirs *et al.*, 1996; Madsen & Shine, 1999).

To investigate *a posteriori* if rainfall patterns might have influenced KLWR population, we examined monthly rainfall data during the wet season (May–September) for each study period from the US Weather Service Station in Tavernier, FL, on the Island of Key Largo and supplemented missing data with records from the nearest continually operational weather station in Miami Beach, FL. The study period with the lowest f , 2005, corresponded to the lowest rainfall totals (1995–1996 = 110 cm, 2000–2001 = 83 cm, 2005 = 64 cm, 2007 = 94 cm), suggesting a possible link between f and rainfall. Rainfall in the hardwood hammocks of the Key Largo has been positively correlated with the production of fruits (Bancroft *et al.*, 2000) that are an important part of the KLWR's diet (Humphrey, 1992). Thus, a possible mechanism for changes in f may be variation in food supplies caused by seasonal and/or annual variation in rainfall patterns. Alternatively, reductions in f may have been due to poor survival of nestlings (birth to 2–3 months), predation of dispersing juveniles or juvenile KLWRs leaving the trapping grids before being detected. As such, there is a need to better understand the demographics of KLWRs before they reach a trappable age.

Captive-breeding and release program

Not surprisingly, the estimate of true survival for captive KLWRs was higher than the estimate for the wild-born KLWRs. Released KLWRs had low survival rates during the first 3 months post-release, with only a few released KLWR surviving long enough to make a meaningful contribution to population growth through reproduction. Using current protocols, it appears that captive release of KLWR is not an effective management tool for augmenting the population. This finding should not be surprising; the reintroductions of most endangered species are unsuccessful, particularly when captive-bred animals are released into the wild (Snyder *et al.*, 2002; Mathews *et al.*, 2005).

The rapid mortality of most of the reintroduced KLWRs suggests that released animals were not prepared for integration into the wild population. Research on captive animals shows that captivity may lead to a reduction in anti-predator behaviors (McPhee, 2004) or a loss of opportunities for captive animals to learn how to recognize and avoid predators (Griffin, Blumstein & Evans, 2000; Seddon *et al.*, 2007). To reduce post-release mortality, many release programs using captive-bred animals utilize pre-release conditioning (Seddon *et al.*, 2007). Although not a panacea, conditioning programs can increase the survival rates of released captive-bred animals (Shier & Owings, 2006). Another viable option may be an *in situ* captive-breeding program, raising KLWR in an outdoor facility in Key Largo. This type of program has the advantage of exposing captive animals to natural environmental and climatic conditions, as well as potentially reducing the stress of captive animals once they are released into free-ranging conditions (Kock, Soorae & Mohammed, 2007).

Conclusion

The demographic insights from this study force scientists and managers to rethink how they understand and mitigate

declines in the KLWR population. Our results suggest that high predation was the primary cause of mortality of released KLWR, leading to the failure of a CBRP. However, there was little evidence that predation of post-juvenile KLWRs caused precipitous declines in the population. KLWR population dynamics appear to be driven by temporal variation in recruitment, with variation in survival playing a relatively minor role. This study clearly illustrates the importance of simultaneously considering reproductive and survival parameters when attempting to discern demographic mechanisms underlying population declines in rare or endangered species. Finally, our research illustrates the difficulties with CBRP and the necessity of preparing captive animals for release in their native habitats.

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References

- Aaltonen, K., Bryant, A.A., Hostetler, J.A. & Oli, M.K. (2009). Reintroducing endangered Vancouver Island marmots: survival and cause-specific mortality rates of captive-born versus wild-born individuals. *Biol. Conserv.* **142**, 2181–2190.
- Alligood, C.A., Daneault, A.J., Carlson, R.C., Dillenbeck, T., Wheaton, C.J. & Savage, A. (2011). Development of husbandry practices for the captive breeding of Key Largo woodrats (*Neotoma floridana smalli*). *Zoo Biol.* **30**, 318–327.
- Bancroft, G.T., Bowman, R. & Sawicki, R.J. (2000). Rainfall, fruiting phenology, and the nesting season of White-crowned pigeons in the upper Florida Keys. *Auk* **117**, 416–426.
- Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd edn. New York: Springer-Verlag.
- Clotfelter, E.D., Pedersen, A.B., Cranford, J.A., Ram, N., Snajdr, E.A., Nolan, V. & Ketterson, E. (2007). Acorn mast drives long-term dynamics of rodent and songbird populations. *Oecologia* **154**, 493–503.
- Cole, L. (1954). The population consequences of life-history phenomena. *Q. Rev. Biol.* **29**, 103–137.
- Elias, S.P., Witham, J.W. & Hunter, M.L. (2004). *Peromyscus leucopus* abundance and acorn mast: population fluctuation patterns over 20 years. *J. Mammal.* **85**, 743–747.
- Forys, E.A. & Humphrey, S.R. (1999). Use of population viability analysis to evaluate management options for the endangered Lower Keys marsh rabbit. *J. Wildl. Mgmt.* **63**, 251–260.
- Greene, D.U., Potts, J.M., Duquesnel, J.G. & Snow, R.W. (2007). Geographic distribution: *Python molurus bivittatus* (Burmese python). *Herpetol. Rev.* **38**, 355.
- Greene, D.U., Mengak, M.T. & Castleberry, S.B. (2013). A methodology for long-term population monitoring of the endangered Key Largo cotton mouse. *Wildl. Soc. Bull.* doi: 10.1002/wsb.282.
- Griffin, A.S., Blumstein, D.T. & Evans, C.S. (2000). Training captive-bred or translocated animals to avoid predators. *Conserv. Biol.* **14**, 1317–1326.
- Hersh, S.L. (1981). Ecology of the Key Largo woodrat (*Neotoma floridana smalli*). *J. Mammal.* **62**, 201–206.
- Hines, J.E. & Nichols, J.D. (2002). Investigations of potential bias in the estimation of lambda using Pradel's 1996 model for capture–recapture data. *J. Appl. Stat.* **29**, 573–587.
- Humphrey, S.R. (1992). Key Largo woodrat. In *Rare and endangered biota of Florida*: Vol. I, 119–130. Humphrey, S.R. (Ed.). Gainesville: University of Florida Press.
- Jule, K.R., Leaver, L.A. & Lea, S.E.G. (2008). The effects of captive experience on reintroduction survival in carnivores: a review and analysis. *Biol. Conserv.* **141**, 355–363.
- Kaplan, E.L. & Meier, P. (1958). Nonparametric estimation from incomplete observations. *J. Am. Stat. Assoc.* **53**, 457–481.
- Karim, A. & Main, M.B. (2009). Habitat fragmentation and conservation strategies for a rare forest habitat in the Florida Keys archipelago. *Urban Ecosyst.* **12**, 359–370.
- Kleinbaum, D.G. & Klein, M. (2005). *Survival analysis: a self-learning approach*. 2nd edn. New York: Springer.
- Kock, R.A., Soorae, P.S. & Mohammed, O.B. (2007). Role of veterinarians in re-introductions. *Int. Zoo Yearb.* **41**, 24–37.
- Laake, J. & Rextad, E. (2008). RMark – an alternative approach to building linear models in MARK. In *Program MARK: a gentle introduction*: C1–C115. Cooch, E. & White, G. (Eds). Available at <http://www.phidot.org/software/mark/docs/book/>. Accessed 15 March 2012.
- Leirs, H., Verhagen, R., Verheyen, W., Mwanjabe, P. & Mbise, T. (1996). Forecasting rodent outbreaks in Africa: an ecological basis for mastomys control in Tanzania. *J. Appl. Ecol.* **33**, 937–943.
- Lima, M. & Jaksic, F.M. (1999). Survival, recruitment and immigration processes in four subpopulations of the leaf-eared mouse in semiarid Chile. *Oikos* **85**, 343–355.
- Madsen, T. & Shine, R. (1999). Rainfall and rats: climatically-driven dynamics of a tropical rodent population. *Aust. J. Ecol.* **24**, 80–89.
- Marcello, G.J., Wilder, S.M. & Meikle, D.B. (2008). Population dynamics of a generalist rodent in relation to variability in pulsed food resources in a fragmented landscape. *J. Anim. Ecol.* **77**, 41–46.
- Mathews, F., Orros, M., McLaren, G., Gelling, M. & Foster, R. (2005). Keeping fit on the ark: assessing the suitability

- of captive-bred animals for release. *Biol. Conserv.* **121**, 569–577.
- McCleery, R.A., Lopez, R.R., Silvy, N.J., Frank, P.A. & Klett, S.B. (2006). Population status and habitat selection of the endangered Key Largo woodrat. *Am. Midl. Nat.* **155**, 197–209.
- McCleery, R.A., Lopez, R.R., Silvy, N.J. & Grant, W.E. (2005). Effectiveness of supplemental stockings for the endangered Key Largo woodrat. *Biol. Conserv.* **124**, 27–33.
- McPhee, M.E. (2004). Generations in captivity increases behavioral variance: considerations for captive breeding and reintroduction programs. *Biol. Conserv.* **115**, 71–77.
- Oli, M.K. & Dobson, F.S. (2003). The relative importance of life-history variables to population growth rate in mammals: Cole's prediction revisited. *Am. Nat.* **161**, 422–440.
- Potts, J.M., Buckland, S.T., Thomas, L. & Savage, A. (2012). Estimating abundance of cryptic but trappable animals using trapping point transects: a case study for Key Largo woodrats. *Method. Ecol. Evol.* **3**, 695–703.
- Pradel, R. (1996). Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics* **52**, 703–709.
- Pradel, R., Johnson, A.R., Viallefont, A., Nager, R.G. & Cézilly, F. (1997). Local recruitment in the greater flamingo: a new approach using capture-mark-recapture data. *Ecology* **78**, 1431–1445.
- R Development Core Team (2011). *R: a language and environment for statistical computing in R foundation for statistical computing*. Vienna. Available at <http://www.r-project.org>. Accessed 15 March 2012.
- Rave, E.H. & Holler, N.R. (1992). Population dynamics of beach mice (*Peromyscus polionotus ammobates*) in southern Alabama. *J. Mammal.* **73**, 347–355.
- Reed, A.W. & Slade, N.A. (2008). Density-dependent recruitment in grassland small mammals. *J. Anim. Ecol.* **77**, 57–65.
- Reid, J.M., Bignal, E.M., Bignal, S., McCracken, D.I., Bogdanova, M.I. & Monaghan, P. (2008). Investigating patterns and processes of demographic variation: environmental correlates of pre-breeding survival in red-billed choughs *Pyrrhonorax pyrrhonorax*. *J. Anim. Ecol.* **77**, 777–788.
- Sasso, C.R. & Gaines, M.S. (2002). Population ecology of three species of small mammals on Key Largo, Florida. *Fla. Sci.* **65**, 115–125.
- Schorr, R.A. (2012). Using a temporal symmetry model to assess population change and recruitment in the Preble's meadow jumping mouse (*Zapus hudsonius preblei*). *J. Mammal.* **93**, 1273–1282.
- Seddon, P.J., Armstrong, D.P. & Maloney, R.F. (2007). Developing the science of reintroduction biology. *Conserv. Biol.* **21**, 303–312.
- Selås, V. (1997). Cyclic population fluctuations of herbivores as an effect of cyclic seed cropping of plants: the mast depression hypothesis. *Oikos* **80**, 257–268.
- Shier, D.M. & Owings, D.H. (2006). Effects of predator training on behavior and post-release survival of captive prairie dogs (*Cynomys ludovicianus*). *Biol. Conserv.* **132**, 126–135.
- Sinclair, A.R.E., Pech, R.P., Dickman, C.R., Hik, D., Mahon, P. & Newsome, A.E. (1998). Predicting effects of predation on conservation of endangered prey. *Conserv. Biol.* **12**, 564–575.
- Skalski, J.R., Ryding, K.E. & Millspaugh, J.J. (2005). *Wildlife demography: analysis of sex, age, and count data*. Burlington: Elsevier Academic Press.
- Snyder, N.F., Derrickson, S.R., Beissinger, S.R., Wiley, J.W., Smith, T.B., Toone, W.D. & Miller, B. (2002). Limitations of captive breeding in endangered species recovery. *Conserv. Biol.* **10**, 338–348.
- Taylor, K.D. & Green, M.G. (1976). The influence of rainfall on diet and reproduction in four African rodent species. *J. Zool. (Lond.)* **180**, 367–389.
- Therneau, T. & Lumley, T. (2011). *Survival: survival analysis, including penalized likelihood, 2011*. R package version, 2.36.
- White, G.C. & Burnham, K.P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**, 120–138.
- Winchester, C. (2007). *An evaluation of habitat selection and an abundance estimate for the endangered Key Largo woodrat*. MS thesis, University of Georgia, Athens, GA.
- Winchester, C., Castleberry, S.B. & Mengak, M.T. (2009). Evaluation of factors restricting distribution of the endangered Key Largo woodrat. *J. Wildl. Mgmt.* **73**, 374–379.
- Wood, P.B. (2008). Woodrat population dynamics and movement patterns. In *The Allegheny woodrat: ecology, conservation and management of a declining species*: 45–62. Peles, J.D. & Wright, J. (Eds). New York: Springer.