



## Research Article

# Monitoring Coyote Population Dynamics With Fecal DNA and Spatial Capture–Recapture

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**ABSTRACT** Estimating coyote (*Canis latrans*) density and other demographic parameters is difficult, particularly for populations that exist at low density. This is the situation for recently established coyote populations in the eastern United States where populations may be below carrying capacity and growth unregulated. We used non-invasive fecal DNA collected from 5 scat sampling sessions over 2.5 years to estimate population parameters (i.e., density, apparent survival, recruitment, and population growth) for coyotes at 2 different sites in the Ridge and Valley region of the central Appalachians in Virginia, USA. We identified individuals using microsatellite genotypes and estimated apparent survival for the local population at both sites across the 5 sessions in a single Cormack–Jolly–Seber model. We estimated density for each site and session separately using single session spatial replicates of 0.5-km transect segments as traps in a spatial capture–recapture model. Finally, we derived estimates of recruitment and population growth using an ad hoc robust design approach. We were able to estimate population parameters, even though coyote densities at both sites were low. Generally, derived recruitment and apparent survival were inversely related across sites, however, precision in estimates was poor. Thus, although there appeared to be some differences in demographic estimates for local coyote populations, uncertainty in parameters was too great to detect changes in demographic rates over short periods of time using ad hoc robust design. However, the non-invasive genetic sampling and spatial capture–recapture approach provides a useful methodology and framework for future research intended to estimate population dynamics for coyotes. This method will also be useful for other species that occur at low densities, over large spatial scales, and lack distinguishing marks for camera-trap surveys. Finally, we believe this method will allow for detection of population trends over greater periods of time, and we consider alternate sampling strategies and modeling approaches that may improve the ability to estimate demographic rates of change for coyote populations using noninvasive genetics and spatial capture–recapture. © 2016 The Wildlife Society.

**KEY WORDS** ad hoc robust design, apparent survival, *Canis latrans*, coyote, density dependence, density estimation, non-invasive genetic sampling, population dynamics, recruitment, spatial capture–recapture.

Over the last 2 centuries coyotes (*Canis latrans*) have expanded their range from the central plains of the United States, prior to European settlement, to most of North America (Bekoff 1978, Parker 1995, Gompper 2002a, Kays et al. 2008). As a result, human–coyote conflicts have increased, inciting concerns about the potential impacts to prey and competitors (Litvaitis and Harrison 1989, Gompper 2002b, Kilgo et al. 2012). As coyote populations expanded into each new area, the natural resource agencies and state legislatures often responded with attempts to limit expansion, reduce coyote densities, and manage conflict with humans using lethal removals (Houben 2004). However, lethal

removal efforts have yielded little to no success (Conner and Morris 2015). Therefore, it is of practical use to obtain estimates of coyote demographic parameters to evaluate population responses to management efforts and to understand why current management strategies are unsuccessful.

Management of animal populations requires influencing  $\geq 1$  of 4 population processes (i.e., inputs [births and immigration] and outputs [mortality and emigration]), and success is ideally measured by changes in local abundance or density (Cole 1954, Nichols et al. 2000, Williams et al. 2002). Thus, estimating and understanding local densities and population dynamics is critical to making informed management decisions (Kéry and Schaub 2012). Eastern coyote populations may have high mortality rates, exhibit complex adaptive social structures, and can occur at low densities over broad spatial scales (Kamler and Gipson 2000, Patterson and Messier 2001, Hinton et al. 2015). As a result, obtaining unbiased estimates of coyote population parameters has been difficult and often requires problematic

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assumptions about closure, counts, or detection (Bozarth et al. 2015, Gulsby et al. 2015, Hansen et al. 2015).

Effectively estimating population parameters requires a way to count individuals and a way to account for imperfect detection of individuals. Traditionally, these concepts have been addressed with capture–recapture models using repeated encounters with marked individuals over time through the visual observation of natural or applied individual marks (Otis et al. 1978, Williams et al. 2002). Application of capture–recapture methods has been limited with coyotes because they are difficult to capture and recapture at encounter rates required for reliable parameter estimation (Gulsby et al. 2015). Although camera traps have improved our ability to monitor many carnivore populations (O’Connell et al. 2010, Meek et al. 2014), coyotes do not typically have distinguishing marks to allow for use of traditional camera trap designs. Although it is possible to collar coyotes and use mark–resight models (McClintock and White 2009; Sollmann et al. 2013 $a,b$ ; Alonso et al. 2015) based on camera trap resightings of collared individuals at specific locations, this would violate the assumption of equal capture–recapture probabilities across space, resulting in biased estimates (Royle et al. 2013 $b$ ). In addition, coyote movement and space use are highly variable (Hinton et al. 2015). Therefore, recent development of unmarked individual count models that use minimal encounter information (Royle 2004, Chandler and Royle 2013) are unemployable because model assumptions of similar movement, critical for accurate estimates, are unlikely met for coyote populations. Finally, coyote individual behavior and space use can result in an unknown amount of capture heterogeneity determined solely by where a capture grid is placed in relation to individual home ranges. This likely violates assumptions about geographic closure and impedes our ability to estimate an effective sampling area (Royle et al. 2013 $b$ ).

Two recent advancements in population monitoring improve our ability to identify individual coyotes and to account for detection in estimating density and effective trapping area given large-scale coyote space use. Non-invasive genetic sampling (NGS) allows for detection of individuals without the need for physical capture (Waits and Paetkau 2005). This method has seen prolific recent use, particularly for monitoring carnivores and other elusive and wide-ranging species (Lampa et al. 2013). Spatial capture–recapture (SCR) models allow for the estimation of density based on the movement of marked individuals around activity centers over multiple possible encounters (Royle and Young 2008, Royle et al. 2013 $b$ ). Thus, SCR allows for explicit modeling of inherent spatial heterogeneity in encounter probabilities and can provide unbiased estimates of density (no. individuals over a unit of area) for an area of interest.

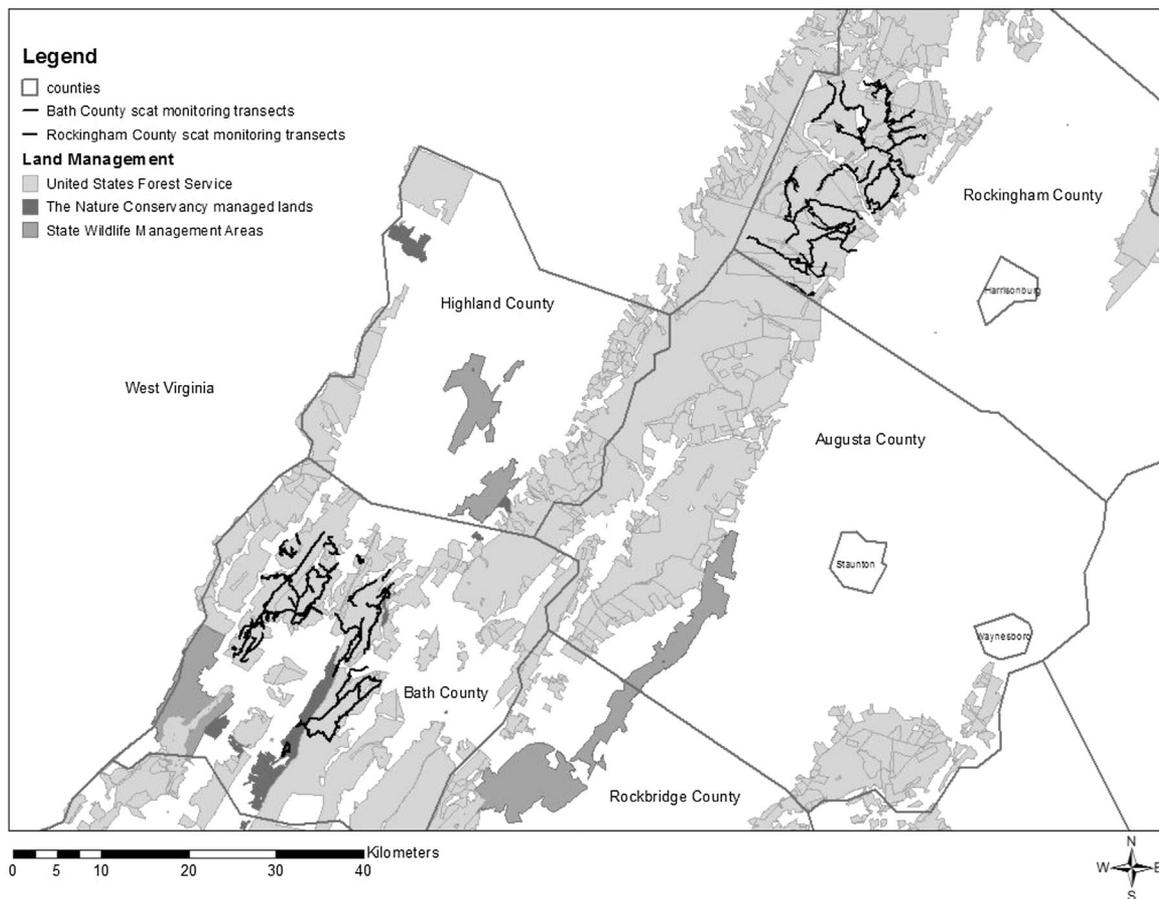
We combined NGS and SCR methods to estimate local coyote densities over multiple sessions at 2 sites in western Virginia, USA. We expected to find differences in local population dynamics between sites as a result of different intensities of harvest (permitted year-round) and available resources. We predicted that mortality and subsequent

recruitment would be greater in areas with higher human population density and private inholdings that allowed for greater opportunity for coyote harvest compared to areas with lower human density. Because annual density was also expected to be dependent on prey availability (Knowlton et al. 1999), we predicted density would be greater at sites with greater habitat diversity and potential anthropogenic food resources from interspersed human and agricultural habitats (Rose and Polis 1998, Fedriani et al. 2001). Finally, we predicted local densities would fluctuate seasonally as a result of reproduction and dispersal (Knowlton et al. 1999) with greater densities in the summer following birth of pups and lower densities in the winter following dispersal.

## STUDY AREA

We conducted surveys from June 2011 to July 2013 in 2 study areas, 1 in each of 2 counties in Virginia: Bath and Rockingham counties. Both are located along the eastern divide in the northern Ridge and Valley province of the central Appalachians, bordering West Virginia, USA (Fig. 1). The region, transitioning from the Shenandoah Valley to the Appalachian Plateau, is characterized by karst topography with elongated mountain ridges and narrow valleys. Elevation in Bath County ranges from 350 m to 1,365 m, and 363 m to 1,335 m in Rockingham County. Average monthly temperature can range from 0.7°C to 25.1°C, with a mean minimum temperature of –4.6°C in January and a mean maximum temperature of 31.6°C in July (National Oceanic and Atmospheric Administration, public data 2012). Average annual precipitation was 97.79 cm, with most precipitation occurring between March and September (National Oceanic and Atmospheric Administration, public data 2012). Both study areas consisted primarily of mature hardwood forest habitat with low coyote densities (Tremblay et al. 1998, Richer et al. 2002, Kays et al. 2008). Forest habitat structure consists of a canopy including chestnut oak (*Quercus prinus*), red oak (*Q. rubra*), white oak (*Q. alba*), and tulip poplar (*Liriodendron tulipifera*), and an understory including rhododendron (*Rhododendron maximum*) and eastern mountain laurel (*Kalmia latifolia*). There was a diversity of potential prey species including white-tailed deer (*Odocoileus virginianus*), rabbits (*Sylvilagus* spp.), squirrels (*Sciurus* spp.), voles (*Microtus* spp.), and mice (*Peromyscus* spp.). However, all animal populations were potentially limited by low nutritional carrying capacity in the region (DeCalesta 1997, Diefenbach et al. 1997). In addition, 2 other predators in the region, bobcats (*Lynx rufus*) and American black bears (*Ursus americanus*), likely competed with coyotes for limited resources.

Outdoor recreation was the primary land use in both study areas. The Bath County study area is located in the northwest portion of the county and movement of individuals within this study area extended into Highland and Allegheny Counties, Virginia, and Pocahontas and Greenbrier Counties, West Virginia. The Rockingham study area was located in the western portion of the county, and estimated home ranges extended into Pendleton County, West Virginia. The



**Figure 1.** Locations of roughly 200 km of scat transects in each of 2 study areas (Bath County to the south, and Rockingham County to the north) in western Virginia. Transects were located on existing dirt roads and trails on public managed lands and surveys repeated over 5 periods from 2011 to 2013 to estimate density and population demographics for coyotes.

Rockingham County study area was located in a large block of contiguous forest in the George Washington National Forest, whereas the Bath County study area was placed in predominantly forest habitat on federal and state public lands (~57% of Bath County), and was interspersed with veins of more productive pasture, hayfields, and human development along linear valley bottoms (Morin 2015). We focused sampling within a 250-km<sup>2</sup> survey area at each site, but because of the size of coyote home ranges overlapping with the survey area, the size of each study area was much larger (estimated state space size varied between ~900 km<sup>2</sup> and ~1,200 km<sup>2</sup>; see below).

## METHODS

### Sample Collection

We collected fecal DNA samples over 5 closed sessions at each study site, 3 summer sessions (Jul 2011, 2012, and 2013) and 2 winter sessions (Feb 2012 and Mar 2013), to estimate rates of change over intervals with expected population inputs (reproduction in spring) and population outputs (dispersal and potential for increased mortality during fall hunting seasons). We established approximately 200 km of scat transects along dirt roads, hiking trails, and well-defined

game trails on publicly managed lands (predominantly George Washington National Forest) in each study area: 213 km in Bath County, 208.5 km in Rockingham County. Scat accumulation rates can be slow for highly mobile, low-density populations (Lonsinger et al. 2015). Conducting repeated secondary sampling sessions (temporal replicates) to estimate detection within sessions can violate closure assumptions when scat accumulation periods are lengthy, especially if apparent survival is low. Thus, we chose to use single-session detections over spatial replicates during a single month for each sampling session to satisfy the population closure assumption. We first cleared scat from all transects and then collected fecal DNA samples and recorded global positioning system (GPS) locations for all newly accumulated scats 1 month later.

In addition to the samples collected for the closed sessions for this study, we collected samples for separate surveys in the same study areas (concurrent sampling sessions). We used all closed session and concurrent session scat samples for genetic analysis to identify individuals, and then used a subset of data consisting only of the closed session samples to create encounter histories for closed population models. Sampling methods were approved by the Virginia Tech Institutional Animal Care and Use Committee (permit #10-117-FIW)

and permitted by the Virginia Department of Game and Inland Fisheries (permit #041503).

### Identifying Individual Coyotes From Scat Samples

We extracted DNA from feces using Qiagen QIAmp DNA stool kit (Qiagen, Valencia, CA, USA) in a lab designated for low-quality, low-quantity DNA and included an extraction negative in each batch. We screened all samples using a species identification multiplex that allows co-amplification and fragment analysis of 2 segments of the mitochondrial DNA (mtDNA) control region for scoring species-specific fragment sizes (De Barba et al. 2014). The 2 study sites were located in the assumed convergence zone of the northern and southern fronts of eastern coyote range expansion (Parker 1995, Kays et al. 2008), which indicated gray wolf (*Canis lupus*) mtDNA haplotypes may occur in the population. In addition, Adams et al. (2003) reported domestic dog mtDNA haplotypes in coyotes in the southeastern United States. Two tissue samples collected from 19 different individual coyotes captured in the Bath County study area (Morin 2015) were identified as possible domestic dog or gray wolf based on amplified fragment sizes from the mtDNA test. Thus, we attempted to genotype all samples identified as canid (*Canis* spp.) and screened for domestic dogs using a more sensitive nuclear DNA (nDNA) genotype assignment test as described below. To determine genotypes, we combined 9 nuclear microsatellite loci and canid sex-specific identification primers (Seddon 2005) in a multiplex for polymerase chain reaction (PCR) amplification and analyzed samples using the Applied Biosystems 3130xl ABI capillary machine (Applied Biosystems, Foster City, CA, USA) and associated software as described in Stenglein et al. (2011). We included a PCR positive (known coyote tissue sample) and PCR negative control in each PCR plate to identify PCR failure or potential contamination.

We initially performed PCR for each sample twice to cull poor quality nDNA samples (i.e., samples with <50% amplification across the 9 loci not associated with sex chromosomes). We then repeated PCR 1–3 more times for each sample to confirm alleles for each locus. We required 2 repetitions to confirm heterozygous loci and 3 repetitions to confirm homozygous loci to minimize potential genotyping errors in low quality-low quantity DNA samples from allelic dropout and polymerase errors (Taberlet et al. 1996). We used RELIOTYPE (Miller et al. 2002) to confirm >95% accuracy of genotypes observed in only a single sample.

Finally, we added scat sample genotypes collected for this study (closed sessions for population monitoring) to scat sample genotypes identified from concurrent monitoring efforts from other surveys in both study areas. Although these other samples were not collected during the established closed-density monitoring sessions, we combined samples from all scat collection efforts in the 2 study areas only for genetic analyses to improve sample sizes for assignment tests and estimation of summary population genetics statistics required to estimate probability of identity siblings,  $P_{ID(sibs)}$  (Waits et al. 2001). We did not include the additional samples in models to estimate population demographic

parameters described below. We calculated  $P_{ID(sibs)}$  in GenAlEx 6.501 (Peakall and Smouse 2006, 2012) using an allele frequency data set consisting of individual coyotes identified with fecal DNA with alleles confirmed at all loci and tissue samples from 19 captured individuals in the study area (Morin 2015). We matched genotypes from different scat samples to the same individual canid using GenAlEx 6.501 and the calculated  $P_{ID(sibs)}$  to conservatively distinguish between genetically similar siblings ( $P_{ID(sibs)} < 0.001$  at 7 loci required for a match,  $P_{ID(sibs)} = 0.000069$  at all 9 codominant loci). We combined all individual canid genotypes from fecal samples with genotypes from 19 coyotes captured in the Bath County study area and 28 domestic dogs and screened the canid genotypes in STRUCTURE version 2.3.4 (Pritchard et al. 2000) with 9 loci, 2 assumed populations, 100,000 burn-in and 200,000 iterations. We removed all genotypes that clustered with known domestic dog samples and used the remaining confirmed individual genotypes from the 5 closed-session population monitoring surveys to construct SCR encounter histories for both study sites, resulting in 10 SCR data sets to estimate density (i.e., 5 sessions for each of the 2 sites). To estimate survival, we created a capture history by recording whether an individual was detected during a session and noted site as a grouping factor.

### Population Parameter Estimates

*Apparent survival.*—We estimated apparent survival ( $\phi$ ) and detection ( $p$ ) using the Cormack–Jolly–Seber (CJS) model in Program MARK (Lebreton et al. 1992, White and Burnham 1999) implemented through the RMark package (Laake 2013) in Program R (R Core Team 2015) with individual encounters for 5 sessions grouped by both sites. The apparent survival parameter is an estimate of population outputs including mortality and permanent emigration from the study area. We constructed a candidate model set consisting of 25 candidate models testing whether survival and detection were best estimated by site (Bath or Rockingham), session (Jul 2011, Feb 2012, Jul 2012, Mar 2013, and Jul 2013), season (winter or summer), or combinations of site and session or season (site  $\times$  session or site  $\times$  season). We imported the most parameterized model [ $\phi(\text{site} \times \text{session}) p(\text{site} \times \text{session})$ ] to MARK and estimated goodness of fit using parametric bootstrap with 999 simulations and estimated the overdispersion parameter ( $\hat{c}$ ) by dividing the observed  $\hat{c}$  by the mean  $\hat{c}$  for the simulations. We selected the best model using quasi-Akaike's Information Criterion corrected for small sample sizes ( $QAIC_c$ ) and assessed usefulness of estimates of survival based on precision (Burnham and Anderson 2002).

*Density.*—We estimated coyote density for each site for all 5 sessions separately. We used a hierarchical SCR single occasion model for each closed session at each site. We used 0.5-km transect segments as spatial replicates and fit the SCR<sub>0</sub> model (Royle et al. 2013b). The model consists of encounter histories of individuals detected by fecal DNA at specific transect segment locations ( $J$ ) over a single sampling occasion ( $K = 1$ ). The process model assumes that individual

animals use space around an individual activity center ( $s$ ), and that probability of detection at a specific trap decreases with distance of that trap from activity centers, represented by a scaling parameter ( $\sigma$ ). We assumed a bivariate Gaussian (half-normal) distribution detection function defined by parameter  $\sigma$ . We recognize a monotonically decaying detection rate from an activity center may not be ideal for detection of scat for territorial animals. Thus, estimates of  $\sigma$  may be biased by this assumption and 95% home range size should not be inferred from  $\sigma$ . However, our primary interest was estimating density, and although the size of estimated home ranges may be biased by violation of this assumption, the estimate of the number of activity centers in the state space should not be (Royle et al. 2013b). Additionally, the bivariate Gaussian detection function has been tested and density estimates from models employing the bivariate Gaussian detection function are robust to most assumption violations (Russell et al. 2012).

We used data augmentation to account for individuals present but not detected during the study (Royle and Young 2008). For each of the 10 data sets, we set a maximum number of possible activity centers ( $M$ ) within an area ( $S$ ) for each site- and session-specific state space (Table 1). We associated an indicator variable ( $z_i$ , outcome of a Bernoulli trial) with each possible unobserved activity center to estimate whether those possible activity centers were representative of individuals that were present in the area but that had capture histories consisting of all zeros, or whether they were structural zeros (not representative of undetected individuals), with a binomial distribution characterizing all trials ( $\psi$ ). We summed all activity centers (detected and estimated nonstructural zeros) and derived density by dividing the sum of activity centers within the state space by the total area of the state space. The choice of  $S$  is not arbitrary but is a prior of the binomial point process model

and is determined by testing the sensitivity of resulting parameter estimates to changes in the size of  $S$ , and thus may vary by site and session (Table 1).

We formatted data using the SCR23darray() function in the analysis package scrbook (Royle et al. 2014) in R (R Core Team 2015) and implemented each model using the rjags (Plummer 2014), and coda (Plummer et al. 2006) packages. We ran each model with 3 Markov chain Monte Carlo (MCMC) chains with 100 adaptations for the Metropolis-within-Gibbs algorithm, and then used coda to sample 200,000 iterations from the posterior distributions of each monitored parameter at a thinning rate of 1 (no thinning), including a burn-in of 100,000 iterations. We assessed MCMC convergence by visually inspecting trace plots for each monitored parameter, and comparing  $\hat{R}$  statistics to 1.1 (Gelman and Rubin 1992). In addition, we used subsets of 30,000 iteration posteriors from different locations within each 100,000 iteration posteriors and confirmed similar estimates within reasonable MCMC error. We reported the posterior means and standard deviations, medians, and 95% credible intervals for baseline encounter rate ( $\lambda_0$ ),  $\sigma$ , and  $\psi$ , and we reported the posterior mode for density ( $D$ ) as it is unbiased compared to the posterior mean in SCR models (Chandler and Royle 2013).

*Recruitment and population growth rate.*—We used an ad hoc robust design approach combining the apparent survival estimates (population outputs) from the CJS model and the site- and session-specific density estimates from the SCR models to derive estimates of net new recruits (population inputs via reproduction or immigration) to the population ( $B_i$ ) and per capita recruitment ( $f_i$ ) over each interval (Pollock 1981, 1982; Williams et al. 2002). We estimated  $B_i$  and  $f_i$  using a Jolly–Seber estimator (Jolly 1965, Seber 1965, Williams et al. 2002). We estimated approximate variance for  $B_i$  following Pollock et al. (1990) and variance for  $f_i$  by calculating the

**Table 1.** Recapture rates, priors, and parameter values used in the spatial capture–recapture (SCR<sub>0</sub>) model to estimate coyote density for each site and session in Bath and Rockingham Counties, Virginia, USA, July 2011–July 2013.

Site session	Captures (total detections)	Individuals recaptured (range of recaptures)	Max. no. possible individuals ( $M$ )	Area of site- and session-specific state space ( $S$ )	$\sigma$ prior
Bath Jul 2011	15 (21)	4 (2–3)	200	997.50 km <sup>2</sup> ~5.0-km buffer	Uniform (0,5)
Bath Feb 2012	22 (41)	8 (2–10)	250	934.89 km <sup>2</sup> ~4.5-km buffer	Uniform (0,5)
Bath Jul 2012	14 (21)	5 (2–4)	240	874.29 km <sup>2</sup> ~4.0-km buffer	Uniform (0,3)
Bath Mar 2013	31 (79)	17 (2–12)	165	874.29 km <sup>2</sup> ~4.0-km buffer	Uniform (0,4)
Bath Jul 2013	14 (18)	2 (2–4)	280	1,267.92 ~7-km buffer	Uniform (0,8)
Rockingham Jul 2011	7 (11)	3 (2–3)	150	995.80 km <sup>2</sup> ~4.5-km buffer	Uniform (0,5)
Rockingham Feb 2012	19 (33)	8 (2–4)	175	995.80 km <sup>2</sup> ~4.5-km buffer	Uniform (0,4)
Rockingham Jul 2012	12 (16)	4 (2)	225	1,194.67 km <sup>2</sup> ~6.0-km buffer	Uniform (0,6)
Rockingham Mar 2013	25 (51)	14 (5)	175	995.80 km <sup>2</sup> ~4.5 km buffer	Uniform (0,4)
Rockingham Jul 2013	17 (52)	11 (2–13)	175	1,060.09 km <sup>2</sup> ~5.0-km buffer	Uniform (0,4)

variance of a ratio of random variables (Mood et al. 1974). We derived population growth as the ratio of posterior mode density estimates from the SCR model ( $\hat{\lambda}_i = \frac{\hat{D}_{i+1}}{\hat{D}_i}$ ) between each session. We estimated variance for  $\hat{\lambda}_i$  by calculating the variance of a ratio of random variables (Mood et al. 1974).

## RESULTS

We collected 5,048 fecal samples across the 5 closed sessions and all concurrent scat collection monitoring efforts and identified 1,003 (19.87%) as canid using mtDNA species identification. We successfully amplified nDNA microsatellites and confirmed genotypes at 7 loci for 579 of 1,003 samples (57.7%). The average of allelic dropout/sample genotype was 0.75 (range: 0–8), the average number of false alleles/sample genotype 0.06 (range: 0–4), and the average PCR replicates/sample was 4.39 (range: 2–6). Our final dataset contained no individuals mismatched at only 1 locus and no individuals mismatched at 2 out of 9 loci. After removing genotypes identified as domestic dog (39 samples, 32 individuals) we identified 146 individual coyote genotypes across the 2 study sites. For the closed session population monitoring, we genotyped 347 scat samples and confirmed 107 individual coyotes over 5 sessions at the 2 study sites.

### Population Parameter Estimates

*Apparent survival.*—Bootstrap goodness of fit indicated evidence of lack of fit ( $P < 0.001$ ) so we used  $\hat{c} = 2.20$  (observed deviance of most parameterized model/ $\bar{x}$  simulation deviance) to estimate a quasi-likelihood adjustment

(QAIC<sub>c</sub>) for model selection. There were several competing models that all included site-specific survival and nested parameterizations of detection including site and season (Table 2). These models suggested detection was higher in the summer than the winter at the Bath County site but lower in the summer compared to winter at the Rockingham County site, so we did not attempt to constrain detection with a post hoc additive model (Appendix A). Because the top 3 models were all nested and had approximately equivalent model weights (Table 2), we chose to use the  $\phi(\text{site})p(\text{site} \times \text{season})$  model for further population parameter estimates (Table 3). This model produced practical estimates of apparent survival and was not affected by constraints on detection. Model selection indicated survival at the 2 sites was different (the top 4 models included site as a covariate on apparent survival and their combined relative QAIC<sub>c</sub> weight ( $w_i$ ) = 0.68). The Bath County site 6-month apparent survival estimate was 0.442 (95% CI = 0.259–0.643) across seasons and the Rockingham County site apparent survival estimate was 0.863 (95% CI = 0.269–0.991).

*Density.*—Density estimates were low at both sites, (Fig. 2, Table 3, Appendix B). At the Rockingham County study area, density was generally less precise during the winter sessions (Feb 2012 posterior mode = 7.53/100 km<sup>2</sup>, 95% credible interval = 4.52–14.46; Mar 2013 posterior mode = 8.53/100 km<sup>2</sup>, 95% credible interval = 6.43–15.16) than during the summer sessions (Jul 2011 = 2.41/100 km<sup>2</sup>, 95% credible interval = 1.21–10.54; Jul 2012 = 4.68/100 km<sup>2</sup>, 95% credible interval = 2.51–16.07; Jul 2013 = 3.77/100 km<sup>2</sup>,

**Table 2.** Cormack–Jolly–Seber (CJS) model selection for apparent survival ( $\phi$ ) and detection ( $p$ ) over 5 scat sampling sessions (July 2011–July 2013) for coyotes in Bath and Rockingham Counties, Virginia, USA (sites). The time models allow parameters for each session or interval to be estimated and season constrains survival or detection to be the same for each season (winter or summer). We compared models using Akaike’s Information Criterion with a quasi-likelihood adjustment (QAIC<sub>c</sub>), differences in QAIC<sub>c</sub> compared to the top model ( $\Delta$ QAIC<sub>c</sub>), model weight based on QAIC<sub>c</sub> ( $w_i$ ), and quasi-likelihood adjusted deviance (QDeviance).

Model	<i>K</i>	QAIC <sub>c</sub>	$\Delta$ QAIC <sub>c</sub>	$w_i$	QDeviance
$\phi(\sim\text{site})p(\sim\text{season})$	4	126.84	0.00	0.19	26.73
$\phi(\sim\text{site})p(\sim\text{site})$	4	127.15	0.31	0.16	27.04
$\phi(\sim\text{site})p(\sim\text{site} \times \text{season})$	6	127.41	0.57	0.14	22.96
$\phi(\sim\text{site} \times \text{season})p(\sim\text{site} \times \text{season})$	7	127.93	1.09	0.11	21.26
$\phi(\sim\text{season})p(\sim\text{site})$	4	128.78	1.94	0.07	28.67
$\phi(\sim\text{season})p(\sim\text{season})$	4	128.92	2.08	0.07	28.81
$\phi(\sim\text{season})p(\sim\text{site} \times \text{season})$	6	129.49	2.65	0.05	25.04
$\phi(\sim\text{site})p(\sim\text{time})$	6	130.17	3.33	0.04	25.72
$\phi(\sim\text{time})p(\sim\text{season})$	6	130.26	3.42	0.03	25.81
$\phi(\sim\text{time})p(\sim\text{site})$	6	130.66	3.82	0.03	26.21
$\phi(\sim\text{site} \times \text{season})p(\sim\text{site})$	6	130.93	4.09	0.02	26.48
$\phi(\sim\text{time})p(\sim\text{site} \times \text{season})$	8	131.02	4.18	0.02	22.10
$\phi(\sim\text{site} \times \text{season})p(\sim\text{season})$	6	131.11	4.27	0.02	26.66
$\phi(\sim\text{season})p(\sim\text{time})$	6	132.10	5.26	0.01	27.65
$\phi(\sim\text{time})p(\sim\text{time})$	7	132.13	5.29	0.01	25.46
$\phi(\sim\text{site} \times \text{season})p(\sim\text{time})$	8	134.38	7.54	0.00	25.45
$\phi(\sim\text{site})p(\sim\text{site} \times \text{time})$	10	135.27	8.43	0.00	21.73
$\phi(\sim\text{site} \times \text{time})p(\sim\text{time})$	10	136.32	9.48	0.00	22.78
$\phi(\sim\text{site} \times \text{time})p(\sim\text{site})$	10	137.13	10.29	0.00	23.59
$\phi(\sim\text{season})p(\sim\text{site} \times \text{time})$	10	137.27	10.43	0.00	23.73
$\phi(\sim\text{site} \times \text{time})p(\sim\text{season})$	10	137.28	10.44	0.00	23.74
$\phi(\sim\text{site} \times \text{time})p(\sim\text{site} \times \text{season})$	12	138.23	11.39	0.00	19.92
$\phi(\sim\text{site} \times \text{season})p(\sim\text{site} \times \text{time})$	12	138.37	11.53	0.00	20.07
$\phi(\sim\text{time})p(\sim\text{site} \times \text{time})$	12	139.88	13.04	0.00	21.58
$\phi(\sim\text{site} \times \text{time})p(\sim\text{site} \times \text{time})$	13	140.55	13.71	0.00	19.81

**Table 3.** Population parameter estimates for coyotes in Bath and Rockingham Counties, Virginia, USA for 6-month seasonal intervals and for each session from July 2011 to July 2013.

Site	Session	Apparent survival ( $\phi$ ) <sup>a</sup>	Density ( $D$ , per 100 km <sup>2</sup> ) <sup>b</sup>	Births ( $B_i$ ) <sup>c</sup>	Recruitment ( $f_i$ ) <sup>d</sup>	Population growth rate ( $\lambda$ ) <sup>e</sup>
Bath	Jul 2011	0.442 (0.103, 0.259–0.643)	8.02 (4.21–17.74)	5.12 (3.31)	0.64 (0.50)	1.08 (0.58)
	Feb 2012		8.66 (4.92–15.83)	4.05 (4.87)	0.47 (0.58)	0.91 (0.63)
	Jul 2012		7.88 (4.69–23.33)	5.56 (2.01)	0.71 (0.50)	1.15 (0.73)
	Mar 2013		9.04 (7.32–14.18)	1.53 (0.95)	0.17 (0.11)	0.61 (0.12)
	Jul 2013		5.53 (2.76–19.72)			
Rockingham	Jul 2011	0.863 (0.172, 0.269–0.991)	2.41 (1.21–10.54)	5.45 (3.27)	2.26 (2.57)	3.12 (3.20)
	Feb 2012		7.53 (4.52–14.50)	–1.82 (3.70)	–0.24 (0.50)	0.62 (0.50)
	Jul 2012		4.68 (2.51–16.07)	4.45 (2.45)	0.96 (0.88)	1.82 (1.42)
	Mar 2013		8.53 (6.4 –15.16)	–3.59 (1.80)	–0.42 (0.24)	0.44 (0.16)
	Jul 2013		3.77 (2.74–6.51)			

<sup>a</sup> Maximum likelihood point estimate (SE, 95% CI) from Cormack–Jolly–Seber model, estimated constant across all sessions.

<sup>b</sup> Posterior mode from 1 chain (95% credible interval).

<sup>c</sup> New entrants in the population between  $i$  and  $i + 1$  where  $\hat{B}_i = \hat{N}_{i+1} - \hat{\phi}_i(\hat{N}_i)$ ,

$$\left( SE(\hat{B}_i) = \sqrt{\text{var}(\hat{N}_{i+1}) + \phi_i^2 * \text{var}(\hat{N}_i) + N_i^2 * \text{var}(\hat{\phi}_i) + \text{var}(\hat{\phi}_i) * \text{var}(\hat{N}_i)} \right).$$

<sup>d</sup> Number of new animals at session  $i + 1$  per the number present at  $i$  where  $f_i = \frac{\hat{B}_i}{N_i}$ ,  $\left( SE(f_i) = \sqrt{f_i^2 * \left( \frac{\text{var}(B_i)}{\hat{B}_i^2} + \frac{\text{var}(N_i)}{\hat{N}_i^2} \right)} \right).$

<sup>e</sup> Ratio of posterior mode density estimates from the spatial capture–recapture (SCR) model ( $\hat{\lambda}_i = \frac{\hat{D}_{i+1}}{\hat{D}_i}$ ) between each session

$$\left( SE(\lambda_i) = \sqrt{\lambda_i^2 * \left( \frac{\text{var}(N_i)}{\hat{N}_i^2} + \frac{\text{var}(N_{i+1})}{\hat{N}_{i+1}^2} \right)} \right).$$

95% credible interval = 2.74–6.51). The Bath County study area reflected more consistent density estimates than Rockingham across all sessions regardless of season (median density for Bath County study area = 8.02/100 km<sup>2</sup>; min. density Jul 2013 = 5.53/100 km<sup>2</sup>, 95% credible interval = 2.76–19.72; max. density Mar 2013 = 9.04, 95% credible interval = 7.32–14.18). The estimate for the final session in Bath County was much less precise because of the small sample size and very small number of recaptures (Table 1). This may have been a result of excessive rainfall during the accumulation period following initial clearing for the session in Bath County, which likely removed scats and decreased DNA amplification success rates for remaining scats (Lonsinger et al. 2016). Clearing for the Rockingham transects followed clearing for Bath County and occurred during the persistent heavy rains and individuals detected and recapture rates were much higher. Thus, we do not have as much confidence in the final density estimate for Bath County (Jul 2013).

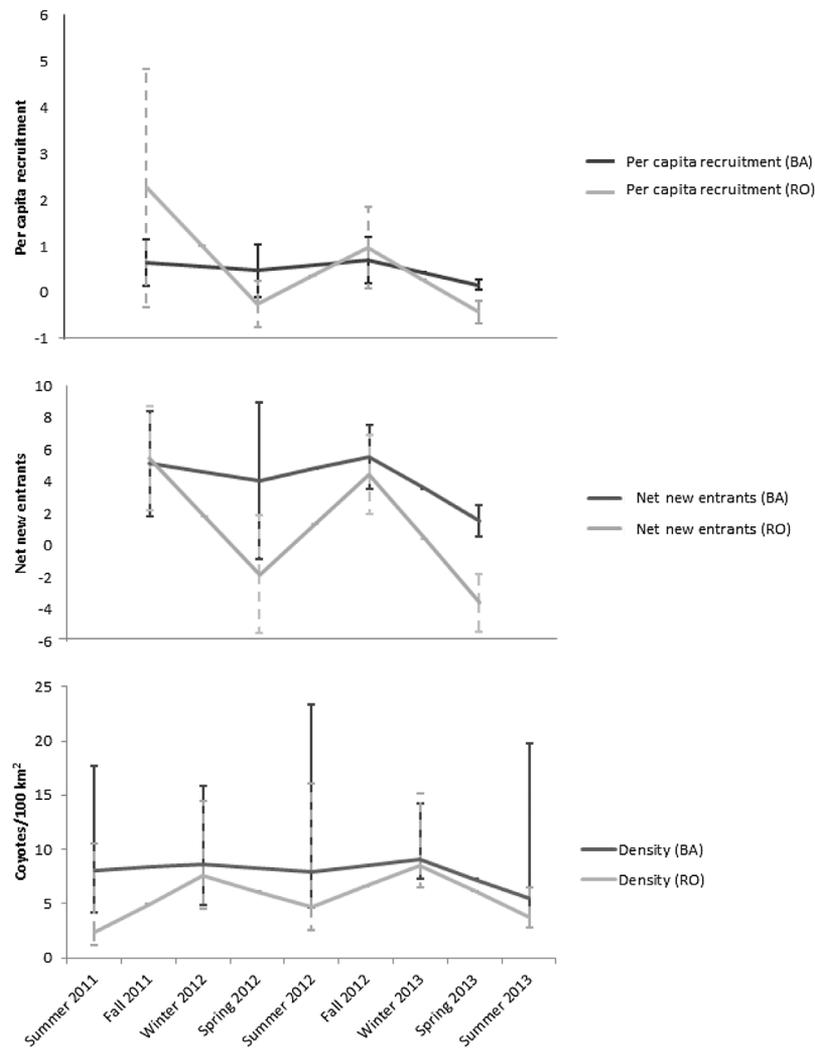
**Recruitment and population growth rate.**—Over 6-month intervals, point estimates of  $B_i$  and  $f_i$  in Bath County ranged from 1.53 to 5.56 new recruits/100 km<sup>2</sup> and from 0.17 to 0.71 recruits/capita, respectively (Fig. 2, Table 3). However, precision in estimates was variable and poor and we were unable to determine if recruitment was consistently positive given the uncertainty in estimates. At the Rockingham County study area,  $B_i$  appeared to alternate between seasons with greater numbers of recruits between the summer and winter sessions and no recruits (negative estimates of recruits) between winter and summer sessions (point estimate range = –3.59 to 5.45), and point estimates of  $f_i$  demonstrated the same fluctuating seasonal pattern (point estimate range = –0.42 to 2.26). However, precision in estimates was again too poor to determine differences with certainty. Population growth rate ( $\hat{\lambda}_i$ ) was variable, exhibited

a large amount of uncertainty, and overlapped 1.0 across seasons for both study areas (Table 3).

## DISCUSSION

Estimating density and demographic rates of change is critical to wildlife management. The use of NGS and SCR to estimate local coyote population parameters is an improvement compared to traditional monitoring methods because it is unaffected by capture and geographic closure constraints that can be problematic with wide-ranging carnivores (Royle et al. 2008). We found combining single-season scat surveys with NGS and a spatial replicate SCR model was a successful approach for estimating coyote density in our study area. However, precision in estimates was relatively poor. As a result, direct comparisons between sites and seasons included a large amount of overlap in error estimates and inconclusive results. In addition, poor precision also hindered our ability to evaluate hypotheses about demographic rates of change between seasons. Thus, although we were able to combine SCR density estimates with CJS apparent survival estimates to derive local recruitment and population growth estimates, we were unable to detect meaningful differences over space and time because of the amount of uncertainty in the estimates.

Although we were not entirely successful in estimating all population parameters of interest with precision, there is room for improvement based on the lessons learned here. The use of a site-specific pilot study could have allowed for better determination of an appropriate accumulation period (Lonsinger et al. 2015, Woodruff et al. 2015). Recapture rates were highest for both sites during winter 2013. This session was completed prior to denning but was slightly later than intended because of periods of high snowfall that prohibited detection of scats for both the clearing and the



**Figure 2.** Coyote per capita recruitment ( $f_i$ ), new recruits into the population ( $B_i$ ), and density ( $D = \text{coyotes}/100 \text{ km}^2$ ) estimates for the 2 sites, Bath County (BA) and Rockingham County (RO) for the 5 scat sampling sessions ( $D$ ) and the 4 intervals between sampling sessions ( $F_i$  and  $B_i$ ). Error bars for  $D$  represent the 95% credible intervals for estimates and error bars for  $F_i$  and  $B_i$  represent standard errors.

collection sessions. Thus, the accumulation period was 1–2 weeks longer for this session and that likely contributed to larger sample sizes, better recapture rates, and more precise estimates. For our study area, it may be preferable to increase the length of the closed session sampling period to 6 weeks to improve estimates. In addition, we found initially clearing transects to be a critical step because test samples collected during clearing sessions detected 2 individuals known to be killed 1–4 months before the session. Thus, it is important to consider closure and accumulation rates to provide an adequate sample for density estimates (Lonsinger et al. 2015).

There are several other considerations that could improve estimates from the SCR models. First, coyote space use and home range were variable, and often determined by class structure (Hinton et al. 2015, Morin 2015). Including habitat covariates or estimating landscape resistance could result in some improvement to model estimates (Royle et al. 2013a, Sutherland et al. 2015). However, biases or uncertainty due to differences in habitat, especially in our

study area, were likely less important than the challenges associated with class structure. Although there was no evidence for differences in home range size by sex in a concurrent space use study in Bath County, there was support for differences in home range size between adults and subadults, and especially between residents and transients (Morin 2015). Although density estimates are robust to the presence of transience, estimates of the spatial scalar ( $\sigma$ ) could be dramatically improved if allowed to differ for residents and transients, which could provide a substantial increase in precision (Royle et al. 2015). In addition, incorporating resource selection functions could also improve accuracy and precision (Royle et al. 2013c).

Estimates of  $\sigma$  may also be affected by the chosen detection function (Gaussian bivariate half-normal). The initial Gaussian bivariate SCR model was developed to estimate carnivore densities from camera-trap photographs, which are direct observations of the animals, so the assumption that detection is highest at an individual's activity center is often reasonable. However, detection based on collection of fecal

DNA from transects may result in behavioral biases if detection is uniform throughout a home range or greater towards the outer portions of the home range for territorial animals such as coyotes (Allen et al. 1999, Gese 2001). There may also be a sampling bias because detections can only occur along transects. Validation of detection functions for this sampling method could dramatically improve identifiability, accuracy, and precision for estimates of all parameters within the model. Finally, recent developments for SCR CJS (Gardner et al. 2010) would likely allow for more useful session-specific estimates for apparent survival compared to the maximum likelihood estimates we used here. This would be true for low-density populations and would improve derived estimates and our ability to identify trends over time and across sites.

Although precision in parameter estimates was not sufficient for strong inference of demographic processes, there were some patterns in the point estimates that warrant further investigation. Interestingly, density point estimates at the Rockingham site were more than twice as high for the winter sessions than the summer, opposite of our initial predictions that density would increase in the summer with reproductive inputs. It is possible this difference is a reflection of the detection sensitivity of our sampling method. Previous studies reported whelping to occur in late March to late May and dens abandoned after 2–3 months of age, with increasing pup independence at 4 months of age (Harrison 1992, Parker 1995). In our study area, births seemed to occur in mid-late April, which would mean pups may not have been moving around independently until August, after our summer sampling sessions. Because we were sampling transects and not rendezvous sites (Stenglein et al. 2011), it is possible we were not detecting the reproductive input in the summer but were instead detecting new individuals in the winter session, resulting in increased densities. In addition, the higher density in winter possibly was a result of increased transients or individuals attempting to immigrate into the Rockingham study area and that fewer residents defending territories comprised the summer population.

The possible differences in point estimate trends between the 2 study areas should also be explored in future studies. Although the sites were only approximately 100 km apart, there were tentative indications of demographic spatial structure within the region. This finding was surprising because the habitat was similar across our study areas and the only discernible differences were private inholdings and increased year-round interaction with humans in Bath County. The Bath County study area density point estimates were generally higher than the Rockingham County study area as predicted, despite very low 6-month apparent survival across seasons in Bath County. Conversely, although point estimates suggest density may have been lower at the Rockingham study area, population parameter estimates appeared to fluctuate seasonally as would be expected for a saturated local population with few new available territories for recruits (Knowlton et al. 1999). Thus, our findings may indicate the presence of a density-dependent compensatory

feedback mechanism (Murdoch 1994, Turchin 1999, Hixon et al. 2002), similar to recent studies investigating the ineffectiveness of culling efforts for red foxes (*Vulpes vulpes*) in agricultural areas in England (Baker and Harris 2006) and France (Lieury et al. 2015), and black-backed jackals (*Canis mesomelas*) in South Africa (Minnie et al. 2015).

Coyote survival in western states and urbanized areas has been relatively high compared to survival rates of eastern coyotes (Bogan 2004, Gehrt 2007, Grubbs and Krausman 2009), yet densities varied with resource availability, not mortality rates. Mortality in eastern coyote populations was primarily human-caused, including trapping, shooting, other forms of lethal removal, road mortality, and incidental poisoning (Harrison 1986, Crête et al. 2001, Houben 2004, Van Deelen and Gosselink 2006, Schrecengost et al. 2009). Even in an eastern population where annual survival was unusually high (0.80–0.98), the prevalent cause of mortality was harvest (Chamberlain and Leopold 2001). However, despite continued coyote harvest and removals, populations continued to expand in the eastern United States and local densities in areas with coyote bounties and intensive lethal removal efforts have not appeared to decrease (Kays et al. 2008, Kilgo et al. 2014, Conner and Morris 2015). In addition, past studies suggest local coyote populations were regulated by competition with other coyotes for territories and resources, and not harvest or mortality (Knowlton et al. 1999, Conner and Morris 2015). Although density dependence has been difficult to identify in single studies of coyote populations, the uncertain emerging pattern in our study, and trends in survival, recruitment, and density from previous studies, suggest density dependence should be considered when planning future management objectives for coyote populations. Further investigation into local coyote population dynamics including local and regional differences is required to elucidate the true nature of population regulation for this adaptable predator.

## MANAGEMENT IMPLICATIONS

As coyote populations have expanded across eastern North America, effective population management strategies have been elusive. The NGS SCR approach provides a non-invasive method to monitor local coyote population dynamics using easily implemented single session scat surveys. This method estimates each session at each site separately and results may be comparable across separate monitoring efforts (regions and over time). Although results from our study were inconclusive because of large variances for estimates, the estimated density at both study areas was very low. Low density resulted in small numbers of individuals captured using NGS methods and lower precision in density estimates and in estimates of apparent survival, and therefore, all derived parameters. However, we expect this method would be very effective in areas with greater densities, which is useful because high-density populations may be more likely to create human-coyote conflict. In addition, when the objective is to estimate low-density populations, increasing the size of the study area, and therefore the number of individuals available to be sampled,

would improve precision. Although we were not able to detect differences in population growth rates and recruitment between seasons in our study, estimating inputs and outputs over a longer period of time could yield population trend information, particularly if differences between one time period and the next are great. Thus, to produce useful results, monitoring objectives should be well defined prior to implementation, specific hypotheses should be outlined, and sampling designed to achieve those objectives. Spatial and temporal scale of the processes of interest need to be considered. Finally, we recommend local pilot studies to estimate general population densities and identify appropriate study area size to provide sufficient power to detect differences in the population parameters of interest across space and time.

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## LITERATURE CITED

Adams, J. R., J. A. Leonard, and L. P. Waits. 2003. Widespread occurrence of a domestic dog mitochondrial DNA haplotype in southeastern US coyotes. *Molecular Ecology* 12:541–546.

Allen, J. J., M. Bekoff, and R. L. Crabtree. 1999. An observational study of coyote (*Canis latrans*) scent-marking and territoriality in Yellowstone National Park. *Ethology* 105:289–302.

Alonso, R. S., B. T. McClintock, L. M. Lyren, E. E. Boydston, and K. R. Crooks. 2015. Mark-recapture and mark-resight methods for estimating abundance with remote cameras: a carnivore case study. *Plos One* 10: e0123032.

Baker, P. J., and S. Harris. 2006. Does culling reduce fox (*Vulpes vulpes*) density in commercial forests in Wales, UK? *European Journal of Wildlife Research* 52:99–108.

Bekoff, M. 1978. *Coyotes: biology, behaviour and management*. Academic Press, New York, New York, USA.

Bogan, D. A. 2004. Eastern coyote (*Canis latrans*) home range, habitat selection, and survival rates in the suburban Albany Pine Bush landscape of New York. State University of New York at Albany, Albany, New York, USA.

Bozarth, C. A., B. Gardner, L. L. Rockwood, and J. E. Maldonado. 2015. Using fecal DNA and spatial capture-recapture to characterize a recent coyote colonization. *Northeastern Naturalist* 22:144–162.

Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information theoretic approach*. Second edition. Springer, New York, New York, USA.

Chamberlain, M. J., and B. D. Leopold. 2001. Survival and cause-specific mortality of adult coyotes (*Canis latrans*) in central Mississippi. *American Midland Naturalist* 145:414–418.

Chandler, R. B., and J. A. Royle. 2013. Spatially explicit models for inference about density in unmarked or partially marked populations. *Annals of Applied Statistics* 7:936–954.

Cole, L. C. 1954. The population consequences of life history phenomena. *The Quarterly Review of Biology* 29:103–137.

Conner, L. M., and G. Morris. 2015. Impacts of mesopredator control on conservation of mesopredators and their prey. *Plos One* 10:e0137169.

Crête, M., J. P. Ouellet, J. P. Tremblay, and R. Arsenault. 2001. Suitability of the forest landscape for coyotes in northeastern North America and its implications for coexistence with other carnivores. *Ecoscience* 8:311–319.

De Barba, M., J. R. Adams, C. S. Goldberg, C. R. Stansbury, D. Arias, R. Cisneros, and L. P. Waits. 2014. Molecular species identification for multiple carnivores. *Conservation Genetics Resources* 6:821–824.

DeCalesta, D. S. 1997. Deer and ecosystem management. Pages 267–279 in W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. *The science of overabundance: deer ecology and population management*. Smithsonian Institution Press, Washington, D.C., USA.

Diefenbach, D. R., W. L. Palmer, and W. K. Shope. 1997. Attitudes of Pennsylvania sportsmen towards managing white-tailed deer to protect the ecological integrity of forests. *Wildlife Society Bulletin* 25:244–251.

Fedriani, J. M., T. K. Fuller, and R. M. Sauvajot. 2001. Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. *Ecography* 24:325–331.

Gardner, B., J. Reppucci, M. Lucherini, and J. A. Royle. 2010. Spatially explicit inference for open populations: estimating demographic parameters from camera-trap studies. *Ecology* 91:3376–3383.

Gehrt, S. D. 2007. Ecology of coyotes in urban landscapes. Pages 303–311 in *Proceedings of the 12th Wildlife Damage Management Conference*. D. L. Nolte, W. M. Arjo, and D. H. Stalman, editors. *Wildlife Damage Management*, Internet Center for USDA National Wildlife Research Center, Lincoln, Nebraska, USA.

Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. *Statistical Science* 7:457–511.

Gese, E. M. 2001. Territorial defense by coyotes (*Canis latrans*) in Yellowstone National Park, Wyoming: Who, how, where, when, and why. *Canadian Journal of Zoology* 79:980–987.

Gompper, M. E. 2002a. The ecology of northeast coyotes. *Wildlife Conservation Society* 17:1–47.

Gompper, M. E. 2002b. Top carnivores in the suburbs? Ecological by conservation issues raised by colonization of northeastern North America by coyotes. *BioScience* 52:185–190.

Grubbs, S. E., and P. R. Krausman. 2009. Use of urban landscape by coyotes. *The Southwestern Naturalist* 54:1–12.

Gulsby, W. D., C. H. Killmaster, J. W. Bowers, J. D. Kelly, B. N. Sacks, M. J. Statham, and K. V. Miller. 2015. White-tailed deer fawn recruitment before and after experimental coyote removals in central Georgia. *Wildlife Society Bulletin* 39:248–255.

Hansen, S. J. K., J. L. Frair, H. B. Underwood, and J. P. Gibbs. 2015. Pairing call-response surveys and distance sampling for a mammalian carnivore. *Journal of Wildlife Management* 79:662–671.

Harrison, D. J. 1986. *Coyote dispersal, mortality, and spatial relationships with red foxes in Maine*. Dissertation, University of Maine, Orono, USA.

Harrison, D. J. 1992. Dispersal characteristics of juvenile coyotes in Maine. *Journal of Wildlife Management* 56:128–138.

Hinton, J. W., F. T. van Manen, and M. J. Chamberlain. 2015. Space use and habitat selection by resident and transient coyotes (*Canis latrans*). *Plos One* 10:e0132203.

Hixon, S. W., M. A. Pacala, and S. A. Sandin. 2002. Population regulation: historical context and contemporary challenges of open vs. closed systems. *Ecology* 83:1490–1508.

Houben, J. M. 2004. Status and management of coyote depredations in the eastern United States. *Sheep & Goat Research Journal* 19:16–22.

Jolly, G. M. 1965. Explicit from estimates data with both death and immigration-stochastic model. *Biometrika* 52:225–247.

Kamler, J. F., and P. S. Gipson. 2000. Space and habitat use by resident and transient coyotes. *Canadian Journal of Zoology* 78:2106–2111.

Kays, R. W., M. E. Gompper, and J. C. Ray. 2008. Landscape ecology of eastern coyotes based on large-scale estimates of abundance. *Ecological Applications* 18:1014–1027.

Kéry, M., and M. Schaub. 2012. *Bayesian population analysis using WinBUGS: a hierarchical perspective*. Elsevier, London, United Kingdom.

- Kilgo, J. C., H. S. Ray, M. Vukovich, M. J. Goode, and C. Ruth. 2012. Predation by coyotes on white-tailed deer neonates in South Carolina. *Journal of Wildlife Management* 76:1420–1430.
- Kilgo, J. C., M. Vukovich, H. Scott Ray, C. E. Shaw, and C. Ruth. 2014. Coyote removal, understory cover, and survival of white-tailed deer neonates. *Journal of Wildlife Management* 78:1261–1271.
- Knowlton, F. F., E. M. Gese, and M. M. Jaeger. 1999. Coyote depredation control: an interface between biology and management. *Journal of Range Management* 52:398–412.
- Laake, J. L. 2013. RMark: an interface for analysis of capture-recapture data with MARK. Alaska Fisheries Science Center, NOAA, National Marine Fisheries Service, Processed Report 2013-01, Seattle, Washington, USA.
- Lampa, S., K. Henle, R. Klenke, M. Hoehn, and B. Gruber. 2013. How to overcome genotyping errors in non-invasive genetic mark-recapture population size estimation—A review of available methods illustrated by a case study. *Journal of Wildlife Management* 77:1490–1511.
- Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- Lieury, N., S. Ruette, S. Devillard, M. Albaret, F. Drouyer, B. Baudoux, and A. Millon. 2015. Compensatory immigration challenges predator control: an experimental evidence-based approach improves management. *Journal of Wildlife Management* 79:425–434.
- Litvaitis, J. A., and D. J. Harrison. 1989. Bobcat-coyote niche relationships during a period of coyote population increase. *Canadian Journal of Zoology* 67:1180–1188.
- Lonsinger, R. C., E. M. Gese, S. J. Dempsey, B. M. Kluever, T. R. Johnson, and L. P. Waits. 2015. Balancing sample accumulation and DNA degradation rates to optimize noninvasive genetic sampling of sympatric carnivores. *Molecular Ecology Resources* 15:831–842.
- Lonsinger, R. C., E. M. Gese, R. N. Knight, T. R. Johnson, and L. P. Waits. 2016. Quantifying and correcting for scat removal in noninvasive carnivore scat surveys. *Wildlife Biology* 22:45–54.
- McClintock, B. T., and G. C. White. 2009. A less field-intensive robust design for estimating demographic parameters with mark-resight data. *Ecology* 90:313–320.
- Meek, P. D., G. Ballard, a. Claridge, R. Kays, K. Moseby, T. O'Brien, A. O'Connell, J. Sanderson, D. E. Swann, M. Tobler, and S. Townsend. 2014. Recommended guiding principles for reporting on camera trapping research. *Biodiversity and Conservation* 23:2321–2343.
- Miller, C. R., P. Joyce, and L. P. Waits. 2002. Assessing allelic dropout and genotype reliability using maximum likelihood. *Genetics* 1:357–366.
- Minnie, L., A. Gaylard, and G. I. H. Kerley. 2015. Compensatory life history responses of a mesopredator may undermine carnivore management efforts. *Journal of Applied Ecology* 53:379–387.
- Mood, A. M., F. A. Graybill, and B. C. Boes. 1974. Introduction to the theory of statistics. Third edition. McGraw-Hill, New York, New York, USA.
- Morin, D. J. 2015. Spatial ecology and demography of eastern coyotes (*Canis latrans*) in western Virginia. Virginia Tech, Blacksburg, USA.
- Murdoch, W. W. 1994. Population regulation in theory and practice. *Ecology* 75:271–287.
- Nichols, J. D., J. E. Hines, J. Lebreton, and R. Pradel. 2000. Estimation of contributions to population growth: a reverse-time capture-recapture approach. *Ecology* 81:3362–3376.
- O'Connell, A. F., J. D. Nichols, and K. U. Karanth. 2010. Camera traps in animal ecology: methods and analyses. Springer, New York, New York, USA.
- Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 62:3–135.
- Parker, G. R. 1995. Eastern coyote: the story of its success. Nimbus, Halifax, Nova Scotia Canada.
- Patterson, B. R., and F. Messier. 2001. Social organization and space use of coyotes in eastern Canada relative to prey distribution and abundance. *Journal of Mammalogy* 82:463–477.
- Peakall, R., and P. E. Smouse. 2006. GenAlEx 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes* 6:288–295.
- Peakall, R., and P. E. Smouse. 2012. GenAlEx 6.5: Genetic analysis in Excel. Population genetic software for teaching and research—an update. *Bioinformatics* 28:2537–2539.
- Plummer, M. 2014. rjags: Bayesian graphical models using MCMC. <http://cran.r-project.org/package=rjags>. Accessed 20 Sep 2014.
- Plummer, M., N. Best, and K. Cowles. 2006. CODA: convergence diagnosis and output analysis for MCMC. *R News*. Volume 6. <http://cran.r-project.org/doc/Rnews/>. Accessed 20 Sep 2014.
- Pollock, K. H. 1981. Capture-recapture models: a review of current methods, assumptions, and experimental design. Pages 426–435 in C. M. Ralph and J. M. Scott, editors. Estimating numbers of terrestrial birds. *Studies in Avian Biology*. Allen Press, Lawrence, Kansas, USA.
- Pollock, K. H. 1982. A capture-recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 46:752–757.
- Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* 107: 3–97.
- Pritchard, J. K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. *Genetics* 155:945–959.
- R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Richer, M. C., M. Crête, J. P. Ouellet, L. P. Rivest, and J. Huot. 2002. The low performance of forest versus rural coyotes in northeastern North America: inequality between presence and availability of prey. *Ecoscience* 9:44–54.
- Rose, M. D., and G. A. Polis. 1998. The distribution and abundance of coyotes: the effects of allochthonous food subsidies from the sea. *Ecology* 79:998–1007.
- Royle, J. A. 2004. N-mixture models for estimating population size from spatially replicated counts. *Biometrics* 60:108–115.
- Royle, J. A., R. B. Chandler, K. D. Gazenski, and T. A. Graves. 2013a. Spatial capture-recapture models for jointly estimating population density and landscape connectivity. *Ecology* 94:287–294.
- Royle, J. A., R. B. Chandler, R. Sollmann, and B. Gardner. 2013b. Spatial capture-recapture. Academic Press, San Diego, California, USA.
- Royle, J. A., R. B. Chandler, R. Sollmann, and B. Gardner. 2014. *scrbook: companion to the book: Spatial Capture Recapture*. <https://sites.google.com/site/spatialcapture/recapture/scrbook-r-package>. Accessed 20 Sep 2014.
- Royle, J. A., R. B. Chandler, C. C. Sun, and A. K. Fuller. 2013c. Integrating resource selection information with spatial capture-recapture. *Methods in Ecology and Evolution* 4:520–530.
- Royle, J. A., A. K. Fuller, and C. Sutherland. 2015. Spatial capture-recapture models allowing Markovian transience or dispersal. *Population Ecology* 58:53–62.
- Royle, J. A., T. R. Stanley, and P. M. Lukacs. 2008. Statistical modeling and inference from carnivore survey data. Pages 293–312 in R. A. Long, P. McKay, J. C. Rey, and W. Zielinski, editors. *Noninvasive survey methods for carnivores*. Island Press, Washington, D.C., USA.
- Royle, J. A., and K. V. Young. 2008. A hierarchical model for spatial capture-recapture data. *Ecology* 89:2281–2289.
- Russell, R. E., J. A. Royle, R. Desimone, M. K. Schwartz, V. L. Edwards, K. P. Pilgrim, and K. S. Mckelvey. 2012. Estimating abundance of mountain lions from unstructured spatial sampling. *Journal of Wildlife Management* 76:1551–1561.
- Schreckengost, J. D., J. C. Kilgo, H. S. Ray, and K. V. Miller. 2009. Home range, habitat use and survival of coyotes in western South Carolina. *American Midland Naturalist* 162:346–355.
- Seber, G. A. F. 1965. A note on the multiple-recapture census. *Biometrika* 52:249–259.
- Seddon, J. M. 2005. Canid-specific primers for molecular sexing using tissue or non-invasive samples. *Conservation Genetics* 6:147–149.
- Sollmann, R., B. Gardner, R. B. Chandler, D. B. Shindle, D. P. Onorato, J. A. Royle, and A. F. O'Connell. 2013a. Using multiple data sources provides density estimates for endangered Florida panther. *Journal of Applied Ecology* 50:961–968.
- Sollmann, R., B. Gardner, A. W. Parsons, J. J. Stocking, B. T. McClintock, T. R. Simons, K. H. Pollock, and A. F. O'Connell. 2013b. A spatial mark-resight model augmented with telemetry data. *Ecology* 94:553–559.
- Stenglein, J. L., L. P. Waits, D. E. Ausband, P. Zager, and C. M. Mack. 2011. Estimating gray wolf pack size and family relationships using noninvasive genetic sampling at rendezvous sites. *Journal of Mammalogy* 92:784–795.

- Sutherland, C., A. K. Fuller, and J. A. Royle. 2015. Modelling non-Euclidean movement and landscape connectivity in highly structured ecological networks. *Methods in Ecology and Evolution* 6:169–177.
- Taberlet, P., S. Griffin, B. Goossens, S. Questiau, V. Manceau, N. Escaravage, L. P. Waits, and J. Bouvet. 1996. Reliable genotyping of samples with very low DNA quantities using PCR. *Nucleic Acids Research* 24:3189–3194.
- Tremblay, J. P., J. Huot, and M. Crête. 1998. Summer foraging behaviour of eastern coyotes in rural versus forest landscape: a possible mechanism of source-sink dynamics. *Ecoscience* 5:172–182.
- Turchin, P. 1999. Population regulation: a synthetic view. *Oikos* 84:153–159.
- Van Deelen, T. R., and T. E. Gosselink. 2006. Coyote survival in a row-crop agricultural landscape. *Canadian Journal of Zoology* 84:1630–1636.
- Waits, L. P., G. Luikart, and P. Taberlet. 2001. Estimating the probability of identity among genotypes in natural populations: Cautions and guidelines. *Molecular Ecology* 10:249–256.
- Waits, L. P., and D. Paetkau. 2005. Noninvasive genetic sampling tools for wildlife biologists: a review of applications and recommendations for accurate data collection. *Journal of Wildlife Management* 69:1419–1433.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:S120–S139.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, California, USA.
- Woodruff, S. P., T. R. Johnson, and L. P. Waits. 2015. Evaluating the interaction of faecal pellet deposition rates and DNA degradation rates to optimize sampling design for DNA-based mark-recapture analysis of Sonoran pronghorn. *Molecular Ecology Resources* 15:843–854.

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## APPENDIX A

Real parameter estimates from selected Cormack–Jolly–Seber (CJS) model of apparent survival ( $\phi$ ) and detection ( $p$ ) for coyotes in Bath and Rockingham Counties, Virginia, USA, 2011–2013.

Model	Parameter	Estimate	SE	Lower 95% CI	Upper 95% CI
$\phi(\text{site})$ $p(\text{site} \times \text{season})$	$\phi(\text{Bath})$	0.442	0.103	0.259	0.643
	$\phi(\text{Rockingham})$	0.863	0.172	0.269	0.991
	$p(\text{Bath, summer})$	0.711	0.140	0.393	0.903
	$p(\text{Bath, winter})$	0.342	0.090	0.192	0.531
	$p(\text{Rockingham, summer})$	0.294	0.095	0.145	0.505
	$p(\text{Rockingham, winter})$	0.415	0.112	0.223	0.636

## APPENDIX B

Spatial capture–recapture (SCR) model parameter estimates, standard errors, and credible intervals for coyotes in the Bath and Rockingham County study areas of Virginia, USA, 2011–2013.

Site and session	Parameter	$\bar{x}$	SE	Mode	Quantile 0.025	Quantile 0.50	Quantile 0.975
Bath Jul 2011	$\sigma^a$	1.544	0.455		0.946	1.450	2.694
	$\lambda_0^b$	0.050	0.030		0.012	0.043	0.125
	$\psi^c$	0.465	0.174		0.204	0.436	0.883
	$D^d$		3.45	8.02	4.21	8.72	17.74
Bath Feb 2012	$\sigma$	1.974	0.398		1.375	1.912	2.926
	$\lambda_0$	0.045	0.018		0.019	0.043	0.088
	$\psi$	0.338	0.108		0.178	0.322	0.596
	$D$		2.80	8.66	4.92	8.56	15.83
Bath Jul 2012	$\sigma$	1.301	0.376		0.785	1.227	2.271
	$\lambda_0$	0.051	0.029		0.014	0.045	0.123
	$\psi$	0.414	0.175		0.165	0.379	0.851
	$D$		4.78	7.88	4.69	10.29	23.33
Bath Mar 2013	$\sigma$	1.543	0.150		1.284	1.531	1.871
	$\lambda_0$	0.109	0.024		0.069	0.107	0.160
	$\psi$	0.545	0.100		0.369	0.539	0.760
	$D$		1.77	9.04	7.32	10.18	14.18
Bath Jul 2013	$\sigma$	3.615	1.313		1.868	3.306	7.010
	$\lambda_0$	0.009	0.007		0.002	0.008	0.026
	$\psi$	0.394	0.202		0.121	0.349	0.892
	$D$			5.53	2.76	7.65	19.72
Rockingham Jul 2011	$\sigma$	2.516	0.834		1.376	2.327	4.564
	$\lambda_0$	0.030	0.024		0.005	0.024	0.093
	$\psi$	0.255	0.156		0.075	0.214	0.705
	$D$		2.3	2.41	1.72	3.20	5.57
Rockingham Feb 2012	$\sigma$	2.081	0.418		1.450	2.016	3.089
	$\lambda_0$	0.040	0.018		0.015	0.037	0.083
	$\psi$	0.468	0.146		0.243	0.447	0.824
	$D$		2.5	7.53	4.52	7.83	14.5
Rockingham Jul 2012	$\sigma$	2.408	0.806		1.326	2.238	4.503
	$\lambda_0$	0.026	0.019		0.005	0.021	0.075
	$\psi$	0.373	0.183		0.130	0.330	0.853
	$D$		3.44	4.68	2.51	6.19	16.07
Rockingham Mar 2013	$\sigma$	1.629	0.228		1.260	1.602	2.152
	$\lambda_0$	0.071	0.021		0.037	0.069	0.120
	$\psi$	0.576	0.131		0.354	0.563	0.867
	$D$		2.23	8.53	6.43	9.84	15.16
Rockingham Jul 2013	$\sigma$	2.208	0.289		1.738	2.176	2.871
	$\lambda_0$	0.093	0.026		0.051	0.090	0.151
	$\psi$	0.266	0.067		0.153	0.260	0.413
	$D$		0.97	3.77	2.74	4.25	6.51

<sup>a</sup> Scaling parameter for Gaussian bivariate detection model.

<sup>b</sup> Encounter rate at hypothetical activity center.

<sup>c</sup> Data augmentation parameter.

<sup>d</sup> Density (coyotes/100 km<sup>2</sup>).