Journal of Applied Ecology

Journal of Applied Ecology 2010, **47**, 1083–1093 doi: 10.1111/j.1365-2664.2010.01846.x

Combining ground count, telemetry, and mark–resight data to infer population dynamics in an endangered species

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Summary

1. To successfully manipulate populations for management and conservation purposes, managers must be able to track changes in demographic rates and determine the factors driving spatial and temporal variation in those rates. For populations of management concern, however, data deficiencies frequently limit the use of traditional statistical methods for such analyses. Long-term demographic data are often piecemeal, having small sample sizes, inconsistent methodologies, intermittent data, and information on only a subset of important parameters and covariates.

2. We evaluated the effectiveness of Bayesian state-space models for meeting these data limitations in elucidating dynamics of federally endangered Sierra Nevada bighorn sheep *Ovis canadensis sierrae*. We combined ground count, telemetry, and mark–resight data to: (1) estimate demographic parameters in three populations (including stage-specific abundances and vital rates); and (2) determine whether density, summer precipitation, or winter severity were driving variation in key demographic rates.

3. Models combining all existing data types increased the precision and accuracy in parameter estimates and fit covariates to vital rates driving population performance. They also provided estimates for all years of interest (including years in which field data were not collected) and standardized the error structure across data types.

4. Demographic rates indicated that recovery efforts should focus on increasing adult and yearling survival in the smallest bighorn sheep population. In evaluating covariates we found evidence of negative density dependence in the larger herds, but a trend of positive density dependence in the smallest herd suggesting that an augmentation may be needed to boost performance. We also found that vital rates in all populations were positively associated with summer precipitation, but that winter severity only had a negative effect on the smallest herd, the herd most strongly impacted by environmental stochasticity.

5. *Synthesis and applications*. For populations with piecemeal data, a problem common to both endangered and harvested species, obtaining precise demographic parameter estimates is one of the greatest challenges in detecting population trends, diagnosing the causes of decline, and directing management. Data on Sierra Nevada bighorn sheep provide an example of the application of Bayesian state-space models for combining all existing data to meet these objectives and better inform important management and conservation decisions.

Key-words: Bayesian state-space models, demographic parameter estimation, fecundity, ground count, mark–resight, *Ovis canadensis sierrae,* Sierra Nevada bighorn sheep, survival, telemetry

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Introduction

To successfully manipulate populations for management and conservation purposes, managers must be able to track changes in demographic parameters, identify vital rates (survival and reproductive rates) having the greatest influence on population growth, and determine the factors driving spatial and temporal variation in those key rates (Franklin *et al.* 2000; Morris & Doak 2002; Bakker *et al.* 2009). Unfortunately, data deficiencies prohibit these critical analyses for many populations of management interest (Tear *et al.* 1995; Fieberg & Ellner 2001; Morris *et al.* 2002). Demographic data are often piecemeal, having small sample sizes, inconsistent methodologies, intermittent data collection, and information on only a subset of important parameters and covariates. Traditional statistical approaches are limited in their ability to analyse such demographic data, and as a result, critical management decisions are routinely made with limited quantitative analysis.

Bayesian state-space models provide a powerful statistical tool for evaluating the dynamics of populations with messy or incomplete datasets. These models can account for multiple data types, small sample sizes, and missing data to estimate key demographic parameters and simultaneously fit covariates to those parameters (Brooks, King & Morgan 2004; Goodman 2004; Schaub *et al.* 2007; King *et al.* 2008). As such, they effectively 'integrate' all available demographic data into a single, comprehensive model that can describe the behaviour of a population while standardizing the error structure across different data types (Besbeas *et al.* 2002; Brooks, King & Morgan 2004; Goodman 2004). Another benefit of these models is that they are highly mechanistic, explicitly linking variation in population size to changes in stage-specific vital rates and covariate values. While this method holds tremendous potential for combining a wide range of demographic data types, its application to wildlife populations has been limited largely to merging ground surveys with capture–recapture data (Besbeas *et al.* 2002; Brooks, King & Morgan 2004; Schaub *et al.* 2007; Véran & Lebreton 2008).

We used the Bayesian state-space approach to evaluate the dynamics of federally endangered Sierra Nevada bighorn sheep, *Ovis canadensis sierra* (SNBS), the rarest subspecies of bighorn sheep in North America (U.S. Fish and Wildlife Service 2007). Although data have been collected intermittently on this subspecies for > 30 years, limitations of the dataset have prohibited comprehensive demographic analyses; despite the value of such information for directing recovery efforts. Data available on SNBS include ground counts, telemetry based known-fate survival and reproductive success, and mark–resight surveys. Our objectives were to evaluate the effectiveness of the Bayesian state-space approach for combining SNBS data types to (i) estimate annual population size and vital rate parameters and, (ii) determine factors potentially driving variation in key vital rates.

To meet our second objective we specifically evaluated the factors determining those vital rates that are most important to this subspecies. A recent sensitivity analysis found that most variation in SNBS growth rates was attributable to variation in adult female survival and fecundity (Johnson *et al.* 2010). We assessed variation in these 'key' vital rates with respect to variation in population density, winter severity, and summer precipitation. These covariates are likely to affect bighorn sheep in the Sierra Nevada and are commonly associated with the dynamics of other ungulate populations (Portier *et al.* 1998; Coulson, Milner-Gulland & Clutton-Brock 2000; Gaillard *et al.* 2000; Jacobson *et al.* 2004).

Materials and methods

SNBS POPULATIONS

Seven SNBS populations currently exist, but we focus only on the three for which there are long-term demographic data: Warren, Wheeler, and Langley. These populations were reintroduced between 1979 and 1986 (Bleich *et al.* 1990), with Warren the northernmost population, Langley the southernmost, and Wheeler in the central part of the range (Fig. S1, Supporting Information). These herds represent approximately 60% of the overall subspecies population, and exhibit high spatial and temporal variation in population trends, density, and environmental conditions. All populations are known to be geographically isolated so that their dynamics are independent. Detailed information about the history of the populations and the study area is described in Johnson *et al.* (2010).

DATA TYPES

Ground count data (y_C)

Annual ground counts were performed by experienced observers, who systematically hiked and scanned each herd area for bighorn sheep by sex and stage class (lambs, yearlings and adults). Due to small population sizes and repeated surveys, in many cases counts were successful at being complete, or near-complete, censuses of numbers in each stage class. We used counts collected at Warren from 1988 to 2008, at Wheeler from 1981 to 2009, and at Langley from 1987 to 2008 (Table 1). Annual surveys at Warren and Langley occurred in July or August, shortly after new lambs were born (post-birth pulse), while surveys at Wheeler occurred in March or April just before new lambs were born (pre-birth pulse). The lambing period primarily occurs from mid-April to mid-June with adult females giving birth to one offspring/year (Wehausen 1980, 1996). Although three stage classes were observed during both pre- and post-birth pulse surveys, the timing of surveys resulted in distinct differences in the field data that translate into different parameterizations of our demographic models. Throughout the *Methods* we describe data and models relevant to post-birth pulse surveys, and provide details on the pre-birth pulse modifications in Appendix S1 Supporting Information. Post-birth pulse surveys counted the number of adult females ($\geq$2·2 years; y_A), yearling females ($\sim$1·2 years; y_Y), and newborn lambs ($\sim$0·2 years; y_L).

Telemetry data (y_T)

California Department of Fish and Game (CDFG) personnel radio-collared adult female SNBS for information on individual survival and reproduction. Radio-collars were deployed in each herd one to

Table 1. Number of years (n) that ground count, telemetry, and mark–resight data were collected on the Warren, Wheeler, and Langley populations of Sierra Nevada bighorn sheep. The minimum and maximum numbers of adult females that were radio-collared for telemetry and mark–resight surveys are given in parentheses

	Ground count		Telemetry – adult survival		Telemetry – fecundity		Mark–resight	
Population	Years collected	n	Years collected	n	Years collected	n	Years collected	n
Warren	1988–1999, 2001–2008	20[a]	2003–2008	6 (1–6)	2002, 2005–2008	4 (1–5)	N/A	N/A
Wheeler	1981, 1983, 1984, 1987, 1992, 1995–2009	20	2002–2009	8 (7–21)	2001–2009	9 (5–17)	2006–2009	4 (13–18)
Langley	1987, 1990, 1996–2008	14[b]	2004–2008	5 (3–17)	2005–2008	4 (7–15)	2006–2008	3 (8–17)

[a] No ground count for adult females in 1994 and for yearling females from 1991 to 1994.
[b] No ground count for adult females in 2005.

two times/year using a net-gun fired from a helicopter. Collaring efforts began at Wheeler in 2001, Warren in 2002, and Langley in 2004. Collared females were monitored twice/month by ground and aerial telemetry for survival (systematic survival monitoring began at Wheeler in 2002 and at Warren in 2003) and they were observed annually to determine whether or not they had a lamb (reproductive monitoring began in Langley in 2005). While telemetry data should yield precise parameter estimates, small sample sizes limit statistical power in many years (Table 1).

Mark–resight data (y_{MR})

Mark–resight data were collected in Wheeler and Langley from 2006 onward, following McClintock and White (2007; Table 1). During mark–resight surveys herd areas were systematically searched (without telemetry) for all adult females, and the identities of marked (collared) females and the numbers of unmarked adult females were recorded. Surveys were conducted in a single day by multiple observers such that sampling of marked animals was done without replacement. We often performed multiple (two or three) mark–resight surveys within a season to estimate adult female population size. We did not collect mark–resight data on the same days as ground counts to ensure independence among data types.

Covariate data

We evaluated the effects of population density, winter severity, and summer rainfall on SNBS survival and reproductive rates. The effect of density on vital rates in year t was modelled as the number of adult and yearling females estimated in year $t-1$ (described in *State Process*). We indexed winter severity by the monthly average depth of snowpack from February to April (cm). Snow data were obtained from weather stations operated by the California Department of Water Resources (CDEC; http://cdec.water.ca.gov). We selected population-specific stations to reflect differences in local conditions, with stations located within or adjacent to each herd area and situated at 2775–3050 m, an average winter elevation for SNBS. For summer rainfall we calculated mean monthly precipitation from June to August (cm), as rain during these months is likely to be important for maintaining growth and nutrient quality of forage in the arid eastern Sierra Nevada. We obtained precipitation data from NOAA weather stations (http://lwf.ncdc.noaa.gov/oa/climate) located in the towns closest to each herd because CDEC stations have not tracked long-term precipitation patterns.

MODEL FORMULATION AND PARAMETERIZATION

General approach

The Bayesian state-space approach identifies *state* processes (equations describing the dynamics of the system) and *observation* processes (equations linking state processes to empirical field data; Besbeas *et al.* 2002; Brooks, King & Morgan 2004; Buckland *et al.* 2004; Schaub *et al.* 2007). For SNBS, the state process describes annual changes in the size of each SNBS stage class as a function of changes in stage-specific vital rates, modelled with a series of likelihood functions. The observation process then links our various data types to the population size and vital rate parameters describing our system.

For populations surveyed post-birth pulse the observed stage classes were adult females, yearling females, and lambs, and the vital rates describing changes in these stages were annual adult female survival (Φ_A), yearling female survival (Φ_Y), and fecundity (F; the number of lambs born/number of adult females). For Wheeler, surveyed during the pre-birth pulse, the observed stage classes were adult females, two-year-old females, and yearlings, and the associated vital rates were adult female survival, two-year-old survival and recruitment (the number of lambs that were born and survived their first year/adult female; see Appendix S1, Supporting Information). A consequence of this difference was that we were able to estimate fecundity for Warren and Langley, and recruitment for Wheeler.

Each of our data types, count (y_C), telemetry (y_T), and mark–resight data (y_{MR}), provide information on a subset of demographic parameters (Fig. 1). Annual ground counts provide direct information on the numbers of animals in each stage class, and consecutive annual counts provide indirect information on survival rates. Meanwhile, telemetry data can be used to estimate adult female survival and fecundity, and mark–resight data can be used to estimate the population size of adult females. We modelled the Warren, Wheeler, and Langley populations independently, parameterizing models with demographic and covariate data specific to each herd.

State process

We used a binomial distribution to model the number of adult females in year t as a function of the adult female survival rate from $t-1$ to t ($\Phi_{A(t-1)}$) and the number of adult and yearling females in year $t-1$:

$$N_{A\female}(t) \sim \text{Binomial}(\Phi_{A(t-1)}, N_{A\female(t-1)} + N_{Y\female(t-1)})$$

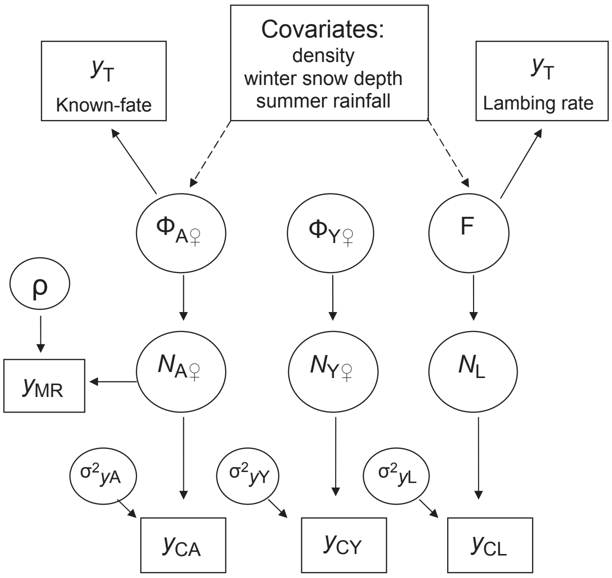

Fig. 1. Sierra Nevada bighorn sheep demographic model for populations surveyed post-birth pulse. Data are represented by boxes while estimated parameters are represented by circles. Solid arrows depict stochastic dependencies between data and parameters and dashed arrows represent deterministic dependencies. The model combines ground count (y_{CA}, y_{CY}, y_{CL}), telemetry (y_T), and mark-resight (y_{MR}) data to estimate numbers of adult females (N_A), yearling females (N_Y) and lambs (N_L), adult female survival (Φ_A), yearling female survival (Φ_Y), and fecundity (F). The model also estimates detection probability for mark-resight surveys (ρ) and the variance of ground counts for each stage class (σ^2_{yA}, σ^2_{yY}, σ^2_{yL}).

Because field data did not identify lambs by sex, we assumed a 50:50 sex ratio and described the number of yearling females at time t as a function of their survival from $t - 1$ to t ($\Phi_{Y(t-1)}$) and half the total number of lambs in $t - 1$:

$$N_{Y♀}(t) \sim \text{Binomial}(\Phi_{Y(t-1)}, 0{\cdot}5 * N_{L(t-1)})$$

We assumed that yearlings did not produce offspring, as ultrasonography on eight yearlings (captured from 2003 to 2009) found only one to be pregnant (CDFG unpublished data). We therefore modelled the number of lambs in year t as a function of the annual fecundity rate ($F_{(t)}$) and the number of adult females in year $t - 1$ multiplied by their survival rate ($\Phi_{A(t-1)}$):

$$N_L(t) \sim \text{Binomial}(F_{(t)}, N_{A♀(t-1)} * \Phi_{A(t-1)})$$

We could model this process using a binomial distribution because SNBS only give birth to one offspring per year (Wehausen 1980).

Ground count likelihood functions

Given that ground counts of SNBS have been complete or near-complete censuses in most years we assumed that counts of adult females ($y_{CA♀}$), yearling females ($y_{CY♀}$), and lambs (y_{CL}) in year t were normally distributed as a function of the true number of adult females ($N_{A♀}$), yearling females ($N_{Y♀}$), and lambs (N_L) in year t:

$$y_{CA♀(t)} \sim \text{Normal}(N_{A♀(t)}, {\sigma_{yA}}^2)$$

$$y_{CY♀(t)} \sim \text{Normal}(N_{Y♀(t)}, {\sigma_{yY}}^2)$$

$$y_{CL(t)} \sim \text{Normal}(N_{L(t)}, {\sigma_{yL}}^2)$$

where ${\sigma_y}^2$ terms represent the variance associated with counts of each stage class, and the normal distribution is truncated at 0. These equations describe how ground count data are linked to the true, but unknown, number of animals in the population.

Telemetry likelihood functions

While we obtained indirect information on adult female survival and fecundity from consecutive annual counts, we also obtained direct information on these vital rates from collared adult females. Given known-fate telemetry data ($y_{\text{TKnown-Fate}}$), we used a parametric exponential model to estimate annual adult female survival. This model only required estimation of a single parameter which could be accommodated by limited telemetry data. This model assumes that the baseline hazard rate (H_0; the probability that death occurs in a given interval) is constant and is expressed as the negative log of the survival rate (Hosmer & Lemeshow 1999; Ibrahim, Chen & Sinha 2001). To approximate the baseline hazard rate we described the probability of mortality ($D_{(i,t)}$) for female i in year t as a function of the population-specific hazard rate in that year:

$$D_{(i,t)} \sim \text{exponential}(H_{0(t)} | \text{Number of days at risk}_{(i,t)})$$

We needed to account for different numbers of days-at-risk because animals were collared following a staggered-entry design. For females collared at the start of the year the days-at-risk was 365, and for females collared after the start of the year the days-at-risk was reduced to reflect monitoring time. This model provided an estimate of the daily (instantaneous) hazard rate. Annual adult female survival was then calculated by taking the exponent of the negative daily hazard rate multiplied by 365:

$$\Phi_{A(t)} = e^{-(H0(t)*365)}$$

We calculated annual known-fate survival rates to match the timing of ground counts (i.e. the timing of pre-birth pulse vs. post-birth pulse surveys).

To incorporate data on the reproductive success of collared females (y_{TLambing}) into fecundity estimates, we used a binomial distribution to describe the number of collared females with a lamb in year t ($l_{(t)}$) as a function of the annual fecundity rate ($F_{(t)}$) and the number of collared females monitored in that year ($c_{(t)}$):

$$l_{(t)} \sim \text{binomial}(F_{(t)}, c_{(t)})$$

Mark–resight likelihood functions

We included mark–resight data (y_{MR}) into estimates of annual adult female population size (N_A) by using a modified Bayesian binomial model (McClintock & Hoeting 2009). This model describes the probability of sighting individual i in year t ($x_{(i,t)}$) as a function of the annual detection probability ($\rho_{(t)}$) and the number of surveys (sampling occasions) conducted in that survey season ($k_{(t)}$):

$$x_{(i,t)} \sim \text{binomial}(\rho_{(t)}, k_{(t)})$$

Assumptions are that the number of marked animals is known, sampling is without replacement, and there is no individual heterogeneity in sighting probabilities. Our study design satisfied the first two assumptions. While there may be some heterogeneity in sighting probabilities, small numbers of marked animals limited our ability to fit more complex models. We assumed that the total number of unmarked adult females observed across sampling occasions for a given year ($\text{UF}_{(t)}$) was a binomial function of the annual detection probability ($\rho_{(t)}$) and $\text{Uk}_{(t)}$, or the number of sampling occasions that occurred in year *t* multiplied by the total number of unmarked adult females observed during those occasions (the total number of adult females minus the number of marked females ($m_{(t)}$)), as described by the equations:

$$\mathrm{UF}_{(t)} \sim \mathrm{binomial}(\rho_{(t)}, \mathrm{Uk}_{(t)}), \text{and}$$
$$\mathrm{Uk}_{(t)} = (\mathrm{N}_{A♀(t)} - \mathrm{m}_{(t)}) * k_{(t)}$$

While the mark–resight model was developed by McClintock and Hoeting (2009) for populations where the number of marked animals was unknown, the model could be simplified to assess the abundance of populations like SNBS where the number of marks is known with certainty.

Combined model

Likelihoods from different data types were combined to form a joint model, where parameter estimates were maximized across individual component likelihoods (Besbeas *et al.* 2002; Brooks, King & Morgan 2004; Buckland *et al.* 2004; Goodman 2004). A key assumption in pooling multiple data types into a joint likelihood is sampling independence among those data types (not independence among sampled animals). Because count, mark–resight, and telemetry data were collected independently of one another their component likelihoods in our post-birth pulse model can be represented as:

$$\begin{array}{ll} \text{Ground count}: & L(y_{\mathrm{C}}|N_{\mathrm{A}}, N_{\mathrm{Y}}, N_{\mathrm{L}}, \phi_{\mathrm{A}}, \phi_{\mathrm{Y}}, F) \\ \text{Telemetry}: & L(y_{\mathrm{T}}|\phi_{\mathrm{A}}, F) \\ \text{Mark}-\text{Resight}: & L(y_{\mathrm{MR}}|N_{\mathrm{A}}, \rho) \end{array}$$

The demographic parameters adult female survival (Φ_{A}), fecundity (F), and adult female population size (N_{A}) are present in multiple independent component likelihoods so we combined likelihoods from the three different data types to yield the joint function:

$$L(y_{\mathrm{C}}, y_{\mathrm{T}}, y_{\mathrm{MR}}|N_{\mathrm{A}}, N_{\mathrm{Y}}, N_{\mathrm{L}}, \Phi_{A}, \Phi_{\mathrm{Y}}, F, \rho)$$

In addition to estimating annual population numbers and vital rates, we calculated annual population growth rates (λ_t) for each herd, a derived parameter. This was obtained by dividing the number of adult and yearling females in year *t* by the number of adult and yearling females in year $t - 1$:

$$\lambda_t = (N_{\mathrm{A}(t)} + N_{\mathrm{Y}(t)})/(N_{\mathrm{A}(t-1)} + N_{\mathrm{Y}(t-1)})$$

We used the geometric mean of annual λ_t's for each population to estimate the mean long-term growth rate over the time each herd was monitored.

Fitting covariates to key vital rates

After estimating baseline population size and vital rate parameters we fit the covariates density, winter snowpack, and summer precipitation to adult survival and fecundity/recruitment rates, assessing covariate effects for each vital rate independently in separate models. We modelled these factors for periods of complete or near-complete consecutive annual surveys: 1988–2008 for Warren, 1995–2009 for Wheeler, and 1996–2008 for Langley. Because vital rates were constrained between 0 and 1, we used a logit transformation to model covariates as a linear function of adult female survival and fecundity:

$$\begin{aligned} \mathrm{logit}(\Phi_{\mathrm{A(t)}}) &= \beta_0 + \beta_1(\mathrm{density}_{(\mathrm{t})}) + \beta_2(\text{snow depth}_{(\mathrm{t})}) \\ &\quad + \beta_3(\mathrm{precipitation}_{(\mathrm{t})}), \text{and} \\ \mathrm{logit}(F_{(\mathrm{t})}) &= \beta_0 + \beta_1(\mathrm{density}_{(\mathrm{t})}) \\ &\quad + \beta_2(\text{snow depth}_{(\mathrm{t})}) + \beta_3(\mathrm{precipitation}_{(\mathrm{t})}) \end{aligned}$$

Model implementation

We made inferences about demographic parameters by drawing samples from the joint posterior distribution using Markov Chain Monte Carlo techniques in WinBUGS (Lunn *et al.* 2000). We ran each model for 1 100 000 iterations, discarding the first 100 000 iterations as 'burn-in' and sampling one out of every 10 iterations thereafter to estimate posterior distributions (PD) for parameter values. Convergence occurred within 5 000 iterations, as indicated by the Brooks–Rubin–Gelman diagnostic (Brooks & Gelman 1998). We estimated adult female survival, fecundity, and the total number of adult females (parameters with data from multiple sources) based on each data type independently, and in combination, to evaluate the effectiveness of pooling across data types. We also estimated regression coefficients for overall covariate effects, annual detection probabilities for mark–resight surveys, variance terms for stage-specific ground counts, and annual population growth rates (Fig. 1).

We used uninformative priors to specify demographic parameters. We used 10, 5, and 5, as prior initial sizes of adult, yearling, and lamb stage classes in all populations for the first year of the simulation (values that reflected the small sizes of these reintroduced populations), using large variances of 10^4 (Brooks, King & Morgan 2004; Schaub *et al.* 2007). We used an inverse gamma prior for estimates of $\sigma_y{}^2$ with distribution parameters equal to 0·001 (Brooks, King & Morgan 2004). We assumed uniform prior distributions for detection probabilities that ranged from 0 to 1, and beta distributions (mean and variance parameters of 1) for vital rates modelled without covariate effects. For vital rates estimated with covariates we assumed all priors on regression coefficients were normally distributed with a mean of 0 and variance of 2. To demonstrate the combination of count, telemetry and mark–resight data we provide the baseline WinBUGS code in Appendix S2 (Supporting information).

Results

PARAMETER ESTIMATES

The inclusion of telemetry data in demographic models consistently reduced posterior standard deviations (SD) around estimates of adult female survival, recruitment, and fecundity, from those obtained from ground count data alone (Table 2; Fig. 2). When estimates from ground count and telemetry data were quite different, the values obtained from the combined model were generally intermediate, and weighted more strongly towards the data providing higher precision (Table 2). Similarly, mark–resight data increased the precision in estimates of adult female population size, although the effect was slight (Table 3). When female population size was estimated independently for each data type, posterior standard deviations around N_{A} were significantly larger for mark–resight estimates than for ground count estimates (~2–3 times as large; Table 3). As a result, the combined estimate was consistently

Table 2. Annual adult female survival (Φ_A), recruitment (*R*; for pre-birth pulse surveyed Wheeler) and fecundity (*F*; for post-birth pulse surveyed Warren and Langley) rates for Sierra Nevada bighorn sheep populations. Estimates were obtained from ground count data only, telemetry data only, and with the combined data model (count and telemetry data; SD in parentheses)

	Ground count only		Telemetry only		Combined model	
Population & year	Φ_A	*R/F*	Φ_A	*R/F*	Φ_A	*R/F*
Wheeler						
2001	0·82 (0·10)	0·95 (0·05)	0·86 (0·12)	0·71 (0·16)	0·88 (0·08)	0·91 (0·06)
2002	0·91 (0·08)	0·79 (0·11)	0·89 (0·10)	0·75 (0·14)	0·94 (0·05)	0·81 (0·09)
2003	0·85 (0·09)	0·70 (0·11)	0·83 (0·11)	0·67 (0·15)	0·87 (0·07)	0·69 (0·09)
2004	0·91 (0·07)	0·65 (0·10)	0·80 (0·10)	0·55 (0·14)	0·86 (0·06)	0·61 (0·08)
2005	0·92 (0·07)	0·79 (0·09)	0·93 (0·07)	0·62 (0·13)	0·95 (0·04)	0·73 (0·07)
2006	0·76 (0·09)	0·58 (0·09)	0·77 (0·10)	0·57 (0·13)	0·80 (0·06)	0·58 (0·08)
2007	0·92 (0·07)	0·34 (0·08)	0·85 (0·08)	0·59 (0·12)	0·89 (0·05)	0·41 (0·07)
2008	0·89 (0·07)	0·32 (0·08)	0·94 (0·05)	0·26 (0·10)	0·95 (0·04)	0·28 (0·06)
2009	NA	0·46 (0·08)	NA	0·53 (0·12)	NA	0·47 (0·07)
Warren						
2004	0·73 (0·16)	0·75 (0·17)	0·57 (0·27)	NA	0·82 (0·13)	0·74 (0·18)[a]
2005	0·76 (0·13)	0·57 (0·20)	0·47 (0·23)	0·40 (0·20)	0·72 (0·13)	0·50 (0·16)
2006	0·76 (0·14)	0·72 (0·18)	0·71 (0·16)	0·57 (0·18)	0·81 (0·09)	0·65 (0·15)
2007	0·69 (0·13)	0·70 (0·18)	0·44 (0·17)	0·67 (0·18)	0·54 (0·13)	0·78 (0·12)
2008	NA	0·76 (0·17)	NA	0·50 (0·22)	NA	0·63 (0·19)
Langley						
2003	0·91 (0·07)	0·79 (0·12)	0·70 (0·22)	NA	0·91 (0·07)	0·79 (0·12)[a]
2004	0·94 (0·05)	0·63 (0·13)	0·87 (0·11)	NA	0·95 (0·04)	0·63 (0·12)[a]
2005	0·86 (0·09)	0·90 (0·07)	0·81 (0·12)	0·89 (0·10)	0·86 (0·06)	0·93 (0·05)
2006	0·76 (0·11)	0·76 (0·11)	0·94 (0·06)	0·60 (0·15)	0·93 (0·05)	0·72 (0·08)
2007	0·79 (0·11)	0·67 (0·14)	0·69 (0·10)	0·53 (0·12)	0·76 (0·06)	0·55 (0·08)
2008	NA	0·32 (0·13)	NA	0·43 (0·13)	NA	0·33 (0·08)

[a] The combined model value reflects only the ground count data because no telemetry data was available in that year.

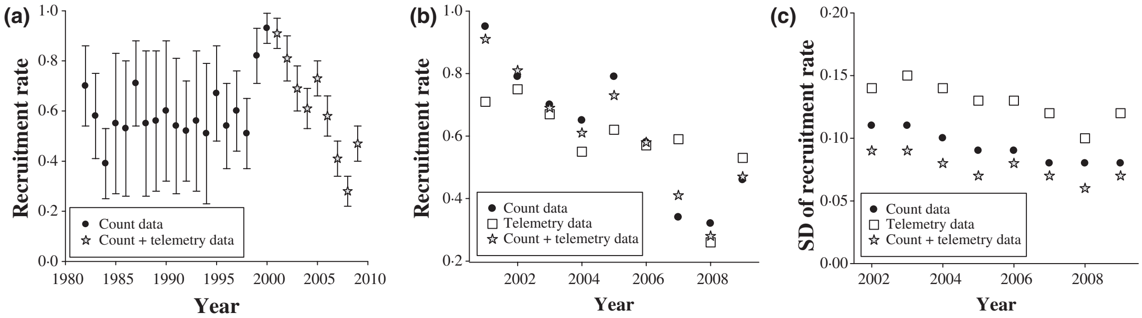

Fig. 2. Estimates from the Wheeler population of Sierra Nevada bighorn sheep. (a) Annual recruitment rates (and SD) across all years of the study (1981–2009). From 1981 to 2000 estimates were based only on ground count data and from 2001 to 2009 estimates were based on the combined model (count and telemetry data). (b) Recruitment rate estimates when using only count data, only telemetry data, and both data types combined. (c) SD around recruitment estimates when using only count data, only telemetry data, and both data types combined.

weighted towards values obtained from counts (the data type with the higher precision). With the exception of Langley in 2006 (only eight marked females), mark–resight abundance estimates were also consistently higher than those generated from count data.

The models estimated demographic parameters even in years when field data were not collected, although the posterior standard deviations of those estimates were substantially larger than years for which data existed (N_A estimates shown in Fig. 3). These estimates can be derived because only some values are logically possible given the population structure in the previous and following years. Models also provided PD credible intervals (CIs) for parameters obtained from ground counts, for which there had been no previous estimates of error. In total, 85% of the ground counts of each stage class fell within the credible intervals of predicted abundance values (see example of estimates vs. count data for adult females at Warren in Fig. 4).

We report estimated numbers of adult females, mean vital rate values, and mean population growth rates for each herd

Table 3. Annual estimates of the number of adult females (N_A) in the Wheeler and Langley populations of Sierra Nevada bighorn sheep when estimated from ground count data only, mark–resight (MR) data only, and with the combined data model (count and mark–resight data; SD in parentheses)

Population	Year	# Marked females	# MR surveys	MR (N_A)	Ground count (N_A)	Combined
Wheeler						
	2006	13	2	36 (5·96)	33 (2·02)	34 (1·62)
	2007	18	1	42 (5·81)	33 (1·94)	35 (1·39)
	2008	16	2	41 (6·71)	35 (1·82)	36 (1·50)
	2009	16	1	44 (6·52)	35 (2·07)	38 (1·53)
Langley						
	2006	8	3	29 (3·5)	33 (2·97)	32 (2·13)
	2007	17	1	50 (10·9)	34 (3·49)	40 (2·38)
	2008	12	2	47 (6·7)	35 (3·75)	40 (2·15)

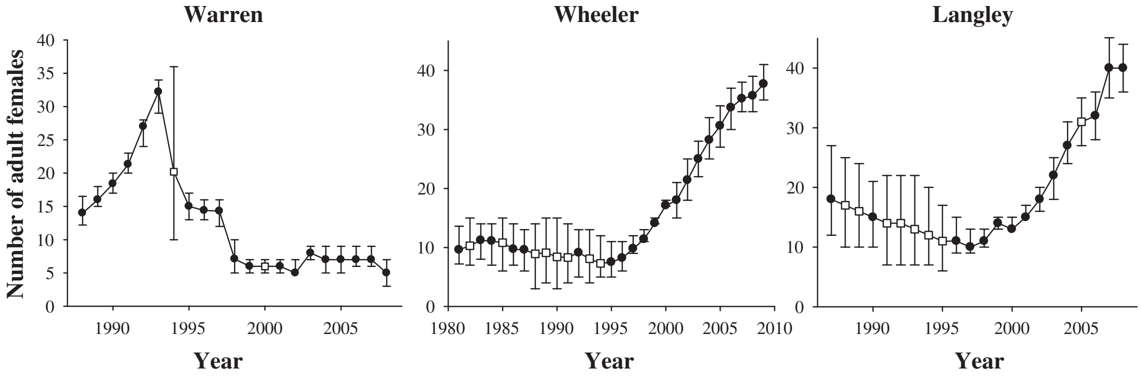

Fig. 3. Estimated number of adult female Sierra Nevada bighorn sheep (and 95% CI) in the Warren, Wheeler, and Langley populations. Black circles (●) signify years that demographic data were collected on the populations and open squares (□) signify years that no demographic data were collected.

from baseline demographic models (year-specific estimates are provided in Table S1, Supporting information). The Warren population was estimated to have grown from 14 adult females in 1988, to a maximum of 32 in 1993. This herd subsequently declined to an estimated six adult females in 1999, and has remained relatively static since then with five adults estimated in 2008. Over all the years in which data were collected, mean adult female survival was 0·83 (SD = 0·02), yearling survival was 0·50 (SD = 0·10), fecundity was 0·62 (SD = 0·05), and the mean growth rate was 0·97 (95% CI = 0·86 – 1·08). For Wheeler 10 adult females were estimated in 1981, which declined to a low of seven in 1994, and grew to an estimated 38 as of 2009. From 1981 to 2008, average adult female survival was 0·90 (SD = 0·02), two-year-old survival was 0·67 (SD = 0·07), recruitment was 0·55 (SD = 0·03), and the mean growth rate was 1·04 (95% CI = 1·00–1·08). The Langley herd was estimated at 18 adult females in 1987, declining to a low of 10 in 1997, and subsequently increasing to 40. From 1987 to 2008 the average adult female survival was 0·91 (SD = 0·02), yearling survival was 0·77 (SD = 0·06), fecundity was 0·63 (SD = 0·05), and the mean growth rate was 1·05 (95% CI = 1·00–1·11).

COVARIATE EFFECTS

The increasing populations, Wheeler and Langley, exhibited negative density dependence in both vital rate parameters (95% CIs of regression coefficients did not overlap zero with the exception of adult survival at Wheeler which had 86% PD < 0; Table 4). Meanwhile, there was a trend suggesting positive density dependence in survival rates at Warren (regression coefficient had 90% PD > 0; Table 4; Fig. 5). Generally summer rainfall had a positive influence on survival and reproductive rates in all populations although the effect was greatest on fecundity rates for bighorn sheep in Warren (95% CI of regression coefficients did not overlap 0; Table 4; Fig 5). Regression coefficients demonstrated that increases in snow depth were positively associated with adult survival at Wheeler (>83% PD > 0) and with reproduction at Langley (95% CIs did not overlap zero). At Warren, however, both adult survival and fecundity were strongly negatively associated with winter snow depth (95% CIs did not overlap zero; Fig. 5).

Discussion

The Bayesian state-space models developed here, combining ground count, telemetry, and mark–resight data, allowed us to integrate all the available data to increase accuracy and precision in parameter estimates and to fit covariates to vital rates driving population performance. Imprecise parameter estimates are one of the greatest limitations in detecting population trends, diagnosing causes of declines, and directing management actions (Taylor & Gerrodette 1993; Gibbs, Droege & Eagle 1998). By integrating all available data to better track the spatial and temporal dynamics of SNBS populations we are able to prioritize populations for management

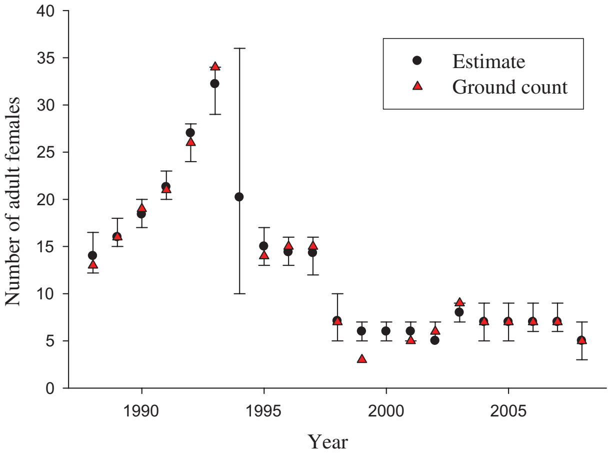

Fig. 4. Number of adult female Sierra Nevada bighorn sheep counted during annual ground surveys and estimated from the Bayesian state-space demographic model (with 95% CI) in the Warren population from 1988 to 2008.

intervention, identify vital rates that should be increased, and direct future recovery strategies.

We found that combining SNBS data types significantly improved the precision of demographic parameter estimates, as has been found in other studies combining data types (Fig. 2; Besbeas *et al.* 2002; White & Lubow 2002; Brooks, King & Morgan 2004; Schaub *et al.* 2007). Given the wide application of telemetry in wildlife research and monitoring, the integration of telemetry data with other data types, such as ground counts, has tremendous potential for enhancing demographic parameter estimation. While the integration of count and telemetry data dramatically decreased the variation in adult survival and fecundity, the combination of count and mark–resight data just slightly decreased the variation in estimates of adult female population size (Table 3). This occurred because the count data model had a constant relationship to population size while the mark–resight model replaced this assumption with an estimate of detection probability, thus increasing the variance around abundance estimates. Given that the count data yielded a much more precise estimate of adult abundance, the estimates from the combined data model were biased towards those from counts. We suspect that heterogeneity in resighting probabilities among individuals (unaccounted for in the current model) may have caused the mark–resight data to overestimate the numbers of adult females, while count data may have underestimated them, particularly as populations increased in size. By combining data types, estimates were more intermediate in value and were likely to be more accurate (Table 3).

Given the piecemeal nature of the SNBS data, this approach was also beneficial for standardizing the error structure across different data types. For the first time, demographic rates of SNBS can be directly compared among populations, regardless of the various data types used in different years. The models also estimated parameter values for years when field data were not collected, filling in gaps in our data set, and estimating precision around ground counts that had no previous measurement of error (Fig. 3).

With these improved demographic parameter estimates we have greater power to prioritize populations of conservation concern and detect demographic rates indicative of decline. For example, Wheeler and Langley have been increasing in size with long-term growth rates of 1·04 and 1·05, respectively. Meanwhile, Warren has had a negative long-term growth rate of 0·97 and is the clear management priority. While fecundity rates at Warren were comparable to the other herds, adult and yearling survival rates were ~10% and 20% lower, respectively; suggesting that recovery activities should focus on increasing these rates (Johnson *et al.* 2010). Greater precision in parameter estimates can also be used to more quickly identify key changes in population trajectories. Since 2000, growth rates at Langley have been > 1·13; however, in 2008 this rate dropped dramatically. Based on only the ground count data, the annual growth rate was estimated at 0·88 with a 95% CI ranging from 0·66 to 1·08, yielding uncertainty about the status of the population. Given the improved combined data model, the annual growth rate was estimated at 0·86 with a credible interval from 0·76 to 0·96, signalling to managers the likelihood of a definitive short-term decline.

The results of our models can also be used to improve population monitoring efficiency (Goodman 2004). For example, it appears that telemetry-based vital rate estimates have comparable precision to ground counts, but only in the large populations and when > 30% of the females are collared. As populations increase in size and near-complete census counts are harder to obtain, information on adult survival, fecundity, and adult female abundance could be entirely derived from telemetry data. While telemetry data were highly informative for estimating demographic rates in large SNBS populations, count data were more effective for elucidating rates in small herds like Warren, where small sample sizes caused telemetry estimates to be less precise (Table 2). In the future, simulation studies could be used to identify the value of different data types (both those currently collected and novel ones) to estimate parameters under a wide range of conditions to improve monitoring programmes given logistical and budgetary constraints.

By including covariates into demographic models we found evidence of negative density dependence in both adult female survival and recruitment/fecundity in the increasing populations of Wheeler and Langley (Fig. 5), despite their relatively small sizes. Negative density effects may arise from a combination of high site fidelity, limited female dispersal, and discrete habitat patches in the Sierra Nevada; all factors that may constrain bighorn sheep from expanding into unoccupied ranges. In Wheeler and Langley reproductive rates were impacted at lower densities than adult survival (Fig. 5), a pattern commonly observed in other ungulates, as younger stage classes tend to be disproportionately influenced by negative density dependence (Gaillard, Festa-Bianchet & Yoccoz 1998; Gaillard *et al.* 2000).

While vital rates were depressed by density in Wheeler and Langley, adult female survival appeared to be positively

Table 4. Posterior mean estimates, SD, and 95% credible intervals (95% CI) for regression coefficients from covariate models of adult female survival and fecundity/recruitment rates from Sierra Nevada bighorn sheep populations. The proportion of the coefficient posterior distribution (PD) on either side of zero is also reported

Vital rate and population	Parameter	Estimate	SD	Lower 95% CI	Upper 95% CI	% PD < 0	% PD > 0
Adult survival							
Warren	Intercept	2·667	0·906	0·955	4·423	–	–
	Density*	0·030	0·026	–0·016	0·088	9·7	90·3
	Snowpack**	–0·011	0·004	–0·020	–0·002	99·4	0·6
	Summer Rain*	0·564	0·439	–0·274	1·481	7·8	92·2
Wheeler	Intercept	2·579	1·018	0·563	4·571	–	–
	Density*	–0·025	0·024	–0·077	0·017	86·1	13·9
	Snowpack*	0·008	0·008	–0·008	0·023	16·8	83·2
	Summer Rain*	0·951	0·898	–0·759	2·771	14·2	85·8
Langley	Intercept	3·923	0·726	2·394	5·352	–	–
	Density**	–0·061	0·015	–0·091	–0·026	99·9	0·1
	Snowpack	0·003	0·004	–0·005	0·012	21·4	78·6
	Summer Rain*	1·138	1·092	–0·962	3·320	14·9	85·1
Fecundity/Recruitment							
Warren	Intercept	1·734	0·849	0·047	3·40	–	–
	Density	–0·009	0·024	–0·053	0·040	67·2	32·8
	Snowpack**	–0·006	0·003	–0·013	0·000	97·8	2·2
	Summer Rain**	0·624	0·391	0·029	1·590	1·8	98·2
Wheeler	Intercept	1·804	0·658	0·563	3·159	–	–
	Density**	–0·059	0·023	–0·107	–0·057	99v9	0·1
	Snowpack	0·002	0·005	–0·009	0·002	38·0	62·0
	Summer Rain	–0·300	0·668	–1·601	1·031	67·8	32·2
Langley	Intercept	2·454	0·935	0·707	4·376	–	–
	Density**	–0·073	0·023	–0·119	–0·029	99·6	0·4
	Snowpack**	0·009	0·004	0·001	0·018	1·1	98·9
	Summer Rain*	2·180	1·252	–0·306	4·619	5·3	94·7

*Indicates covariate coefficients that have > 80% of their posterior probability distributions > or < than zero.

**Indicates covariate coefficients with confidence intervals non-overlapping zero and having > 95% of their posterior probability distributions > or < than zero.

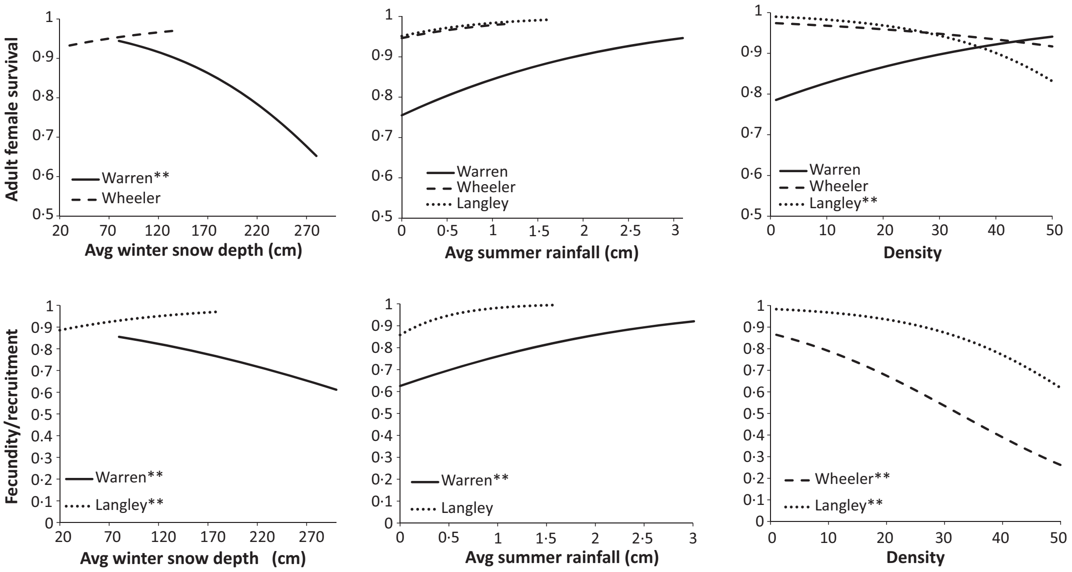

Fig. 5. Predicted effects of winter snow depth, summer rainfall, and density on adult female survival and fecundity/recruitment rates for populations of Sierra Nevada bighorn sheep. Predictions are only shown for populations with > 80% of their regression coefficient posterior distributions > or < 0; populations marked with a double asterisk (**) had > 95% of their posterior distributions > or < 0. Predictions for weather covariates were only modeled for the range of values experienced by each herd during the study period.

associated with density at Warren (Fig. 5). Studies of density in ungulate populations have largely focused on negative effects, with few studies observing Allee effects, or positive density dependence, in small populations (Treydte *et al.* 2001; Matson, Goldizen & Jarman 2004; Wittmer, Sinclair & McLellan 2005). While the mechanism driving an Allee effect at Warren is unknown, small SNBS herds may need to be augmented to alleviate depressed survival and/or reproductive rates. The large herds, showing signs of negative density effects, could potentially be used as the source stock for such augmentations.

Similar to density, climate factors differentially influenced the small Warren population compared to the larger populations of Wheeler and Langley. At Warren, winter snow depth negatively affected both adult female survival and fecundity, as has been found in other ungulates (Gaillard *et al.* 2000; Jacobson *et al.* 2004). Contrary to this pattern, however, snow depth had a minor positive effect on survival at Wheeler and on reproduction at Langley. This disparity may be due to the relative amounts of snowfall each herd receives, as the weather station at Warren reported snow depths almost double those reported for other herds (Fig. 5). Additionally, low elevation winter range is abundant in Wheeler and Langley, and SNBS in these herds routinely descend below snow line. Meanwhile, a majority of the winter observations of SNBS at Warren have been at high elevations on slopes blown-free from snow, where snow patterns are expected to have a greater effect (CDFG, unpublished data). Given that most precipitation in the arid Sierra Nevada is received as snow in winter, the positive effects of snow depth at Wheeler and Langley may reflect a longer growing season the following spring and summer. Unlike snow, summer precipitation affected all populations in a similar way, having a positive influence on both survival and reproduction. While this effect was slight at Wheeler and Langley, rainfall dramatically increased vital rates in Warren. As with snow, this may be a function of the range of rainfall values that occurred during the study, which were greatest at Warren (Fig. 5).

Although weather factors typically have a greater influence on younger stage classes than older ones (Gaillard *et al.* 2000), we did not see this pattern in SNBS. Weather covariates had weak effects on both adult survival and reproduction at Wheeler and Langley, but elicited strong effects on the vital rates of both young and old stage classes at Warren. The powerful influence of weather on adult survival in this herd is disconcerting, as this is atypical of ungulates and may contribute to Allee effects. We are uncertain whether the strong influence of environmental stochasticity in this population reflects a difference in habitat quality or is simply a function of its small size and demographic stochasticity.

Mountain lions, *Puma concolor*, are the main predator of SNBS (Wehausen 1996) and lion predation is the primary known-cause of mortality (CDFG, unpublished data). Because consistent long-term data on mountain lions in SNBS populations were unavailable, this factor could not be included in our demographic models. Thus, observed negative density dependence could be due to food-based or predator-based carrying capacity; further work on the role of predation in SNBS dynamics will be required. Other factors that may significantly influence SNBS vital rates, including disease, habitat use patterns, and genetic diversity, were not included in our analysis but are suspected to play a significant role in the dynamics of these populations.

To successfully manage and conserve populations we must be able to accurately estimate key demographic parameters and identify the deterministic and stochastic factors driving the variation in those rates. Using traditional statistical methods, such analyses have been limited for populations with piecemeal datasets, common for both endangered and harvested species. We found that Bayesian state-space models were a powerful tool for integrating count, telemetry and mark–resight data available for SNBS, identifying the information content of different data types, determining demographic trends, and elucidating the ecological processes driving dynamics (King *et al.* 2008; Véron & Lebreton 2008). For SNBS, our model results can be used to prioritize populations of conservation concern, better detect population declines, improve monitoring schemes, and direct management strategies; all capabilities that will improve recovery success in this subspecies.

Acknowledgements

We thank E. Crone and M. Hebblewhite for discussion and statistical modelling support, B. McClintock for providing code for Bayesian mark–resight estimation, and D. German for compiling demographic data. We are grateful to all the people who have collected data on SNBS including T. Blankinship, L. Bowermaster, L. Brown, M. Cahn, K. Chang, L. Chow, K. Ellis, D. German, A. Feinberg, J. Fusaro, L. Greene, D. Jensen, M. Kiner, K. Knox, P. Moore, R. Ramey II, C. Schroeder, T. Taylor, and S. Thompson. CDFG and the Canon National Parks Scholars Program provided funding for this work; L.S.M. also acknowledges NSF (DEB-0415 604).

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Received 30 December 2009; accepted 21 June 2010
Handling Editor: Paul Lukacs

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Location of Warren, Wheeler, and Langley Sierra Nevada bighorn sheep populations, CA.

Appendix S1. Pre-birth pulse survey modifications to the Sierra Nevada bighorn sheep demographic model.

Appendix S2. WinBUGS code for Sierra Nevada bighorn sheep post-birth pulse demographic model.

Table S1. Estimated annual vital rates and population growth rates (λ) from Bayesian state-space models of Sierra Nevada bighorn sheep populations.