JOINT EFFECTS OF DENSITY DEPENDENCE AND RAINFALL ON ABUNDANCE OF SAN JOAQUIN KIT FOX

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Abstract: We analyzed time-series abundances of San Joaquin kit fox estimated during 1983–95 on the Naval Petroleum Reserves in California (NPRC). For the analysis, we modified a model of density-dependent, stochastic population growth to include the lagged effects of a weather covariate (vegetation growing season rainfall). Without the covariate in the model, a statistical test failed to detect significant density dependence in fluctuating kit fox abundances. However, when the covariate was added, strong density dependence was detected. According to an information-theoretic model-selection index, the model with both density dependence and rainfall is far superior to the models that result from deleting one or more of these factors. The 2-year time lag in the response of kit fox abundances to changes in rainfall is consistent with biological expectations of how rainfall affects habitat carrying capacity for kit fox. An additional covariate, a coyote abundance index, failed to improve the model. A population viability analysis (PVA) performed with the combined density dependence–rainfall model suggests that the San Joaquin kit fox on NPRC could face a risk of up to 52% of falling to low levels within 20 years.

Time-series statistical methods for wildlife ecology are maturing. New approaches convert deterministic, biologically-based population models into stochastic models in order to account for the unpredictable variability present in animal populations (Dennis et al. 1995). The population models used as the bases for stochastic models include exponential growth (Dennis et al. 1991), density-dependent growth (Turchin and Taylor 1992, Turchin 1993, Dennis and Taper 1994, Saitoh et al. 1997, Fryxell et al. 1998, Zeng et al. 1998), stage-structured models (Dennis et al. 1995, 1997), models of multiple populations varying spatially (Bjornstad et al. 1995, Stenseth et al. 1996, Dennis et al. 1998), and models of multiple species (Carpenter et al. 1994, Pascual and Kareiva 1996, Stenseth et al. 1997, Fryxell et al. 1999). The stochastic components serve as connections between models and time-series data and allow for statistical inferences such as parameter estimation, hypothesis testing, model selection, model evaluation, and forecasting.

From a management standpoint, one of the more potentially useful developments in time-series modeling is the incorporation of environmental covariates into the models (Marmorek 1996, Rotella et al. 1996, Rothery et al. 1997). Environmental covariates can be weather or climate conditions (Turchin and Ostfeld 1997; Zhou et al. 1997; Forchhammer et al. 1998; Lewellen and Vessey 1998a,b; Post and Stenseth 1999), or even other species (Fryxell et al. 1999). If environmental covariates are part of the data base, they can be added and tested as adjustments to model parameters in order to improve site- and year-specific population forecasts.

The endangered population of San Joaquin kit foxes (*Vulpes macrotis mutica*) inhabiting the NPRC poses challenging problems for time-series analysis. Estimates of abundance extend back only to 1983 and reveal erratic, wide fluctuations in population size. Immense variability of demographic parameters in the population is associated with variable environmental conditions (Otten and Cypher 1998). The kit fox feeds primarily on small mammalian herbivores (Cypher and Spencer 1998) that depend on vegetation (Beatley 1969), suggesting kit fox

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abundance may reflect rainfall amounts during the growing season 2 years earlier. Appropriate statistical analyses for examining this hypothesis must account for the time-series nature of the kit fox data as well as the main biological features of kit fox population growth. Due to the short length of the series, however, complex analysis approaches are severely constrained by the number of parameters that can be estimated.

We analyzed the relationship of rainfall and kit fox abundance by modifying a simple stochastic model of density-dependent population growth to include covariates. The base model for the kit fox population was the stochastic Ricker–logistic model used by Dennis and Taper (1994) to construct a statistical test of density dependence. The carrying capacity of the modified model fluctuates from year to year with covariate levels, the main covariate of interest being growing season rainfall (2-yr lag).

We examined other covariates with this modeling approach. Among the covariates, coyote abundance was of particular interest. Coyotes are known to compete with kit foxes as well as to kill foxes opportunistically (White and Garrott 1997, Cypher and Spencer 1998), although coyote control as a means for enhancing the kit fox population on NPRC was shown to be ineffective (Cypher and Scrivner 1992). A coyote abundance index was incorporated in the model jointly with growing season rainfall, in order to test whether coyotes had any detectable effect on population fluctuations of kit foxes. Additional covariates analyzed included alternative lags for growing season precipitation, calendar year rainfall (various lags), and 2-year lag in fox abundance (second-order density dependence).

We hypothesized that combining the effects of density dependence and growing season rainfall in one model would account for a large amount of variability in kit fox abundances. Under the hypothesis, a model with both factors included should describe the data better than models with either density dependence alone or rainfall alone. Furthermore, model selection and model evaluation analyses should indicate that the joint density dependence–rainfall model is not overparameterized and that it adequately describes the statistical properties of the noise in the system. Finally, under the hypothesis we would not expect the additional covariates, including coyote abundance, to improve the model.

With the best model that emerged from the analyses, we conducted a preliminary PVA for the San Joaquin kit fox population on NPRC. Two conceptual problems with PVA in this setting arose: first, how to incorporate the weather covariate information, and second, how to estimate the uncertainty in the risk assessments. We adapted some bootstrapping approaches to handle both problems.

In this paper, our purpose is twofold. First, we thoroughly describe the stochastic model and its associated statistical methods. Although the methods are not currently available as a part of any statistical or ecological computer packages, the necessary calculations are fairly simple and easily programmed. Second, through our kit fox analysis we attempt to provide a completely worked example of how the model might be helpful to wildlife managers. We discuss the biological interpretation of the model and the management ramifications of the analysis results. We believe these novel statistical methods could find useful applications in many wildlife management problems.

STUDY AREA

The time-series data consist of annual estimates of abundance of San Joaquin kit fox and were collected within a 135-km^2 study area on the NPRC from 1983–95. The NPRC is located approximately 40 km west–southwest of Bakersfield, California and is composed of well-developed oil fields interspersed with areas of relatively undeveloped grassland-shrub habitat. The study area encompassed approximately the southern two-thirds of NPRC. The vegetative community on NPRC is broadly described as valley grassland (Heady 1977) and specifically described as belonging to the Allscale Series (Sawyer and Keeler-Wolf 1995). Vegetative compositions are dominated by annual grasses and forbs. Xerophytic shrubs are locally common, but trees are rare (Heady 1977).

The climate of the NPRC region is Mediterranean in type and is characterized by hot, dry summers and mild, wet winters (Major 1977). Mean annual rainfall is 15.1 cm (National Climatic Data Center 1996). Over the years of this study (1983 through 1995), annual rainfall varied between 7.3 and 27.6 cm (15.9 ± 1.8 cm, $\bar{x}$ ± SE, $n = 13$). Most rainfall on NPRC occurs from 1 October to 31 March (defined as annual growing season rainfall) and coincides with the primary vegetative growing season. We there-

Table 1.   Maximum likelihood estimates ($\hat{a}$, $\hat{b}$, $\hat{c}$, $\hat{\sigma}^2$) of parameters in the density dependence–rainfall model (Eq. 1), generalized R^2, and Schwarz information criterion (SIC) for 4 model hypotheses (H_i) fitted to the San Joaquin kit fox data. The population estimates (and SE) for the winters of 1983–84 to 1995–96 were 117 (11.5), 220 (16.6), 161 (15.9), 164 (14.3), 135 (13.4), 166 (14.7), 131 (13.9), 117 (13.0), 46 (9.2), 88 (9.2), 196 (15.9), 363 (23.5), and 133 (11.0); the precipitation levels (cm) for the growing seasons of 1982–83 to 1993–94 were 22.0, 8.6, 8.7, 15.2, 12.9, 10.2, 8.4, 5.9, 14.8, 17.6, 22.5, and 11.3, respectively.

Hypothesis	$\hat{a}$	$\hat{b}$	$\hat{c}$	$\hat{\sigma}^2$	R^2	SIC
H_0	0.01068	—	—	0.3305	0.00	25.7
H_1	0.7408	−0.004647	—	0.2055	0.09	22.5
H_2	−1.089	—	0.08346	0.1446	0.23	18.3
H_3	−0.3607	−0.003835	0.07437	0.06165	0.82	10.6

fore modeled precipitation effects on kit fox abundance using annual growing season rainfall rather than total annual rainfall. For the 12 years 1982–83 through 1993–94, annual growing season rainfall varied between 5.9 and 22.5 cm (Table 1; overall mean of 13.1 ± 1.6 cm).

METHODS

Population Estimation

Annual abundance estimates of San Joaquin kit fox were made as a part of a large study of population dynamics (Brian Cypher, NPRC Endangered Species and Cultural Resources Program, unpublished data). Adult and yearling foxes were captured each winter (Nov, Dec, Jan) between 1983–95 to estimate annual abundances and to determine annual distribution patterns. One wire-mesh model 208 Tomahawk live-trap (Tomahawk, Tomahawk, Wisconsin, USA) was placed within each quarter section of the study area and operated for 4 consecutive nights. Trap locations were consistent between years, differing only when a particular location was destroyed (e.g., road construction) or became unusable or unsafe (e.g., presence of feral dogs). In these instances, new trap locations were established as close as possible to previous locations while minimizing the risk to captured animals. Captured kit foxes were marked with individually numbered eartags, sexed, aged, weighed, measured, and released at the capture location.

Annual abundances (Table 1) were estimated from capture–recapture histories using program CAPTURE (Otis et al. 1978, Rexstad and Burnham 1991). Model selection criteria in CAPTURE indicated that models M_o (equal catchability model) and M_{bh} (heterogeneity and trap response model) were best. To aid in model selection, Pollock et al. (1990) recommended utilizing pertinent biological information, if such information is available. Previous research on

NPRC suggests that kit foxes exhibit both heterogeneity in trapability and a response to trapping and that model M_{bh} is probably the most appropriate (Harris 1987). As a result, we selected the jackknife-type estimator of Pollock and Otto (1983) in program CAPTURE (model M_{bh}), which allows for individual capture probabilities and a trap response.

Density-dependent–Rainfall Model

All statistical methods used in this paper were based on a stochastic population growth model. The model was a discrete-time, stochastic logistic model (Dennis and Taper 1994) that we modified to incorporate weather as a covariate. The model can be written as:

$$N_t = N_{t-1}\exp(a + bN_{t-1} + cW_{t-2} + \sigma Z_t), \quad (1)$$

where N_t is kit fox population abundance at time t (yr: $t = 0, 1, 2, \ldots, 12$; each yr begins in Oct, so that yr 0 includes observations recorded between Oct 1983 and Sep 1984), W_t is the annual growing season rainfall (cm) for time t, and Z_t is normal (0,1) noise (with Z_1, Z_2, ... uncorrelated). Also, a, b, c, and σ^2 are unknown parameters ($\sigma > 0$) to be estimated from the data. Under this model, the population abundances N_t ($t = 1, 2, \ldots$) are random variables that are correlated through time, and N_0 is fixed. The random variables Z_t ($t = 1, 2, \ldots$) represent unpredictable fluctuations in growth rate (on the logarithmic scale) over and above fluctuations accounted for by density dependence and precipitation.

Various models are contained in Eq. 1 as special cases. If $\sigma = 0$, $c = 0$, and $b = 0$, Eq. 1 is the simple deterministic model of exponential increase–decrease (in discrete time). If $\sigma = 0$ and $c = 0$, Eq. 1 is the Ricker (1954) discrete-time logistic model. When $c = 0$ and $b = 0$, Eq. 1 is the stochastic model of exponential increase–decrease (in discrete time) discussed by

Dennis et al. (1991). With $c = 0$, Eq. 1 is the stochastic discrete-time logistic model proposed by Dennis and Taper (1994) as a base model for testing density dependence.

Four biologically interesting cases of Eq. 1 were fitted to the data as separate hypotheses: H_0: $b = 0$ and $c = 0$ (no density dependence, no rainfall effect); H_1: $b \neq 0$ and $c = 0$ (density dependence, no rainfall effect); H_2: $b = 0$ and $c \neq 0$ (no density dependence, rainfall effect); and H_3: $b \neq 0$ and $c \neq 0$ (density dependence, rainfall effect).

We calculated maximum likelihood (ML) estimates of the unknown parameters in Eq. 1 for all 4 hypotheses, using the time-series abundance estimates of kit foxes in conjunction with the rainfall data. The ML estimates for the model are identical to "conditional least squares" estimates (Dennis and Taper 1994, Dennis et al. 1995) and are easily calculated with most ordinary regression packages as follows. Let n_0, n_1, n_2, ..., n_q be the recorded population abundances (the time series data, Table 1). Lower case denotes that they are fixed quantities (outcomes) and not random. Also, let $y_1 = \ln(n_1/n_0)$, $y_2 = \ln(n_2/n_1)$, ..., $y_q = \ln(n_q/n_{q-1})$ be the yearly population changes on the logarithmic scale, and let w_{-1}, w_0, w_1, ..., w_{q-2} be the recorded (and lagged) rainfall levels. For the full model (H_3), a regression is performed with the data triples (y_1, n_0, w_{-1}), (y_2, n_1, w_0), ..., (y_q, n_{q-1}, w_{q-2}), in which the y's are used as the dependent variable and the n's and w's are the predictor variables. The resultant coefficients in the regression equation are the ML point estimates of a (intercept), b, and c. The ML point estimate of σ^2 is the error sum of squares (sum of squared model residuals) divided by q. For hypotheses H_2, H_1, and H_0, the corresponding predictor variables are dropped from the regressions.

While valid point estimates are easily obtained with regression packages (e.g., SAS [SAS Institute 1990], or SYSTAT [SPSS 1996]), associated confidence intervals for the parameters printed by regression packages are not valid for hypotheses H_3 and H_1 (in which the n's are used as a predictor variable). Printed hypothesis tests for whether the parameters are nonzero in H_3 or H_1 are also not valid. This is because the growth increments (y's) have serial dependence in the density-dependent models, which contradicts the distributional assumptions of regression (Dennis and Taper 1994).

Density-dependent–Rainfall–Coyote Model

We performed additional analyses to explore the possible effects of other covariates. In particular, a coyote abundance index based on scent-station visits had been recorded in March of each year since 1985 in a monitoring survey of NPRC (Cypher and Scrivner 1992; Table 2). If coyotes affect fox survival (White and Garrott 1997), the coyote abundance recorded in March of year $t - 1$ would be expected to have a discernable effect on fox abundance observed in November–December of year t (recall that years begin on Oct 1). The coyote abundance index for year $t - 1$ was entered in the model as an additional covariate. The full model was

$$N_t = N_{t-1}\exp(a + bN_{t-1} + c_1W_{t-2} + c_2V_{t-1} + \sigma Z_t), \qquad (2)$$

where V_t is the coyote abundance index at time t, and c_1, c_2 are constants. The time series for this analysis was reduced in length by 1 observation because the coyote index survey began in 1985. Thus, only 11 observations (11 time steps from N_{t-1} to N_t) were available for fitting Eq. 2.

Eight submodels of Eq. 2 were fitted as separate hypotheses, in which the constants b, c_1, and c_2 were fixed at zero singly and in combinations: H_0': $b = 0$, $c_1 = 0$, $c_2 = 0$; H_1': $b \neq 0$, $c_1 = 0$, $c_2 = 0$; H_2': $b = 0$, $c_1 \neq 0$, $c_2 = 0$; H_3': $b = 0$, $c_1 = 0$, $c_2 \neq 0$; H_4': $b = 0$, $c_1 \neq 0$, $c_2 \neq 0$; H_5': $b \neq 0$, $c_1 = 0$, $c_2 \neq 0$; H_6': $b \neq 0$, $c_1 \neq 0$, $c_2 = 0$; H_7': $b \neq 0$, $c_1 \neq 0$, $c_2 \neq 0$.

Other covariates analyzed were calendar year rainfall (Jan–Dec) with various lags, other lags of growing season rainfall, and 2-year lagged fox abundance (second-order density dependence). These models were investigated by fitting Eq. 1 using the covariate of interest in place of W_{t-2}.

Hypothesis Tests

We performed statistical hypothesis tests by parametric bootstrapping (Dennis and Taper 1994, Manly 1997, Rothery et al. 1997). The procedure is straightforward but numerically intensive. We describe the steps for testing H_i (null) vs. H_j (alternative); consult Dennis and Taper (1994) and Manley (1997) for further details. Step-by-step instructions are as follows. (1) Obtain ML parameter estimates for both the null model and the alternative model. (2) Calculate the t-ratio statistic for the particular slope

coefficient being tested. The essence of the hypothesis testing problem in density-dependence models is that the t-ratio statistic does not have a Student's t distribution, and therefore t-tables cannot be consulted for P-values or critical percentiles. The t-ratio is the likelihood ratio statistic for testing H_i vs. H_j; its distribution when the null hypothesis is true is estimated by simulation in the subsequent steps. (3) Simulate B time series (we used $B = 10,000$) of population abundances from the null hypothesis model, using the null hypothesis ML parameter estimates. Each time series should have the same number of observations as the original data and should start at the same initial population value of the original data. The values of the weather covariate are not simulated, but are entered in the simulation model as fixed constants. (4) Refit (i.e., calculate ML estimates via regression) both H_i and H_j to each of the simulated time series. (5) Calculate the t-ratio for each of the simulated time series, yielding B simulated values of the t-ratio (one can also retain the B sets of parameters for the null hypothesis for calculating confidence intervals, CIs). (6) The proportion of the B simulated t-ratios that are more extreme than the original t-ratio from the data is the estimated P-value for the test.

Adapting a regression package to do these bootstrapping calculations requires some provision in the package for looping, such as a macro language. Because the calculations involve repeated regressions (matrix inversions), use of a matrix programming language such as GAUSS (Aptech Systems 1993) or MATLAB (Math Works 1993) rather than a commercial statistics package greatly facilitates the bootstrapping process.

Four statistical hypothesis tests were conducted for the density dependence–rainfall model (Eq. 1): H_0 vs. H_1, H_0 vs. H_2, H_1 vs. H_3, and H_2 vs. H_3. In each test, the null model is contained within the alternative model as a special case and is obtained by setting 1 parameter equal to zero. The bootstrap method for testing H_0 vs. H_1 is the principal topic of Dennis and Taper (1994). It was not necessary to bootstrap the test of H_0 vs. H_2, because the growth increments (y's) are independent in the density-independent models (Dennis et al. 1991), and the t-ratio has a Student's t distribution under H_0.

Hypothesis tests were conducted among all pairs of submodels within the density dependence–rainfall–coyote model (Eq. 2) for which

1 model was nested within the other and had 1 less parameter (H_0' vs. H_1', H_2', and H_3'; H_1' vs. H_5' and H_6'; H_2' vs. H_4' and H_6'; H_3' vs. H_4' and H_5'; H_4' vs. H_7'; H_5' vs. H_7'; H_6' vs. H_7'). It was not necessary to bootstrap the tests that have $b = 0$ (no density dependence) in both null and alternative hypotheses, because the t-ratio has a Student's t distribution under the null hypothesis.

Model Selection

Choosing a model by pairwise-hypothesis testing among several candidate models can lead to ambiguous results (a problem well-known in stepwise regression). We supplemented the hypothesis testing results with the Schwarz information criterion (SIC, Schwarz 1978). The SIC is an information-theoretic, model-selection index used to select the best model from a suite of models, and is an Akaike-style index (Sakamoto et al. 1986) based on the maximized log-likelihood, penalized by the number of parameters estimated in the model. It has performed extremely well in extensive simulation studies of ecological time-series modeling (Hooten 1995). For a model hypothesis H_i contained in Eq. 1 or Eq. 2, the SIC is

$$SIC_i = q[1 + \ln(2\pi\hat{\sigma}_i^2)] + p\ln q, \qquad (3)$$

where $\hat{\sigma}_i^2$ is the ML estimate of σ^2 under model H_i, and p is the number of parameters estimated in model H_i (including the parameter σ^2). The model with the lowest SIC is the best in the sense that the procedure selects in large samples the model closest to the true model (closest according to an information-theoretic measure of discrepancy between the fitted model and the true model; Sakamoto et al. 1986, Bozdogan 1987). A rough guideline states that one will not notice much difference in quality of 2 models with SIC values differing by <2 (Sakamoto et al. 1986). The SIC is easily calculated from the information printed by regression packages.

Overall goodness of fit for each model was measured with a generalized R^2 value, defined as

$$R^2 = 1 - \frac{\sum\limits_{t=1}^{q} (n_t - \hat{n}_t)^2}{\sum\limits_{t=1}^{q} (n_t - \bar{n})^2}, \qquad (4)$$

where $\hat{n}_t$ is the 1-step-ahead predicted value for n_t (e.g., $\hat{n}_t = n_{t-1}\exp(\hat{a} + \hat{b}n_{t-1} + \hat{c}w_{t-2})$ for

model H_3, Eq. 1), and $\bar{n} = \Sigma_{t=1}^{q} n_t$ is the sample mean of the observations (not including the initial observation n_0). The measure compares the 1-step-ahead predictions of the model with the predictions that result from using the sample mean as a predictor. It is possible for the value of R^2 to be <0. A time series model can give worse predictions than the sample mean, and under such circumstances, a value of zero would be reported. The maximum R^2 value is 1 (perfect predictions). Because a high R^2 value can be achieved by an over-parameterized model, it should be interpreted in conjunction with a parameter penalty index such as SIC. When a parameter is added to a model, an increased R^2 value should ideally be accompanied by a decreased SIC.

The modeling approach used here is parametric, and careful attention to model evaluation is essential (Dennis et al. 1991, Dennis and Taper 1994). For nonlinear time-series models, diagnostic techniques focus on the residuals (Tong 1990). We scrutinized the residuals of the best-fitting model with diagnostic plots and tests for normality and autocorrelation. Verifying that the model is an adequate description of the stochastic mechanism that generated the data is particularly important if the model is to be used for forecasting or PVA.

Population Viability Analysis

We conducted a PVA using the density dependence–rainfall model, which emerged as the best model from the hypothesis testing and model selection analyses. A PVA essentially consists of simulating a stochastic model and estimating first-passage properties, such as the median time to reach a low abundance level or the probability of reaching that level within a fixed time (Dennis et al. 1991). However, as pointed out by Dennis et al. (1991), a serious mistake made in many PVA exercises is the failure to propagate the errors of parameter estimation in the estimates of first-passage properties. Propagation of these errors can be accomplished with bootstrapping (Dennis et al. 1991).

We refitted the best model to 2,000 sets of parametrically bootstrapped time series. With each set of parameters, we then estimated the probability that the San Joaquin kit fox population will decrease to n_e individuals within t years, by simulating future trajectories of population abundance. For each pair of values of n_e and t, the resulting 2,000 sets of first-passage

probabilities were used to form bootstrap CIs (Manly 1997).

Simulating potential future population trajectories poses a problem with a covariate in the model. For instance, in the case of rainfall, the covariate values were fixed for parameter estimation, and inferences were conditioned on that particular realization of rainfall values. However, it is not possible to forecast what values rainfall will take in the next 10 years in order to do a 10-year model simulation. Instead, we used the existing rainfall values as an estimate of the stationary probability distribution from which rainfall values arise. Local yearly precipitation typically has little or no autocorrelation and is routinely modeled with a skewed distribution such as a gamma (Rice 1995). We bootstrapped the rainfall values, that is, for each year of a simulation, we selected a value at random, with replacement, from the recorded rainfall values in the data set. Thus, our PVA with the density-dependence–rainfall model (Eq. 1) is based on the assumption that the variability patterns in rainfall characteristic of the last 2 decades will continue.

RESULTS

Density-dependent–Rainfall Model

The 4 fitted submodels of Eq. 1 yielded 4 sets of ML parameter estimates (Table 1). Note that the models with precipitation included (H_2 and H_3) had negative values estimated for the intercept parameter a. The precipitation covariate, however, serves as a yearly intercept adjustor. For these models, the average intercept prevailing over the years of the study can be estimated by $\hat{a} + \hat{c}\bar{w}$, where $\bar{w}$ (=13.175 cm) is the sample average of the covariate values. For model H_3, the estimated average intercept is 0.6191. Recall that in the pure density-dependence model (H_1), the value of $-a/b$ gives the long-term equilibrium, or carrying capacity, of the deterministic logistic model component. The carrying capacity in model H_1 can be estimated by $-\hat{a}/\hat{b} = 161.0$. For model H_3 the carrying capacity estimated using the average intercept is nearly identical in value: $-(\hat{a} + \hat{c}\bar{w})/\hat{b} = 161.4$. Because H_1 and H_3 are stochastic models, these carrying capacities are interpreted as the estimated long-term values around which the population fluctuates.

Hypothesis tests pointed to H_3 as the overall best model among the 4 models considered.
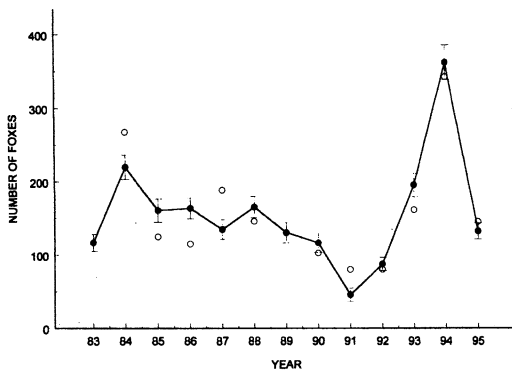
Fig. 1. Estimates of San Joaquin kit fox abundances (solid circles, ±SE) and 1-step-ahead predictions (open circles) from fitted model of density-dependent population growth with growing season rainfall as a covariate.

The tests rejected H_0 in favor of H_2 ($T = 3.59$, $P = 0.005$), rejected H_2 in favor of H_3 ($T = 4.58$, $P = 0.015$), rejected H_1 in favor of H_3 ($T = -3.48$, $P = 0.002$), but failed to reject H_0 in favor of H_1 ($T = -2.47$, $P = 0.139$). In other words, adding rainfall alone to a density independent model is a significant improvement, while adding density dependence alone is not a significant improvement. However, the model with both rainfall and density dependence is a significant improvement over the models with either factor alone. Density dependence is thus detectable only after the rainfall covariate is added to the model.

The SIC also points to H_3 as the overall best model (Table 1). The model with density dependence alone (H_1) is somewhat of an improvement over the density-independent model (H_0), according to the SIC. The model with rainfall alone (H_2) is a substantial improvement over H_0, and a definite improvement over H_1, according to the SIC. The SIC for the the mod-

el with both density dependence and rainfall (H_3), however, is far lower than the SICs for the other models, indicating that the added parameter improves model H_3 substantially.

Indeed, the 1-step predictions for model H_3 are close to the fox abundance estimates (Fig. 1). The fit of the model is reflected in the high generalized R^2 value of 0.82 (Table 1). While having too many parameters can produce such close fits, the SIC results indicate the model is not overparameterized.

Model diagnostic procedures indicate that the residuals from model H_3 are normal, homoscedastic, and uncorrelated. Residual plots (Fig. 2) show lack of variability patterns and approximate normality. The Lin-Mudholkar test for normality (Tong 1990) indicates that the normal distribution is an acceptable model for the residuals ($Z = 0.52$, $P = 0.603$). Tests reveal no significant first- or second-order autocorrelation (Tong 1990) in the residuals ($Z_1 = \hat{\rho}_1\sqrt{q}$ $= -1.02$, $P = 0.306$; $Z_2 = \hat{\rho}_2\sqrt{q} = 0.96$, $P = 0.337$; $\hat{\rho}_1$ and $\hat{\rho}_2$ are the first- and second-order sample autocorrelations). Overall, diagnostic results suggest that the model describes the patterns of stochastic variability in the data extremely well.

Density-dependence–Rainfall–Coyote Model

For the coyote covariate analysis, the 8 submodels of Eq. 2 yielded 8 sets of parameter estimates (Table 2). Model hypotheses ranged in complexity from density independence, no covariates (H_0', Table 2), to density dependence plus 2 covariates (H_7', Table 2).

The hypothesis tests provided no support for the presence of a detectable coyote influence in the kit fox time series. In all cases in which coy-

Table 2. Maximum likelihood estimates ($\hat{a}$, $\hat{b}$, $\hat{c}_1$, $\hat{c}_2$, $\hat{\sigma}^2$) of parameters in the density dependence–rainfall–coyote model (Eq. 2), and Schwarz information criterion (SIC) for 7 model hypotheses (H_i') fitted to the San Joaquin kit fox data, with growing season rainfall (2-yr lag) and coyote abundance index (1-yr lag) as covariates (coefficients c_1 and c_2, respectively). The coyote abundance index values for March 1985 to March 1995 were 110.5, 135.0, 106.06, 45.0, 36.27, 30.15, 25.13, 21.86, 68.42, 100.5, and 116.16, respectively.

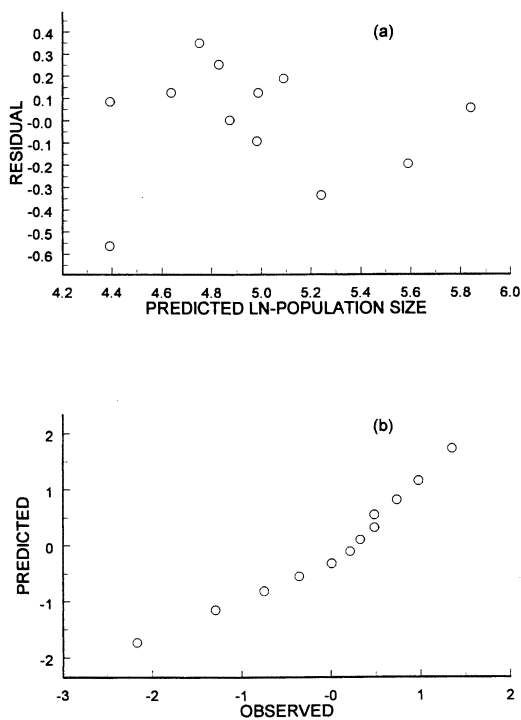| Hypothesis	$\hat{a}$	$\hat{b}$	$\hat{c}_1$	$\hat{c}_2$	$\hat{\sigma}^2$	R^2	SIC
H_0'	−0.04575	—	—	—	0.3223	0.00	23.6
H_1'	0.6625	−0.004360	—	—	0.2055	0.11	21.0
H_2'	−1.137	—	0.08819	—	0.1559	0.12	18.0
H_3'	−0.06824	—	—	−0.001577	0.3183	0.00	25.8
H_4'	−0.9531	—	0.09333	−0.003424	0.1375	0.40	19.0
H_5'	0.5396	−0.006478	—	0.006462	0.1653	0.19	21.0
H_6'	−0.4255	−0.003924	0.08223	—	0.06206	0.84	10.2
H_7'	−0.4019	−0.004969	0.07601	0.003085	0.05372	0.85	11.0

Fig. 2. Model residuals plotted against predicted logarithmic population sizes (a), and normal quantile-quantile plot of model residuals (b).

ote index was in the alternative model but not in the null, the test failed to reject the null model (H_0' vs H_3', $T = -0.34$, $P = 0.742$; H_1' vs H_5', $T = 1.39$, $P = 0.272$; H_2' vs H_4', $T = -1.04$, $P = 0.329$; H_6' vs H_7', $T = 1.04$, $P = 0.218$). In all cases in which rainfall was in the alternative model but not in the null, the likelihood-ratio test rejected the null model (H_0' vs H_2', $T = 3.10$, $P = 0.013$; H_1' vs H_6', $T = 4.30$, $P = 0.004$; H_3' vs H_4', $T = 3.24$, $P = 0.012$; H_5' vs H_6', $T = 3.81$, $P = 0.002$). In all cases in which density dependence was added to a model that already contained rainfall, the test rejected the null hypothesis (H_2' vs H_6', $T = -3.48$, $P = 0.016$; H_4' vs H_7', $T = -3.30$, $P < 0.001$). In all cases in which density dependence was added to a model that did not contain rainfall, the test failed to reject the null hypothesis (H_0' vs H_1', $T = -2.26$, $P = 0.173$; H_3' vs H_5', $T = 2.72$, $P = 0.146$). These results are consistent with the previous hypothesis tests for the density-dependence–rainfall model in that growing season precipitation (2-yr lag) was detected as an important factor in population fluc-

tuations, and density dependence was detected only when precipitation is already in the model.

The model with the smallest SIC included density dependence and growing season precipitation (2-yr lag), but not coyote abundance (H_6', Table 2). This model is identical to model H_3 in the previous growing season precipitation analysis (Table 1), except that H_6' is fitted to 1 less observation. One model with coyote abundance included (H_7', Table 2) had an SIC nearly as low but not as low as that of H_6', indicating that there is no real advantage of adding coyotes to the model once growing season precipitation is included. In fact, the sign of the estimated coefficient $\hat{c}_2$ in model H_7' is positive (Table 2); if coyotes had a detrimental effect on survival, that coefficient would be expected to be negative.

Other covariates analyzed (in place of W_{t-2} in Eq. 1), including calendar year precipitation (various lags), other lags of growing season precipitation, and 2-year lag in fox abundance (second-order density dependence), did not improve the model. For reasons of space, we omit the numerical results; the SIC values were all substantially higher than that of model H_3 (Table 1). We conclude that model H_3 (Table 1), containing growing season precipitation (2-yr lag) and density dependence, gives the best description of the data among all models considered.

Population Viability Analysis

The PVA was conducted with model H_3, using the parameter values from Table 1. The PVA estimated a 19% chance that the population will fall from 133 individuals (recorded in winter of 1995–96) to ≤50 within the next 20 years (Table 3). While the chance that the population will fall to 50 individuals within 5 years was estimated at only 3%, the estimated chance increased to 15% within 10 years. The 95% CIs for these chances revealed a high level of imprecision for time frames >5 years (Table 3). The chance that the population declines to 50 individuals within 20 years could be as high as 52%, according to the bootstrap CI.

When the lower threshold population was set at 30, the estimated chances of the population attaining the threshold were reduced considerably (Table 3). The chance of attaining 30 individuals within 20 years was just 3%, although the 95% CI suggests that the true value could be as high as 12%.

Table 3. Estimated probability (and approximate 95% CI) that the San Joaquin kit fox population will decrease to n_e individuals within t yr, starting in 1995 from a population of 133 individuals.

n_e	t	Estimated probability	95% CI
50	5	0.03	<0.01–0.11
50	10	0.15	0.01–0.44
50	15	0.15	0.01–0.40
50	20	0.19	0.01–0.52
30	5	<0.01	0.00–0.01
30	10	0.02	0.00–0.10
30	15	0.02	0.00–0.08
30	20	0.03	0.00–0.12

DISCUSSION

Our finding that growing season rainfall affects the abundance of kit foxes 2 years later is consistent with current knowledge of their population ecology. The diet of kit foxes consists primarily of small rodents, particularly kangaroo rats (*Dipodomys* spp.), and of leporids (Laughrin 1970, White and Ralls 1993, Cypher and Spencer 1998). These species, in turn, exist principally on a diet of seeds and herbaceous plant parts. In arid regions, primary plant production, and ultimately rodent and leporid abundance, is strongly influenced by annual rainfall quantities and patterns (Beatley 1969, Brown and Munger 1985). In these systems, vegetation responds rapidly to altered precipitation regimes. Rodent and leporid populations, however, may take up to a year to exhibit a significant numerical response to variable rainfall. For example, to maximize persistence during periods of drought, many heteromyid (kangaroo rats, pocket mice) species express behaviors that promote adult survival in lieu of fecundity (Brown and Harney 1993). As a result, these populations do not typically explode immediately after the onset of more favorable environmental conditions.

San Joaquin kit fox populations appear to be regulated primarily by prey availability (Cypher and Scrivner 1992, White and Garrott 1997), expressed chiefly as variation in annual adult reproductive success and survival (White and Ralls 1993, White et al. 1996). Prey availability (habitat carrying capacity), in turn, varies in relation to rainfall. Because fox populations are separated from the direct effect of precipitation, however, the primary rainfall effects on fox abundance are noticeably postponed. Along with the lagged numerical response of prey, the

monestrous fox reproductive cycle also contributes to the delay. Fox breeding occurs primarily in December and parturition occurs in February or March (McGrew 1979).

Thus, the relative timing of the vegetative growing season (Oct–Mar), subsequent prey responses, and the reproductive cycle of kit foxes means that numerical responses by fox populations to fluctuating rainfall is delayed by up to 2 years (White et al. 1996). Such a combination of first-order density dependence (dependence of N_t on N_{t-1}), in which the prevailing habitat carrying capacity (prey abundance) changes annually in relation to the growing season precipitation in the previous year (time $t - 2$), is the central feature of our model.

Our finding that coyote abundance did not significantly affect fox abundances is consistent with earlier studies (Cypher and Scrivner 1992, White and Garrot 1997). While it is unclear whether coyote-related mortality is additive or compensatory, it does not appear to be a major regulatory factor for kit fox populations. An analysis of the efficacy of coyote control on NPRC indicated that, at the intensity of control applied, reductions in coyote density did not lead to an increase in kit fox abundance (Cypher and Scrivner 1992). White and Garrott (1997) suggest that while coyotes may be able to regulate kit fox populations of low to moderate density, prey abundance and spacing patterns are probably the major factors influencing fox population dynamics.

The wide CIs for the population risk estimates (Table 3) are characteristic of PVA, a fact not widely acknowledged in the PVA literature or in endangered species management. Given that there are only 12 observations (time steps) in the data set, the CIs are actually smaller than expected. Dennis et al. (1991) stressed the importance of estimating the uncertainty in the point estimates of risk, and noted that such uncertainty will typically be large. These ideas were reemphasized recently by Ludwig (1999). If preserving the population is an important goal, then the proper interpretation of the risk estimates for the San Joaquin kit fox is that the possibility that the fox population is at high risk cannot be ruled out.

As is the case with most covariate analyses, the model parameter estimates are conditional on the particular realization of the covariate (rainfall values). Rainfall is a stochastic process, and model projections must somehow incorpo-

rate the stochasticity of rainfall. The bootstrapping method we used for the PVA assumes that the rainfall values originate from a stationary probability distribution, and that there is little or no autocorrelation of rainfall from year to year. Under such assumptions, the empirical distribution function of rainfall values is a statistically consistent estimate of the stationary cumulative distribution function, and resampling the values themselves is akin to sampling out of the estimated rainfall stationary distribution.

The stationary distribution model of local rainfall is used reliably and routinely in hydrology, agriculture, and meteorology; nonetheless, the PVA should be interpreted cautiously. Long-term climate change could cause the mean, variance, or autocorrelation of the rainfall to change through time, and such possibility of change is not accounted for in the model. The PVA simply projects past system variability patterns into the future.

Shenk et al. (1998) criticized ecological time-series models, and density-dependence hypothesis tests in particular, for failing to account for sampling variability in estimates of population abundances. They simulated density-dependence tests by generating time-series abundances with sampling noise added that had a constant coefficient of variation. However, the kit fox abundance estimates do not conform to the sampling noise model of Shenk et al. (1998). The kit fox estimates had sampling coefficients of variation that tended to decrease with increasing population abundance (Fig. 1, Table 1), which is a characteristic of most mark–recapture models (Otis et al. 1978). The decreasing coefficient of variation (sampling variance proportional to N_t) conforms to the sampling variation simulations of Dennis and Taper (1994); their simulations suggested that the size of the bootstrap density dependence test remains near the nominal value of 0.05 with moderate amounts of sampling variability. The coefficients of variation for the kit fox estimates averaged around 10% (range from 6.5 to 19.9%). Shenk et al. (1998) noted that the density dependence test had statistical performance problems under their sampling model at coefficients of variation ranging from 30 to 100%, at which levels it is questionable whether population monitoring is worthwhile.

Also, a well-known property in time-series models is that sampling variability tends to induce autocorrelation in the noise (Walker 1960). In practice, lack of autocorrelation in the residuals can be taken to indicate that sampling error is not an important source of variability, provided the model for population abundance is an adequate description of the population growth process. We point out that no significant first- or second-order autocorrelation was detected in the residuals for the density dependent–rainfall model for kit fox abundances.

In the 1950's, ecologists launched a durable debate on the relative importance of density-dependent and density-independent factors in population regulation (Biological Laboratory 1957). The intensity of the debate was fueled by a presumption that regulation is primarily one or the other. Strong (1986) called for a combined approach in which density-dependence analyses would incorporate environmental covariates or contingent variables. In our kit fox model, both density-dependent and density-independent factors contribute to determining population size. Carrying capacity in the model is determined principally by growing season rainfall, which fluctuates considerably from year to year. The long-term average carrying capacity of 161 foxes is just an estimated central value of a stationary probability distribution for population sizes; yearly departures from that central value can be, and have been, substantial. Yearly carrying capacity fluctuates so much that density dependence was barely detectable in the time series of population abundances. The result was a form of "density vagueness" in the time series (Strong 1986). A model with density dependence alone was not adequately predictive, nor was a model with rainfall alone. Instead, the model that blended both types of factors gave a far superior description of the data.

MANAGEMENT IMPLICATIONS

The model developed here should help managers to moderate the risk faced by San Joaquin kit fox populations from the effects of variable annual precipitation. With the 1-step-ahead forecasts, the model can provide a 1-year warning of when the kit fox population is expected to become critically low. During such years, special measures for population protection and habitat enhancement, such as translocating animals, constructing artificial den sites in marginal habitats, or providing supplemental foods, may merit serious consideration.

Given the results of the PVA and the large

amount of variability displayed in the population since 1983, the long-term risk to the San Joaquin kit fox on NPRC must be regarded as potentially high. According to the PVA, there is a fair chance that the population could drop below 50 individuals in the short term (within 20 yr). The short-term chance of dropping below 30 individuals though is low according to the PVA. However, a level of 50 individuals might be low enough to subject the population to small population forces such as an Allee effect (Dennis 1989, Fowler and Baker 1991), demographic variability (Lande 1998), or other forces contributing to the "extinction vortex" (Gilpin and Soulé 1986). None of these forces are incorporated in the model.

If the objective of management policy is to maintain a viable fox population on NPRC, then such policy must accomodate the prospect that the present population might not be viable. This has important repercussions for range-wide conservation of the species, as lands on and adjacent to NPRC have been identified in recent recovery planning as supporting 1 of 3 core kit fox populations (U.S. Fish and Wildlife Service 1998). Further population monitoring would improve the modeling and risk assessment and would help warn of stochastic population declines.

The modeling approach described here consists of: (1) proposing multiple plausible hypotheses about wildlife–environment relationships, (2) formulating the hypotheses as quantitative influences on growth rates in stochastic population growth models, and (3) evaluating the models rigorously using time-series abundance data and nonlinear, time-series statistical methods. The approach has many potential uses for managing other wildlife species. Environmental covariates have important effects in numerous population systems, and using simple correlation analysis to detect those effects can be statistically inappropriate and can fail in the presence of complex ecological relationships. Weather variables, for example, affect wildlife populations in many indirect and direct ways. While direct effects of weather include immediate mortality from floods or freezing, indirect effects include weather-dependent food supply, weather-mediated events elsewhere in the food chain, weather-altered habitat, and weather-influenced parasite loads. Understanding the variability of wildlife populations can be greatly aided by including explicit hypothesized effects

of environmental covariates in biologically-based population models.

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