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Optimizing reserve expansion for disjunct populations of San Joaquin kit fox

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Abstract

Expanding habitat protection is a common strategy for species conservation. We present a model to optimize the expansion of reserves for disjunct populations of an endangered species. The objective is to maximize the expected number of surviving populations subject to budget and habitat constraints. The model accounts for benefits of reserve expansion in terms of likelihood of persistence of each population and monetary cost. Solving the model with incrementally higher budgets helps prioritize sites for expansion and produces a cost curve showing funds required for incremental increases in the objective. We applied the model to the problem of allocating funds among eight reserves for the endangered San Joaquin kit fox (*Vulpes macrotis mutica*) in California, USA. The priorities for reserve expansion were related to land cost and amount of already-protected habitat at each site. Western Kern and Ciervo-Panoche sites received highest priority because land costs were low and moderate amounts of already-protected habitat resulted in large reductions in extinction risk for small increments of habitat protection. The sensitivity analysis focused on the impacts of kit fox reproductive success and home range in non-native grassland sites. If grassland habitat is lower quality than brushland habitat resulting in higher annual variation in reproductive success or larger home ranges, then protecting habitat at the best grassland site (Ciervo-Panoche) is not cost–efficient relative to shrubland sites (Western Kern, Antelope Plain, Carrizo Plain). Finally, results suggested that lowest priority should be given to three relatively high-cost grassland sites (Camp Roberts, Contra Costa, and Western Madera) because protecting habitat at those sites would be expensive and have little effect on the expected number of surviving kit fox populations.
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1. Introduction

Establishing and expanding nature reserves is a cornerstone of species conservation (Noss and Cooperrider, 1994; Pimm and Lawton, 1998). Recognizing that resources are limited and economic development competes with habitat protection, biologists, operations researchers, and economists have explored ways to rationalize the choice and assembly of reserves (Kingsland, 2002). An outcome was the development of reserve site selection models, which typically maximize the number of species protected subject to cost constraints and provide case-specific policy guidance about tradeoffs between conservation goals and reserve costs. Following the pioneering applications in Australia (Margules et al., 1988; Cocks and Baird, 1989), site selection models have been used in countries throughout the world where biodiversity is threatened and in need of protection (see Rodrigues and Gaston, 2002 for a summary of published studies). While most site selection models maximize the number of species included in reserves, they do not assess the probabilities that species survive.

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Ensuring species survival has long been an objective of nature reserve design (Margules et al., 1982; Simberloff and Abele, 1982; Soulé and Simberloff, 1986), and reserve design models that account for species survival probabilities have been built with increasing levels of biological detail. Species survival rates have been directly related to reserve design features such as number, size, and quality of protected sites with the objective of maximizing the expected number of surviving species (Hof and Raphael, 1993; Williams and Araújo, 2002). Models with more biological detail maximized population size using deterministic equations relating population growth to the number, size, and spatial arrangement of habitat reserves (Hof et al., 1994; Bevers et al., 1997; Hof and Raphael, 1997; Rothley, 2002). Stochastic demographic models of population viability are commonly used to make wildlife management decisions (Beissinger and Westphal, 1998), and researchers are beginning to incorporate them into reserve design models with the objective of maximizing survival probabilities (Montgomery et al., 1994; Haight, 1995; Haight and Travis, 1997). Because the stochastic optimization methods used in those applications are computationally intensive, more efficient methods are needed.

Haight et al. (2002) developed an optimization framework for expanding a reserve for a single population of an endangered species. The model was designed to select the amount of habitat by quality class to minimize the extinction risk of the population. The framework was based on the idea that an extinction-risk function that predicts the relative value of increasing the quantity and quality of habitat can be estimated from a response surface generated by a stochastic demographic model of population viability. Then, the risk function was incorporated into an optimization model for determining cost–efficient habitat protection. Because the risk function could be evaluated much faster than the stochastic demographic model, the optimization procedure was much less time consuming.

In this paper, we apply the response-surface methodology developed by Haight et al. (2002) to the problem of allocating a fixed budget for habitat protection among disjunct populations of an endangered species to maximize the expected number of surviving populations. A demographic model of population viability is used to quantify the risk of extinction of each population under different amounts of protected habitat (e.g., Fahrig, 2001). The predictions of the demographic model, in turn, are used to estimate risk–area curves for the populations. The risk–area curves and costs of habitat protection are incorporated into an optimization model to determine how best to allocate limited funds among the populations.

We apply the optimization model to a problem of expanding habitat reserves for disjunct populations of the San Joaquin kit fox (*Vulpes macrotis mutica*), an endangered species in California, USA. The San Joaquin kit fox was granted Federal protection in 1967 (US Department of Interior, 1967) because habitat loss resulting from agricultural, industrial, and urban development significantly reduced its abundance and distribution (US Fish and Wildlife Service, 1998). Currently, kit fox populations are constricted into fragmented areas of varying size and habitat quality, and suspected high mortality of kit fox dispersers may limit the movement of individuals between populations. The recovery plan for upland species of the San Joaquin Valley, California, specified a goal of establishing a viable set of kit fox populations on public and private lands throughout the kit fox's geographic range (US Fish and Wildlife Service, 1998). We focused our analysis on determining cost–efficient reserve expansion for eight sites within the kit fox range. The results address the basic question of which sites and populations should be afforded more protection.

2. Methods

2.1. An optimization model for reserve expansion

Suppose we have a set of disjunct populations of an endangered species and a limited budget to protect the habitat. By disjunct we mean that each population is isolated enough that migration between populations is inconsequential. Further, assume that we have information for each population about the relationship between risk of population extinction and amount of habitat. Using these risk-area curves, we can formulate an optimization model for determining the amount of habitat to protect for each population that maximizes the expected number of populations that survive over the management horizon. The model has the following notation:

i, I: indices for individual populations and total number of populations;

a_i: amount of already-protected habitat for population i;

b: upper bound on budget;

c_i: unit cost of protecting additional habitat for population i;

d_i: upper bound on the amount of habitat available for protection for population i;

x_i: amount of habitat that is selected for protection for population i; and

$p_i (a_i + x_i)$: probability of extinction, population i.

The optimization problem is formulated as follows:

$$\text{Maximize} \sum_{i=1}^{I} 1 - p_i(a_i + x_i) \tag{1}$$

subject to:

$$\sum_{i=1}^{I} c_i x_i \leqslant b \qquad (2)$$

$$0 \leqslant x_i \leqslant d_i \qquad i = 1, \ldots, I. \qquad (3)$$

The objective of the optimization problem (1) is to maximize the expected number of populations that survive over the management horizon. The probability of extinction of each population depends on the total amount of habitat protected, which is the sum of the already-protected habitat and the newly protected habitat. As we show later, the risk function can be estimated using predictions from a demographic model of population viability under different amounts of protected habitat. The first constraint (2) requires that spending for habitat protection does not exceed the budget. Note that the unit cost of protection, c_i, can differ across sites but is constant within a given site. If the cost of protecting habitat in a given site varies (e.g., by location), then the model is easily expanded by subdividing land into cost classes (Haight et al., 2002). The second set of constraints (3) bounds the amount of habitat available for protection.

It is not difficult to write the necessary conditions required for an optimal solution (e.g., Bazaraa and Shetty, 1979, p. 137). The model's optimality conditions state that funds should be allocated so that the marginal costs of increasing the viability of populations are equal while staying within the budget and habitat area constraints. If a solution does not satisfy these conditions, then funding can be taken from the site with relatively high marginal cost and invested in the site with lower marginal cost to achieve a higher level of viability.

For a given set of land costs and an upper bound on funding, the optimization model can be used to determine the best protection strategy in terms of the amount of habitat to secure for each population. Then, by re-solving the model with incrementally higher bounds on funding, a relationship between cost and expected number of surviving populations can be determined. The cost curve shows funding requirements for incremental increases in population viability.

2.2. Study area

The San Joaquin Valley occupies the southern two thirds of California's great Central Valley and encompasses about 20% of the land area of the state (Fig. 1). The climate is semiarid with hot dry summers and cool wet winters. Precipitation occurs as rainfall primarily between November and April in quantities (usually < 31 cm) that vary greatly year to year. Although the Valley was once dominated by grassland, shrubland, and wetland communities, it is now dominated by agricultural, industrial, and urban development. Only a few remnant grasslands and shrublands remain on the Valley's perimeter.

With the loss of its natural communities, the San Joaquin Valley experienced a great loss of biodiversity. As of 1998, 75 species of plants and animals were either listed or candidates for listing as threatened or endangered including the San Joaquin kit fox (US Fish and Wildlife Service, 1998). The recovery plan for upland species designated the kit fox as an umbrella species with a goal of establishing a viable set of kit fox populations on public and private lands throughout the kit fox's geographic range (US Fish and Wildlife Service, 1998).

Although the kit fox once inhabited grasslands and shrublands throughout the San Joaquin Valley (Grinnell et al., 1937), habitat loss and alteration curtailed its distribution to suitable habitat in the San Joaquin Valley floor, side valleys, and surrounding foothills of the coastal ranges, the Sierra Nevada, and the Tehachapi Mountains (Fig. 1). Kit foxes are found in two large populations and several small populations. The two large populations (Western Kern and Carrizo Plain) encompass large amounts of land in public ownership and are designated core populations with high priority for enhancement and protection (US Fish and Wildlife Service, 1998). The Western Kern population occurs in and around the Naval Petroleum Reserves of California, a 313-km^2 area in the southern San Joaquin Valley. The Carrizo Plain population occurs on a 13×18-km long, arid plain separated from the Western Kern population by the Temblor Mountains. A smaller population at the Ciervo-Panoche Natural Area was also designated as a core population because its habitat includes a large expanse of land in public ownership. While the Carrizo Plain and Western Kern populations have been studied (Ralls and White, 1995; Cypher et al., 2000), less is known about the Ciervo-Panoche population.

We used eight sites in our analysis (Fig. 1), including three core populations (Carrizo Plain, Western Kern, and Ciervo-Panoche), three areas that encompass small kit fox populations (Camp Roberts, Antelope Plain, and Santa Nella), and two areas where kit foxes have not been recently sighted (Contra Costa and Western Madera). The Contra Costa site is the northern edge of the kit fox range where state agencies are interested in grassland and oak woodland conservation in the face of increasing urban development. The Western Madera site includes unique alkali shrubland on the floor of the San Joaquin Valley. Together, the eight sites represented pieces of the historical geographic range of the kit fox.

Habitat conditions in the study sites vary spatially with precipitation being the most influential factor. Annual precipitation increases from south to north in

the San Joaquin Valley and from inland to coastal areas. Mean annual precipitation is 15.4 cm in Bakersfield at the southern end of the Valley and increases to 30.9 cm in Stockton at the northern end of the Valley. As a result, habitat conditions at the three southern sites (Western Kern, Carrizo Plain, and Antelope Plain) are arid, shrubs are prevalent, herbaceous cover is sparse, and kangaroo rats (*Dipodomys spp.*) and rabbits are the primary prey of kit foxes. In the five sites to the north and west (Ciervo-Panoche, Camp Roberts, Santa Nella, Western Madera, and Contra Costa), conditions are mesic, shrubs are absent, herbaceous cover (primarily non-native grass) is dense, and California ground squirrels (*Spermophilus beechyi*) are the primary prey.

While shrubs have been removed from parts of the southern sites, we refer to southern habitat as shrubland and the northern and western habitats as grassland. Historically and currently, kit fox abundance is greater in southern shrublands compared with northern grasslands (Grinnell et al., 1937; US Fish and Wildlife Service, 1998).

Kelly et al. (2000) estimated the amount of suitable habitat in the Public Land Survey System townships (58 km^2 land divisions) covering each site. Suitable habitat was defined as land with $\geq 50\%$ grassland or shrubland vegetation and with slopes $\leq 10\%$. Suitable habitat was divided into two management categories: (1) protected public and private conservation land; and (2) unprotected
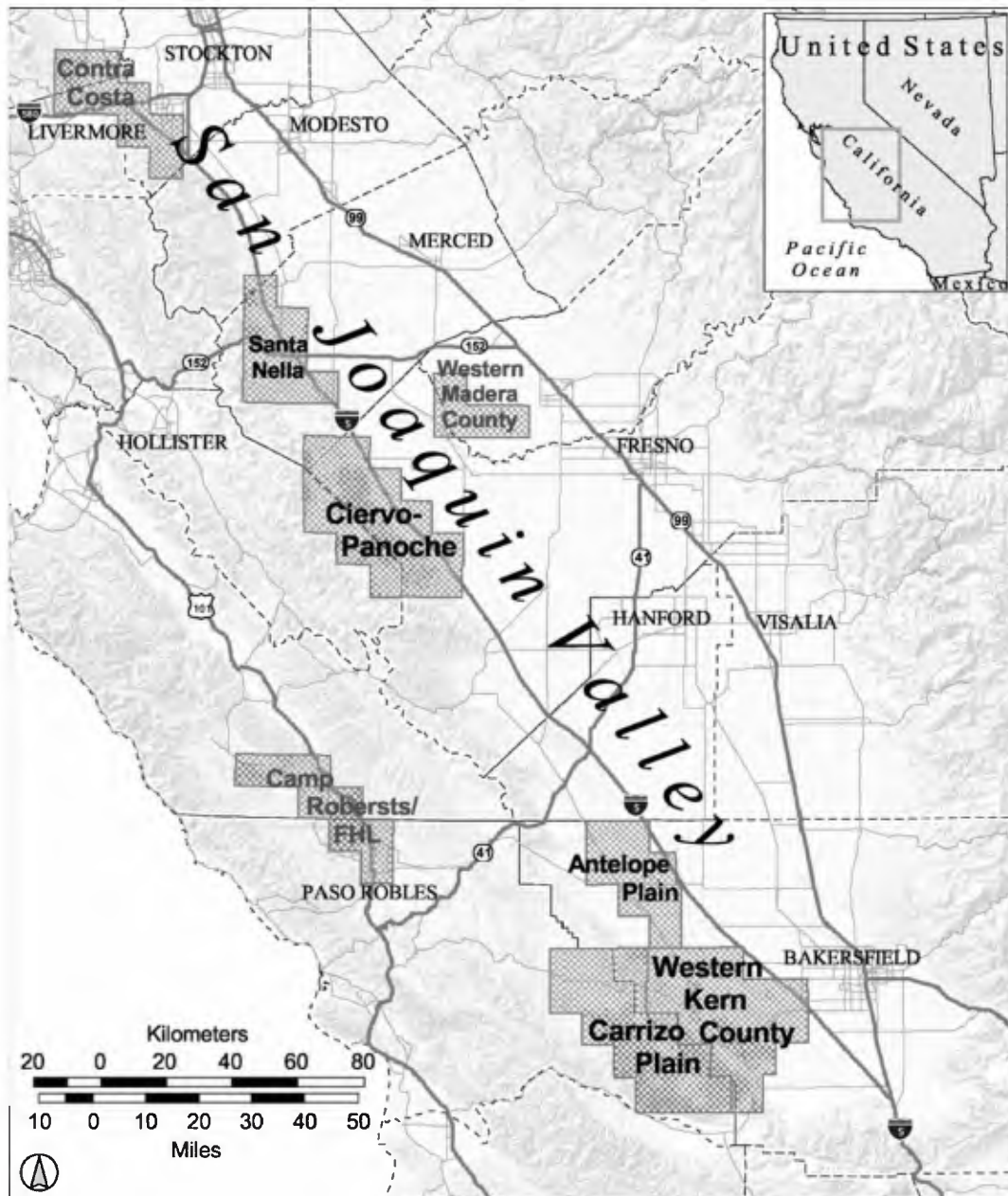

Fig. 1. Kit fox habitat areas used in the analysis.

Table 1
Amount and cost of kit fox habitat at sites in the San Joaquin Valley

Site	Protected public land	Unprotected private land	
	(km²)	(km²)	($1000/km²)
Antelope Plain	1	157	37
Western Kern	238	850	44
Ciervo-Panoche	240	626	74
Carrizo Plain	451	471	91
Santa Nella	54	327	132
Western Madera	1	114	222
Camp Roberts	55	142	141
Contra Costa	35	416	216

private land. While three sites had >230 km² of protected habitat (Ciervo-Panoche, Western Kern, and Carrizo Plain), five sites had <60 km² of protected habitat (Table 1). Each site had >100 km² of unprotected habitat.

2.3. Estimating habitat protection cost

We estimated the costs of protecting habitat in each site using 2001 land values for agricultural land use categories (California ASFMRA, 2001). Although habitat can be protected by conservation easements or landowner incentives as well as land purchase, for simplicity we based our example only on land purchase. Using a GIS with land cover data and irrigation district boundaries, we subdivided each county by agricultural land use (e.g., row crop, rangeland, orchard, vineyard). Then, we overlaid the map of kit fox habitat at each site with the county maps of agricultural land use. The cost of habitat protection was the average land value of privately held habitat in the townships covering each site.

2.4. Simulating kit fox populations

Detailed information and literature reviews of the life history and ecology of the San Joaquin kit fox are available elsewhere (US Fish and Wildlife Service, 1998; White and Garrott, 1999; Cypher et al., 2000), and we only summarize information that we used for model building. Kit foxes are nocturnal predators of rodents and rabbits and use underground dens for shelter, reproduction, and escape. Adult pairs remain together and maintain large and relatively non-overlapping home ranges. Home ranges from less than 2.6 up to 31 km² have been reported. A kit fox pair breeds once a year with a minimum breeding age of 1 year. Mating takes place between December and March. Reproductive success is correlated with prey availability—success drops when prey is scarce. Prey abundance, in turn, varies annually with the previous year's precipitation— prey abundance drops when low rainfall reduces plant productivity. If reproduction is successful, a litter of

two–six pups emerges from the den in spring. Pups become adult-sized and disperse during August through September in search of mates and vacant home ranges. Annual mortality rates for pups and adults are 50–70 and 40–60%, respectively, depending on vegetation and topography.

We designed a stochastic, demographic model of a kit fox population living in a patch of contiguous habitat covering up to 1200 km². The habitat patch consisted of a fixed number of potential kit fox home ranges. Each home range was 4 km² and could support a single kit fox family consisting of a breeding pair and its pups. State variables for each family were the number of foxes of each sex in pup (0–12 months) and adult (>12 months) age classes. The model was spatially structured (Beissinger and Westphal, 1998) because the population was subdivided into breeding pairs; however, the model was not spatially explicit because home range shapes and locations were not included. The model was individually based because demographic events were computed one fox at a time. The model was a variant of one developed by Haight et al. (2002).

Our model simulated birth, mortality, and dispersal of foxes in each home range on an annual cycle beginning midwinter. The values of the demographic parameters were based on 14 years of observations of the Western Kern population in shrubland habitat (Cypher et al., 2000). There were no comparable series of data for populations at the grassland sites.

Breeding pairs produced their pups in late winter. Because temporal variation in prey availability is linked to kit fox reproductive success, we modeled reproduction in a two-step process. First, an average reproductive success rate for the year was chosen from a normal distribution with a mean of 0.61 and a standard deviation of 0.27. The success of each breeding pair was determined by comparing a random number obtained from a uniform 0–1 distribution to the chosen success rate. Then, the litter size of each successful pair was selected from a discrete probability distribution with a mean of four pups and a range of two–six pups. Unsuccessful pairs and solitary foxes remained in their home ranges without producing litters.

All modeled mortality took place in summer. Whether each kit fox died was a Bernoulli random variable with probability depending on kit fox age. Mortality rates were 60% for pups and 40% for adults. Adults reaching the 6-year-old age class died.

All surviving pups dispersed in autumn in search of mates and home ranges. While there is little quantitative information about kit fox dispersal patterns and behavior, we believe that dispersing pups could search for mates and home ranges throughout the habitat patch. In the model, each disperser was randomly assigned to a home range with an available mate. If no mates were available, the disperser was randomly assigned to a

vacant home range. If no vacancies were available, the disperser died. We assumed that adult kit foxes did not disperse. The ages of kit foxes in each home range were updated after pup dispersal.

2.5. Estimating risk-area curves

We used the baseline kit fox population model described above to predict extinction risk in 100 years in habitat patches covering 80–1200 km^2 in increments of 80 km^2. For each patch, the estimator of extinction risk was the percentage of 1000 independent simulations in which population size was <10 individuals in 100 years.

The predictions were used to estimate a relationship between extinction risk in 100 years and the area of the habitat patch. The risk–area relationship was a logistic function estimated using a form of logistic regression called the minimum logit chi-squared method (Maddala, 1983, pp. 28–30). Logistic regression describes a binary response as a function of one or more explanatory variables. In our case, the binary response was extinction or persistence of a population in a habitat patch, and the explanatory variable was patch area.

The minimum logit chi-squared method of estimation is appropriate when there are multiple observations of the binary response for each level of the explanatory variable. In our case, the population model was used to obtain 1000 observations of extinction or persistence for each habitat patch. Let $\hat{p}_i$ be the proportion of the 1000 observations in which the population became extinct in patch i, and $\hat{p}_i/(1 - \hat{p}_i)$ be the estimated odds of extinction. With the logistic model, the log of the odds of extinction is assumed to be a linear function of patch area:

$$\log \frac{\hat{p}_i}{1 - \hat{p}_i} = b_0 + b_1 y_i + \mu_i \tag{4}$$

where y_i is the area of patch i, b_0 and b_1 are the regression coefficients, and μ_i is the regression error. Because the log of the odds of extinction is a continuous variable without limit, ordinary or weighted least squares regression can be used to estimate the parameters of (4). We used weighted least-squares regression to remove heteroscedasticity in the regression error (Maddala, 1983, p. 30). Once the parameters of (4) were estimated, the equation was transformed into a risk–area relationship by solving for p_i on the left-hand-side.

2.6. Optimizing reserve expansion

We incorporated the risk–area relationship computed with predictions from the baseline population model together with information about the amount and cost of kit fox habitat for the eight sites (Table 1) into the optimization model (Eqs. (1)–(3)) to determine priorities for reserve expansion under increasing upper bounds on

funding. The results allowed us to plot a cost curve showing funding required for incremental increases in population viability.

In the sensitivity analysis, we determined how the priorities for reserve expansion changed using risk–area relationships computed with changes in the baseline population model. In the baseline model, we assumed that parameters for kit fox populations at the eight study sites were identical. Those parameter values were based on observations of the Western Kern population in shrubland habitat (Cypher et al., 2000). While the baseline parameter values are appropriate for populations in shrubland habitat (Western Kern, Carrizo Plain, and Antelope Plain), they are likely to be over optimistic for less well-studied populations at grassland sites (Ciervo-Panoche, Camp Roberts, Santa Nella, Western Madera, and Contra Costa). Kit fox sightings are rare in grassland areas, and recent scat surveys suggested kit foxes are much less abundant (Smith et al., 2003). Kit fox density may be lower in grassland habitat because lower prey availability results in larger home ranges and higher annual variability in reproductive success. Thus, we focused our sensitivity analysis on evaluating the effects of assuming higher variability in reproductive success and larger home ranges of populations at the five grassland sites.

To determine how the priorities for reserve expansion changed with increasing variation in reproductive success at the grassland sites, we first estimated extinction risk versus habitat area relationships for two higher standard deviations of reproductive success (0.32 and 0.37). Then, we re-formulated and solved the optimization model using each new risk–area curve to represent the five grassland sites. The risk–area curve computed with the baseline population model was applied to the three shrubland sites.

We created two new risk–area curves for the grassland sites using higher home ranges (6 and 10 km^2). In the population model, increasing the average home range reduced the carrying capacity of a habitat patch. For example, with the baseline home range (4 km^2), a 300-km^2 patch had a carrying capacity of 75 kit fox families. If the average home range increased to 6 km^2, the carrying capacity was 50 kit fox families, or 66% of the baseline value. Further, the predicted extinction risk of a population in a 300-km^2 patch with an average home range of 6 km^2 was the same as the predicted extinction risk of a population in a 200-km^2 patch with an average home range of 4 km^2. Therefore, the risk–area curve for a population with an average home range of 6 km^2 was created by translating the baseline risk–area curve (multiplying the patch area by 0.66) while keeping the parameters of the equation the same. Likewise, the risk–area curve for a population with an average home range of 10 km^2 was obtained by multiplying the patch area in the baseline equation by 0.40. We

re-formulated and solved the optimization model using each of these new risk–area curves to represent the five grassland sites.

The optimization models were solved on an IBM Pentium III laptop computer using the integrated solution package GAMS/MINOS 2.25 (Gams Development Corporation, 1990), which was designed for large and complex linear and nonlinear programming problems. Input files were created using GAMS (Generalized Algebraic Modeling System), a program designed to generate data files in a standard format that optimization programs can read and process. Because the models had nonlinear objective functions with linear constraints, GAMS/MINOS used a reduced-gradient algorithm combined with a quasi-Newton algorithm (Murtagh and Saunders, 1978) to find the solution. Solutions times were less than 1 sec.

3. Results

3.1. Habitat protection costs

The average cost of private land varied widely across sites from \$37,000/km^2 (\$150/ac) at Antelope Plain to \$222,000/km^2 (\$900/ac) at Western Madera (Table 1). Four sites had large amounts (>150 km^2) of relatively low-cost (<\$100,000/km^2) private land, and three of those low-cost sites encompassed core populations (Western Kern, Ciervo-Panoche, and Carrizo Plain). The four sites with higher land costs (>\$100,000/ km^2) included sites on the edges of the kit fox range where few kit foxes had been sighted in recent years.

3.2. Risk–area curves

Predictions of extinction risk from the population model were used to estimate the following logistic model for each level of variation in reproductive success:

$$\log \frac{p}{1-p} = b_0 + b_1 \frac{1}{y} + b_2 \ \log(y) \tag{5}$$

Table 2
Estimated parameter values and standard errors (in parentheses) of risk–area curves for kit fox populations with the baseline standard deviation of reproductive success (SD = 0.27) and two higher levels of variability (SD = 0.32 and SD = 0.37)

SD of reproductive success	Model parameters			Adjusted
	b_0	b_1	b_2	R^2
0.27	13.84	−9.24	−2.39	0.97
	(0.78)	(0.92)	(0.13)	
0.32	11.89	−7.29	−1.87	0.97
	(0.57)	(0.67)	(0.09)	
0.37	11.13	−6.54	−1.59	0.98
	(0.42)	(0.50)	(0.07)	

where p is the probability of extinction in 100 years, y is the amount (km^2) of habitat, and b_0, b_1, and b_2 are the regression coefficients. The values of regression coefficients are listed in Table 2, and all coefficients were significant at the 0.001 probability level. A variety of models with different transformations of the independent variable y were estimated, and the final selection was based on goodness of fit. The adjusted R^2 was >95% for each of the estimated models.

The predicted extinction risk in 100 years versus habitat area for the different models are plotted in Fig. 2. The slope of each curve represents the risk reduction associated with an incremental increase in the area of protected habitat. With the logistic form, the slope decreases (becomes more negative) initially, reaches a minimum, and then increases and approaches zero as the habitat area increases. The greatest reduction in extinction risk for an increment of protected habitat occurs in the mid-range of the function. The implication is that protecting additional habitat will be most fruitful in sites with already-protected habitat but not so much that their populations are secure. The risk–area curve computed with the baseline level of variation in reproductive success (0.27) suggests that extinction risk for kit fox populations is <0.20 in habitat patches >600 km^2. The risk–area curves computed with higher levels of variability suggest that populations approach this risk threshold when their habitat area is >1200 km^2. The risk–area curves computed with higher home ranges had similar shapes (Fig. 3).

3.3. Optimal reserve expansion

In the baseline case, the risk–area curve computed with the lowest level of variation in reproductive success (0.27) was used in the optimization model to represent each of the eight kit fox sites. With no funding, no
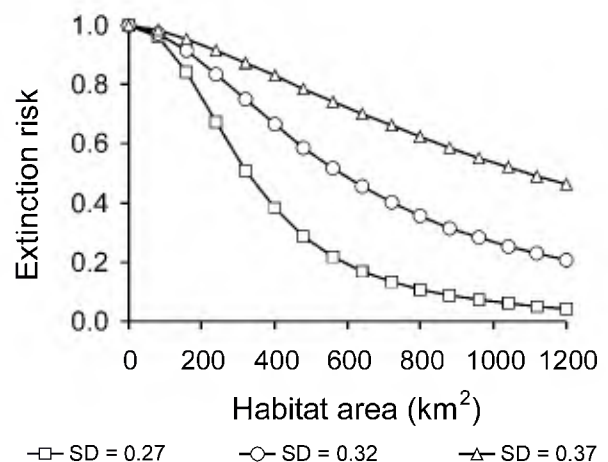

Fig. 2. Predicted extinction risk in 100 years versus habitat area for kit fox publications with the baseline standard deviation of reproductive success (SD = 0.27) and two higher levels of variability (SD = 0.32 and 37).
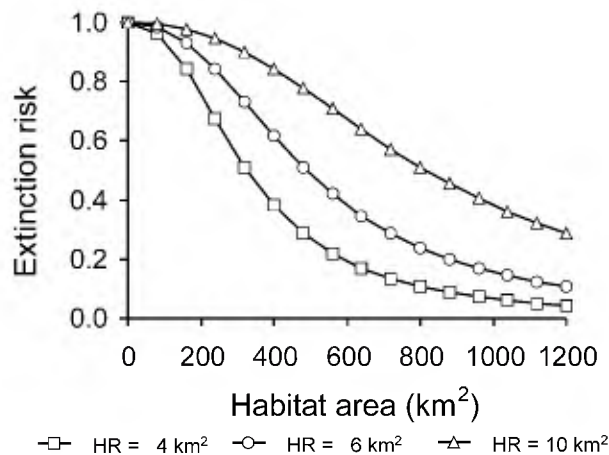
Fig. 3. Predicted extinction risk in 100 years versus habitat area for kit fox publications with the baseline home range (HR = 4 km^2) and two higher levels of home range (HR = 6 and 10 km^2).

habitat beyond existing public land was protected, and the expected number of surviving populations was 1.38 (Table 3). As funding increased, the location and amount of protected habitat depended on the cost of land and the amount of already-protected habitat at each site.

For funding levels of $0–20 million, habitat was protected at Western Kern and Ciervo-Panoche (Table 3). The first $8 million was used to protect 182 km^2 at Western Kern, where land cost was low, 238 km^2 of public land was already protected, and the risk–area curve predicted a relatively steep reduction in extinction risk for sites with 200–400 km^2 of habitat. As a result, the marginal cost of increasing population viability was lower at Western Kern than at any other site. For funding levels of $8–20 million, habitat was protected at Western Kern and Ciervo-Panoche. While Ciervo-

Panoche had more expensive land, it had less protected land and thus was located on a steeper portion on the risk–area curve. As a result, the marginal costs of increasing population viability were the same at the two sites.

At $20 million, a second optimal solution was found involving the protection of all available habitat at Antelope Plain (157 km^2) and smaller amounts at Western Kern and Ciervo-Panoche (Table 3). Even though land cost at Antelope Plain was lowest, protecting its habitat was not a priority at lower levels of funding because Antelope Plain had almost no already-protected habitat. As a result, Antelope Plain was initially located on a flat part of the risk–area curve, and a large amount of funding was required to obtain a reduction in extinction risk.

With funding levels of $20–42 million, all habitat at Antelope Plain plus additional habitat at Western Kern and Ciervo-Panoche was protected (Table 3). With funding levels of $42–55 million, habitat purchase at Carrizo Plain also was cost–efficient. Protecting habitat at Carrizo Plain was not cost–efficient at lower levels of funding primarily because 451 km^2 are already protected. As a result, Carrizo Plain was on a flatter part of the risk–area curve where the reduction in extinction risk for an increment in habitat protection was relatively small.

At $55 million, a second optimal solution was found involving the protection of a portion of Santa Nella (155 km^2), smaller amounts at Western Kern and Ciervo-Panoche, and no additional habitat at Carrizo Plain (Table 3). Despite having higher land cost, Santa Nella received higher priority than Carrizo Plain for budgets of $55–80 million because protecting additional habitat at Santa Nella, which had little already-protected

Table 3
Cost–efficient habitat protection and expected number of surviving populations under alternative budgets[a]

| Budget ($million) | Number of populations | Area (km^2) purchased by site | | | | | | | |
		Antelope Plain	Western Kern	Carrizo Plain	Ciervo-Panoche	Santa Nella	Western Madera	Camp Roberts	Contra Costa
0	1.38	0	0	0	0	0	0	0	0
8	1.71	0	182	0	0	0	0	0	0
20	2.02	0	253	0	120	0	0	0	0
20	2.02	157	212	0	66	0	0	0	0
42	2.44	157	387	0	259	0	0	0	0
55	2.58	157	452	61	321	0	0	0	0
55	2.58	157	322	0	196	155	0	0	0
80	2.95	157	381	0	254	292	0	0	0
100	3.17	157	461	69	330	327	0	0	0
100	3.17	157	381	1	254	292	0	142	0
156	3.63	157	649	235	500	327	0	142	0
156	3.63	157	443	53	313	327	0	142	183
286	4.45	157	850	471	626	327	0	142	416
312	4.52	157	850	471	626	327	114	142	416

[a] In this baseline case, each kit fox population had the same level of variation of reproductive success (SD = 0.27) and the same average home range (HR = 4 km^2).

land, pushed it onto the steep portion of the risk–area curve. Protecting habitat at Carrizo Plain was once again cost-efficient for budget levels of $80–100 million.

For funding levels > $100 million, the priority for protecting habitat at the remaining three sites was directly related to land cost (Table 3). Habitat protection at Camp Roberts ($141,000/ km^2) was cost-efficient with funding levels > $100 million, and protection at Contra Costa ($216,000/km^2) was cost-efficient with funding > $156 million. With $286 million, all available habitat was purchased at all sites except Western Madera, which had lowest priority because of its high land cost ($222,000/km^2) and small amount of available habitat. With funding levels of $286–312 million, habitat was protected at Western Madera, but it did little to increase population viability.

The results of the baseline optimization runs are summarized in the first two columns of Table 4, which show the priority ranking of reserve expansion and the budget level at which habitat protection at each site becomes and remains cost-efficient. In the baseline case, the same risk–area curve was applied to each site. As a result, the rankings were based on the cost and amount

of already-protected habitat and not on the type of habitat. The three sites with shrubland habitat— Western Kern, Antelope Plain, and Carrizo Plain— were ranked 1, 3 and 6, respectively, with the grassland sites ranked in between.

In the sensitivity analysis, we determined how changes in the shape and location of the risk–area curve applied to grassland sites affected the priority ranking of reserve expansion. When the risk–area curve applied to the grassland sites was computed with higher levels of variation in reproductive success, habitat protection at grassland sites was less effective and received lower priority than did protection at shrubland sites (Table 4). For example, habitat protection at Ciervo-Panoche— the highest ranking grassland site in the baseline case— dropped in rank from 2 to 4 as the standard deviation in reproductive success increased from 0.27 to 0.37. Further, the budget at which habitat protection at Ciervo-Panoche was cost-efficient increased from 8 to $43 million. When the risk–area curve applied to grassland sites was computed assuming larger home ranges at these sites, the changes in priority ranking of reserve expansion were almost the same (Table 5).

Table 4
Priority ranking of expansion of kit fox reserves under alternative assumptions about the variability in kit fox reproductive success[a]

Site	SD = 0.27		SD = 0.32		SD = 0.37	
	Rank	Budget[b]	Rank	Budget[b]	Rank	Budget[b]
Western Kern	1	0	1	0	1	0
Ciervo-Panoche	2	8	3	21	4	43
Antelope Plain	3	20	2	13	2	13
Santa Nella	4	55	5	104	5	130
Camp Roberts	5	100	6	150	6	174
Carrizo Plain	6	100	4	41	3	22
Contra Costa	7	156	7	196	7	196
Western Madera	8	286	8	286	8	286

[a] In the baseline case (SD = 0.27), each kit fox population had the same level of variation. In the other two cases, populations in grassland habitat (Ciervo-Panoche, Santa Nella, Western Madera, Camp Roberts, Contra Costa) had higher levels of variability (SD = 0.32 and SD = 0.37).
[b] Budget represents the level of funding ($million) where reserve expansion became and remained cost-efficient.

Table 5
Priority ranking of expansion of kit fox reserves under alternative assumptions about kit fox home range[a]

Site	HR = 4 km^2		HR = 6 km^2		HR = 10 km^2	
	Rank	Budget[b]	Rank	Budget[b]	Rank	Budget[b]
Western Kern	1	0	1	0	1	0
Ciervo-Panoche	2	8	3	19	4	40
Antelope Plain	3	20	2	13	2	13
Santa Nella	4	55	5	98	5	137
Camp Roberts	5	100	6	155	6	176
Carrizo Plain	6	100	4	49	3	22
Contra Costa	7	156	7	196	7	196
Western Madera	8	286	8	286	8	286

[a] In the baseline case (HR = 4 km^2), each kit fox population had the same average home range. In the other two cases, populations in grassland habitat (Ciervo-Panoche, Santa Nella, Western Madera, Camp Roberts, Contra Costa) had larger home ranges (HR = 6 km^2 and HR = 10 km^2).
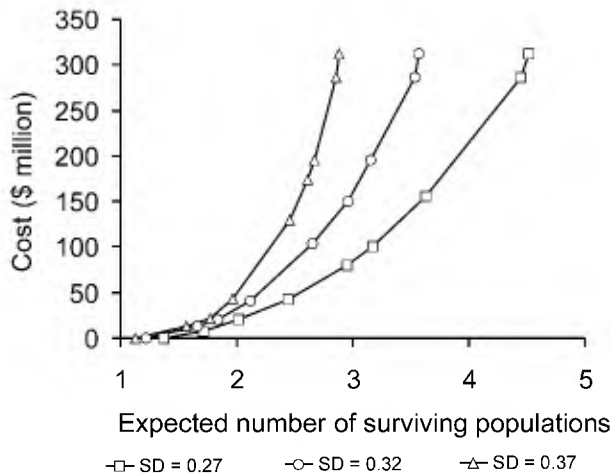[b] Budget represents the level of funding ($million) where reserve expansion became and remained cost-efficient.

Fig. 4. Cost curves for kit fox populations with the baseline standard deviation of reproductive success (SD = 0.27) and two higher levels of variability (SD = 0.32 and 0.37).

3.4. Cost curves

We used solutions of the optimization model to construct cost curves for each level of variation in reproductive success (Fig. 4). Each curve shows the funding required for incremental increases in population viability. The cost curve for the baseline case with low variation in reproductive success (0.27) was flat initially and gradually got steeper. While increasing the number of surviving populations from 1.38 to 2.95 (114%) required $80 million for habitat protection at four sites (Antelope Plain, Western Kern, Ciervo-Panoche, and Santa Nella), additional increments required larger amounts of funding. For example, increasing the expected number of surviving populations from 2.95 to 4.45 (50%) required an additional $206 million for habitat protection at all but the Western Madera site. An additional $26 million was required to protect the available habitat at Western Madera and raise the number of surviving populations from 4.45 to 4.52 (2%). Increasing the variation in reproductive success at grassland sites resulted in steeper cost curves, especially for costs > $50 million. Cost curves were similar for cases with increasing levels of home range (not shown).

4. Discussion

We addressed the problem of allocating a fixed budget for reserve expansion among disjunct populations of an endangered species with the objective of maximizing the expected number of surviving populations. The model included benefits of reserve expansion in terms of likelihood of persistence of each population as well as monetary costs. Under a given budget, the model allocates funds according to the marginal costs of increasing

population viability: sites with the least expensive habitat and greatest reduction in extinction risk for an increment of protected habitat usually receive the most funding. Solving the model with incrementally higher budgets helps identify the priority order of reserve expansion and produces a cost curve showing the funding required for incremental increases in population viability. The cost–efficient ranking of reserve expansion and the cost curve are valuable tools for decision makers who must justify their use of scarce conservation resources.

Model application to reserve expansion for San Joaquin kit fox conservation illustrated an important result: the priorities for reserve expansion are related to both land cost and amount of already-protected habitat at each site. For example, with low budgets for habitat protection, Western Kern and Ciervo-Panoche received highest priority for expansion because land prices were relatively low and already-protected habitat put the kit fox populations on the steepest part of the risk–area curve. In contrast, protecting habitat at Antelope Plain, which had the lowest land cost, was not cost–efficient at low funding levels because it had almost no already-protected habitat and required a large amount of funding to obtain a reduction in extinction risk.

The sensitivity analysis helped to determine how changes in the shape and location of the risk–area curve applied to grassland sites affected the priority ranking of reserve expansion. We concluded that, if grassland habitat is lower quality than shrubland habitat resulting in higher variation in reproductive success or larger home ranges, then protecting habitat at shrubland sites should receive priority at lower levels of funding even though those sites are relatively small (Antelope Plain) or relatively secure (Carrizo Plain). The best grassland site—Ciervo-Panoche—is not cost–efficient under this assumption despite having low land cost and a large amount of already-protected habitat because the reduction in extinction risk for an increment of habitat protection in a grassland site is relatively low.

Taken together, the optimization results suggest that available funding for habitat protection, up to $8 million, should be used at Western Kern. There are other reasons to target Western Kern. The site was designated by the recovery plan as high priority for enhancement and protection because it encompassed a large amount of already-protected public land and contained other listed species in addition to kit foxes (US Fish and Wildlife Service, 1998). Many small conservation areas have been established, and funding could be used to acquire land that joins those areas. Organizations are actively acquiring land, which presents opportunities for partnerships and pooling of resources. Future expansion of nearby cities could increase demand for development, increase land price, and reduce the number of willing sellers.

The results also suggest the importance of research at Ciervo-Panoche to determine prey availability in grassland habitat and its effect on kit fox reproductive success and home range. Ciervo-Panoche is an attractive place for reserve expansion because of its low land cost and moderate amount of already-protected land. However, if the grassland habitat quality is low, then reserve expansion will not produce large increases in population viability relative to reserve expansion at shrubland sites such as Western Kern, Antelope Plain, and Carrizo Plain.

Finally, the results suggest that lowest priority should be given to reserve expansion at three relatively high-cost grassland sites: Camp Roberts, Contra Costa, and Western Madera. In the recovery plan, those sites were important for securing the range of kit fox habitat. The cost curves suggested that protecting habitat at those sites would be expensive and have little effect on the expected number of surviving kit fox populations.

A limitation of our model was the assumption that kit fox populations were isolated and migration between populations was inconsequential. However, a recent study found evidence of gene flow among populations, with gene flow between pairs of populations decreasing with distance between them (Schwartz et al., 2002). For example, there was good gene flow between Carrizo Plain and Western Kern, slightly less gene flow between Ciervo-Panoche and Western Kern, and still less gene flow between Camp Roberts and both Western Kern and Ciervo Panoche. The relatively small number of migrating individuals necessary to maintain gene flow between two populations (Mills and Allendorf, 1996) might be insufficient for demographic rescue of a failing population, especially if dispersal is male-biased. Nevertheless, because our predictions of population viability do not consider possible rescue effects of migration between populations, the risk–area curves may underestimate the effects of increasing habitat protection, especially in smaller populations on the edges of the kit fox range. Accounting for the effects of migration may change the priorities for reserve expansion reported here. To address this issue, our next step is to formulate and solve an optimization model for reserve expansion with the objective of maximizing the expected number of surviving populations while accounting for migration and regional stochasticity. This is not a trivial optimization problem because the value of each candidate solution needs evaluation using a stochastic metapopulation model (e.g., Moilanen and Cabeza, 2002). More work is needed on algorithms for such problems.

Another model limitation was the assumption that habitat within each site had uniform quality and could be acquired all at once. In practice, habitat may be fragmented by development and have uneven quality. Furthermore, the landscape is not static: habitat not protected now may become developed or habitat not immediately available may be for sale in the future. Thus, knowledge of the spatial distribution, quality, and availability of habitat parcels in each site should be considered alongside the results of this reserve expansion model. Tools have been developed to create fine-grained maps of kit fox habitat quality (Gerrard et al., 2001) and determine optimal site selection strategies over time that account for parcel availability (Costello and Polasky, 2004, in press). It may be possible to create a dynamic parcel selection model that maximizes population persistence at a site while accounting for the spatial distribution, quality, and availability of habitat, adding a new and important dimension to the analysis of reserve expansion strategies.

Acknowledgements

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