

---

# Optimizing Habitat Protection Using Demographic Models of Population Viability

ROBERT G. HAIGHT,\* BRIAN CYPHER,† PATRICK A. KELLY‡, SCOTT PHILLIPS,‡  
HUGH P. POSSINGHAM,§ KATHERINE RALLS,\*\* ANTHONY M. STARFIELD,††  
P. J. WHITE,‡‡ AND DANIEL WILLIAMS§§

\*U.S. Forest Service, North Central Research Station, 1992 Folwell Avenue, St. Paul, MN 55108, U.S.A.,  
email rhaight@fs.fed.us

†California State University, Stanislaus, Endangered Species Recovery Program, P.O. Box 9622, Bakersfield, CA  
93389, U.S.A.

‡California State University, Stanislaus, Endangered Species Recovery Program, 1900 N. Gateway Boulevard,  
Suite 101, Fresno, CA 93727, U.S.A.

§Departments of Zoology and Mathematics, The University of Queensland, St Lucia, QLD 4072, Australia

\*\*Conservation and Research Center, Smithsonian National Zoological Park, Washington, D.C. 20008, U.S.A.

††Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, MN 55108, U.S.A.

‡‡U.S. Fish and Wildlife Service, 2730 Loker Avenue West, Carlsbad, CA 92008, U.S.A.

§§California State University, Stanislaus, Department of Biological Sciences, 801 W. Monte Vista Avenue, Turlock,  
CA 95382, U.S.A.

---

**Abstract:** *Expanding habitat protection is a common tactic for species conservation. When unprotected habitat is privately owned, decisions must be made about which areas to protect by land purchase or conservation easement. To address this problem, we developed an optimization framework for choosing the habitat-protection strategy that minimizes the risk of population extinction subject to an upper bound on funding. The framework is based on the idea that an extinction-risk function that predicts the relative effects of varying the quantity and quality of habitat can be estimated from the results of a demographic model of population viability. We used the framework to address the problem of expanding the protected habitat of a core population of the endangered San Joaquin kit fox (*Vulpes macrotis mutica*) in the Panoche area in central California. We first developed a stochastic demographic model of the kit fox population. Predictions from the simulation model were used to estimate an extinction-risk function that depended on areas of good- and fair-quality habitat. The risk function was combined with costs of habitat protection to determine cost-efficient protection strategies and risk-cost curves showing how extinction risk could be reduced at minimum cost for increasing levels of funding. One important result was that cost-efficient shares of the budget used to protect different types of habitat changed as the budget increased and depended on the relative costs of available habitat and the relative effects of habitat protection on extinction risk. Another important finding was the sensitivity of the location and slope of the risk-cost curve to assumptions about the spatial configuration of available habitat. When the location and slope of the risk-cost curve are sensitive to model assumptions, resulting predictions of extinction risk and risk reduction per unit cost should be used very cautiously in ranking conservation options among different species or populations. The application is an example of how the results of a complex demographic model of population viability can be synthesized for use in optimization analyses to determine cost-efficient habitat-protection strategies and risk-cost tradeoffs.*

Optimización de la Protección de Hábitat Utilizando Modelos de Viabilidad Poblacional

**Resumen:** *La protección de hábitat y expansión es una táctica común para la conservación de especies. Cuando el hábitat sin protección es propiedad privada, las decisiones deben ser tomadas sobre las áreas a*

---

*Paper submitted November 8, 1999; revised manuscript accepted October 3, 2001.*

1386

*proteger mediante la compra de terrenos o la expropiación para conservación. Para tratar este problema, desarrollamos un marco de optimización para elegir la estrategia de protección del hábitat que reduce al mínimo el riesgo de extinción de la población conforme a un límite superior de financiamiento. El marco se basa en la idea que se puede estimar una función extinción - riesgo que prediga los efectos relativos de variar la cantidad y la calidad del hábitat a partir de los resultados de un modelo demográfico de viabilidad de la población. Utilizamos el marco para tratar el problema de ampliar el hábitat protegido de una población núcleo del zorro de San Joaquín (*Vulpes mutica macrotis*) en el área de Panoche en California central. Primero desarrollamos un modelo demográfico estocástico de la población del zorro. Las predicciones del modelo de simulación fueron utilizadas para estimar una función de riesgo de extinción que dependió de áreas de hábitat de buena y mediana calidad. La función del riesgo fue combinada con costos de protección del hábitat para determinar estrategias de protección costo-eficientes y curvas de riesgo-costo que mostraban cómo el riesgo de la extinción se podría reducir al mínimo costo para niveles de financiamiento en aumento. Un resultado importante fue que las acciones costo-eficientes del presupuesto utilizadas para proteger diversos tipos de hábitat cambiaron a medida que el presupuesto aumentó y dependieron de los costos relativos de hábitat disponible y de los efectos relativos de la protección del hábitat sobre el riesgo de extinción. Otro resultado importante fue la sensibilidad de la localización y de la pendiente de la curva de riesgo-costo a suposiciones sobre la configuración espacial del hábitat disponible. Cuando la localización y la pendiente de la curva de riesgo-costo son sensibles a las suposiciones del modelo, las predicciones del riesgo de extinción y de reducción del riesgo por costo unitario resultantes se deben utilizar muy cautelosamente al jerarquizar opciones de conservación de diversas especies o poblaciones. La aplicación es un ejemplo de cómo los resultados de un complejo modelo demográfico de la viabilidad de la población se pueden sintetizar para el uso en el análisis de la optimización para determinar estrategias de protección de hábitat costo-eficientes y compensaciones del riesgo-costo.*

## Introduction

Protecting species on private lands is essential to conserving biodiversity in the United States, because the habitat of more than half of all federally listed species is located on private land (Wilcove et al. 1996). Although essential, strategies for protecting species on private lands are expensive, because securing habitat requires purchase of title, conservation easement, or land-use incentives. Consequently, methods for designing habitat-protection strategies need to account for financial considerations in addition to the benefits of protection.

We developed a method for determining the habitat-protection strategy that minimizes the risk of population extinction within a given budget. The method is based on the idea that a demographic model of population viability can be used to predict and compare the probabilities of extinction under different options for habitat protection (Boyce 1992; Ralls & Taylor 1997; Beissinger & Westphal 1998; Groom & Pascual 1998). The predictions of the demographic model, in turn, are synthesized into a risk function that predicts the relative effects of varying the quantity and quality of habitat (see also McCarthy et al. 1995). The risk function and the costs of habitat protection are incorporated into an optimization model for determining cost-effective protection strategies.

Although demographic models of population viability are routinely used to determine the relative effects of habitat-management options (e.g., Armbruster & Lande 1993; Liu et al. 1995; Lindenmayer & Possingham 1996),

only a few studies address the problem of choosing a management option when there are competing objectives of maximizing species persistence and minimizing economic cost. For example, structured decision-making approaches can be used to inform decision-makers about the benefit-cost tradeoffs among predefined management options (Possingham et al. 1993; Ralls & Starfield 1995; Possingham 1997). Optimization methods can further inform decision-makers by determining the best option from a wider array of potential management strategies, and the results can be used to generate cost curves that show gains in terms of risk reduction associated with incremental increases in the budget. Optimization methods have been widely applied to the problem of reserve-site selection to maximize the number of species covered within budget constraints (e.g., Church et al. 1996; Ando et al. 1998). Optimization has also been used to search for efficient land-use allocations when protection of biodiversity, as measured by a weighted sum of species viabilities, is one of several land-management objectives (Beverly et al. 1995; Montgomery et al. 1999).

There are only a few studies in which optimization has been combined with demographic models of species viability to determine cost-effective protection strategies (Montgomery et al. 1994; Haight & Travis 1997). The computational difficulties of incorporating stochastic demographic models into optimization algorithms required these studies to address problems with only one decision variable representing the total area of protected habitat. The optimization framework we present avoids

those computational difficulties by using model predictions to estimate a risk function that is incorporated into the optimization analysis. The general idea was developed by Hof and Raphael (1997), who used predictions from a stochastic demographic model to estimate dispersal parameters in an optimization model. In our application, the risk function can include decision variables for the amounts of habitat of different qualities and locations, thereby enhancing the range of habitat-protection options that can be considered.

We first present the optimization model and then describe its application to expanding the area of protected habitat of a core population of the San Joaquin kit fox (*Vulpes macrotis mutica*), an endangered species in central California. The San Joaquin kit fox was granted federal protection in 1967 (U.S. Fish and Wildlife Service 1967) because habitat loss resulting from agricultural, industrial, and urban development had significantly reduced its abundance and distribution (U.S. Fish and Wildlife Service 1998). Currently, kit fox populations are constricted into fragmented areas of varying size and habitat quality, and the suspected high mortality of kit fox dispersers may limit the movement of individuals between populations. To limit the threat from continued habitat fragmentation, the recovery plan for upland species of the San Joaquin Valley (U.S. Fish and Wildlife Service 1998) specifies the enhanced protection and management of three geographically distinct populations, which form the core of a kit fox metapopulation. We focused our analysis on one of the core populations of kit foxes.

## An Optimization Model for Habitat Protection

Demographic models of population viability are often used to estimate probabilities of population extinction under existing habitat conditions and alternative scenarios for habitat expansion or contraction. Our approach assumed that we could find a suitable risk function to express the probability of population extinction as a function of habitat area by using extinction probabilities obtained from a demographic model of population viability. Based on the risk function, we formulated an optimization model for selecting areas for habitat protection to minimize the risk of population extinction under a given set of protection costs and an upper bound on funding. The model was formulated with the following notation:

- $j, J$  = individual habitat type and number of habitat types;
- $a_j$  = area of already-protected habitat, type  $j$ ;
- $b$  = upper bound on protection budget;
- $c_j$  = unit cost of protecting additional habitat, type  $j$ ;
- $d_j$  = upper bound on the area of habitat type  $j$  that is available for protection;

- $x_j$  = area of habitat type  $j$  that is selected for protection;
- $y_j$  = total area of protected habitat, type  $j$ ;
- $P(y_1, \dots, y_J)$  = probability of population extinction.

The optimization problem was formulated as follows:

$$\text{minimize } P(y_1, \dots, y_J) \quad (1)$$

subject to

$$y_j = a_j + x_j \quad j = 1, \dots, J \quad (2)$$

$$\sum_{j=1}^J c_j x_j \leq b \quad (3)$$

$$0 \leq x_j \leq d_j \quad j = 1, \dots, J \quad (4)$$

The objective of the optimization problem (Eq. 1) was to minimize the probability of population extinction, which was a function of the area of protected habitat by type. The first set of constraints (Eq. 2) defined the area of protected habitat by type as the sum of the already-protected area and the newly protected area. The second constraint (Eq. 3) ensured that the total amount of funding required for additional habitat protection did not exceed the budget. The unit cost of protection,  $c_j$ , can differ by habitat type, but the unit cost is constant for a given type. The third set of constraints (Eq. 4) bounded the area of habitat available for protection.

To make the model more realistic, we relaxed the assumption of constant unit costs because the cost of protecting land of a given habitat quality may vary depending on property enhancements, location, and method of securing protection (e.g., with an easement or purchase of title). Unit costs of protecting land of each habitat type were represented with a piecewise linear total cost curve (Murty 1976). First, land of habitat type  $j$  was divided into  $K$  different cost classes, ordered from lowest to highest. Let  $c_j^k$  be the unit cost of class  $k$ , and  $c_j^1 < c_j^2 < \dots < c_j^K$ . Furthermore, let  $x_j^k$  be a decision variable for the amount of habitat selected for protection in cost class  $k$ , and  $d_j^k$  be the upper bound on the amount of habitat available in class  $k$ , so that

$$0 \leq x_j^k \leq d_j^k, \quad k = 1, \dots, K. \quad (5)$$

Then, the decision variable  $x_j$  was eliminated from the model by substituting  $x_j = x_j^1 + \dots + x_j^K$  in constraint set equation 2 and substituting  $c_j x_j = c_j^1 x_j^1 + \dots + c_j^K x_j^K$  in the cost constraint Eq. 3. Finally, each area constraint  $0 \leq x_j \leq d_j$  in Eq. 4 was replaced with constraint set Eq. 5. It should be noted that, if the model selects any habitat of type  $j$  for protection, the model will select the habitat with the lowest unit cost first. As a result, for any  $k$ , if  $x_j^k > 0$ , then  $x_j^t = d_j^t$  for all  $t < k$ , and the total cost of protecting habitat of type  $j$  is a piecewise linear convex curve (Murty 1976).

For each habitat type with varying unit costs, the decision variable for the amount of habitat to protect can be

partitioned and included in the model as above. Then, for a given set of prices 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 by quality class. Furthermore, by re-solving the model with incrementally higher upper bounds on funding, a relationship between extinction risk and funding can be determined. This risk-cost curve shows the benefit in terms of a reduced extinction risk as a result of increased funding.

## Application to Kit Fox Conservation

### Background

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 that vary greatly from year to year. For example, annual rainfall in Bakersfield, California, was 5–25 cm from 1980 to 1995 (Cypher et al. 2000). Although the valley floor was once

dominated by grassland, scrubland, and wetland communities, it is now dominated by agricultural, industrial, and urban development. Only a few remnant grasslands remain on the valley's perimeter.

With the loss of its natural communities, the San Joaquin Valley has experienced a great loss of biodiversity. As of 1998, 75 species of plants and animals were listed or candidate species, including the San Joaquin kit fox (U.S. Fish and Wildlife Service 1998). The recovery plan for upland species of the San Joaquin Valley designated the kit fox as an umbrella species and has a goal of establishing a viable complex of populations of kit foxes on public and private lands throughout their geographic range (U.S. Fish and Wildlife Service 1998).

Although the San Joaquin kit fox once inhabited relatively flat grasslands and scrubland throughout the San Joaquin Valley (Grinnell et al. 1937), habitat loss and alteration curtailed its distribution so that high-density populations of kit foxes are now found primarily on a few public and private grasslands. Three geographically distinct populations have been designated a high priority for enhancement and protection: the Carrizo Plain and western Kern County populations in the southern part of the valley and the Panoche-area population in the

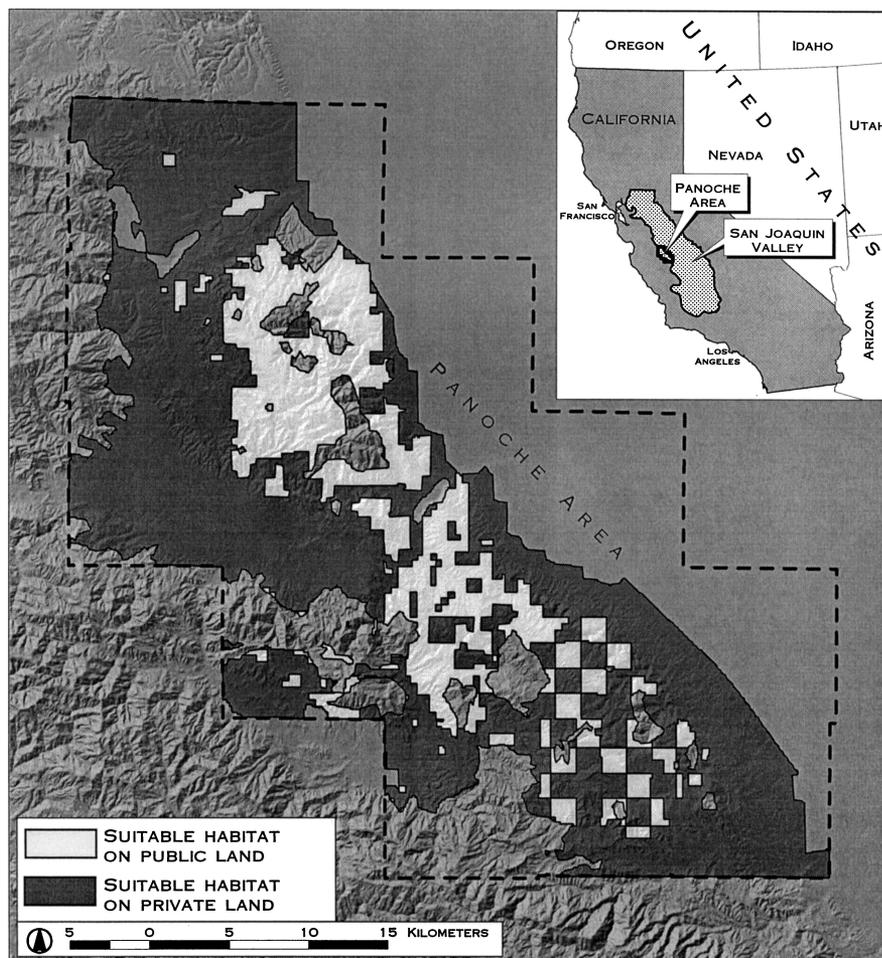


Figure 1. Habitat of San Joaquin kit fox on public and private land in the Panoche area of California.

western portion of the valley (U.S. Fish and Wildlife Service 1998). These are viewed as core populations in the recovery plan because each inhabits a large amount of good-quality, publicly owned habitat, each is subject to a different set of environmental conditions, and each can serve as a source of kit foxes for neighboring satellite populations.

Detailed information and literature reviews of the life history and ecology of the San Joaquin kit fox have been provided by the U.S. Fish and Wildlife Service (1998), White and Garrott (1999), and Cypher et al. (2000), and we only summarize the information important to model building. Kit foxes are nocturnal predators of rodents and rabbits. Adult pairs remain together and maintain large and relatively nonoverlapping home ranges. Home ranges from  $<2.6$  km<sup>2</sup> up to approximately 31 km<sup>2</sup> have been reported. A kit fox pair breeds once a year and has 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 (White & Ralls 1993; White & Garrott 1997). If reproduction is successful, a litter of two to six pups emerges from the den in spring. Pups reach adult size and disperse from August through September in search of mates and vacant home ranges. Dispersal distances vary widely, with male foxes known to travel over 40 km. Pups and adults are known to disperse through disturbed habitat, including agricultural fields, oil fields and rangelands, and across highways and aqueducts.

Because of the endangered status of the kit fox, considerable research has been conducted in the last 15 years to identify natural factors that have influenced the dynamics of the western Kern County and Carrizo Plain populations. Food availability was the most important factor. Prey abundance and kit fox numbers varied annually with a previous year's precipitation (Ralls & Eberhardt 1997; Cypher et al. 2000). Kit fox numbers had a strong positive relationship with prey availability (White et al. 1996; Cypher et al. 2000), probably because prey reductions caused lower reproductive success in kit foxes (White & Ralls 1993; White & Garrott 1997). An important conclusion is that high-amplitude fluctuations in kit fox numbers may be intrinsic to the desert systems they inhabit because of large fluctuations in annual precipitation and prey availability (White & Garrott 1999; Dennis & Otten 2000).

We used these observations to construct a demographic model of a kit fox population for the evaluation of habitat-protection strategies in the Panoche area. We focused on the Panoche area because a large amount of kit fox habitat is located on public land and because opportunities exist to secure additional habitat on nearby private land. In the Panoche area, public land administered by the U.S. Bureau of Land Management (BLM) contains 312 km<sup>2</sup> of relatively flat grassland suitable for kit foxes (Fig. 1). Because kit foxes occur in higher den-

sities and are less vulnerable to mortality from larger canids on flat or rolling grasslands (Warrick & Cypher 1998), we classified habitat quality based on slope (for an alternative approach to defining kit fox habitat see Gerrard et al. 2001). Good habitat had slopes of 0–5% and fair habitat had slopes of 5–10%. Places with slopes of  $>10\%$  were assumed to be unsuitable for kit foxes. Good and fair habitat cover 62 km<sup>2</sup> and 250 km<sup>2</sup>, respectively. Over 600 km<sup>2</sup> of suitable habitat exist in private ownerships surrounding the BLM land (Fig. 1). None of the suitable habitat on private land is currently protected.

To estimate the maximum number of home ranges in good and fair habitat on BLM land, we used observations of kit fox density in the western Kern County population (B.C., unpublished data). There, kit fox density in good habitat (0.51/km<sup>2</sup>) was twice the density in fair habitat (0.26/km<sup>2</sup>). Lower kit fox density in fair habitat probably resulted from a combination of higher predation risk and lower food availability. Assuming two kit foxes per home range, we estimated that home ranges in good and fair habitat averaged 3.9 km<sup>2</sup> and 7.8 km<sup>2</sup>, respectively. Using these home-range sizes and the amounts of good and fair habitat, we estimated that BLM land in the Panoche area contained a maximum of 16 and 32 home ranges in good and fair habitat, respectively. To demonstrate the optimization model, we assumed that enough private land to make 48 home ranges each of good and fair habitat was adjacent to the BLM land and available for protection.

We wanted to predict and compare the probabilities of extinction of the kit fox population in the Panoche area under different options for protecting additional habitat. As a baseline, we predicted kit fox population viability on 312 km<sup>2</sup> of already-protected BLM land, assuming that surrounding private land was unsuitable for kit foxes. We then predicted how the viability of the kit fox population would change if additional habitat adjacent to the BLM land was protected. Finally, we predicted the effect of protecting a disjunct area of habitat separated from the BLM land by unprotected areas of unsuitable habitat.

### Simulating Kit Fox Populations

The structure of the stochastic demographic model of kit fox population viability was similar to models of other territorial animals (Lamberson et al. 1994; Haight et al. 1998). We assumed that a contiguous habitat patch consisted of a fixed number of potential kit fox home ranges, each classified as good or fair habitat. Each home range could support a single kit fox family. The annual change in each kit fox family was predicted with an age-structured model describing the number of kit foxes by age and sex beginning midwinter prior to birth. Predictions were made sequentially for birth, mortality, and dispersal.

Birth took place in late winter. Reproduction in each kit fox family required a male and female  $\geq 12$  months old.

Because temporal variation in prey availability is linked to kit fox reproductive success and litter size, we modeled reproduction using a two-step process (for a similar approach see Loison et al. 2001). In the first step, we picked the reproductive success rate for the year from a normal distribution with a mean of 0.60 and a standard deviation of 0.20, based on the observed reproductive success of kit fox families in the western Kern County population from 1981 to 1995 (Cypher et al. 2000). The reproductive success of each kit fox pair was determined by comparing a random number chosen from a uniform distribution between 0 and 1 to the chosen success rate. In the second step, the litter size of each successful pair was selected from a discrete probability distribution of three to five pups, with a mean of four pups, again based on observations of Cypher et al. (2000). Unsuccessful pairs were assumed to hold their territories without producing litters.

Mortality took place during spring and summer. The number of kit foxes that died in each age class was a binomial random variable with probability depending on age and habitat quality. In good habitat, mortality rates of pups and adults were 0.60 and 0.30, respectively, consistent with recent estimates from survival studies of kit fox populations in western Kern County (Cypher & Spencer 1998) and the Carrizo plain (Ralls & White 1995). In fair habitat, we used pup and adult mortality rates of 0.65 and 0.35, respectively, to account for the higher risk of mortality caused by larger canids (Warwick & Cypher 1998). We assumed that all kit foxes reaching the 6-year-old age class died.

All surviving pups dispersed in autumn in search of mates and home ranges. Although there is little quantitative information about kit fox dispersal patterns and behavior, we believe that dispersing kit foxes seek home ranges in good-quality habitat rather than dispersing at random. In the simulation model, we assumed that dispersing pups could search for mates and territories throughout the contiguous habitat patch. Furthermore, we assumed that pups distinguished between good and fair habitat and searched first in areas of good habitat. Each disperser was randomly assigned to a home range with an available mate. If there were no available mates, the disperser was randomly assigned to a vacant home range. If vacancies were not available in areas of good habitat, the same search routine was applied to areas of fair habitat. If no vacancies were available in fair habitat, dispersers were assumed to leave the patch and die. In the sensitivity analysis, we assumed that 10% of the dispersers from the saturated core patch could reach a disjunct patch of good habitat that was separated from the core area by unsuitable and unprotected habitat.

Following dispersal, we updated the age distribution of kit foxes in each family unit. The updated age distribution approximated the situation in February and was the basis for the next year's projection.

### Estimating the Extinction-Risk Function

The goal of the simulation analysis was to estimate a suitable risk function that related the probability of kit fox population extinction to habitat area. We used the stochastic demographic model to predict probabilities of extinction of the kit fox population in contiguous habitat patches with different amounts of good and fair habitat. The baseline patch represented the already-protected BLM land covering 16 home ranges of good habitat and 32 home ranges of fair habitat. To predict the effects of protecting additional habitat adjacent to the BLM land, we predicted extinction risks of populations in patches with up to 64 home ranges in good habitat and 80 home ranges in fair habitat. Altogether, simulations were performed for 49 different patch configurations, each with a different combination of habitat area and quality class. Each simulation had 1000 replicates in which we assumed that the initial patch was fully occupied by kit fox families. The outcome of each simulation was the proportion of replicates in which population size was <10 in 100 years. This proportion was our estimator of the probability of population extinction. Although our choice of 10 individuals as the threshold for quasi-extinction was arbitrary, we used the threshold because smaller populations would almost certainly go extinct from causes ranging from unbalanced sex ratios to difficulties of individuals finding mates.

We used the minimum logit chi-squared method, as defined by Maddala (1983), to estimate the relationship between extinction risk and the amounts of good and fair habitat. This logit model is appropriate when there are multiple observations of the binary response variable for each level of the independent variables in the experimental design. In our case, the binary response variable was whether or not the kit fox population was extinct after 100 years in a given habitat configuration, and 1000 observations of this response variable were obtained from simulation. We let  $\hat{p}_i$  be the proportion of the 1000 replicates in which the population became extinct in habitat configuration  $i$ , and we let  $\hat{p}_i/(1 - \hat{p}_i)$  be the estimated odds of extinction. In the logit model, the log of the odds of extinction was assumed to be a linear combination of habitat configuration

$$\log \frac{p_i}{1-p_i} = \beta' \mathbf{y}_i, \quad (6)$$

where  $\mathbf{y}_i$  is a vector of habitat amounts and  $\beta'$  is a vector of parameters. Because the log of the odds of extinction is a continuous variable and  $-\infty \leq \log[p_i/(1 - p_i)] \leq \infty$ , ordinary linear regression can be used to estimate  $\beta'$ :

$$\log \frac{\hat{p}_i}{1-\hat{p}_i} = \beta' \mathbf{y}_i + \mu_i, \quad (7)$$

where  $\mu_i$  is the regression error. However, because  $\text{Var}(\mu_i) = 1/[n_i p_i (1 - p_i)]$ , weighted least-squares regression with weights  $[n_i \hat{p}_i (1 - \hat{p}_i)]^{1/2}$  was used to estimate  $\beta'$  in Eq. 6 to remove heteroscedasticity in the regression error (Maddala 1983).

### Optimizing Habitat Protection

With the estimated extinction-risk function, we solved the optimization model (Eqs. 1–5) for a given set of unit costs of habitat protection and increasing upper bounds on available funding. The optimization results allowed us to plot a risk-cost curve showing how much extinction risk could be reduced by incrementally increasing the available funding. Finally, we repeated the analysis using a different assumption about the spatial configuration of habitat available for protection.

Although habitat can be protected by conservation easements, landowner incentives, or outright land purchase, for simplicity we based our example only on land purchase. The cost and availability of land varied by habitat quality (Table 1). Good-quality habitat was \$500–\$2000/ha (\$200–\$800/acre), and fair-quality habitat was \$125–\$500/ha (\$50–\$200/acre). The difference in cost between good and fair habitat reflected slope and ranchland productivity. Good habitat was flat and suitable for dryland farming, whereas fair habitat included rolling hills suitable for cattle grazing. The unit costs were in the range of prices from recent ranch sales in surrounding San Benito and Fresno counties (Sergio Garcia, Range/Livestock Advisor, University of California Cooperative Extension, San Benito County, personal communication). The amounts of land available for protection by quality and price class (Table 1) were devised to illustrate the optimization model. We assumed that relatively small amounts of good-quality habitat were available in

the lower cost classes and that a large amount of fair habitat was available in the smallest cost class.

It is well known that interpatch dispersal and between-patch variation in habitat quality can affect predictions of risk for populations in fragmented habitat (Lindenmayer et al. 2000). Therefore, the purpose of the sensitivity analysis was to determine whether a different assumption about the spatial configuration of kit fox habitat available for protection affected the location and shape of the extinction-risk surface and optimal protection strategy. In the simulation methods described above, all habitat available for protection was assumed to be adjacent to BLM land, and dispersing kit foxes searched for mates and vacant home ranges throughout a contiguous habitat patch formed by the BLM land and protected private land. In the sensitivity analysis, we assumed that the only good-quality habitat available for protection was in a contiguous patch separated from the already-protected BLM land by unsuitable habitat. As before, fair-quality habitat available for protection was adjacent to the BLM land. In this configuration, we assumed that dispersing kit foxes first searched for mates and vacant home ranges within the contiguous core patch formed by the BLM land and the protected fair habitat on adjacent private land. If this core patch was saturated, we assumed that dispersers could reach the disjunct patch of protected good habitat on private land with a probability of 0.10, which represented a relatively high rate of dispersal mortality. The kit fox population in the disjunct patch was simulated with the same demographic model, and kit foxes that dispersed from a saturated disjunct patch could reach the core patch with a probability of 0.10.

The optimization model was solved on an IBM300PL personal 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 with GAMS (General Algebraic Modeling System), a program designed to generate data files in a standard format that optimization programs can read and process. Because the model (Eqs. 1–5) had a nonlinear objective function with linear constraints, GAMS/MINOS used a reduced-gradient algorithm combined with a quasi-Newton algorithm (Murtagh & Saunders 1978) to find the solution. Solution times were <1 second.

### Results

Predictions of extinction risk in 100 years are plotted in Fig. 2a for the case in which all habitat available for protection is adjacent to BLM land. If kit fox habitat was limited to the already-protected BLM land (16 good-quality home ranges and 32 fair-quality home ranges), the pre-

**Table 1.** Cost and availability of good- and fair-quality habitat for San Joaquin kit foxes.

Habitat	Cost		Availability	
	\$/ha	\$/home range*	ha	no. home ranges
Good	500	195,000	1,560	4
	1,000	390,000	1,560	4
	1,500	585,000	6,240	16
	2,000	780,000	9,360	24
Fair	125	97,500	18,720	24
	250	195,000	6,240	8
	375	292,500	6,240	8
	500	390,000	6,240	8

\* Home ranges of good and fair habitat are 390 and 780 ha, respectively.

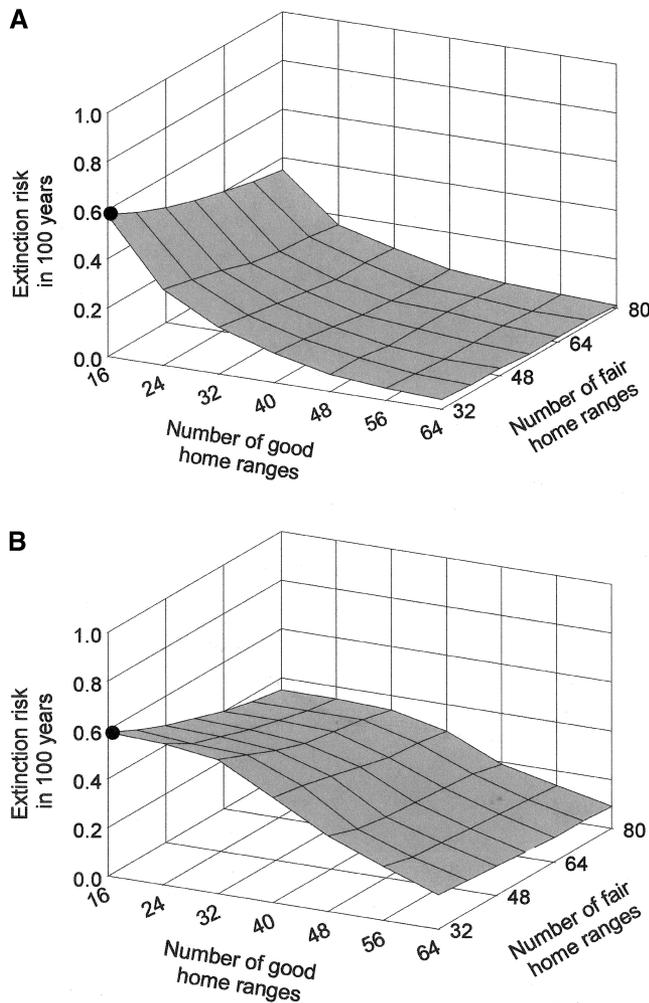


Figure 2. Probability of extinction in 100 years versus amount of protected kit fox habitat when (a) available habitat is adjacent to the habitat on already-protected land of the Bureau of Land Management (BLM) and (b) good habitat is a disjunct patch separated from the habitat on BLM land. The black dot represents extinction risk if kit fox habitat were limited to BLM land (16 good-quality home ranges and 32 fair-quality home ranges).

dicted probability of extinction of a kit fox population that initially occupied the BLM land was 0.58 (Fig. 2a). We used this risk prediction for comparative purposes, and it should not be viewed as an absolute estimate of kit fox population risk in the Panoche area because of uncertainties in various components of the demographic model. Relative to this prediction, the greatest risk reduction was obtained by protecting additional good habitat adjacent to the BLM land (Fig. 2a). For example, predicted extinction risk dropped to 0.04 when 48 additional good-quality home ranges were protected.

In contrast, predicted extinction risk dropped to 0.35 when 48 additional fair-quality home ranges were protected. Protecting good-quality habitat resulted in greater reductions in extinction-risk predictions because good-quality habitat had lower pup and adult mortality rates.

The predictions from the simulations were used to estimate the following risk function:

$$\log \frac{p}{1-p} = 3.0244763 - 0.151321y_1 - 0.0193473y_2 + 0.000979y_1^2 + (0.040858) (0.002093) (0.000365) (0.000027) \tag{8}$$

where  $p$  is the probability of extinction in 100 years and  $y_1$  and  $y_2$  are the numbers of home ranges in good and fair habitat, respectively. The numbers in parentheses are the standard errors of regression coefficients, and all coefficients were significant at the 0.001 probability level. A variety of models with quadratic and interaction terms were estimated, and the final selection was based on the goodness of fit (adjusted  $R^2 = 0.990$ ). The plot of residuals versus estimates suggested that the error variance was homogenous.

We used the risk function (Eq. 8), the optimization model (Eqs. 1-5), and the habitat cost and availability information in Table 1 to determine cost-efficient strategies for protecting additional habitat adjacent to the BLM land for increasing levels of funding. With zero funding, 16 and 32 home ranges of good and fair habitat, respectively, were protected on BLM land (Table 2). As funding increased, the amounts of good and fair habitat protected depended on the relative cost of available habitat and the relative reduction in predicted extinction risk. For example, when the upper bound on funding increased from zero to \$2 million, the cost-efficient

Table 2. Cost-efficient habitat protection under alternative funding levels when both good and fair habitat are adjacent to the core habitat on already-protected land of the Bureau of Land Management.

Funding* (\$, millions)	Extinction risk	No. home ranges	
		good	fair
0	0.580	16	32
2	0.340	24	32
5	0.235	24	56
14	0.073	40	56
16	0.061	40	64
24	0.033	51	64
27	0.027	51	72
32	0.021	58	72
35	0.018	58	80
40	0.015	64	80

\*Each funding level represents a point where the cost-efficient strategy switched from protecting one habitat type to another.

strategy was to secure up to 8 home ranges of good habitat, reducing extinction risk from 0.580 to 0.340. In this range of funding, protecting a home range of good habitat was preferred despite a cost two to four times that of protecting a home range of fair habitat. Good habitat was preferred because each additional home range of good habitat provided a four to six times greater reduction in extinction risk compared with protecting a home range of fair habitat. When the upper bound on funding increased from \$2 million to \$5 million, the cost-efficient strategy was to protect 8 home ranges of good habitat and up to 24 home ranges of fair habitat, reducing extinction risk from 0.340 to 0.235. Once 8 home ranges of good habitat had been secured, protecting a home range of fair habitat was preferred, despite its relatively small reduction in extinction risk because the cost of protecting an additional home range of fair habitat (\$0.097 million) was less than one-fifth of the cost of the available good habitat (\$0.585 million per home range).

We used the solutions of the optimization model to construct a risk-cost curve showing how the risk of extinction in 100 years could decrease for increasing levels of funding (Fig. 3). Extinction risk decreased rapidly from 0.58 to 0.10 for funding levels of up to \$10 million. An additional \$10 million was required to reduce extinction risk from 0.10 to 0.05. Additional increments of funding resulted in very small reductions in extinction risk.

The risk-cost curve (Fig. 3) is a frontier showing the minimum extinction risk obtainable for different levels of funding. The frontier is useful for identifying suboptimal protection strategies, which result in higher probabilities of extinction for any given level of funding. For example, with \$10 million, the optimal strategy was to protect 17 home ranges of good habitat and 24 home ranges of fair habitat with an extinction risk of 0.10 on the risk-cost frontier. If \$10 million was used instead to protect 48 home ranges of fair habitat, extinction risk would be 0.33 (point A). If \$10 million was used to protect 21 home ranges of good habitat, extinction risk would be 0.13 (point B). In this case, the strategy of protecting as much good habitat as possible is almost as effective in reducing extinction risk as the optimal strategy, which involves the protection of a mix of good and fair habitat.

In the sensitivity analysis, we changed an assumption about the spatial configuration of available kit fox habitat so that the only available good-quality habitat was in a contiguous patch separated from the already-protected BLM land. This change affected the shape of the extinction-risk surface (Fig. 2b). The biggest changes were risk predictions associated with protecting small amounts of good-quality habitat. Protecting a small patch of up to 16 good home ranges did not reduce the predicted extinction risk because successful movement of kit foxes between the core BLM land and the disjunct patch was un-

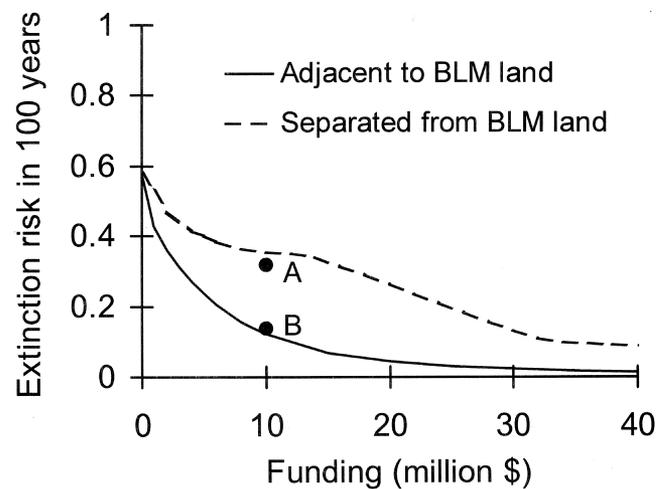


Figure 3. Risk-cost curves for protection of cost-efficient kit fox habitat. The solid line is the risk-cost curve when available habitat is adjacent to the habitat on already-protected land of the Bureau of Land Management (BLM). Points A and B show extinction risks associated with suboptimal protection strategies at the \$10 million funding level. The dashed line is the risk-cost curve when the only good habitat available for protection is separated from the habitat on BLM land.

likely and the disjunct patch was not large enough to sustain a population. When a larger disjunct patch of good habitat was protected, the reduction in extinction risk was larger.

We used the predictions of extinction risk in Fig. 2b to estimate the risk function:

$$\log \frac{p}{1-p} = 1.234696 + 0.017624y_1 - 0.035868y_2 + (0.065231)(0.001626) + (0.002010) - 0.000917y_1^2 + 0.000102y_2^2 + 0.000252y_1y_2 + (0.000017) + (0.000017) + (0.000015). \quad (9)$$

A model with quadratic and interaction terms was selected based on its goodness of fit (adjusted  $R^2 = 0.981$ ). The numbers in parentheses are the standard errors of regression coefficients, and all coefficients were significant at the 0.005 probability level. The plot of residuals versus estimates suggested that the error variance was homogenous.

With risk function equation 9, cost-efficient protection strategies differed from those obtained with risk function equation 8. When the upper bound on funding increased from \$0 to \$10 million, the cost-efficient strategy was to secure up to 48 home ranges of fair habitat, reducing extinction risk from 0.580 to 0.352 (Table 3). In this range of funding, protecting a home range of fair habitat was preferred because it was cheaper and produced a greater reduction in extinction risk than protecting a home range of good habitat. When funding was in the range of \$10–\$12 million, the best strategy

**Table 3.** Cost-efficient habitat protection under alternative funding levels when good habitat is a disjunct patch separated from the core habitat on already-protected land of the Bureau of Land Management.

Funding* (\$, millions)	Extinction risk	No. home ranges	
		good	fair
0	0.580	16	32
10	0.352	16	80
12	0.351	24	80
18	0.291	43	64
33	0.101	64	56
40	0.089	64	80

\*Each funding level represents a point where the cost-efficient strategy switched from protecting one habitat type to another.

was to protect all 48 home ranges of fair habitat and up to 8 home ranges of good habitat, reducing predicted extinction risk from 0.352 to 0.351. Fair habitat continued to be preferred because not enough funding was available to secure a large patch of good habitat. When funding increased from \$12 to \$18 million, the optimal strategy switched to protecting 32 home ranges of fair habitat and 18–27 home ranges of good habitat, reducing extinction risk from 0.351 to 0.291. Here, enough funding was available to protect a relatively large patch of good habitat, which provided a greater reduction in predicted extinction risk than did protecting a large amount of fair habitat adjacent to the BLM land. As a result, fewer home ranges of fair habitat were protected than with lower levels of funding. With funding levels of \$18–\$33 million, an even greater share of the budget was spent protecting a large patch of good-quality habitat, reducing extinction risk from 0.291 to 0.101. With funding greater than \$33 million, the focus was on protecting fair habitat once all 48 available good-quality home ranges had been protected.

Changing the assumption about the location of good-quality habitat available for protection not only affected the optimal protection strategy but also the location of the risk-cost frontier (Fig. 3). The risk-cost curve obtained when good habitat was separated from the already-protected BLM land is located above the curve obtained when the habitat was adjacent, indicating that increments of funding do not produce as much risk reduction. This is an example of how the location and slope of the risk-cost curve is sensitive to the assumptions in the underlying demographic model.

## Discussion

One of the strengths of our optimization framework is its recognition of the conflicting objectives of species conservation planning (Possingham et al. 1993; Montgomery et al. 1994; Ralls & Starfield 1995; Haight & Travis 1997; Possingham 1997). On the one hand, decision-makers

seek those activities that maximize population viability, whereas on the other hand they must minimize cost because funds for conservation are limited. Developing cost-effective conservation plans and analyzing risk-cost tradeoffs are important when planning involves expanding habitat protection on expensive private lands. Cost considerations are also important on public lands where habitat protection precludes benefits from other land uses such as logging or developed recreation. The methods that we described for developing cost-effective habitat-protection strategies and analyzing risk-cost tradeoffs should promote and focus discussion among decision-makers about conservation actions and priorities on both public and private lands.

Another strength of the optimization framework is its focus on the relative effects of different habitat-protection options. There is an emerging consensus among people involved in endangered-species management that demographic models should be used cautiously in population viability analysis because of concerns about the accuracy of predictions (Beissinger & Westphal 1998; Lindenmayer et al. 2000; Ralls et al. 2002). Rather than taking a prediction of extinction risk at face value to make a decision, demographic models of population viability are better used to compare the effects of different management options with the goal of setting priorities (Beissinger & Westphal 1998; Ralls et al. 2002). Our optimization framework applies this strategy by synthesizing model predictions of the effects of different habitat-protection options into an extinction-risk function. Then, the risk function is combined with management costs to determine which options are cost-effective under different budget constraints.

One important result of our kit fox application was that cost-efficient shares of the budget used to protect different types of habitat changed as the budget increased and depended on the relative costs of available habitat and the relative effects on extinction risk. For example, protecting a unit of high-quality habitat was usually cost-efficient because it reduced extinction risk much more than protecting a unit of fair-quality habitat. However, if a unit of fair-quality habitat was much cheaper, then funding was better spent protecting many units of fair-quality habitat. The sensitivity analysis highlights the need to accurately determine the costs and effects of protecting habitat of different qualities. For example, we did not explore the costs of conservation easements that protect habitat at lower cost than land purchase.

Another important result of our application was the sensitivity of the location and slope of the risk-cost curve to assumptions built into the kit fox population model. The location of a risk-cost curve shows predictions of extinction risk under different budgets, whereas the slope of the curve predicts how much extinction risk can be reduced with incremental budget increases. These quantities can be used as parameters in ranking formulas to help decision-makers set priorities among

conservation projects for different species or populations (e.g., Weitzman 1998). In our application, changing the assumption about the location of habitat available for protection affected the location and slope of the risk-cost curve (Fig. 3). When the location and slope of risk-cost curves are sensitive to model assumptions, resulting predictions of extinction risk and risk reduction per unit cost should be used cautiously in ranking conservation options among different species or populations.

Previous attempts to incorporate stochastic demographic models of population viability into optimization programs were limited by computational difficulties, so that applications involved only one decision variable representing the total amount of habitat protected (Montgomery et al. 1994; Haight & Travis 1997). Our approach avoids some of those difficulties by using the simulation model in an experimental design that gives predictions of extinction risk as a response surface. The decision variables defining the response surface can represent the amounts of habitat of different qualities and locations. Then, an appropriate risk function can be fit to the response surface and incorporated into an optimization model. Because the fitted risk function is much simpler than the demographic model, optimization models that evaluate a wider range of habitat-protection strategies are tractable.

Estimating an equation that relates the parameters of a demographic model of population viability to predicted extinction risk has been done. McCarthy et al. (1995) used logistic regression to investigate the sensitivity of extinction-risk predictions from a population model to changes in population-model parameters. They used an experimental design in which the binary response variable for whether or not a population went extinct was observed for a random sample of values of the population-model parameters. Because fewer than 10 observations of the response variable were obtained at each level of the independent variable, maximum-likelihood methods were used to estimate the relationship between extinction risk and the population-model parameters. The experimental design of McCarthy et al. (1995) was more efficient than the one we used in the sense that it used fewer replications of the population model. Furthermore, McCarthy et al. (1995) found that extinction-risk predictions obtained from their logistic-regression model were almost the same as predictions obtained from the population model. As a result, logistic regression should be considered an alternative to the minimum-logit chi-square method used here when computational effort is an important consideration in experimental design.

The relatively simple optimization model we used in our kit fox application can be extended to handle more complex problems. For example, the optimization framework could be applied to conservation decisions for a set of interacting subpopulations in fragmented habitat. This could be accomplished by defining a decision variable for the protection of each patch and using a spa-

tially explicit population model to simulate extinction risk for predefined combinations of patches. Then, an extinction-risk function could be fit to the predictions and incorporated into an optimization model. The optimization model, in turn, could be used to determine cost-effective habitat location and sensitivity to assumptions about interpatch dispersal and between-patch variation in habitat quality, two parameters that can greatly affect population predictions (Lindenmayer et al. 2000).

We focused our optimization framework on habitat-protection strategies for one kit fox population. If risk-cost curves are computed for many independent populations, a larger-scale optimization model could be formulated to help allocate limited funds among the populations (Hof & Raphael 1993; Bevers et al. 1995; Montgomery et al. 1999). For example, suppose we have  $I$  independent populations and  $X_i$  is a decision variable for the amount of funding spent on habitat protection for population  $i$ . For each population there is a risk-cost curve  $P_i(X_i)$  giving the probability of extinction in 100 years as a function of the amount of funding spent on habitat protection. If the upper bound on funding is  $B$ , then the allocation problem can be formulated to minimize the extinction risk of all populations subject to the upper bound on funding:

$$\text{minimize } \prod_{i=1}^I P_i(X_i) \quad (10)$$

$$\text{subject to } \sum_{i=1}^I X_i \leq B \quad (11)$$

$$X_i \geq 0 \quad i = 1, \dots, I. \quad (12)$$

Results of this optimization model can help determine which populations should be given highest priority for additional habitat protection. By incrementally increasing the upper bound on funding and re-solving the problem, we can generate a risk-cost curve for the set of populations. We are currently applying this larger-scale model to the problem of allocating limited funds among independent populations of San Joaquin kit foxes.

## Acknowledgments

This work was conducted as part of the Farmland Retirement Strategies Working Group supported by the National Center for Ecological Analysis and Synthesis, a center funded by the National Science Foundation (grant #DEB-94-21535), the University of California at Santa Barbara, and the State of California. We also received support from the Sisley Fund of the Smithsonian Institution, the North Central Research Station of the U.S. Forest Service, and the Australian Research Council. We are grateful to C. Montgomery for suggesting the logit method for estimating the extinction-risk function and E. Main and four reviewers for thoughtful suggestions for improving earlier drafts.

## Literature Cited

- Ando, A., J. Camm, S. Polasky, and A. Solow. 1998. Species distributions, land values, and efficient conservation. *Science* **279**:2126–2128.
- Armbruster, P., and R. Lande. 1993. A population viability analysis for African elephant (*Loxodonta africana*): how big should reserves be? *Conservation Biology* **7**:602–610.
- Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* **62**:821–841.
- Beyers, M., J. Hof, B. Kent, and M. G. Raphael. 1995. Sustainable forest management for optimizing multispecies wildlife habitat: a coastal Douglas-fir example. *Natural Resource Modeling* **9**:1–23.
- Boyce, M. S. 1992. Population viability analysis. *Annual Review of Ecology and Systematics* **23**:481–506.
- Church, R. L., D. M. Stoms, and F. W. Davis. 1996. Reserve selection as a maximal coverage location problem. *Biological Conservation* **76**:105–112.
- Cypher, B. L., and K. A. Spencer. 1998. Competitive interactions between coyotes and San Joaquin kit foxes. *Journal of Mammalogy* **79**:204–214.
- Cypher, B. L., G. D. Warrick, M. R. M. Otten, T. P. O'Farrell, W. H. Berry, C. E. Harris, T. T. Kato, P. M. McCue, J. H. Scrivner, and B. W. Zoellick. 2000. Population dynamics of San Joaquin kit foxes at the Naval Petroleum Reserves in California. *Wildlife Monographs* **145**.
- Dennis, B., and M. R. M. Otten. 2000. Joint effects of density dependence and rainfall on abundance of San Joaquin kit fox. *Journal of Wildlife Management* **64**:388–400.
- GAMS Development Corporation. 1990. General algebraic modeling system. Version 2.25.090. GAMS Development Corporation, Washington, D.C.
- Gerrard, R., P. Stine, R. Church, and M. Gilpin. 2001. Habitat evaluation using GIS: a case study applied to the San Joaquin kit fox. *Landscape and Urban Planning* **52**:239–255.
- Grinnell, J., J. S. Dixon, and J. M. Linsdale. 1937. *Fur-bearing mammals of California*, Volume 2. University of California Press, Berkeley.
- Groom, M. J., and M. A. Pascual. 1998. The analysis of population persistence: an outlook on the practice of viability analysis. Pages 4–26 in P. L. Fiedler and P. M. Kareiva, editors. *Conservation Biology*. 2nd edition. Chapman and Hall, New York.
- Haight, R. G., and L. E. Travis. 1997. Wildlife conservation planning using stochastic optimization and importance sampling. *Forest Science* **43**:129–139.
- Haight, R. G., D. J. Mladenoff, and A. P. Wydeven. 1998. Modeling disjunct gray wolf populations in semi-wild landscapes. *Conservation Biology* **12**:879–888.
- Hof, J. G., and M. G. Raphael. 1993. Some mathematical programming approaches for optimizing timber age class distributions to meet multispecies wildlife population objectives. *Canadian Journal of Forest Research* **23**:828–834.
- Hof, J. G., and M. G. Raphael. 1997. Optimization of habitat placement: a case study of the Northern Spotted Owl in the Olympic Peninsula. *Ecological Applications* **7**:1160–1169.
- Lamberson, R. H., B. R. Noon, C. Voss, and K. S. McKelvey. 1994. Reserve design for territorial species: the effects of patch size and spacing on the viability of the Northern Spotted Owl. *Conservation Biology* **8**:185–195.
- Lindenmayer, D. B., and H. P. Possingham. 1996. Ranking conservation and timber management options for Leadbeater's possum in southeastern Australia using population viability analysis. *Conservation Biology* **10**:235–251.
- Lindenmayer, D. B., R. C. Lacy, and M. L. Pope. 2000. Testing a simulation model for population viability analysis. *Ecological Applications* **10**:580–597.
- Liu, J., J. B. Dunning, and H. R. Pulliam. 1995. Potential effects of a forest management plan on Bachman's Sparrow (*Aimophila aestiva*): linking a spatially explicit model with GIS. *Conservation Biology* **9**:62–75.
- Loison, A., O. Strand, and J. D. C. Linnell. 2001. Effect of temporal variation in reproduction on models of population viability: a case study for remnant arctic fox (*Alopex lagopus*) populations in Scandinavia. *Biological Conservation* **97**:347–359.
- Maddala, G. S. 1983. *Limited-dependent and qualitative variables in econometrics*. Cambridge University Press, New York.
- McCarthy, M. A., M. A. Burgman, and S. Ferson. 1995. Sensitivity analysis for models of population viability. *Biological Conservation* **73**:93–100.
- Montgomery, C. A., G. M. Brown Jr., and D. M. Adams. 1994. The marginal cost of species preservation: the Northern Spotted Owl. *Journal of Environmental Economics and Management* **26**:111–128.
- Montgomery, C. A., R. A. Pollak, K. Freemark, and D. White. 1999. Pricing biodiversity. *Journal of Environmental Economics and Management* **38**:1–19.
- Murtagh, B. A., and M. A. Saunders. 1978. Large-scale linearly constrained optimization. *Mathematical Programming* **14**:41–72.
- Murty, K. G. 1976. *Linear and combinatorial programming*. Wiley, New York.
- Possingham, H. P. 1997. State-dependent decision analysis for conservation biology. Pages 298–304 in S. T. A. Pickett, R. S. Ostfeld, M. Shachak, and G. E. Likens, editors. *The ecological basis of conservation: heterogeneity, ecosystems and biodiversity*. Chapman and Hall, New York.
- Possingham, H. P., D. B. Lindenmayer, and T. W. Norton. 1993. A framework for improving management of threatened species based on population viability analysis (PVA). *Pacific Conservation Biology* **1**:39–45.
- Ralls, K., and L. Eberhardt. 1997. Assessment of abundance of San Joaquin kit foxes by spotlight surveys. *Journal of Mammalogy* **78**:65–73.
- Ralls, K., and A. M. Starfield. 1995. Choosing a management strategy: two structured decision-making methods for evaluating the predictions of stochastic simulation models. *Conservation Biology* **9**:175–181.
- Ralls, K., and B. Taylor. 1997. How viable is population viability analysis? Pages 228–235 in S. T. A. Pickett, R. S. Ostfeld, M. Shachak, and G. E. Likens, editors. *The ecological basis of conservation: heterogeneity, ecosystems and biodiversity*. Chapman and Hall, New York.
- Ralls, K., and P. J. White. 1995. Predation on San Joaquin kit foxes by larger canids. *Journal of Mammalogy* **76**:723–729.
- Ralls, K., S. Beissinger, and J. F. Cochrane. 2002. Guidelines for using PVA for endangered species management in "population viability analysis." Pages 521–550 in D. McCullough and S. Beissinger, editors. *University of Chicago Press*, Chicago.
- U.S. Fish and Wildlife Service. 1967. Native fish and wildlife endangered species. *Federal Register* **32**:4001.
- U.S. Fish and Wildlife Service (USFWS). 1998. Recovery plan for upland species of the San Joaquin Valley, California. USFWS, Portland, Oregon.
- Warrick, G. D., and B. L. Cypher. 1998. Factors affecting the spatial distribution of a kit fox population. *Journal of Wildlife Management* **62**:707–717.
- Weitzman, M. L. 1998. The Noah's Ark problem. *Econometrica* **66**:1279–1298.
- White, P. J., and R. A. Garrott. 1997. Factors regulating kit fox populations. *Canadian Journal of Zoology* **75**:1982–1988.
- White, P. J., and R. A. Garrott. 1999. Population dynamics of kit foxes. *Canadian Journal of Zoology* **77**:486–493.
- White, P. J., and K. Ralls. 1993. Reproduction and spacing patterns of kit foxes relative to changing prey availability. *Journal of Wildlife Management* **57**:861–867.
- White, P. J., C. A. Vanderbilt White, and K. Ralls. 1996. Functional and numerical responses of kit foxes to a short-term decline in mammalian prey. *Journal of Mammalogy* **77**:370–376.
- Wilcove, D. S., M. J. Bena, R. Bonnie, and M. Macmillan. 1996. Rebuilding the ark: toward a more effective Endangered Species Act for private land. Environmental Defense Fund, Washington, D.C.