# Evaluating the Effectiveness of Predator Control: the Non-Native Red Fox as a Case Study

ELAINE K. HARDING,*§ DANIEL F. DOAK,† AND JOY D. ALBERTSON‡

*Department of Environmental Studies, University of California, Santa Cruz, CA 95064, U.S.A.
†Department of Biology, University of California, Santa Cruz, CA 95064, U.S.A.
‡U.S. Fish and Wildlife Service, Don Edwards San Francisco Bay National Wildlife Refuge, P.O. Box 524, Newark, CA 94560, U.S.A.

**Abstract:** *Non-native vertebrate predators pose a severe threat to many native species, and a variety of management programs are aimed at reducing predator effects. We sought to assess the effects of predator-control programs by analyzing changes in prey and predator populations based on data commonly collected in these programs. We examined data from a predator-control program that primarily targets the introduced red fox (*Vulpes vulpes regalis*) in central California. Red foxes negatively affect populations of native waterbirds, particularly the endangered California Clapper Rail (*Rallus longirostris obsoletus*). Using a combination of matrix population modeling, simple difference equations, and statistical analysis, we analyzed data on removed predators and monitored prey populations. Past control efforts succeeded in depressing fox numbers in local areas over 3-month intervals, and there was a significant, positive relationship between the growth rate of local Clapper Rail populations and the successful trapping of red foxes in the preceding year. By modeling the effect of different fox-removal rates, we found that a stable or declining population could be achieved by removing a minimum of 50% of the adults and 25% of the juveniles. Under trapping rates of 50–70%, the proportion of the fox population composed of immigrants averaged 20–52%. In contrast to the current management approach, elasticity analyses suggested that changes in adult survival rates had relatively little effect on long-term population growth. Overall, our approach indicated that predator control was effective in the short term, but for longer-term success it may be necessary to redirect efforts to control juvenile and immigrant foxes. Our analytical approach is potentially useful for evaluating current control programs aimed at reducing the effects of predators on native species.*

Evaluación de la Efectividad del Control de Depredadores: el Zorro Rojo no Nativo Como Estudio de Caso

**Resumen:** *Los depredadores introducidos son una amenaza severa para muchas especies nativas y una variedad de programas de manejo están orientados a reducir los efectos de los depredadores. Tratamos de evaluar los efectos de los programas de control de depredadores mediante el análisis de los cambios en las poblaciones de presas y de depredadores basados en datos obtenidos en esos programas. Examinamos los datos de un programa de control de depredadores enfocado principalmente sobre el zorro rojo introducido (*Vulpes vulpes regalis*) en California central. El zorro rojo afecta negativamente a las poblaciones de aves acuáticas nativas, particularmente* Rallus longirostris obsoletus *que está en peligro de extinción. Por medio de una combinación de modelaje poblacional matricial, ecuaciones diferenciales sencillas y análisis estadístico analizamos datos de remoción de depredadores y de monitoreo de poblaciones de presas. Esfuerzos de control en el pasado fueron exitosos al reducir el número de zorros en áreas locales a lo largo de intervalos de tres meses y hubo una relación significativa, positiva, entre la tasa de crecimiento de poblaciones locales de* Rallus longirostris obsoletus *y el éxito de trampeo de zorro rojo durante el año anterior. Modelando el efecto de distintas*

*§Current address: School of Tropical Environment Studies and Geography, James Cook University of North Queensland, P.O. Box 6811, Cairns, Queensland, 4870 Australia, email elaine.harding@jcu.edu.au*
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*tasas de remoción de zorros, encontramos que se podría alcanzar una población estable o en declinación removiendo al menos el 50% de los adultos y el 25% de los juveniles. Con tasas de trampeo de 50–70%, la proporción de la población de zorros compuesta por inmigrantes promedió 20–52%. En contraste con la aproximación de manejo actual, el análisis de elasticidad sugirió que los cambios en la supervivencia de adultos tuvieron poco efecto en el crecimiento poblacional a largo plazo. En general, nuestra estrategia indicó que el control del depredador fue efectivo a corto plazo, pero para un éxito de largo plazo posiblemente sea necesario redireccionar los esfuerzos hacia el control de zorros juveniles e inmigrantes. Nuestra estrategia analítica es potencialmente útil para evaluar los programas actuales de control dirigidos a la reducción de los efectos de depredadores en las especies nativas.*

## Introduction

Introduced vertebrate predators are an increasingly common, and often unwelcome, component of both human and natural landscapes, and they can have significant effects on native species taken as prey (Kinnear et al. 1988; Hone 1995; May & Norton 1996; Cote & Sutherland 1997; Yerli et al. 1997). Entire assemblages of species and specific populations of rare and endemic fauna are under siege from increased numbers of opportunistic, non-native predators such as feral cats (*Felis catus*) (May & Norton 1996; Barratt 1997) and red foxes (*Vulpes vulpes*) (Kinnear et al. 1988; U.S. Fish and Wildlife Service and U.S. Navy 1990; Priddel & Wheeler 1997; Harding et al. 1998; Risbey et al. 1999). Introduced predators pose a particularly strong threat to endangered species inhabiting fragmented landscapes or other areas where top carnivores have been removed (Sargeant 1972; Soulé et al. 1988; Zembal et al. 1995; Crooks & Soulé 1999). Almost 50% of all rare vertebrates in the United States are threatened by alien species, including many invasive predators (Wilcove et al. 1998). As the abundance and variety of introduced predators increases, the need becomes urgent to develop and implement effective control programs to alleviate or eliminate the destructive effects of these non-native species.

Although a multitude of predator-management programs exists (Hone 1994; Cote & Sutherland 1997; Short et al. 1997; Yerli et al. 1997), less work has been devoted to analyzing the effectiveness of control efforts (Connolly & Longhurst 1975; Hone 1994; Cote & Sutherland 1997; Conner et al. 1998). The success of predator control is most often judged by an increase in prey species, with a focus on local and short-term results (Boggess et al. 1990; Conner et al. 1998), and little effort is made to directly evaluate effects on the predator species themselves (Connolly & Longhurst 1975; Conner et al. 1998). When control effects on predators are assessed, it is often without regard to the species' biology or distribution across a landscape. Yet the longer-term and larger-scale success of control programs will be profoundly influenced by the life-history traits and habitat-use patterns of the target species (Hone 1990; Conner et al. 1998). Effective evaluation of long-term management therefore requires careful consideration of the demographic factors most likely to influence predator population growth, and should use information on age-specific vital rates such as survival and reproduction. Although age- or stage-specific analyses of optimal management for protected species is now commonplace (Doak et al. 1994; Smith & Trout 1994; Wisdom & Mills 1997), similar approaches investigating the particular life-history stages of exotic species for population control are rarely performed (Smith & Trout 1994).

Because few evaluations of predator-management programs consider both predator and prey species, it seems logical to begin more careful assessments with programs targeting widespread and well-known exotic predators. The introduced red fox (*Vulpes vulpes regalis*), the focus of our study, is one of the most commonly targeted species in control programs worldwide. Introduced red foxes have been documented to reduce populations of native mammalian and avian species (Lloyd 1980; Hone 1994) and have caused the extinction of at least one marsupial (Kinnear et al. 1988; May & Norton 1996). A major impetus for the U.S. Fish and Wildlife Service (USFWS) program that we evaluate is protection of the federally and state endangered California Clapper Rail (*Rallus longirostris obsoletus*) found exclusively in tidal wetlands within the San Francisco (S.F.) Bay area. By 1991 the rail population had declined by 50% in less than 5 years (Foerster & Takekawa 1991), with evidence implicating the red fox as the primary proximate threat to rail persistence (Albertson 1995).

To provide a framework for assessing the efficacy of the red fox program and to allow researchers to utilize a similar approach for other species, we developed a set of analyses to address two broad questions. First, what is the current effect of management on both the prey and the managed predator? Second, how can the effectiveness of a specific management program be assessed and improved with limited data? In attempting to answer the second question, we considered three important issues: (1) Is the current level of control likely to cause population decline? (2) Which life-history stages and rates are most important to target? and (3) How can we use the simple data sets available to make useful inferences about complex population dynamics (e.g., is spatial structure an important consideration)?

We addressed these questions with statistical and modeling techniques tailored to the data generally available from control programs and minimized the need for additional, usually unobtainable, information describing the population patterns of the target predator. The data we used included the usual measurement of success, prey abundance, and temporal trends in estimated and actual numbers of predators removed across a human-modified landscape. Although we attempted to answer our questions through available data on the red fox, our emphasis was on the development of useful questions and simple analytical approaches that could be utilized to clarify the effect of predator control in multiple situations.

## Methods

### Study Site and Data Set

The project area encompassed approximately 12,000 ha of a highly fragmented urban landscape, including a large portion of the Don Edwards San Francisco Bay National Wildlife Refuge (refuge) in south S.F. Bay. Habitats within this area included commercial salt ponds, salt and brackish marshes, and a small amount of ruderal grassland. The red fox was the primary target of the predator-control program (Foerster & Takekawa 1991) and constituted 65% of all predators captured annually (Harding et al. 1998). Predators were captured primarily with padded leghold traps and secondarily with cage traps and opportunistic shooting. Where possible, their movements were deterred by fence barriers (Foerster & Takekawa 1991).

We used two USFWS data sets covering the period from October 1991 to September 1996: (1) winter population surveys of the California Clapper Rail at 24 sites and (2) the number of foxes caught, with the corresponding number of leghold traps used, in 34 mapped locations. The number of leghold traps and foxes caught by leghold traps were used for most analyses, because 87% of foxes were caught by this method. To evaluate the temporal population patterns of both predator and prey, we grouped the data into four seasons (spring, January–March; summer, April–June; fall, July–September and winter, October–December) and five years (October through September). We similarly divided the study area into four large "regions" that were composed of groupings of nine smaller areas encompassing a total of 34 trapping locations (Harding et al. 1998). The areas were not designed to be equal in size but represented natural constellations of marshes and their corresponding predator-control areas. Although the areas were somewhat isolated, the barriers between them were modest for the red fox, which is known to move easily and readily over most urban landscapes (Lloyd 1980) and has the ability to swim across small sloughs in S.F. Bay (E.K.H., personal observation).

### Effects of Removal on Predator and Prey

To estimate the likely effect of predator removal on the red fox, we first accounted for changes in trapping effort across time and space. We defined trapping "success" as the ratio of foxes caught to the number of trap-nights expended. To test for control of fox numbers by trapping, we used logistic regression analysis to relate current seasonal trapping success to the prior season's success in each region (Sokal & Rohlf 1995). We assessed the response of California Clapper Rail populations to fox removal using a linear regression of rail annual population growth rate to fox trapping success in the prior year within each of four areas (for details see Harding et al. 1998). Prior complete survey data on rail populations were not available before trapping began.

### Improving Control of Predator Populations

We used two modeling approaches to examine possible improvements to the management program. First, we developed a simple matrix model of the red fox population in south S.F. Bay with the goal of enhancing management by (1) determining which age-specific vital rates effect the greatest changes in growth rate, (2) assessing a range of likely removal rates and their consequences for population growth, and (3) examining whether temporal changes in managed populations may be influenced by immigration. We created an age-structured model with two classes: juveniles (birth to 1 year old) and adults (1 year and older) (Caswell 1989). Juveniles (also called subadults after about 6 months) often breed within their first year and have differing rates of reproduction and survival (Storm et al. 1976). No data currently exist on red fox demographics in the S.F. Bay region, so we based our model on data primarily from an urban study in Los Angeles, California (Sallee et al. 1992), that was likely to reflect similar environmental conditions. We also used some information from a study of a hunted population in the midwestern United States (Storm et al. 1976) and from a British study on urban foxes (Harris & Smith 1987) (Table 1). We used two versions of the demographic model. Model 1 assumed normal reproduction using the data described above. Model 2 assumed reduced reproduction in which the proportion of juvenile females breeding each year was halved to simulate the possibility of decreased opportunities for juveniles to establish breeding territories either because of suppression by dominant females or lack of resources (von Schantz 1981) (Table 1).

**Table 1. Demographic parameters and their corresponding elasticity values for two matrix models of red fox populations.[a]**

| Estimate | *Model 1: normal reproduction* juvenile | *Model 1: normal reproduction* adult | *Model 2: reduced reproduction[b]* juvenile | *Model 2: reduced reproduction[b]* adult |
|---|---|---|---|---|
| Reproduction[c] | 0.91 | 0.91 | 0.46 | 0.91 |
| elasticity value | 0.36 | 0.25 | 0.16 | 0.30 |
| Survival[d] | 0.65 | 0.58 | 0.65 | 0.58 |
| elasticity value | 0.25 | 0.15 | 0.30 | 0.24 |

[a] *Juvenile class contains individuals from birth to 1 year; adult class contains those 1 year and older.*
[b] *The reduced-reproduction model contains a 50% reduced reproductive rate by juveniles.*
[c] *Reproduction (post-breeding survey) was estimated for each model and class by pups × 0.5 females × juvenile survival × 90 females breeding/year. Model 1/juvenile: $3.5^1 \times 0.5 \times 0.65^1 \times 0.80$ (Harris & Smith 1987); model 1/adult: $3.5^1 \times 0.5 \times 0.58^1 \times 0.90$ (Storm et al. 1976); Model 2/juvenile: $3.5^1 \times 0.5 \times 0.65^1 \times 0.40$; model 2/ adult: $3.5^1 \times 0.5 \times 0.58^1 \times 0.90$ (Storm et al. 1976) (pups and juvenile survival from Sallee et al. 1992).*
[d] *Survival rates were from Sallee et al. (1992).*

We first determined the annual population growth rate (λ) for models 1 and 2, and the sensitivities and elasticities for each vital rate. Sensitivities reflect the effect of the absolute change in a parameter on the growth rate, whereas elasticities show the effects of proportional change in parameters on λ, facilitating comparisons of different vital rates (Caswell 1989). Second, to simulate the effect of trapping on the growth rate of the red fox population, we chose a reasonable range of likely removal rates: 50%, 70%, or 90% annual removal of the existing population. Because the rate of removal for juveniles may be substantially lower than for adults (Harding et al. 1998), for each rate of adult removal we simulated two scenarios for juveniles: (1) one-half the adult rate or (2) the same rate as adults. The two matrix models were each modified by the six removal scenarios (by multiplication of natural survival and survival of trapping), producing 12 estimated growth rates for each combination of removal rates and regular or reduced juvenile reproductive values.

Finally, we compared model predictions about foxes removed through time to temporal trends in the actual number of fox removed per year to infer the removal rate (percentage of foxes removed) that was likely to have occurred during the 5-year period. To do this, model 1 was initialized to predict the actual number of removed female foxes in 1992 (the first full year of the program). We then used the model to estimate the number of foxes removed during the next 4 years under three removal scenarios: 50%, 70%, and 90% adult removal rates, with juveniles removed at half these rates. Preliminary analysis indicated that the most likely model was within this range of removal rates. Because effort was uneven across years, the actual number of foxes removed was scaled by trapping effort (leghold and cage traps combined): foxes multiplied by number of trapnights in year 1, divided by number of trapnights in year *x*. We then graphically compared the temporal pattern of actual foxes removed to the patterns produced by the three removal scenarios to assess the most likely removal rate.

We used a second modeling approach to investigate fox movement rates and their influence on the control program. Because trapping may induce fox movements by creating vacancies in territories, there is a high likelihood that foxes may quickly migrate into managed areas. To estimate the proportion of foxes immigrating, we developed a non-age-structured difference-equation model that used adult survival and reproductive rates for model 1, assumed constant trapping efficiency, and allowed immigration into the local population (Table 2). We transformed the basic model into a form requiring only demographic rates, a trapping efficiency estimate, and an observable measure of relative fox density, (i.e., numbers of foxes removed). Because we had no estimates of trapping efficiency ($e$), we performed analyses assuming that 50% and 70% represent reasonable average trapping rates ($eT$, where $T$ is number of traps) based on the prior demographic analysis. We used equation 3 in Table 2 to estimate the annual proportion of foxes that were immigrants averaged over three regions during the period 1993–1996.

## Results

### Effects of Removal on Predator and Prey

From 1991 to 1996, the number of red foxes removed remained nearly constant, despite an increasing number of leghold traps deployed each year (Fig. 1). Adult foxes were caught at 14 times the rate of juveniles; this difference may be an overestimate because after 6 months of age it is difficult to visually differentiate the two age classes. The total number of traps set per fox removed increased consistently over time from 37 traps/fox in 1991–1992 to 73 traps/fox in 1995–1996. This pattern indicates a probable reduction in fox numbers over the 5-year period, which was probably due to the control program.

Logistic regression of current seasonal trapping success on past success showed a strong and positive relationship ($r^2 = 0.44$, current success = exp($a + b$*past success)/(1 + exp($a + b$*past success)); means and 95% confidence limits: $a = -4.261$ C.L. $\pm 0.357$ and $b =$ 12,888 C.L. $\pm$ 6.620). With a slope of much less than 1, there is evidence that control succeeds in depressing fox numbers in local areas over a 3-month period; current success is always lower than past success, except when the previous rate is very low. But the positive slope between past and future trapping success also indicates that trapping has not caused collapse of local fox

**Table 2. Equations, calculated on an annual basis, used in red fox immigration model.**

| *Description*[a] | *Equation*[b] |
|---|---|
| (1) Basic population equation | $N_{t+1} = (N_t + Z_t)(1 - eT_t)(s_n + s_n r)$ |
| (2) Transformation to removal rates | $Y_{t+1} = C_{t+1} - C_t(T_{t+1}/T_t)$ $(1 - eT_t)(s_n + s_n r)$ |
| (3) Transformation to proportion of immigrants[c] | $F_{t+1} = 1 - (C_t/C_{t+1})$ $[(T_{t+1}/T_t)(1 - eT_t)((s_n)(1+r))]$ |

[a] *The basic model directly predicts fox dynamics as a function of survival, reproduction, and trapping. The subsequent transformations express dynamics in the observed, relative measures of abundance (details of derivations available from authors).*
[b] *Variables:* e, *trapping efficiency (probability of a fox being caught per trap);* T, *number of traps;* N, *number of resident foxes;* Z, *number of immigrant foxes;* P, *number of resident and immigrant foxes (* P = Z + N*);* R, *number of resident foxes removed (* R = eTN*);* Y, *number of immigrant foxes removed (* Y = eTZ*);* C, *number of resident and immigrant foxes removed (* C = R+Y*);* F, *proportion of immigrants in the total fox population (* F = Z/P*);* $s_n$, *fox natural survival rate (0.58); (1 − eT), survival rate of foxes under removal;* r, *fox reproductive rate (0.91).*
[c] *Equation 3 was used to predict the proportion (* F*) of immigrants in the fox population within a region each year.*

populations and is unlikely to result in long-term declines. If trapping strongly depressed fox numbers over longer time periods and immigration rates were low, we would expect to find negative relationships between past and current success.

There was a significant, positive relationship between the growth rate of Clapper Rail populations and red fox trapping success in the preceding year ($r^2 = 0.59$, $p < 0.05$) (Fig. 2). Even with the removal of a high outlying value for clapper rail growth rate (>5), this result remained significant, indicating that when red fox removal is high, growth rates of clapper rail populations respond quickly. Examining the rail population at one large marsh in S.F. Bay, we found a dramatic increase before and after predator control. Forty birds were recorded in 1989, and 104 by the end of 1994 (USFWS).

## Improving Control of Predator Populations

Two-class Leslie matrices for untrapped foxes predicted an annual growth (λ) of 1.53 (normal reproduction) or 1.29 (reduced reproduction). To evaluate the degree to which reductions in survival or reproduction could influence these high growth rates, we calculated sensitivity and elasticity values for each vital rate. For both models, the sensitivity values indicated that juvenile reproduction was more important than adult reproduction and that juvenile survival had more influence than adult survival. Elasticity values generally reinforced this pattern: juvenile reproduction had the highest elasticity for the normal-reproduction model but the lowest elasticity for the reduced-reproduction model (Table 1). In both models, elasticity of juvenile survival and adult reproduction were equal, but with normal reproduction they were second in importance to juvenile reproduction. Thus, it appears that changes in reproduction by juveniles will

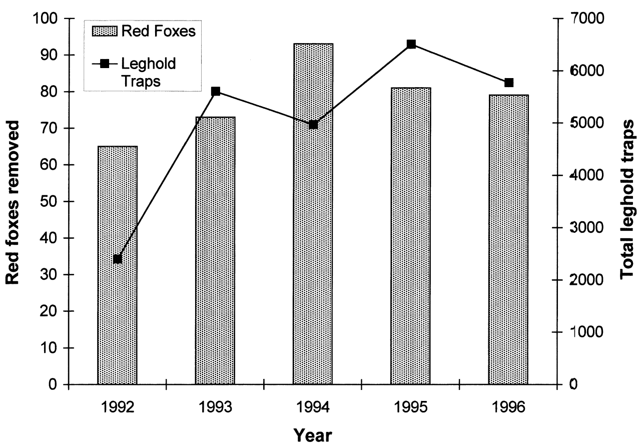


*Figure 1. Total number of red foxes removed by leghold traps and total leghold traps used in the U.S. Fish and Wildlife Service predator-management program in south San Francisco Bay, California, during the 5-year period 1991–1996.*

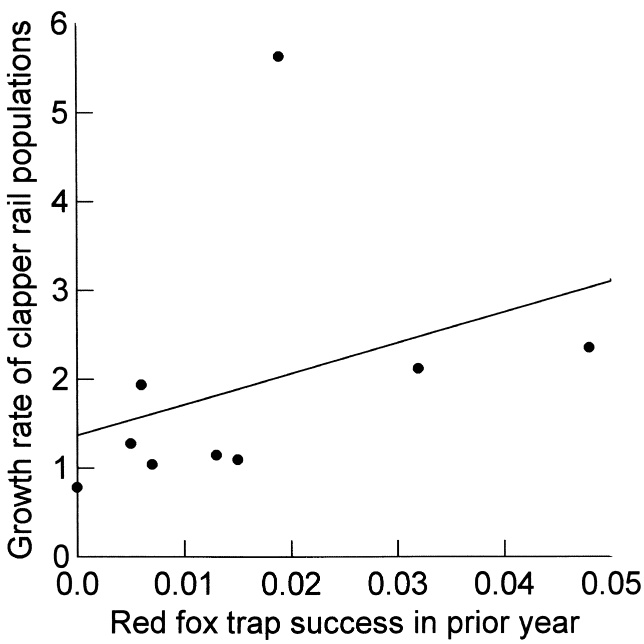


*Figure 2. Relationship between growth rate of the California Clapper Rail population (number in year* t+1*/ number in year* t*) and red fox trapping success (number foxes removed/number leghold traps) in the prior year in each of four areas (*$r^2 = 0.59$*,* $p < 0.05$*,* $n = 9$*).*

exact the greatest influence on population growth unless this parameter is quite low. Juvenile survival may be of secondary importance, perhaps equal to adult reproduction, but it is certainly of greater consequence than adult survival.

In adding trapping effects to our model, we found that a stable or decreasing population ($\lambda < = 1.0$) could be achieved with minimum removal rates of approximately 50% of adults and 25% of juveniles. This annual trapping level resulted in declining populations for all scenarios but one, with higher trapping rates predicted to rapidly deplete populations. To further scrutinize the possible trends in fox removal over time, we used the normal reproduction model and three removal rate scenarios to project removed populations through time (Fig. 3a). The 50% removal rate predicted the actual number of foxes removed quite well (adjusted for increasing trap numbers), except for a modest increase that was in the actual data in 1994 but not in our simulations. But these trends must also be evaluated in light of the missing element of immigration, which could be particularly strong in the second or third year following initial removal.

Although initial declines in fox numbers attributable to the predator-control program indicate that foxes should be rapidly annihilated (presumably with trapping rates greater than 50% annually), this was not the case, suggesting that movement into the managed area may be subsidizing fox numbers. Immigration is therefore a potentially important factor to consider in understanding the effects of trapping on the dynamics of red foxes in S.F. Bay. Under annual removal rates of 50–70%, an average of 20–52% of the annual fox population is predicted to be immigrants (Fig. 3b), with a higher amount of immigration associated with a greater removal rate. This model, fit to the actual removals (Table 1, equation 3), predicts that the peak in number of foxes caught in 1994 was due to higher immigration in that year relative to resident numbers. A possible explanation for this result is that the initial lowering of fox numbers allowed for still large neighboring populations to migrate into the area. Thus, immigration is a likely explanation for the rapid increase seen in foxes removed during 1994 and in the subsequent decline in 1995.

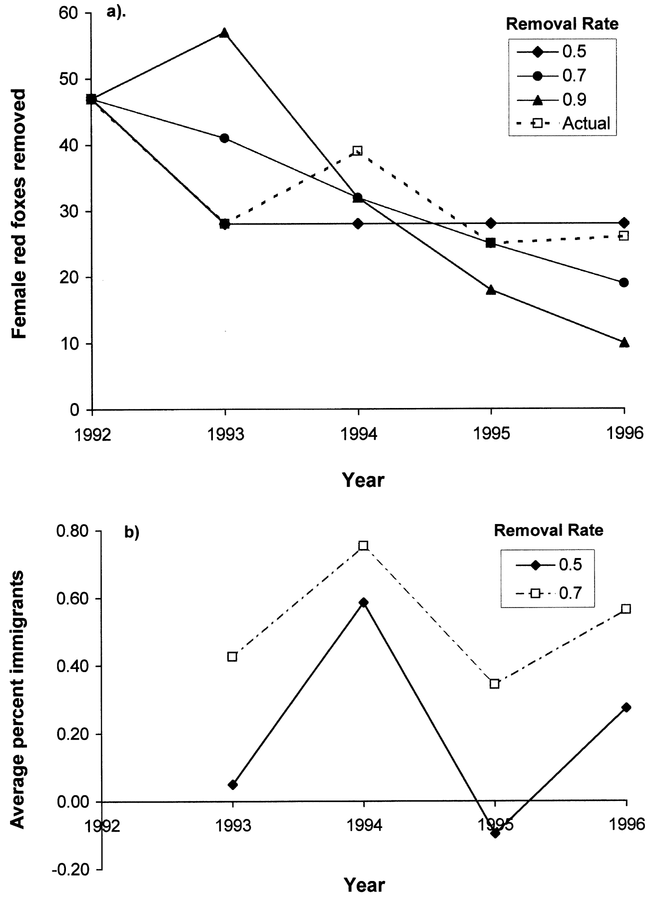


*Figure 3. (a) Number of female red foxes removed annually in the U.S. Fish and Wildlife Service predator-management program in south San Francisco Bay, California. Actual values are adjusted for changing trap effort (see methods). The projected values were calculated for the 5-year period under three removal scenarios: 50%, 70%, and 90% for adults, half each rate for juveniles. (b) Average annual proportion of foxes predicted to be immigrants under two removal rates, 50% and 70%, combined for three regions. The peak in 1994 also occurs in the actual number of foxes removed (a), indicating the likelihood of an influx of immigrants in that year.*

## Discussion

Our evaluation of a predator-removal program demonstrates that simple data sets can support informative analysis of population change in both predator and prey, including modeling approaches that provide useful insights into the management of exotic predators. The removal of the non-native red fox within south S.F. Bay marshes strongly affected two key indicators of program success: foxes caught per unit effort and the population growth rate of a native endangered species preyed on by the fox. In particular, fox removal had a strong positive effect on California Clapper Rail populations over the period 1991–1996. Thus, it is clear the program is meeting its immediate goal of increasing rail populations by lowering local densities of red foxes. The effects of red foxes on California Clapper Rail populations, and the subsequent effects of predator management on other species, are detailed elsewhere (Albertson 1995; Harding et al. 1998). Other studies have also found that reductions in red fox populations are associated with increased populations of rare and endemic species (Kinnear et al. 1988; Friend 1990), although long-term decreases in predation are not often shown for foxes and other canids (Priddel & Wheeler 1997; Conner et al. 1998).

As a result of the control program, the fox population in S.F. Bay appears to be declining, with an increasing amount of trapping required to catch similar numbers of foxes. Although the amount of predator control has increased over the 5-year period, the number of foxes removed per year has remained relatively constant. This pattern is consistent with dependence of total trapping success on densities of both foxes and traps, with increasing effort needed if the goal is to reduce red fox populations to very low levels (Lloyd 1980). A second explanation for this pattern is that traps are less effective at catching foxes because animals are recognizing traps or trappers have become less productive. Although individual foxes may often become wary of traps if they are exposed and then escape unharmed, there is no evidence that either of these situations is important to our results.

By examining data on predator-removal trends over specified time intervals and merging those results with key information on the habitat characteristics of those sites, our analytical approach could be particularly useful for spatially divided populations. We found that within a management region the number of foxes removed (per number of leghold traps in an area) was positively correlated with the number caught in the prior 3-month period but not for much greater lengths of time, confirming a pattern found by Conner et al. (1998) for coyotes. This pattern could be attributable to a short time lag between the vacancy of a territory and it's occupation by another individual. Three alternative scenarios provide plausible explanations for between-site differences in seasonal success: (1) spatial variation in carrying capacity, (2) degree of connectivity among the sites, or (3) variation in predator density due to other causes, such as competition.

The results of modeling and sensitivity analysis suggest that the targeted removal of juveniles should be a high priority. Our demographic modeling indicates that removal of adult foxes, the principle target of trapping, is less effective in reducing population growth than are reductions in juvenile survival and reproduction. But fox behavior can alter the success of trapping juveniles: the outcome depends on the degree of reproductive suppression exerted by alpha females (von Schantz 1981). If older dominant females are limiting juvenile breeding, then the total proportion of females in reproductive condition could be greatly reduced from the adult level, as in our reduced-reproduction model (Zabel & Taggart 1989). Studies of controlled fox populations in urban environments shows that they often contain a high proportion of juveniles (Harris 1977) and more breeding females than an uncontrolled population (Harris & Smith 1987). Because our data suggest that more adult than juvenile foxes are being removed in S.F. Bay, it is highly likely that the fox population may already contain a high proportion of young breeding foxes. Therefore, the targeted removal of juveniles would be an appropriate strategy to continue in S.F. Bay, but perhaps not in other regions, particularly during the early phases of a control program when juvenile breeding may be limited.

In the case of red fox management, two issues must be addressed before targeted removal of juveniles is instituted: a process to differentiate juveniles from adults must be implemented, and an effective means of trapping young animals must be determined. The low number of juveniles reported in this study could be due to our inability to clearly differentiate 6- to 11-month-old juveniles from adults. By late fall or winter, a juvenile's appearance and weight are very similar to those of an adult, with only tooth annuli (Harris & Smith 1987) or other indicators allowing for more precise age determination (Storm et al. 1976). It is also likely that foxes aged 3–6 months are more difficult to catch with leghold traps because of their lighter weight, although traps can be set to a finer trigger. It is therefore unclear whether juveniles over 6 months in age are more (Storm et al. 1976) or less (Yoneda 1982) susceptible to trapping. In either case, it is highly likely that the number of juveniles removed is greatly underestimated, because the proportion of juveniles in hunted fox populations tends to increase over time (Phillips 1970; Yoneda 1982). Thus, it is imperative to gather more accurate estimates of age and reproduction for foxes living in the S.F. Bay area, because the management strategies we suggest are predicated on knowledge of the ecology and demographics of local fox populations, which is clearly limited at this time. As occurs in many studies of introduced species and control programs, we resorted to using information from other studies to supplement data on our population.

Although modeling of predator population dynamics provided support for the effectiveness of the current removal strategy, it also suggested that immigration could greatly influence long-term management success in this urban area. We estimated that a large but variable percentage of the fox population was removed annually through trapping, averaging 50% or more. This amount of culling is close to the mean of 65% calculated by Hone (1999) as the proportion needed to limit maximum population growth of red foxes throughout Australia. We also estimated the average proportion of immigrants in the trapped population at 36%. It is not surprising that a high proportion of immigration may be occurring, because of a corridor network that can be easily traversed by the highly mobile red fox (Sallee et al. 1992). Our results, however, point to a strategy not currently utilized within S.F. Bay: immigration into sensitive habitats could be prevented by trapping foxes at key entry points or erecting barriers to movement. Particular pathways could be targeted for removal of immigrating foxes, such as flood-control channels leading directly to the wetland areas in our study system. Through intense, focused trapping to hinder movement, predator control may be substantially heightened, allowing a greater number of areas to be controlled more effectively for the same cost.

With invasive species becoming more widespread and abundant, it will become increasingly common to initiate control programs aimed at reducing targeted predator populations. Studies seeking to determine the efficacy of management programs can expand their definitions of success and the resolution of their analyses by using a broader set of analytical tools, as suggested by this project. At minimum, data on the predator and prey population should be gathered before and after initiation of a control strategy. Further, additional information on the spatial distribution of removed animals in relation to habitat characteristics and control efforts could be used to infer density patterns and potential movement pathways and to predict the short- and long-term efficacy of control. Ideally, the development of any new program, or the evaluation of existing ones, should include measurement of both population trends and demographic performance and should delineate spatial dynamics, especially those that capture the fundamental population processes that govern predators at appropriate scales.

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