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Using Population Viability Criteria to Assess Strategies to Minimize Disease Threats for an Endangered Carnivore

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Abstract: *Outbreaks of infectious disease represent serious threats to the viability of many vertebrate populations, but few studies have included quantitative evaluations of alternative approaches to the management of disease. The most prevalent management approach is monitoring for and rapid response to an epizootic. An alternative is vaccination of a subset of the free-living population (i.e., a "vaccinated core") such that some individuals are partially or fully immune in the event of an epizootic. We developed a simulation model describing epizootic dynamics, which we then embedded in a demographic simulation to assess these alternative approaches to managing rabies epizootics in the island fox* (Urocyon littoralis)*, a species composed of only 6 small populations on the California Channel Islands. Although the monitor and respond approach was superior to the vaccinated-core approach for some transmission models and parameter values, this type of reactive management did not protect the population from rabies under many disease-transmission assumptions. In contrast, a logistically feasible program of prophylactic vaccination for part of the wild population yielded low extinction probabilities across all likely disease-transmission scenarios, even with recurrent disease introductions. Our use of a single metric of successful management—probability of extreme endangerment (i.e., quasi extinction)—to compare very different management approaches allowed an objective assessment of alternative strategies for controlling the threats posed by infectious disease outbreaks.*

Keywords: disease, epizootic model, island fox, monitoring, population viability, rabies, vaccination

Utilización de Criterios de Viabilidad Poblacional para Evaluar Estrategias para Minimizar Amenazas de Enfermedades para un Carnívoro en Peligro

Resumen: *Los brotes de enfermedades infecciosas representan serias amenazas para la viabilidad de muchas poblaciones de vertebrados, pero pocos estudios han incluido evaluaciones cuantitativas de métodos alternativos para el manejo de enfermedades. El método de manejo más prevalente es el monitoreo de una epizootia y de la rapidez de la respuesta a la misma. Una alternativa es la vacunación de un subconjunto de la población silvestre (i.e., un "núcleo vacunado") de manera que algunos individuos están parcial o completamente inmunes en el evento de una epizootia. Desarrollamos un modelo de simulación que describe la dinámica de una epizootia, que posteriormente incluimos en una simulación demográfica para evaluar estos métodos alternativos para el manejo de epizootias de rabia en Urocyon littoralis, una especie compuesta de solo 6 poblaciones pequeñas en las Islas del Canal, California. Aunque el método de monitoreo y respuesta fue superior al del núcleo vacunado para algunos modelos de transmisión y valores de parámetros, este tipo de manejo reactivo no protegió de la rabia a la población bajo muchos supuestos de la transmisión de enfermedades. En contraste, un programa logísticamente factible de vacunación profiláctica para parte de la población silvestre produjo bajas probabilidades de extinción en todos los escenarios de transmisión de enfermedades, aun con la introducción recurrente de enfermedades. Nuestro uso de una sola medida del manejo exitoso – probabilidad de riesgo extremo (i.e., cuasi extinción) – para comparar métodos de manejo*

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muy diferentes permitió una evaluación objetiva de estrategias alternativas para controlar las amenazas que representan los brotes de enfermedades infecciosas.

Palabras Clave: enfermedad, modelo, monitoreo, rabia, *Urocyon littoralis*, vacunación

Introduction

Infectious diseases pose an increasing threat to many populations of rare wild animals (Laurenson et al. 1998; Pedersen et al. 2007; Smith et al. 2009). To address this threat, managers typically rely on some form of monitor-and-respond management, in which field personnel watch for indications of disease in radiocollared or visually surveyed individuals (e.g., Muoria et al. 2007; Cunningham et al. 2008; Knobel et al. 2008). The management response, which often includes quarantine or vaccination of uninfected animals, follows detection of disease. However, the speed with which many infectious diseases can spread presents logistical challenges for this approach to disease management.

Some wild animal populations are reservoirs of diseases that threaten the health of humans or domestic animals (e.g., raccoons [*Procyon lotor*] and rabies, elk [*Cervus canadensis*] and bison [*Bison bison*] and brucellosis, African ungulates and foot and mouth disease). Diseases in these populations have sometimes been managed by prophylactic vaccination of a sufficiently high proportion of the population to prevent outbreaks entirely. In a few cases, similar approaches have been attempted with domestic animals thought to be reservoirs for diseases that infect threatened wild hosts (e.g., domestic dogs in proximity to African wild dogs [*Lycaon pictus*] or Ethiopian wolves [*Canis simensis*] [Cleaveland et al. 2006; Randall et al. 2006]). Although potentially highly effective, such efforts require substantial investments of time and money because most of the population must be vaccinated to reduce the reproductive rate of the disease below one (Anderson et al. 1981).

Recently, a new and more limited use of vaccination for disease management has been proposed. In this management method, originally suggested to control rabies in African wild dogs, a small number of individuals are vaccinated prophylactically (creating a population with a "vaccinated core") to minimize the probability of extinction from epizootics, rather than to prevent disease outbreaks altogether (Cleaveland et al. 2006; Vial et al. 2006). In the event of some future epizootic, individuals in the vaccinated core survive and serve as founders to rebuild the population. Because the goal is not complete prevention of epizootics, maintaining immunity in the majority of the population is not imperative, which greatly increases the feasibility of this approach for wild populations. Although the abilities of the monitor-and-respond and vaccinated-core approaches to reduce the probability of population extirpation have been scrutinized in specific circumstances (Haydon et al. 2006; Vial et al. 2006), the relative effectiveness of these approaches has not been compared directly.

We assessed the abilities of monitor-and-respond and vaccinated-core approaches to minimize the probability of population extirpation from rabies for a rare and highly threatened carnivore, the island fox (*Urocyon littoralis*). This fox is endemic to 6 of the 8 Channel Islands in southern California (U.S.A.). The species is considered particularly susceptible to infectious diseases because it evolved and continues to exist in relative isolation. The near loss of the subspecies on Santa Catalina Island in 1999—where the population size decreased from >1300 to <150 after an apparent outbreak of canine distemper (Roemer et al. 1994; Timm et al. 2009)—underscores the gravity of the disease threat, as do the repeated introductions of both domestic and wild animals carrying distemper and non-native parasites to Santa Catalina Island.

As with most threatened species, diseases act in concert with other factors that threaten the small populations of the island fox, requiring managers to carefully consider the most cost-effective and reliable approaches to a constellation of threats. In the late 1990s, Golden Eagle (*Aquila chrysaetos*) predation reduced the number of foxes on the northern Channel Islands. Fox abundance fell from >1300 to approximately 130 on Santa Cruz Island and simultaneously fell from hundreds to <30 individuals on San Miguel and Santa Rosa Islands (Roemer et al. 2001*a*; Coonan 2003). These subspecies and the Santa Catalina subspecies were listed as endangered under the U.S. Endangered Species Act in 2004 (U.S. Fish and Wildlife Service 2004).

In the course of recovery planning, managers (including representatives of the U.S. Fish and Wildlife Service, U.S. National Park Service, The Nature Conservancy, the Catalina Island Conservancy, and the U.S. Navy) sought to develop proactive and cost-effective strategies to counteract the primary threats to the species. Managers initially planned to implement an aggressive monitor-and-respond program to guard against potentially catastrophic outbreaks of infectious disease. In the midst of these planning discussions, the vaccinated-core strategy was introduced in the literature (Cleaveland et al. 2006; Vial et al. 2006), prompting managers to ask which strategy would be more effective and efficient for the abatement of disease threats to the island fox. Both canine distemper and rabies viruses are suspected to be substantial threats to the island fox, and other epizootic diseases also have the potential to affect fox populations (Schwemm 2008; Timm et al. 2009). Here, we focused on rabies. The extreme lethality and prolonged and variable latency period of rabies exacerbate problems of disease control, but a safe and presumably effective vaccine exists (Cleaveland et al. 2006; Randall et al. 2006; Schwemm 2008).

We used the framework of population-viability management (Bakker & Doak 2009) to compare the 2 proposed management options for minimizing disease threats. In particular, we used the risk of quasi extinction as a measure of management success. This approach allows a direct comparison of these very different management strategies. Following the literature on population viability analysis (e.g., Morris & Doak 2002), we refer to population reductions that are close to complete extirpation as quasi extinction. Preventing near-term extinction and fostering recovery (i.e., greatly diminishing the probability of future extinction) is a legal mandate in the management of endangered species in the United States and the least arbitrary and most biologically relevant metric of successful stewardship (Bakker & Doak 2009). To best inform decision making, population-viability management models population dynamics, the interacting effects of monitoring and management, and the inherent uncertainties in these processes (Bakker & Doak 2009). For many species of conservation concern, ongoing exposure to lethal diseases is probable. The approach we outline here provides a framework for comparing the relative effectiveness and feasibility of different disease-management strategies in the face of such ongoing threats to population viability.

Methods

Study System and Disease Threat

Island foxes form socially monogamous pairs and generally defend exclusive territories (Roemer et al. 2001*b*). The Channel Islands are largely undeveloped and have relatively few native mammal species, a situation that results in a low diversity of species to serve as disease reservoirs. Despite this isolation, island foxes are threatened by an ongoing risk of disease exposure. With the exception of Santa Catalina Island, beach landings of boats with domestic dogs are prohibited, but recreational boaters regularly bring dogs to other islands. On Santa Catalina Island, which has approximately 3700 residents and is visited by 1,000,000 people annually, many domestic dogs and cats are routinely transported between the island and the mainland. In at least one instance, a dog adopted by island residents from a mainland shelter developed clinical canine distemper after arrival (R. Denney, personal communication), which could have exposed the native island foxes that commonly move through areas of human habitation. In at least 6 separate instances since 2007, raccoons from the mainland were inadvertently transported to the island (J. King, unpublished), which represents another potential introduction pathway for both canine distemper and rabies.

Serological surveys of island fox populations over the last 2 decades show varying levels of exposure (based on antibody presence) to numerous pathogens, including canine distemper virus (Garcelon et al. 1992; Roemer et al. 2001*a*; Clifford et al. 2006). A variant of canine distemper virus associated with raccoons was the only viral strain isolated from a fox that died on Santa Catalina Island during the population decline in the late 1990s. Antibodies to canine distemper virus were detected in sera samples taken from apparently healthy foxes prior to the decline, which suggests that disease variants were circulating in the population at that time (Timm et al. 2009). No evidence of past exposure to rabies virus has been detected (Timm et al. 2009), but this is expected, even if a past epizootic had occurred, given the limited sampling and high likelihood that exposed foxes would quickly die from the disease.

Previous Model Development

Our work builds on a demographic model (Bakker et al. 2009) that simulates the dynamics of island fox populations and was parameterized with data from 4 islands collected over 17 years. Key features of this model are 2 age classes (first-year animals and adults) with differing survival and breeding probabilities; stochastic sex determination; demographic and environmental stochasticity in all vital rates; variance in vital rates in response to known drivers, including predation by Golden Eagles, density, and unassigned process variance; parameter and model uncertainty; and annual time steps. Probabilities of survival of males and females do not differ, but unequal sex ratios limit reproduction. Strong density dependence in observed survival rates (Bakker et al. 2009) drives large annual fluctuations in abundance in modeled populations, a prediction that is consistent with anecdotal historical observations. Thus, these populations do not reach a stable carrying capacity and frequent declines in abundance exacerbate the probability of extinction posed by epizootics.

Rabies Model

To evaluate the efficacy of different management approaches, we built a susceptible-exposed-infected-removed (SEIR) epizootic model for rabies that we based on the general approach and parameter estimates developed to simulate rabies outbreaks in European red foxes (*Vulpes vulpes*) (Anderson et al. 1981; Smith & Cheeseman 2002) and domestic dogs (Hampson et al. 2009; Beyer 2010). We used a daily time step and simulated the number of foxes transitioning each day from susceptible to latent exposed, from latent exposed to rabid and infectious, and from all classes to death. At the beginning of an epizootic, foxes were assigned to paired or unpaired status, which allowed us to account for the much higher probability of disease transmission between mates (White et al. 1995; Smith & Cheeseman 2002). To generate realistic incubation and infectious periods, we tracked time since infection and time since rabies onset for latent and rabid individuals and simulated time-varying probabilities for the latent to rabid and rabid to dead transitions (Hampson et al. 2009; Beyer 2010). In the absence of high-quality fox-specific estimates, we used estimates of these probabilities from domestic dogs (Beyer 2010). Using binomial probabilities, we incorporated demographic stochasticity into all transition probabilities. We also modeled the daily probability of natural mortality, again accounting for demographic stochasticity (see Supporting Information for details).

The greatest uncertainty in modeling rabies is the rate and functional form of disease transmission between rabid and susceptible animals (McCallum et al. 2001; Sterner & Smith 2006). We followed others in assuming that, given the frequent contacts between mates, when a paired fox becomes rabid, its mate will also rapidly contract the disease (Smith & Cheeseman 2002) (Supporting Information). Daily contact rates between neighboring, unpaired foxes are less certain, so we based our values on the only empirical estimates for wild canids (red foxes) we could find in the literature. We used the lowest observed seasonal estimate (spring, 0.05) as our low contact rate, the highest observed seasonal estimate (winter, 0.76) as our high contact rate, and the overall mean of 0.28 as our midrange contact rate (White & Harris 1994; White et al. 1995) (Supporting Information).

It is also unclear how contacts and thus rabies transmission rates vary as a function of density in foxes or similar species (Sterner & Smith 2006). We used 2 alternative model structures: a frequency-dependent transmission model (number of individuals each fox interacts with is fixed to neighboring territory holders), which results in constant numbers of new infections per rabid fox across all densities, and a density-dependent transmission model (number of individuals each fox interacts with is proportional to the population size), which results in a linear decline in numbers of new infections per rabid fox as density decreases (Supporting Information).

Monitor-and-Respond Strategy

We simulated monitoring for rabies as both mortality checks on radio-collared foxes (i.e., detection of signals from radio-collars that indicate that an animal may have died) and independent detection of extensive die-offs of $\geq$50% of the initial number of individuals. Many factors contribute to the delay between the start of an epizootic and efforts to protect a population: detection of deaths, recovery of carcasses, shipment of carcasses off the island, necropsy and diagnosis, and trapping, vaccination, and release of vaccinated foxes. With no island facilities to individually isolate hundreds or thousands of foxes, vaccination and release of the majority of captured foxes is the most feasible management approach. We based our estimates of the time required for these actions to be implemented on previous data and the expertise of managers (Supporting Information).

We ran 500 replicate simulations of the SEIR model for single epizootics under different biological and management scenarios. These simulations were devised to answer questions regarding allocation of resources between different aspects of the monitor-and-respond program and to identify minimal requirements for a monitor-and-respond program to ensure population sizes remained above the quasi-extinction threshold adopted for this species ($N_{\mathrm{qext}} = 30$) (Bakker et al. 2009; Bakker & Doak 2009). Vital rates for all simulations were from the Santa Cruz Island population, which has an estimated population size when all territories are fully occupied by fox pairs (F) of 1076. Simulations differed in number of radio-collared foxes (0, 20, 40, 60, 80, 100), frequency of mortality checks (once every 3 or 7 days [7 days is logistically possible but fewer than 3 is not]), delays between detection of a mortality due to rabies and initiation of trapping (5, 7, 9, 11, 13, or 15 days), starting population size ($0.25F$, $1F$, or $4F$ [Table 1]), and transmission type (frequency or density dependent). We also modeled the decreasing probability of diagnosing rabies from carcasses recovered multiple days after death (Supporting Information). The population was tracked until the epizootic was detected and the remaining uninfected foxes were captured and vaccinated, or for 364 days, by which point virtually all modeled epizootics have run their course (Fig. 1). We used the lower 10th percentile of the number of uninfected foxes remaining after an epizootic to evaluate the effectiveness of different management strategies.

We then investigated the long-term probabilities of extinction when using a set of potentially feasible and at least minimally effective monitor-and-respond strategies determined by the SEIR-only runs described above. Specifically, we used 3-day radio-collar checks, 70 collared foxes, and 7-day delays as the most intensive monitor-and-respond parameters for 50-year simulations of monitor-and-respond management. We also ran several sets of simulations with longer check intervals and management delays.

We embedded the SEIR and monitor-and-respond models into the previously developed multi-year population model for island fox (Bakker et al. 2009). Rabies introductions occurred on a random day, triggering a run of the SEIR model with monitor-and-respond management. During an epizootic, the simulation time step changed from annual to daily. At the end of epizootics, populations consisted of all unexposed foxes that had also not succumbed to natural mortality or foxes that were captured and vaccinated prior to exposure. We ran these simulations with an annual probability of rabies introduction of

Table 1. Parameter values used in modeling rabies dynamics in island fox (*Urocyon littoralis*) populations on Santa Cruz Island, California (U.S.A.).

Parameter	*Description*	*Value*	*Source*
F	Population size at which all territories are occupied by 2 adult foxes	1076	Estimated from home range size in Roemer et al. 2001*b*
C	Daily contact rate with each neighboring fox	0.05, 0.28, 0.76	White & Harris 1994, derived from empirical observations of red fox (*Vulpes vulpes*) contacts; values are the lowest seasonal rate, overall average rate, and highest seasonal rate
Latent period	Mean and shape parameters for gamma distribution defining probabilities of latent period duration	22.5, 1	Beyer 2010
Rabid period	Mean and shape parameters for gamma distribution defining probabilities of rabid period duration	3.12, 2	Beyer 2010
Others	Natural mortality and reproduction	See source	Bakker et al. 2009

0.05 (approximately 1 introduction every 20 years) and evaluated the monitor-and-respond strategy at 2 levels of predation by Golden Eagles (mortality rates associated with the presence of either 0 or 2 eagles, on the basis of historical data [Bakker et al. 2009]) and for each disease-transmission model. We used a starting population size of F for all simulations and ran 1000 replicates for 50 years, sampling across both model and parameter uncertainty. Outputs were the probability of extinction and the number of foxes before and after the rabies epizootic.

Core Vaccination

To evaluate the long-term probability of extinction associated with a vaccinated-core strategy, we ran 50-year simulations analogous to those described above, except that in place of a monitor-and-respond program we assumed an ongoing vaccination program that maintained a constant number of wild foxes with effective immunity (vaccinated cores of 40, 60, 80, 100, 140, 180, or 220 individuals). Prior to each epizootic, we assigned vaccinations randomly with respect to age and sex classes and assumed no other management response. After epizootics, populations consisted of all foxes that were vaccinated and did not die of natural causes and unvaccinated survivors that had escaped exposure to rabies. We ran 1000 replicates for each scenario.

Results

With the midrange contact rate estimate, rabies usually spread quickly through an island fox population under both transmission models. Essentially all foxes (>95%) were exposed within 200 days under most scenarios (Fig. 1). However, with density-dependent transmission, low-density populations ($0.25F$ or 0.7 foxes/km^2) resulted in slow or no propagation of the disease (Fig. 1). Low contact rates were associated with a lower probability of spread of the disease and more protracted epizootics when they did occur (Supporting Information). High contact rates were associated with rapid disease spread under all starting conditions and both transmission models (Supporting Information).

Starting population size, response delay time, frequency of mortality checks, number of radio-collared foxes, transmission model, and contact rate all had strong, interacting effects on the ability of the monitor-and-respond approach to save a substantial number of foxes from mortality during a single epizootic (Supporting Information). A successful monitor-and-respond program should guarantee numbers of surviving foxes at or well above a predetermined quasi-extinction threshold across all plausible contact rates, transmission models, and starting population sizes. However, even the most logistically challenging programs modeled, with 100 radio-collared foxes and only a 5-day delay in the initiation of captures, did not result in a 10th percentile of numbers of surviving foxes that was above the 30-animal quasi-extinction threshold under all simulation scenarios.

With low contact rates (Supporting Information) a wide range of management parameters yielded good results (i.e., 10th percentile of surviving foxes was above the quasi-extinction threshold). But with high contact rates, and especially under a frequency-dependent transmission model, no monitor-and-respond program yielded high probabilities of survivor numbers reaching this threshold (Supporting Information). For midrange contact rates and a 7-day check period, a 5-day response delay and a large number of radio-collared foxes ensured high probabilities of survival numbers over the quasi-extinction threshold for most, but not all, starting densities and transmission assumptions (Fig. 2). Three-day collar checks, low response delays (e.g., 7 days), and moderate to large numbers of collars (75–100) was the only combination of parameters that yielded minimally effective protection from rabies epizootics in most combinations of starting densities and transmission models, but only for low or midrange contact rates (Fig. 3 & Supporting Information). We do not show equivalent results for

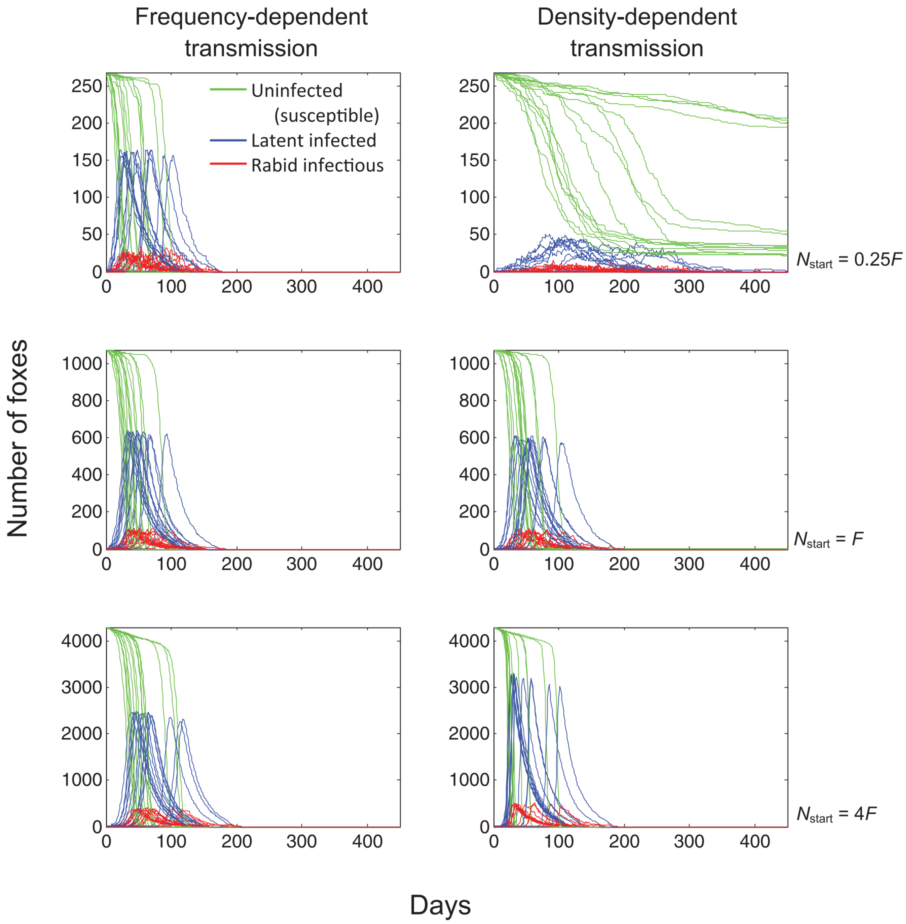

Figure 1. Simulated spread of rabies through an island fox population following the introduction of one rabid individual (frequency-dependent transmission, number of individuals each fox interacts with is fixed [i.e., neighboring territory holders]; density-dependent transmission, number of individuals each fox interacts with is proportional to population size). In all simulations daily contact rates are midrange (0.28) (Table 1). Simulations have different starting population sizes (N_{start}): 0.25F, 1F, or 4 F, where F = 1076 foxes (i.e., the population size at which all territories are occupied by a fox pair). Initial densities determine the background probabilities of survival of foxes (Bakker et al. 2009). The 20 trajectories shown for each scenario illustrate the effects of demographic stochasticity in transitions between model classes of susceptible, latent infected, rabid, and dead. Corresponding results for low and high contact rates are in Supporting Information.

single epizootics for vaccinated-core management models because the number of surviving foxes was near or above the vaccinated-core size across all scenarios.

The 50-year simulations indicated that the ability of monitor-and-respond management to reduce extinction risk as much as the vaccinated-core approach depended strongly on disease-transmission dynamics. With midrange contact rates, a highly ambitious monitor-and-respond program yielded excellent results for the frequency-dependent transmission model, but only small reductions in extinction risk when transmission was density dependent (Fig. 4). In contrast, a vaccinated core of 140 or more foxes dramatically reduced probability of extinction for all scenarios; 50-year quasi-extinction risks were no more than 22% and were lower in most cases. Assuming low contact rates, both approaches reduced extinction risk substantially, but monitor-and-respond management outperformed the vaccinated-core approach (Supporting Information). But for high contact rates, even the most difficult to implement monitor-and-respond program had little effect on extinction probability, whereas vaccinated-core management still greatly reduced extinction risk (Supporting Information).

Population sizes before and after epizootics under the 2 management approaches illustrate the fundamental differences of the approaches (Fig. 5). Under some conditions, the monitor-and-respond approach yielded survivors far in excess of the quasi-extinction threshold of 30 or of the survivors under vaccinated-core management. But this success of monitor-and-respond management only occurred when rabies spread slowly (as with low contact rates) (Fig. 5); when contact

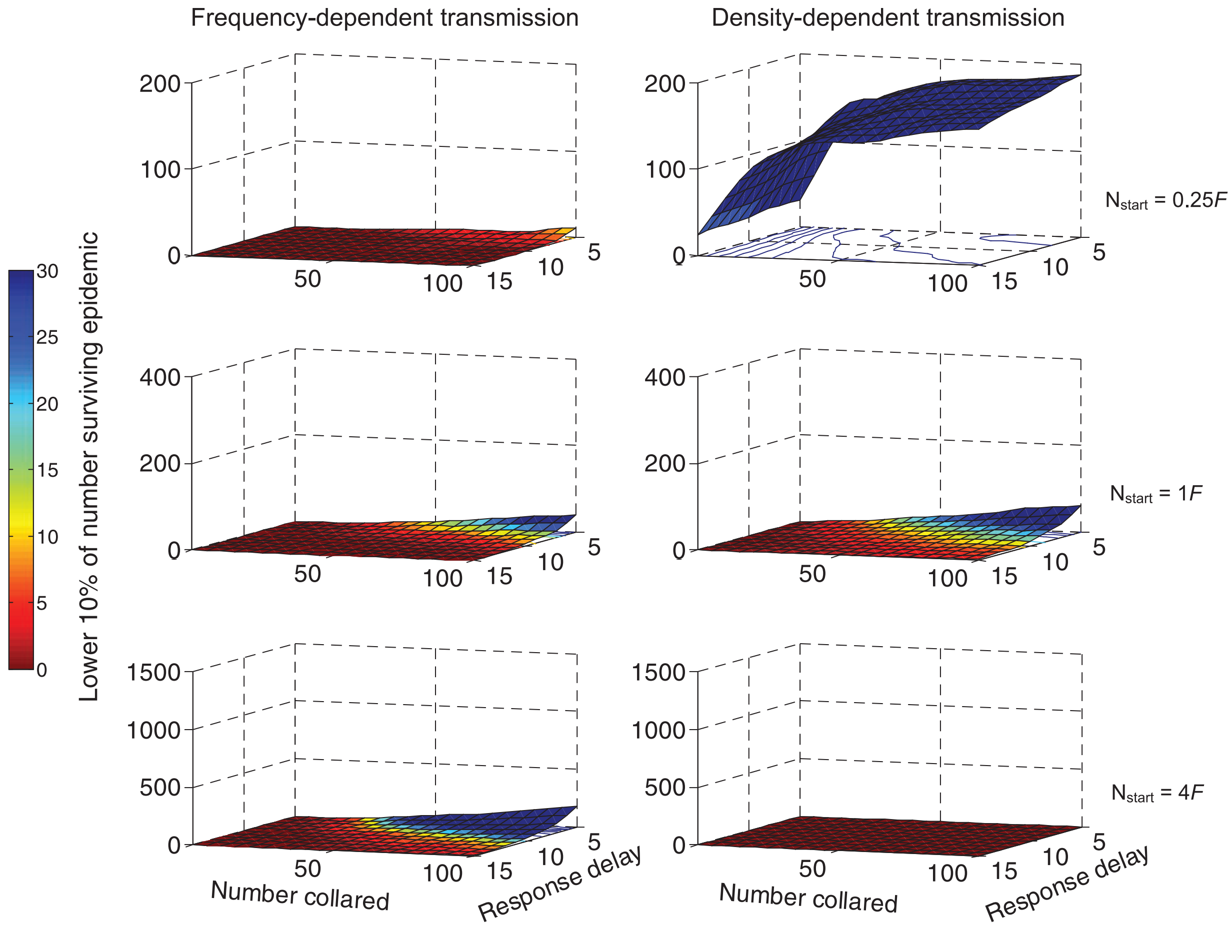

Figure 2. Influence of frequency-dependent and density-dependent transmission (defined in legend of Fig. 1) on numbers of foxes surviving a single epizootic when using monitor-and-respond management. All results are based on weekly mortality checks, no predation by Golden Eagles, and midrange contact rates. Results are shown for 3 starting densities of foxes (N_{start} [defined in legend of Fig. 1]) and for variation in 2 parameters controlling the monitor-and-respond strategy: delay in management response and number of collars deployed. The response (z-axis) variable is the 10th percentile value of the number of uninfected foxes remaining after 500 replicates. Conditions in which the lower 10th percentile number exceeds the quasi-extinction threshold of 30 are in blue. Corresponding results for low and high contact rates are shown in Supporting Information.

rates were moderate, population sizes were small, and transmission was density dependent (Fig. 5); or when contact rates were moderate, population sizes were large, and transmission was frequency dependent (Fig. 5). With other assumptions about disease biology or starting conditions, the monitor-and-respond approach often yielded low or no survival (Fig. 5). In contrast, the vaccinated-core strategy yielded relatively constant minimum numbers of survivors across all scenarios, because the population contracted to no less than the approximate size of the vaccinated core after each epizootic.

Discussion

Many wild populations will require continuing management, potentially in perpetuity, to avoid extinction (Scott et al. 2005), necessitating careful evaluation of the safety and utility of different management methods to combat multiple threats, including disease outbreaks. Given the uncertainty regarding the biology of rabies, we simulated 2 plausible scenarios for disease transmission and a wide range of plausible contact rates, any of which could best represent the true biology of the disease. The monitor-and-respond approaches to rabies management failed to substantially reduce the risk of disease-driven extinction under density-dependent transmission assumptions or high contact rates, whereas a vaccinated core of moderate size substantially reduced extinction risk across all scenarios (Fig. 4). Given the speed with which rabies can spread through canine populations, these results make intuitive sense, but to our knowledge this is the first effort to directly compare these alternative management approaches.

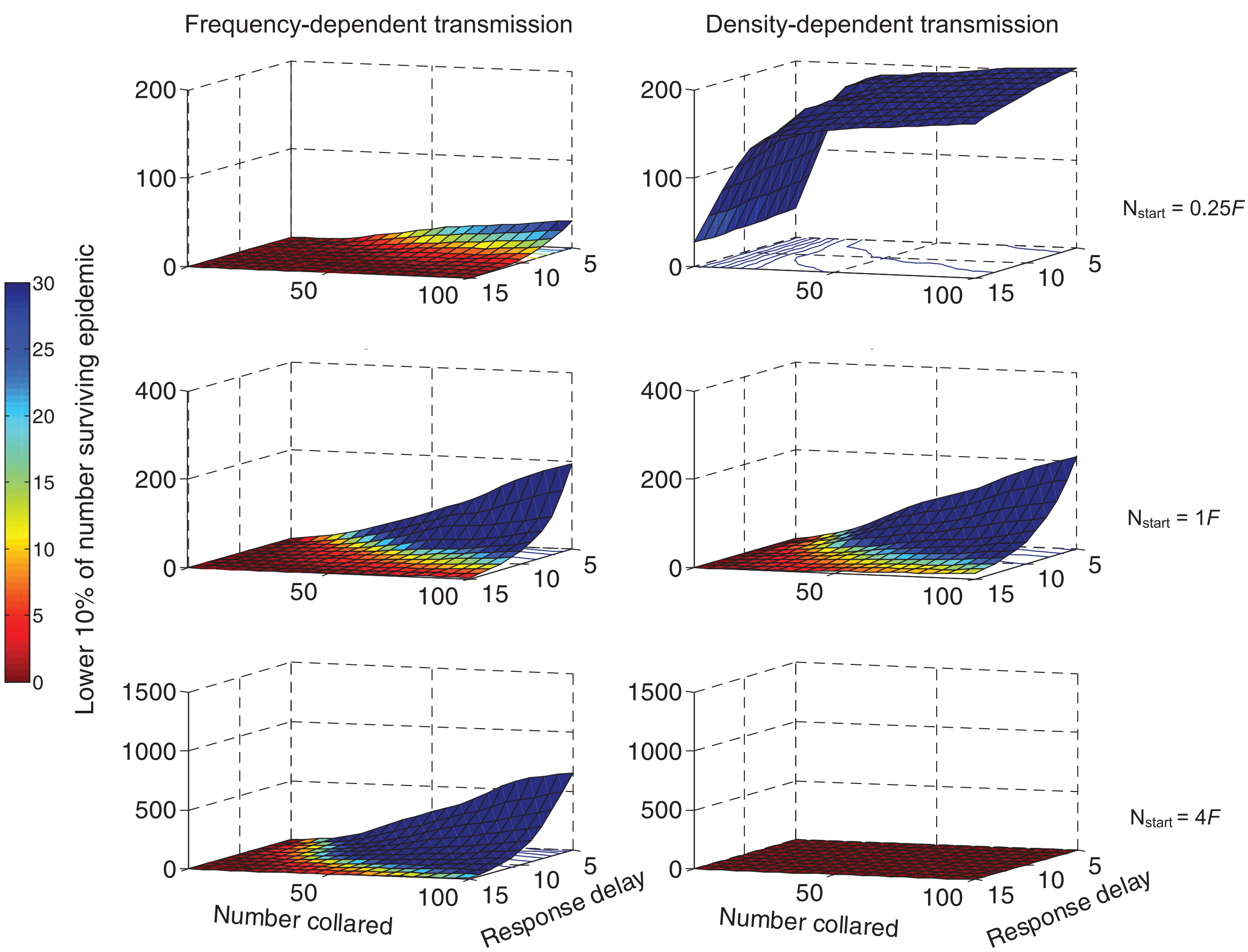

Figure 3. Influence of frequency-dependent and density-dependent transmission (defined in legend of Fig. 1) on numbers of foxes surviving a single epizootic when using monitor-and-respond management. All results are based on 3-day mortality checks, no predation by Golden Eagles, and midrange contact rates. Results are shown for 3 starting densities of foxes (N_{start} [defined in legend of Fig. 1]), and variation in two parameters controlling the monitor-and-respond strategy: delay in management response and number of collars deployed. The response (z-axis) variable is the 10th percentile value of the number of uninfected foxes remaining after 500 replicates. Conditions in which the lower 10th percentile number exceeds the quasi-extinction threshold of 30 are in blue. Corresponding results for low and high contact rates are shown in Supporting Information.

Maintaining large numbers of vaccinated animals requires captures and recaptures in perpetuity, which has spawned debate among island fox managers about the expense and invasiveness of the prophylactic vaccination versus monitor-and-respond strategies (Schwemm 2008). Our results clarify the minimum requirements for either approach to be effective, and thus reveal the costs and difficulties of both approaches. We found that even a minimally effective monitor-and-respond program requires personnel to perform mortality checks every 3 days on 70 radio-collared foxes widely dispersed across rugged island terrain; to rapidly locate, retrieve, package, transport, and necropsy fox carcasses following death; and to mount an extensive vaccination effort across the entire island within 7 days of a rabies mortality. This would require perpetual vigilance and, in the event of an outbreak, seamless coordination of many management agencies. As a result, the personnel and infrastructure costs of this approach are likely to be far higher than those of maintaining an adequate vaccinated core. It would be appealing to directly compare costs of these 2 approaches, but the different sources of funding for each, the multiple duties of the personnel under either scenario, and the as-yet uncalculated costs of maintaining readiness for and implementation of an extensive and rapid mobilization effort make this accounting infeasible at present.

Our results showed that the vaccinated-core approach is likely to be both more feasible and more reliable, but they also indicated the conditions under which a monitor-and-respond strategy worked well: density-dependent transmission and low densities or frequency-dependent

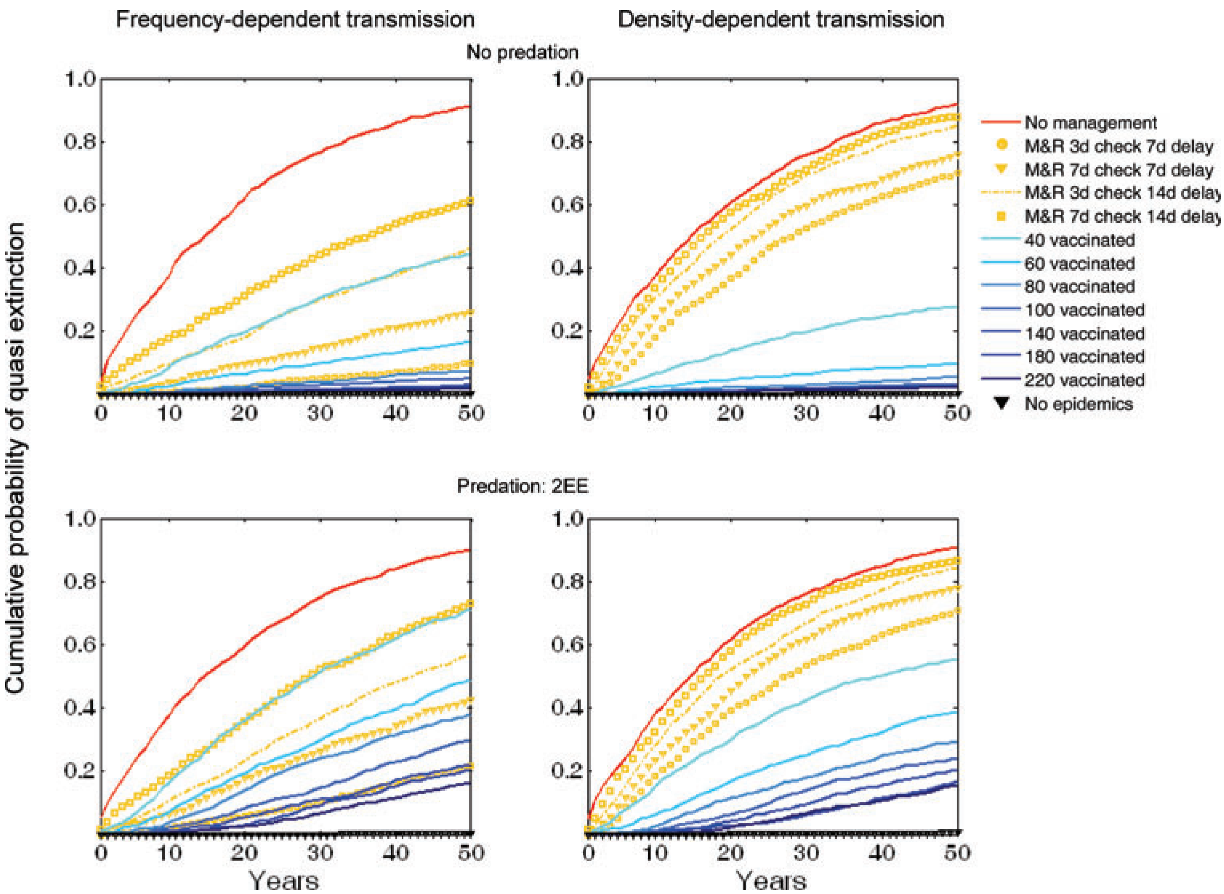

Figure 4. Cumulative quasi-extinction risk associated with monitor-and-respond and vaccinated-core approaches to rabies control under 2 disease-transmission models, Golden Eagle predation (historical predation rate exerted by 2 eagles), and midrange contact rate among island foxes. For all simulations starting population size (N_{start}) = F (where F = 1076, the population size at which all territories are occupied by a fox pair) and the annual probability of disease introduction to the population is 0.05. In the monitor-and-respond strategy, 70 collared foxes are checked for mortality every 3 or 7 days and time elapsed between detection and initiation of extensive management response is 7 or 14 days. Results are from 1000 replicate simulations for each scenario with a quasi-extinction threshold of 30 foxes.

transition and high densities, especially with low to midrange contact rates. Under these conditions, speed of management response is relatively unimportant, and if future research indicates contact rates among foxes are low, supplementing or replacing a vaccinated-core strategy with reactive management in the event of an epizootic may be effective. These results also suggest that more accurate data on contact rates and transmission dynamics for this and other species would allow for more accurate evaluation of alternative disease-control strategies. Such knowledge will also allow extrapolation of results to populations of differing densities and diseases with multiple host species. We suspect that the relatively constant effectiveness of the vaccinated-core strategy will prove even more important in more complex ecological situations, where the speed and shape of epizootic spread will be more variable and hence uncertainty about these processes will remain high.

Although we believe our modeling approach is well suited to the questions we addressed, we ignored many aspects of disease spread. We lacked data to parameterize a spatially explicit model, but spatial structure is a critical element in epizootic processes that could help refine the implementation of any management strategy (Fromont et al. 1998). Our approach likely generates predictions of somewhat more rapid disease spread than would a spatially explicit model. In addition, locations of mortalities could be used to prioritize areas for capture or vaccination, which would increase the efficacy of monitor-and-respond management. Conversely, ability to monitor foxes or recover carcasses is highly variable across most islands, and this variability would reduce the effectiveness of a monitor-and-respond approach to rabies management. Overall, ignoring spatial dynamics is likely to make all our predictions of necessary management effort somewhat precautionary.

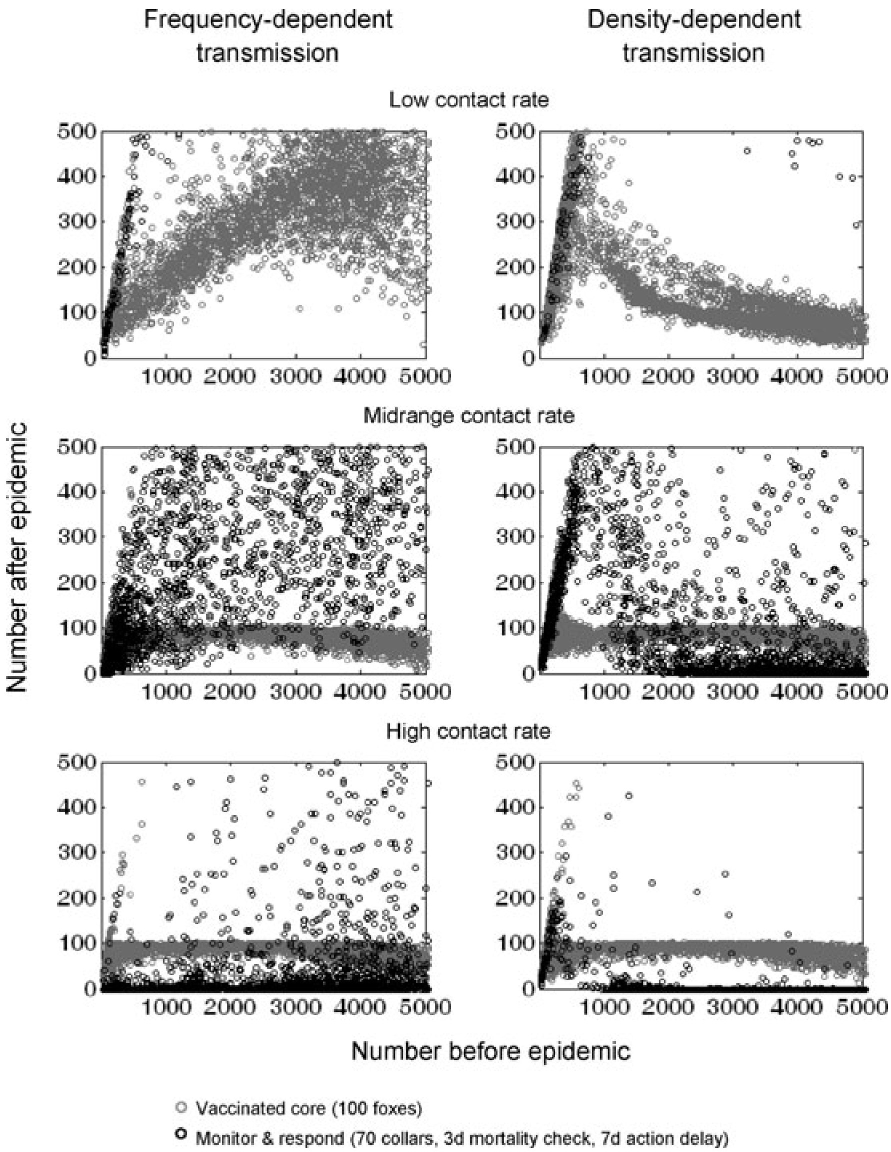

Figure 5. Relation between pre-epizootic population size and numbers of foxes surviving a rabies epizootic for vaccinated-core and monitor-and-respond management approaches in 2 disease-transmission models (defined in the legend of Fig. 1) and low, midrange, and high daily contact rates (Table 1). Graphs combine output for 1000 simulations with no Golden Eagle predation and 1000 simulations with predation rates exerted by 2 eagles. To illustrate conditions resulting in survival of few foxes, only postepizootic populations of 500 or less are shown.

Our work also uses a single disease course model for all individuals, whereas younger animals are likely to be more susceptible to many diseases with epizootic potential. We also ignored spatial heterogeneity in local densities, which may be high, especially for the currently recovering populations. We also assumed introduction of a strain of rabies virus adapted to foxes or closely related canids and thus a transmission rate similar to that in red fox and dog populations (Anderson et al. 1981; Smith & Cheeseman 2002; Beyer 2010). Finally, although island foxes form disease-specific antibodies when administered vaccines for rabies and canine distemper virus (Timm et al. 2009), no one has assessed survival of vaccinated island foxes after challenge with live pathogenic viral strains. Limited immunity, as well as the loss of immunity following one or multiple vaccinations, would require a larger vaccination program to maintain an effective core size.

Other considerations also influence the selection of a management approach. A rabies outbreak would pose a substantial public health threat to the island's human residents, and measures used in mainland rabies outbreaks, such as culling, might be considered. Widespread vaccination of foxes via trapping or distribution of oral baits would be likely, but the effectiveness of barrier vaccination to spatially isolate an outbreak would be decreased by the small size of the islands. Given the high daily capture rates used to model the monitor-and-respond approach, scenarios in which oral vaccines are distributed in bait are unlikely to change results.

We emphasized rabies in our modeling, but our goal was to inform management of both rabies and canine distemper. A monitor-and-respond approach may be more effective at reducing extinction risk due to canine distemper than due to rabies, given that canine distemper is likely to spread at a different rate than rabies, but a vaccinated-core strategy for distemper is expected to result in similar long-term probabilities of extinction as those predicted for rabies. In addition, the superiority of the vaccinated-core strategy for rabies control will affect management decisions for canine distemper because both vaccines can be administered simultaneously. Compared with rabies, monitor-and-respond management of canine distemper is both simpler (no zoonotic potential exists for canine distemper to complicate quarantine or reactive vaccination efforts) and more complicated (canine distemper can be spread by personnel on clothing and trapping equipment). A further complication of application of either approach to canine distemper is the existence in some island fox populations of a wild canine distemper virus strain that appears to be fairly benign (Clifford et al. 2006; Schwemm 2008; Timm et al. 2009). This circulating strain may confer some immunity against more highly pathogenic strains of the virus. Thus, current vaccination strategies try to avoid extirpation of this viral strain by leaving at least half of each fox population permanently unvaccinated once populations reach 50% of *F* (Schwemm 2008).

Despite our support for use of a vaccinated-core approach to control extinction risks from rabies, individual monitoring plays a pivotal role in management for many other threats to island foxes, including eagle predation and outbreaks of other, less lethal diseases. Levels of exposure to other potential epizootic agents such as canine adenovirus and canine parvovirus vary widely in different fox populations (Garcelon et al. 1992; Roemer et al. 2001*a*; Clifford et al. 2006). This suggests that periods of widespread, but mild, disease outbreaks with numerous survivors may be interspersed with periods of low disease prevalence, when a large proportion of foxes may be susceptible. This potential highlights the need for ongoing disease surveillance. In addition, commercially available vaccines against these and other potential diseases have not been tested for safety and efficacy in island foxes or are available only in combinations with other vaccines that may harm foxes (Schwemm 2008), making monitor-and-respond approaches (i.e., quarantine) the only currently feasible approach for these threats.

We followed a population-viability management framework by simulating both natural processes and management and monitoring and then comparing different management strategies through the use of a single biologically based criterion, risk of quasi-extinction (Bakker & Doak 2009). Especially when management methods are strikingly different, the use of a single metric of success that is tied directly to biological and legal criteria (i.e., prevention of extinction) is key to making modeling results relevant to management. We focused on avoiding quasi extinction, but managers may set other biologically based goals and in particular use different quasi-extinction thresholds. Our results indicate that a vaccinated-core approach will more consistently protect fox populations from extinction due to rabies outbreaks. We also found that essentially no realistic monitor-and-respond approach could match the protection from rabies introductions provided by prophylactic vaccination, given our current uncertainty regarding the disease dynamics. In other situations, such as combating slower-moving or less-lethal diseases (Lopez et al. 2009), the same general evaluation might identify monitor-and-respond or other management methods that would be equally effective, thereby allowing cost, logistics, and aesthetics to be considered when choosing among approaches.

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Supporting Information

A detailed description of the epizootic models (Appendices S1-S3) and supplemental outputs (Appendixes S6-S14) is available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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