

Effects of prey metapopulation structure on the viability of black-footed ferrets in plague-impacted landscapes: a metamodelling approach

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Summary

1. Species interactions have been largely ignored in extinction risk assessment. However, the black-footed ferret *Mustela nigripes* exemplifies a class of endangered species for which strong species interactions cannot be ignored. This species is an obligate predator of prairie dogs *Cynomys* spp., and sylvatic plague *Yersinia pestis* epizootics threaten to undermine recovery efforts by functionally eliminating the prey base. Multispecies ‘metamodelling’ techniques offer new opportunities for exploring population dynamics under strong species interdependencies and disease.

2. To investigate ferret extinction risk in plague-affected landscapes, we simultaneously modelled plague epidemiological processes, prairie dog metapopulation dynamics and ferret demographic responses. Ferret population dynamics were investigated at an important release site (Conata Basin in South Dakota) and for 500 artificial prey landscapes spanning a wide range of realistic colony configurations (e.g. total area, # colonies, spatial clustering) and demographic characteristics.

3. Our simulation models indicate that ferrets are unlikely to persist through episodes of plague at Conata Basin unless they can access prey resources from a wider region or unless management actions can otherwise substantially reduce plague transmission.

4. We show that large, diffuse prairie dog metapopulations (those with colonies spread over a region >2500 km²) are most likely to support ferret populations in plague-affected landscapes. Our results also highlight the potential importance of metapopulation connectivity in fuelling plague epizootics and thereby imperilling black-footed ferret conservation efforts.

5. We describe a cycle (c. 5- to 25-year period) of plague-driven population crashes that is an emergent property of our models, and which can destabilize ferret populations.

6. *Synthesis and applications.* On the basis of our models, we conclude that few North American prairie dog complexes cover sufficient land area to sustain black-footed ferret populations through plague-driven crashes in prey abundance. Consequently, our results underscore the importance of working with many constituents to conserve large prairie dog landscapes in addition to continued development of plague mitigation tools. In addition, the strong relationship between plague-induced oscillatory prey cycles and predator population persistence highlights the potential conservation benefits of imposing strategic barriers to connectivity in areas over which plague outbreak cycles are strongly synchronous.

Key-words: connectivity, disease spread, oscillatory population dynamics, predator–prey interactions, sensitivity analysis, spatial structure

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Introduction

Species interactions underpin ecological theory and research, yet they have been largely ignored in extinction risk assessment (Soulé *et al.* 2005; Sabo 2008; Chadès, Curtis & Martin 2012). Failure to consider such feedbacks in conservation biology is particularly notable in the case of population viability analysis (PVA), a set of widely applied simulation modelling techniques for assessing extinction risk and exploring management options (Burgman, Ferson & Akçakaya 1993; Morris & Doak 2002). Typically, PVA models treat populations as isolated single-species systems (but see Fordham *et al.* 2013 for a recent exception), with interspecific interactions grouped with other external forcing factors and handled either as constraints on population growth (e.g. constant mortality term) or as factors that contribute to environmental variability (Sabo 2008). Similarly, disease is usually incorporated within PVAs as one of several stochastic causes of mortality or occasionally as the cause of periodic catastrophes (e.g. Frick *et al.* 2010). However, in reality, diseases have their own dynamics that are often strongly determined by demographic characteristics of their hosts (McCallum & Dobson 1995; Smith, Acevedo-Whitehouse & Pedersen 2009). As with other species interactions, the full interactive dynamics of epizootic disease as a factor that can destabilize or extirpate small populations is rarely modelled explicitly in PVAs (but see Haydon, Laurenson & Sillero-Zubiri 2002).

The endangered black-footed ferret *Mustela nigripes* (Audubon & Bachman 1851), native to the North American shortgrass prairie, is an obligate predator of prairie dogs *Cynomys* spp. and also extensively uses prairie dog colonies and burrows as habitat (Clark 1989; Biggins *et al.* 2006a). The dependence of black-footed ferrets on this single prey species suggests that the tight coupling of population dynamics in these two species cannot be ignored in PVA models. Furthermore, given that epizootics of plague (in prairie dogs and ferrets) and distemper (in ferrets) eliminated the last wild population of ferrets in 1987 (Biggins, Livieri & Breck 2011b) and continue to threaten the persistence of reintroduced populations, there is a clear need to explicitly account for disease dynamics in any PVA for black-footed ferrets. Here, we build a linked predator–prey PVA model that directly accounts for important spatially explicit disease processes and which represents one of the first attempts to model the effects of trophic linkages and disease on an endangered species.

Throughout the 20th century, black-footed ferret populations declined due to human persecution of prairie dogs (e.g. poisoning, rangeland conversion) and sylvatic plague, an exotic flea-borne disease (caused by the bacterium *Yersinia pestis*) that is highly fatal to both prairie dogs and black-footed ferrets. Black-footed ferrets were extinct in the wild by 1987 after the last 18 individuals were

removed for captive breeding (Clark 1989). Since then, more than 7000 black-footed ferrets have been raised in captivity, of which over 3500 have been released into the wild at 19 locations in eight US states, Mexico and Canada (Jachowski *et al.* 2011a; Livieri 2011). Four reintroduction sites are now considered self-sustaining with no further reintroductions required. However, the continued eastward spread of sylvatic plague (Barnes 1982; Abbott & Rocke 2012) has resulted in catastrophic declines in prairie dog populations (e.g. Gage & Kosoy 2005), threatening to undermine recovery efforts (Kotliar, Baker & Whicker 1999; Livieri 2006).

To investigate black-footed ferret population viability in a dynamic, plague-affected landscape, we combined a plague epidemiological model, a prairie dog metapopulation model and a ferret population model. Using this multispecies approach to PVA (Miller & Lacy 2003; Prowse *et al.* 2013), we were able to explore the consequences of strong species interactions in ways not possible using standard PVA methods. We demonstrate that successful black-footed ferret reintroduction efforts in plague-affected landscapes may require large and diffuse prairie dog complexes or management actions to substantially reduce plague transmission rates. Furthermore, these coupled simulations predict oscillatory dynamics in both prey and predator populations, driven by complex interactions between plague epizootics and population recovery in a heterogeneous landscape. We show that this emergent property, which would not have been forecast using a single-species approach, and which is consistent with observations, has important potential consequences for the conservation of black-footed ferrets.

Materials and methods

STUDY SITE: CONATA/BADLANDS REGION

Releases of black-footed ferrets to Conata Basin (located within Buffalo Gap National Grasslands in South Dakota, USA, covering c. 500 km²) began in 1996, resulting in a self-sustaining ferret population of 335 animals by 2007 (Livieri 2006; Wisely *et al.* 2008). To assess the prey base for ferrets, black-tailed prairie dog *Cynomys ludovicianus* colonies across southwestern South Dakota (hereafter, Conata/Badlands region, covering c. 20 000 km²) were mapped by the US Forest Service, Badlands National Park and South Dakota Game, Fish and Parks (Biggins *et al.* 2006b; Sidle, Johnson & Euliss 2001; Cooper & Gabriel 2005; see Appendix S1 in Supporting Information). We used the union of the mapped polygon boundaries from all surveys between 1996 and 2009 to define the spatial extent of all distinct prairie dog colonies within the Conata Basin (area of known black-footed ferret occupancy; Biggins *et al.* 2011a) and the larger Conata/Badlands region, resulting in a metapopulation of 1591 black-tailed prairie dog colonies ranging from 5 ha to c. 10 000 ha in size (median colony area of 16 ha; Appendix S1), of which 71 colonies were identified as part of the Conata Basin and thereby known to be immediately available as prey for the ferret population (Fig. S4-2).

MODELLING OVERVIEW

We developed and linked three separate models (Fig. 1): an individual-based epidemiological model that simulated epizootics of plague; a spatially explicit, age- and sex-structured, stochastic model of the prairie dog metapopulation, and an age- and sex-structured, stochastic, single-population model of black-footed ferrets. These three models are detailed in the following sections. The epidemiological model provided inputs for stochastic ('catastrophe') parameters of the prairie dog model. The total population size of the prairie dogs at each time step of each replicate of the model was used to calculate the carrying capacity of the black-footed ferret population.

EPIDEMIOLOGICAL MODELLING (SYLVATIC PLAGUE)

We developed an individual-based epidemiological model that simulated epizootics of plague spreading through a prairie dog colony (see Appendix S2). Although black-footed ferrets are highly susceptible to plague (Williams *et al.* 1994; Godbey, Biggins & Garelle 2006), we did not model the direct effects of plague on black-footed ferret populations for two reasons. First, our use of a spatially unstructured ferret population model was likely to overstate the direct effects of plague on the ferret population (all ferrets would be exposed to plague simultaneously), preventing subsequent analysis of emergent dynamics and effects of prey spatial structure. Secondly, an effective vaccine has been developed and is currently administered to captive and wild-born ferrets (Abbott & Rocke 2012). Thus, our study assumes that this programme continues to successfully prevent plague outbreaks in the ferret population.

Simulation of basic epidemiological processes in a prairie dog colony and reporting of disease states (Susceptible, Exposed, Infectious, or Recovered) and survivorship were carried out at a daily time step using the software Outbreak (version 1.0; Pollak *et al.* 2008). Outbreak models were initialized with a single infected prairie dog within a colony comprising 1000 individuals, and all simulations were run for 365 days. Although there is some evidence for resistance to *Y. pestis* in black-tailed prairie dogs (Pauli *et al.* 2006; Rocke *et al.* 2012), this process is not yet well understood and was not included in this model. Detailed

output data from Outbreak were used to generate three summary statistics that were subsequently used for modelling prairie dog metapopulation dynamics: (i) overall survival rate in a plague outbreak year, (ii) probability of a potential disperser individual being a carrier of plague and (iii) the probability of a single infected individual initiating an epizootic (Appendix S2).

PRAIRIE DOG METAPOPOPULATION MODEL

We developed an age- and sex-structured matrix model for prairie dogs using RAMAS Metapop (Akçakaya & Root 2013), parameterized using data from Hoogland (1995, 2001, p. 377; Appendix S1). Density dependence was specified as a Ricker function, with a maximum annual population growth rate (R_{max}) of 2.44 (on the basis of populations recovering from plague outbreaks; Appendix S1). Each mapped colony was modelled as a distinct biological population, with carrying capacity (K) defined as a function of colony area and average densities of prairie dogs set at 28.7 ha^{-1} , on the basis of an estimate of prairie dog densities in the Conata region prior to the arrival of plague (Livieri 2006). Dispersal among prairie dog colonies was modelled as a function of inter-colony distances (Appendix S1), on the basis of data from Knowles, Proctor & Forest (2002), Lomolino & Smith (2001) and Garrett & Franklin (1988). We modelled plague dynamics within the prairie dog metapopulation as catastrophes spread by dispersers, with virulence (overall survival) and per-disperser probability of initiating an outbreak estimated from the epidemiological model (Fig. 1). All colonies were initialized at K and at stable age distribution, and all simulations were run with a 10-year burn-in period.

BLACK-FOOTED FERRET DEMOGRAPHIC MODEL

We developed an age- and sex-structured population projection matrix for the black-footed ferret, also using RAMAS Metapop, on the basis of a Wyoming mark-recapture study (Grenier, McDonald & Buskirk 2007) and the observed annual variability of the re-established ferret population in the Conata Basin (Livieri 2006; Appendix S1). On the basis of energetic considerations, we assumed that a population of 766 prairie dogs could sustain a single ferret (Stromberg, Rayburn & Clark 1983; Appendix S1). Thus, K for the ferret population was set at $1/766$ of total prairie dog abundance at each time step. There is a great deal of uncertainty surrounding this estimate, which was derived under the simplifying assumptions that ferrets are monophagous consumers of prairie dogs and that prairie dog populations are exploited by no other major predator. However, although neither assumption is strictly true, violations of these two assumptions exhibit opposing biases, and therefore, no clear bias correction factor could be applied (see Appendix S1). Furthermore, an estimated ferret carrying capacity of 485 at Conata Basin, computed as $1/766$ of estimated total prairie dog carrying capacity, is consistent with the observed growth of the reintroduced ferret population at Conata Basin, which appeared to plateau at abundances *c.* 350 prior to the arrival of plague in 2007 (Livieri 2006; Fig. S1-4). Due to the ferret's strong territorial behaviour, we capped the value of K during periods of high prairie dog densities to prevent ferret densities from exceeding $0.04 \text{ ferrets ha}^{-1}$ (Biggins, Lockhart & Godbey 2006; Appendix S1). We used a Ricker (scramble) density dependence model, with R_{max} set at 1.48 on the basis of records from a rapidly growing Wyoming population

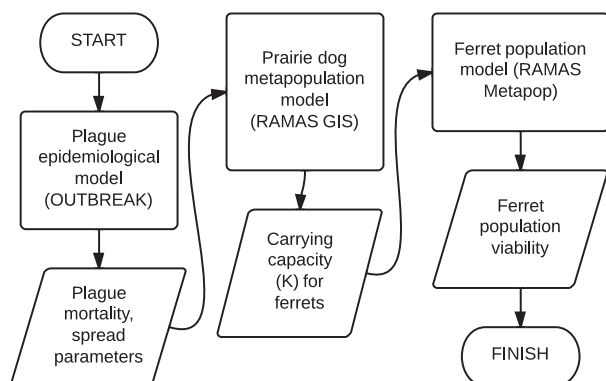


Fig. 1. Schematic flowchart of the metamodelling approach used in this study. Rectangular nodes represent processes (software in parentheses), and parallelogram nodes represent data output, which may be used as input for subsequent processes (indicated by arrows).

(Grenier, McDonald & Buskirk 2007; Appendix S1). Black-footed ferret abundance for each iteration was initialized using reintroduction records from Conata Basin (Livieri 2006).

We ran the black-footed ferret population model assuming either (i) ferrets could only access prairie dog colonies within the Conata Basin or (ii) ferrets could access all 1591 colonies within the larger Conata/Badlands region. Plague outbreaks were initiated in year 11 in a single large, centrally located colony within Conata Basin, reflecting ten plague-free years following the first ferret introductions (Abbott & Rocke 2012). We tested two alternative plague spread scenarios: (i) plague spreads only via prairie dog dispersal and (ii) plague outbreaks arise spontaneously with a probability of 0.05% per year per colony (resulting in a spontaneous plague initiation somewhere in the metapopulation nearly every other year and representing long-distance spread by alternative spread vectors such as coyotes and raptors). Ferret population viability was summarized using two metrics: quasi-extinction risk (defined as the proportion of simulation runs falling below five individuals by the final year of the simulation) and expected minimum abundance (defined as the minimum post-plague abundance averaged across all simulations; McCarthy & Thompson 2001).

SPATIAL SENSITIVITY ANALYSIS

To further investigate the effects of spatially explicit plague dynamics on ferret population viability, we ran the ferret population model with prey availability defined according to 500 distinct artificial prey landscapes. Simulation settings were varied across seven parameters hypothesized to influence the dynamics of plague spread (and thereby affect ferret population viability): (i) total landscape size (square areas varying from 30 km to 200 km per side), (ii) number of distinct colonies (varying from 9 to 1681), (iii) spatial clustering of colonies (regular grid or distinct clusters), (iv) background plague recurrence probability (plague spontaneously recurs somewhere in the metapopulation every 2 years to every 20 years), (v) prey R_{max} (varying from 1.8 to 2.8), (vi) intrinsic prey dispersal rate (intercept term from Eq. 1, varying from 0.061 to 0.105) and (vii) level of temporal variability in prey growth rate (see Appendix S3). Each of the

500 scenarios was selected by randomly sampling a single value from within the low-high range for each uncertain parameter (Table 1; Appendix S3). To study the effects of spatial configuration and fragmentation *per se* (Fahrig 2003), initial abundance and carrying capacity were set at two million individuals (approximating the initial estimated abundance of prairie dogs in the Conata/Badlands region) for all scenarios, representing sufficient prey resources to support a robust population of over 2000 black-footed ferrets in the absence of plague.

We assessed the relative importance of each variable as a predictor of black-footed ferret population viability using a Random Forest algorithm (Breiman 2001; Appendix S3). Relationships were visualized with conditional inference trees (Hothorn, Hornik & Zeileis 2006) and bivariate scatterplots. We also assessed the relationship between ferret population viability and mean nearest-neighbour distance among colonies in artificial prey landscapes, a derived variable closely related to landscape connectivity due to its role in determining prairie dog dispersal rates (and thereby affecting plague transmission risk; Appendix S3). To assess univariate relationships between sensitivity analysis variables and ferret population viability, we also fitted logit-linear models of ferret extinction risk as a function of each predictor variable.

After observing unexpected emergent oscillatory dynamics in the Conata/Badlands model and in many of the artificial prey landscapes, we assessed the contribution of each predictor variable (Table 1) to the emergence of oscillatory dynamics and the amplitude and frequency of the oscillations using the analytic approach outlined above (see Appendix S3). To assess the potential role of plague-driven oscillatory cycles in destabilizing ferret populations, we also examined the correspondence between ferret population viability and the occurrence of oscillations.

Results

EPIDEMIOLOGICAL MODEL

From the Outbreak output ($n = 1000$ replicates), we estimated that a single exposed prairie dog disperser had a 97% chance of initiating a plague epizootic in the

Table 1. Hypothesized influence of seven prairie dog metapopulation parameters on black-footed ferret population viability in artificial prey landscapes

Prairie dog variable	Range of values (see Table S3-1)	Hypothesized influence on black-footed ferret population viability
Metapopulation size (number of distinct colonies)	9–1681	More populations spread the risk of prey extinction.
Landscape size (km per side)	30–200	Larger and more diffuse landscapes will correspond to higher ferret viability via lower connectivity and plague transmission rates (e.g. McCallum & Dobson 2002).
Spatial clustering of colonies	Gridded, clustered	Clustered prairie dog landscapes will enable persistence of ferrets in smaller landscapes than gridded landscapes, by reducing global connectivity (and thereby plague transmission) relative to an equivalent gridded landscape.
Mean period of spontaneous plague outbreak recurrence	2–20	Presence of multiple plague initiation events (average of 1 colony every 2 years) will reduce ferret viability relative to single plague initiation event.
Intrinsic dispersal ability	0.061–0.105	Higher dispersal tendencies will result in more plague transmission events and therefore will lower ferret viability.
R_{max}	1.8–2.8	Higher R_{max} will correspond to faster recovery from plague and therefore higher ferret viability.
Temporal fluctuations in vital rates	See Table S1-1	Higher temporal variability will increase risk of ferret extinction after plague episodes, when ferret (and prey) abundance is lowest.

receiving colony. Once a plague epizootic was initiated, only 2.9% of the population survived to the next year (SE 0.8%). Averaged over an entire year, a prairie dog disperser from an infected colony had a 9.3% chance of carrying plague (see Appendix S1 for details on how we incorporated these results in the prey metapopulation model).

CASE STUDY: CONATA BASIN

Overall, the temporal pattern of plague prevalence (Fig. 2a,b) and prairie dog abundance (Fig. 2c,d) differed little between Conata Basin and the larger Conata/Badlands region. However, post-plague prairie dog abundance within the Conata Basin nearly always descended below levels capable of supporting a black-footed ferret population (Fig. 2c,e), whereas the ferret population tended to persist if available prey resources included all mapped colonies in the Conata/Badlands region (Fig. 2e). Simulated prairie dog (and ferret) population trajectories for the Conata/Badlands region frequently exhibited strong emergent oscillatory dynamics (Fig. S4-4). This

cyclic pattern was not observed in the absence of spatial structure or sylvatic plague outbreaks (Fig. 3a,b). In models without explicit spatial structure (i.e. all colonies treated as a single panmictic population), prairie dog abundance crashed almost instantaneously (Fig. 3b), sharply contrasting with observed rates of plague spread in the Conata/Badlands region (plague took 3 years to travel *c.* 38 km; Travis M. Livieri, unpublished data). Rates of spread in spatially explicit models with a background rate of infection were consistent with the observed rate of spread at Conata Basin (Fig. S4-5). Limiting the initiation of plague to a single event resulted in a less frequent oscillatory pattern and higher mean prairie dog abundance (Fig. 3c) relative to scenarios with a background rate of infection due to occasional extirpation of plague from simulated landscapes (see link to plague spread animation in Appendix S4).

SPATIAL SENSITIVITY ANALYSIS

Black-footed ferret extinction risk was most sensitive to the spatial extent of artificial prairie dog metapopulations

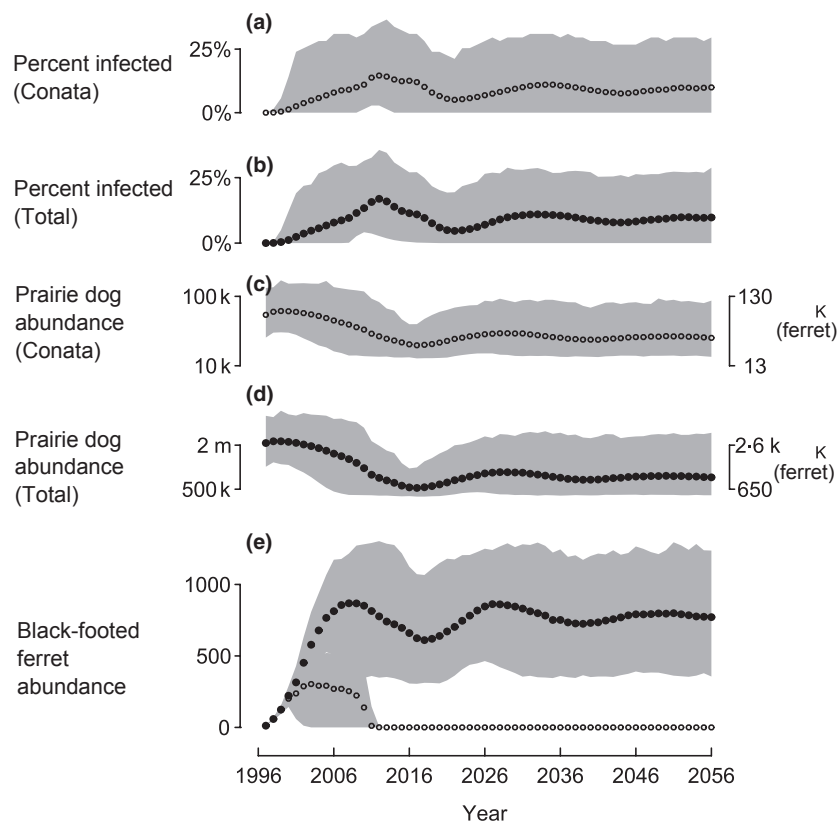


Fig. 2. Simulated abundance and infection rates for a plague-affected black-footed ferret study system in southwestern South Dakota. The top two panels illustrate regional plague severity (% of populations infected each year) for (a) the area observed to be used by ferrets (Conata Basin, open circles) and (b) the region potentially available to ferrets (Conata/Badlands region; filled circles). The next two panels display the simulated abundance of prairie dogs (c) in the Conata Basin area and (d) in the Conata/Badlands region. Secondary y axes display carrying capacity (K) for black-footed ferrets, computed as $1/766$ of prairie dog abundance (see text). The final panel (e) displays simulated abundance of ferrets under two scenarios: K determined on the basis of prairie dog abundance in the Conata Basin (open circles), and K determined on the basis of prairie dog abundance in the larger Conata/Badlands region (filled circles). Ferret abundance starts from zero in the year 2000, the year ferret reintroduction began in the Conata Basin. Grey regions encompass 95% of the results from all simulation runs.

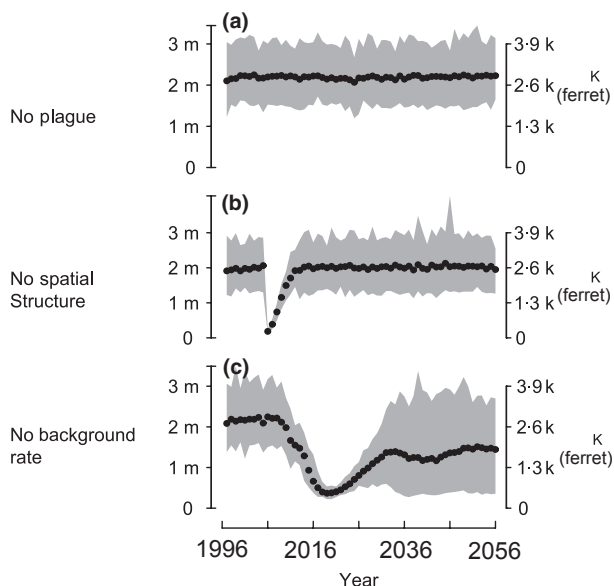


Fig. 3. Simulation results (total abundance of prairie dogs; cf. Fig. 2d) from the same model presented in Fig. 2, but run in the absence of (a) plague, (b) metapopulation structure (i.e. a single panmictic prairie dog population) and (c) background rate of plague (small probability of spontaneous infection), respectively.

(Fig. 4a), such that landscapes smaller than 50×50 km (2500 km^2 , corresponding to regional densities >8 prairie dogs per ha) were less likely to sustain reintroduced ferret populations through plague epizootics (Figs 4b and 5a). The total number of colonies in the landscape ranked second in importance as a predictor of black-footed ferret extinction risk (Fig. 4a). The degree of fragmentation (# distinct colonies) and the configuration of colonies (gridded vs. clustered) influenced ferret viability for relatively dense prey landscapes (≤ 40 km per side), such that extinction risk was maximized at an intermediate level of fragmentation ($9 < \# \text{ colonies} \leq 441$; Fig. 4b). The remaining variables included in the sensitivity analysis – presence of periodic plague initiation events, maximum intrinsic rate of growth of the prairie dog populations and the strength of temporal variation in prairie dog vital rates – had little detectable impact on black-footed ferret population viability (Fig. 4a). Landscape spatial extent exhibited a stronger association with black-footed ferret extinction risk than mean nearest-neighbour distance (mean distance from colony centre to nearest-neighbouring colony edge). A univariate logit-linear model of ferret extinction risk as a function of landscape extent (Fig. 5a) outperformed an analogous model with mean nearest-neighbour distance (Fig. 5b) with ΔAIC of 160. The observation that total landscape extent was a superior predictor of ferret extinction risk compared with mean nearest-neighbour distance (Fig. 5) suggests that plague spread was driven by the absolute numbers of dispersers rather than dispersal rates *per se*.

Prairie dog metapopulations with strong oscillatory dynamics generally corresponded to reduced ferret viability;

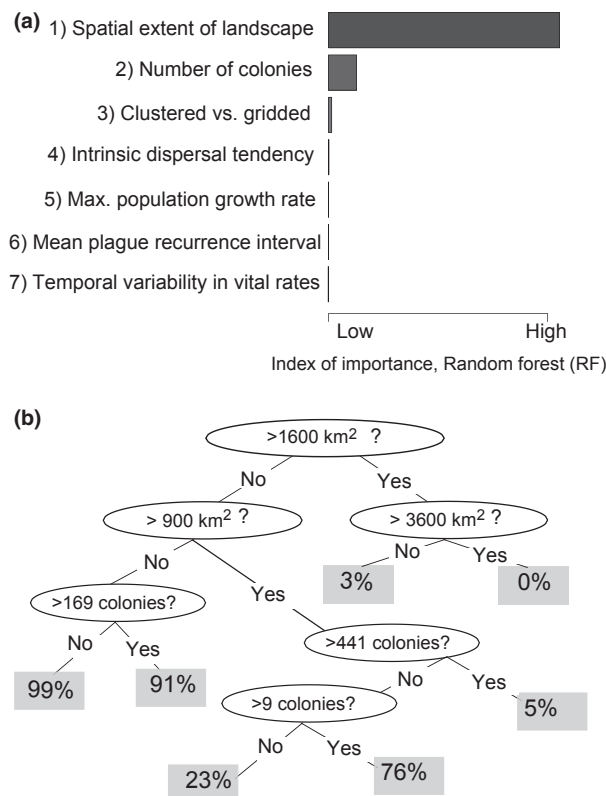


Fig. 4. Sensitivity of black-footed ferret extinction risk to seven variables hypothesized to influence the dynamics of plague spread in artificial prey landscapes: landscape extent, metapopulation size (number of colonies), spatial clustering of prairie dog colonies, intrinsic tendency of prairie dogs to disperse, maximum population growth rate (R_{\max}), mean period between spontaneous plague recurrence and magnitude of annual fluctuations in prairie dog population growth. (a) Relative importance of each variable for predicting ferret extinction risk, derived from a Random Forest algorithm; (b) results from a single conditional inference tree. Splitting rules are indicated within ovals, and final predictions of extinction risk are shaded in grey.

expected minimum ferret abundance averaged 261 (95% CI: 244–278) in the absence of oscillatory cycles and 110 (95% CI: 79–140) in simulated landscapes with strong oscillatory cycles (Fig. 6a) across all 500 simulations in the spatial sensitivity analysis. Similarly, extinction risk increased from 0.08 (95% CI: 0.05–0.10) to 0.42 (95% CI: 0.34–0.50) in the presence of strong oscillations in landscape-level prairie dog abundance. When plotted across a two-dimensional slice of parameter space defined by the two highest importance variables for predicting ferret extinction risk (landscape extent and number of colonies), regions of high oscillation probability overlapped substantially with regions of high ferret extinction risk (Fig. 6b).

Discussion

Our modelling results suggest that black-footed ferret extinction risk may be higher in plague-affected landscapes

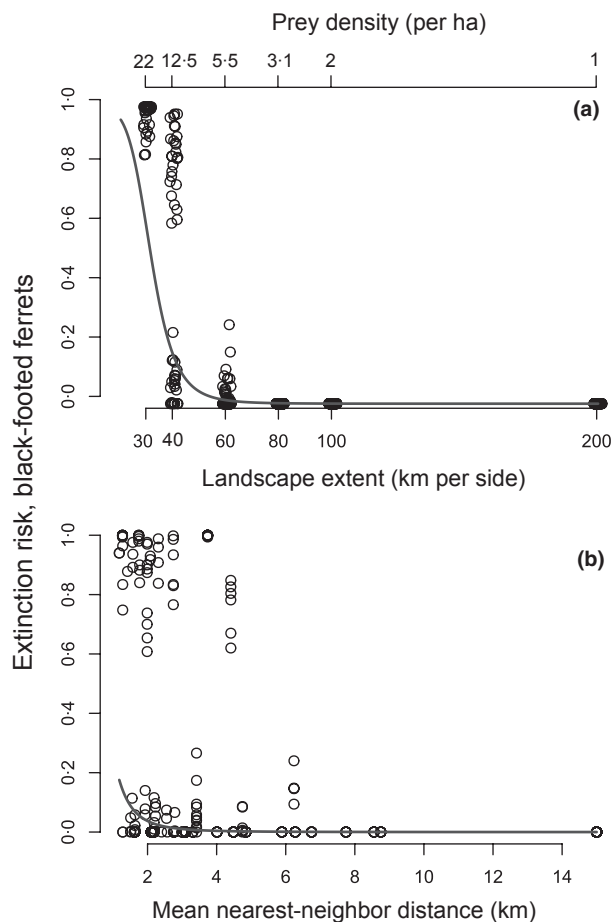


Fig. 5. Black-footed ferret extinction risk as a function of (a) spatial extent of artificial prey landscape (km per side) and (b) mean nearest-neighbour distance among colonies (km). For clarity, simulated landscapes with clustered colony structure are excluded.

with dense, closely spaced prairie dog colonies than in landscapes with colonies spread over larger areas (<8 prairie dogs ha⁻¹ and covering >2500 km²). Conata Basin, deemed high-quality habitat for reintroduced black-footed ferrets due to its large and densely packed black-tailed prairie dog colonies (Jachowski *et al.* 2011b; Livieri & Anderson 2012), provides an interesting case in point. This site was plague-free until 2008 and displayed growing or stable population dynamics of prairie dogs and black-footed ferrets from the date of first release (1996) to the date of plague arrival (Livieri 2006; Wisely *et al.* 2008). With regional black-tailed prairie dog densities measured as high as 30 to 50 per hectare (Biggins *et al.* 2011a), Conata Basin falls into a high-risk zone according to our models, whereby plague-induced extinction of black-footed ferrets is predicted in the absence of exogenous influences (e.g. influx of prey, relocation of ferrets or costly plague mitigation efforts). In reality, the ferret population at Conata Basin has declined dramatically since sylvatic plague was detected in 2008, falling from 335 in 2007 to only 71 animals in 2012 (Travis M. Livieri, unpublished data). Plague mitigation efforts at

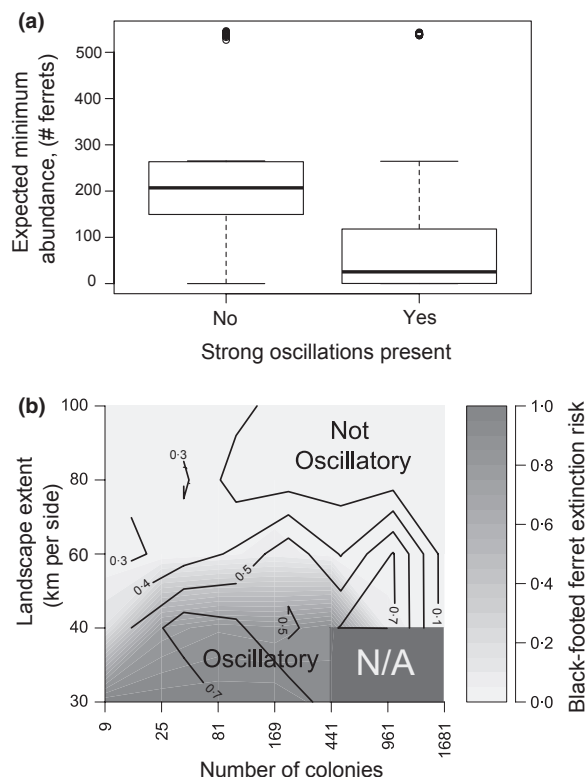


Fig. 6. Relationship between ferret population viability and the presence of strong plague-driven oscillatory dynamics in artificial prey landscapes. (a) expected minimum abundance for ferrets occupying prairie dog metapopulations with weak or no oscillatory dynamics (labelled ‘No’) vs. metapopulations with strong oscillatory dynamics (labelled ‘Yes’). (b) Oscillatory dynamics and ferret extinction risk across a two-dimensional slice of parameter space covering a wide range of landscape sizes (km per side) and metapopulation sizes (number of colonies). Dark grey areas denote high risk of black-footed ferret extinction, and contour lines show the frequency of strong plague-driven oscillatory dynamics. The grey region labelled ‘N/A’ represents a constrained region of parameter space (i.e. unable to fit further distinct colonies without colony overlap).

Conata Basin, including vaccination of black-footed ferrets, dusting (i.e. insecticide treatment) of prairie dog burrows and experimental oral vaccination of prairie dogs (Abbott & Rocke 2012), have thus far helped to avert extirpation of ferrets at this important release site.

This study highlights the potential importance of meta-population connectivity in fuelling plague epizootics and thereby imperilling black-footed ferret conservation efforts. Empirical evidence supports the link between meta-population connectivity and disease spread in this predator–prey–disease system. White-tailed prairie dogs *Cynomys leucurus* tend to occur in lower densities than black-tailed prairie dogs (Hoogland 1995), and some research indicates that black-footed ferret populations established on large, low-density white-tailed prairie dog complexes may have higher probabilities of surviving a plague epizootic than ferret populations occupying higher-density black-tailed prairie dog complexes (Cully &

Williams 2001). Notably, the ferret population at Shirley Basin, Wyoming (Grenier, McDonald & Buskirk 2007), occupying a large (>1200 km²) complex of white-tailed prairie dogs, persisted through a plague epizootic in 1994 (Wisely *et al.* 2008) without plague mitigation or other exogenous influences. Furthermore, evidence suggests that the last wild black-footed ferret population (at Meeteetse, Wyoming), also occupying white-tailed prairie dog habitat, experienced at least one plague epizootic prior to ferret extirpation (but plague ultimately led to the demise of this population). Nonetheless, plague currently affects populations of white-tailed, black-tailed, Gunnisons *C. gummisoni* and Utah prairie dogs *C. parvidens* and the mechanisms underlying epizootics remain unclear, underscoring the need for continued research on plague persistence and transmission.

EMERGENT PATTERNS

Our study highlights the interesting demographic dynamics that can emerge in a spatially complex landscape with density-dependent, disperser-mediated disease transmission. Among the emergent patterns observed in our simulation models, perhaps most notable was the oscillatory fluctuations in predator and prey abundance exhibited in the Conata Basin case study and many of the artificial prey landscapes. This oscillatory pattern was driven by disperser-mediated disease transmission, whereby plague epizootics were suppressed by insufficient transmission rates at low population densities. As prairie dog populations grew and connectivity was restored, a wave of renewed outbreaks of plague became inevitable, generating a cycle of collapse and recovery that could be sustained as long as *Y. pestis* persisted within the metapopulation (see link to animation in Appendix S4). Not surprisingly, the strongest oscillatory dynamics tended to correspond with compact, high-connectivity artificial landscapes in which plague could spread rapidly and synchronously through the prairie dog metapopulation (Fig. 6b). Similar cycles (5–10 years) of plague outbreaks have also been observed in natural systems (Barnes 1982; Cully & Williams 2001; Cully *et al.* 2010), although the underlying mechanisms are unclear. For example, an unmanaged black-tailed prairie dog colony at Rocky Mountain Arsenal National Wildlife Refuge has exhibited a *c.* 5-year interval between plague epizootics from 1988 to 2000 (Seery & Matiatos 2000; Seery *et al.* 2003).

ADVANTAGES AND DISADVANTAGES OF LINKED METAMODELS RELATIVE TO SINGLE-SPECIES MODELS

In this study, we used linked models – what has been termed a ‘metamodel’ approach (Miller & Lacy 2003; Lacy *et al.* 2013; Prowse *et al.* 2013) – to reveal dynamics that can emerge from interactions among species and with disease (Fig. 1). The oscillatory dynamics of prairie dog abundance, in turn driving oscillations and sometimes

extinction of the ferret population, did not occur in models that lacked epidemic disease, spatial structure of the prairie dog metapopulation or occasional arrival of infected animals from outside the modelled system. Therefore, a more traditional single-species PVA model of the black-footed ferret population, even if incorporating the requirement for a sufficient prey base and the threat from occasional disease, would not have led to the same predictions regarding the importance of habitat extent in mediating the impact of epidemic disease on the predator–prey system.

However, there are also disadvantages of a metamodel compared to models that focus on one primary process or species. Each submodel requires many parameters that are at best uncertain. While a metamodel usefully allows dynamic processes to cascade through the linkages, the uncertainty also propagates. Therefore, sensitivity tests will be necessary to identify dependence of results on uncertain parameters (e.g. Figs 4, 5 and 6) as well as the dependence of results on metamodel structure (e.g. presence or absence of specific metamodel components; Fig. 3).

CAVEATS

We used sensitivity analysis to reveal which factors and processes in the model had largest effect on results and to test whether alternative estimates would have led to different general conclusions. However, we recognize that uncertain or omitted factors beyond the scope of our sensitivity analysis could alter simulation results and subsequent management recommendations. In our models, black-footed ferret populations behaved as a single panmictic group regardless of the size or spatial structuring of prey populations. However, spatial structuring of ferret populations may have important consequences for population viability via local prey deficiencies (potentially damaging viability) and extinction–recolonization dynamics (potentially conferring dynamic metapopulation stability; Hanski, Moilanen & Gyllenberg 1996). Although it is clear that black-footed ferret spatial ecology is strongly dependent on the spatial distribution of their primary prey (Jachowski *et al.* 2010; Eads *et al.* 2011), the conditions (e.g. spatial extent and clustering of prey colonies) under which metapopulation dynamics emerge in black-footed ferrets remain unclear. Black-footed ferrets are capable of long-distance movements and have been known to cover more than 49 km in short periods (Biggins *et al.* 1999). In Conata Basin, annual net displacement distances of 10 km by both males and females were documented (Travis M. Livieri, unpublished data), suggesting that it may not be unreasonable to assume that ferrets could occupy a 200 × 200 km prairie dog complex (largest artificial landscapes in this study) after 10 years. Clearly, the spatial ecology of ferret populations occupying heterogeneous, low-density prairie dog landscapes merits further research.

In our models, plague transmission among colonies primarily occurred via disperser-mediated transmission of infected fleas. However, carnivores and raptors are likely to play a role in transporting plague-infected fleas to distant prairie dog colonies (Abbott & Rocke 2012), and small mammals – notably, grasshopper mice *Onychomys leucogaster* – have been strongly implicated in plague spread at smaller spatial scales (Salkeld *et al.* 2010). However, the mechanisms of plague transmission among colonies by these organisms are not yet well understood, especially at large spatial scales. For simplicity, we modelled the composite contribution of alternative transmission vectors using a single constant background rate of infection. We also did not attempt to model enzootic plague, which affects both prairie dogs (Biggins *et al.* 2010) and black-footed ferrets (Matchett *et al.* 2010). We emphasize that very different demographic outcomes and management recommendations may emerge if alternative mechanisms were found to play a more dominant role in plague transmission. As additional data on plague transmission (and other demographic processes) become available at sites like Conata Basin, refined versions of our models can be used to produce robust site-specific management recommendations.

MANAGEMENT IMPLICATIONS

The recovery goal for black-footed ferrets, as stated in the current recovery plan (U.S. Fish & Wildlife Service 2013), is 3000 black-footed ferrets in 30 or more populations across the historic range. Our models suggest that vast prairie landscapes (>2500 km²) may be necessary to sustain a single ferret population through recurring plague epizootics. Although other studies (Forrest *et al.* 1985; Richardson *et al.* 1986; US Fish & Wildlife Service 1988, 2013; Conservation Breeding Specialist Group 2004; Jachowski *et al.* 2011a) have also concluded that 'large' areas of habitat are necessary to maintain black-footed ferrets, the areas mentioned in these studies range only from 25 to 200 km². Unfortunately, few landscapes >2500 km² occupied by prairie dogs exist today (Proctor, Haskins & Forrest 2006). For the foreseeable future, it is likely that successful efforts to achieve recovery goals for black-footed ferrets in plague-affected areas will depend upon effective plague mitigation tools such as dusting of prairie dog burrows and vaccination of ferrets (Abbott & Rocke 2012). Extensive field trials of an oral prairie dog vaccine for prairie dogs are currently underway (T. E. Rocke, personal communication). In addition, the strong relationship between plague-induced oscillatory prey cycles and predatory population persistence, as suggested by our models (Fig. 6), suggests the use of field surveys to assess the spatial extent over which plague outbreak cycles are strongly synchronous. Targeting these high-risk areas with management interventions to disrupt connectivity and subsequent plague transmission may help to minimize the extent of plague epizootics and overall impact on the

prairie dog metapopulation (Fig. S4-4). Our findings underscore the importance of working with many constituents to conserve large prairie dog landscapes (Proctor, Haskins & Forrest 2006; Jachowski *et al.* 2011a; Livieri 2011) and to develop improved plague mitigation tools. More generally, this study illustrates the insights that multispecies modelling yields for population viability assessment and conservation planning, especially for strongly interacting or co-dependent species ensembles that include threatened taxa.

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Data accessibility

Detailed model descriptions are available in the online supporting information and R scripts are available from the authors upon request.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Demographic and spatial model specifications.

Appendix S2. Details of the plague transmission model.

Appendix S3. Details of the sensitivity analysis routine.

Appendix S4. Supplementary Results and Figures.