



Simulated effects of habitat loss and fragmentation on a solitary mustelid predator

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Abstract

Brine spills associated with petroleum extraction can reduce the amount of suitable habitat and increase habitat fragmentation for many terrestrial animals. We conducted a simulation study to quantify the effects of habitat loss and fragmentation on a solitary mammal predator. To provide focus, we adopted biological attributes of the American badger (*Taxidea taxus*) and environmental attributes of the Tallgrass Prairie Preserve in Oklahoma. We simulated badger activities on landscapes with different degrees of habitat loss and fragmentation using a spatially explicit and individual-based population model. Both habitat loss and fragmentation increased the incidence of habitat-related mortality and decreased the proportion of eligible females that mated, which decreased final population sizes and the likelihood of persistence. Parameter exploration suggested that steep, threshold-like, responses to habitat loss occurred when animals included high-risk habitat in their territories. Badger populations showed a steeper decline with increasing habitat loss on landscapes fragmented by spills than on less fragmented landscapes. Habitat fragmentation made it difficult for badgers to form high-quality territories, and exposed individuals to higher risk while seeking to establish a territory. Our simulations also suggest that an inability to find mates (an Allee effect) becomes increasingly important for landscapes that support a sparse distribution of territories. Thus, the presence of unmated females with territories may foreshadow population decline in solitary species that do not normally tolerate marginal adults.

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1. Introduction

Habitat loss is the most significant cause of species extinctions (Wilcove et al., 1998). Fragmentation of the remaining habitat often occurs during habitat loss, and this has been linked to decreased species diversity in a variety of taxonomic groups (e.g., Crooks, 2002; Drinnan, 2005). Habitat loss and fragmentation are a

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particular concern for America's native grasslands, a vanishing ecosystem whose species are disappearing with the prairie habitats on which they depend (US Fish and Wildlife Service, 1998). Few ecosystems have experienced as great a degree of loss and alteration. Prior to European settlement, tallgrass prairies covered nearly 1-million km² (Howe, 1994). Today, tallgrass prairies occupy less than 0.1% of their historical range. The loss of tallgrass prairie has resulted from cultivation (conversion to agricultural use), altered grazing and burning regimes (Briggs et al., 2002), development of roads and residential areas, and other human activities.

This theoretical study focuses on habitat loss and fragmentation caused by brine spills associated with petroleum extraction, and represents part of a larger risk assessment (Efroymsen et al., 2004). Brine spills cause severe and long-lasting damage to vegetation. Rock interstices of some geologic formations contain brine that is extracted with oil and gas. When spills of this mixture occur, affected vegetation dies and gradually recovers over a time scale of decades, if not centuries. For example, Tallgrass Prairie Preserve (TPP) in Oklahoma has denuded soils caused by spills 80 years ago. Furthermore, the effects of brine often spread to surrounding areas because of soil erosion. Improving drainage, preventing erosion and stimulating microbial activity can hasten recovery (Atalay et al., 1999).

Our goal is to separate the influence of habitat fragmentation, which we define here as the partitioning of a fixed area into fewer or more distinct patches, from that of habitat loss. In field studies (e.g., Schmiegelow et al., 1997), the term "habitat fragmentation" is often used to refer to both the loss of habitat and partitioning of habitat into smaller patches (Andren, 1994). Because this is a simulation study, we are able to vary loss and fragmentation of habitat independently. In this study, we increase habitat fragmentation by increasing the number of brine spills that create areas of unsuitable habitat. The spatially explicit individual-based approach adopted here does not assume that patch isolation can be inferred from the characteristics of the landscape without knowing about the organism. Instead, metapopulation structure is an emergent property of the behaviors (movements and activities) of animals traversing the landscape, which are influenced by the configuration of suitable habitat in the landscape. Whereas distinct areas of suitable habitat

that remain may be isolated (i.e., separated by barriers to movement) from the perspective of some lifestages, they may not be for others.

As it is useful to have a particular species and ecosystem in mind, we focus on the American badger in a tallgrass-prairie habitat. A solitary predator adapted to burrowing, the American badger uses its burrowing ability to dig dens and forage on fossorial small mammals. In this study, we assume that petroleum extraction influences badger populations indirectly through habitat availability, and not through exposure to toxic substances or indirect trophic pathways. We examine the effects of both the fragmentation and loss of habitat associated with brine spills on this species.

2. Study area

Although this study is intended to be general, we focus on a particular site, the Tallgrass Prairie Preserve in Oklahoma owned by The Nature Conservancy. We describe spatial variation in vegetation cover in the TPP using a land cover map with 30 m resolution from the Oklahoma GAP program (Dr. William Fisher; Oklahoma State University). The TPP covers 157.2 km² and consists of 71% tallgrass prairie, 20% woodland and savanna and the remainder in other categories, such as streams, roads and oil wells (Fig. 1).

Approximately 126 brine scars covering approximately 1.1% of the TPP are evident from maps digitized by Elizabeth Word from digital ortho-quarter quadrangle photos taken by Bryan Tapp (University of Tulsa). Spill areas ranged from 7 to 49,000 m², with an average spill area of 1380 m² (S.D. = 4800 m²). Our simulations are designed to evaluate the impacts of much larger total areas of disturbance than those observed in the TPP.

3. Simulated environment

Spatial input data used by the population model partitions the TPP into 30 m × 30 m cells. We characterize each cell by its vegetation cover, whether or not it contains a brine spill, and information about the simulated individual badgers that it contains. To predict the effects of brine spill impacts on badger populations, the population model reads in spill landscapes that are generated with a specified percentage of area covered by spills,

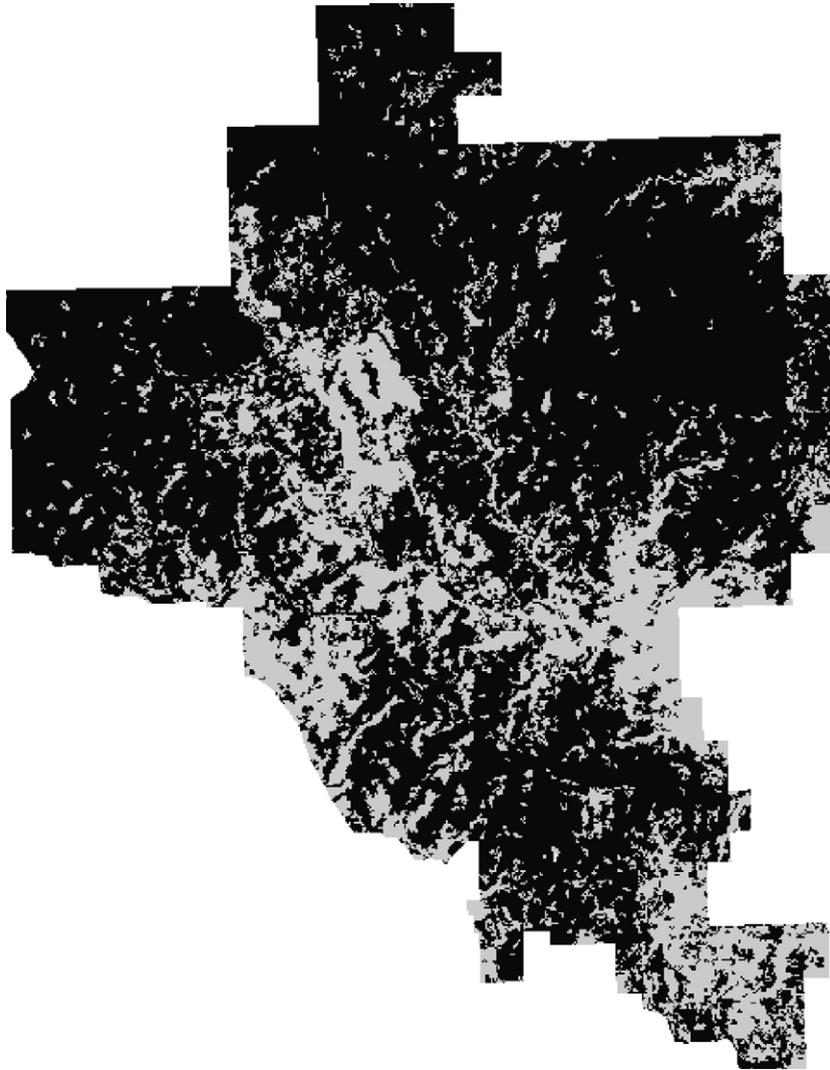


Fig. 1. Map of simulated badger habitat quality at the Nature Conservancy Tallgrass Prairie Preserve, Oklahoma, USA. National Gap Analysis Program data from Mark Gregory, Oklahoma State University provided land cover classifications. Key: white = unsuitable or outside boundary, grey = marginal habitat, black = optimal habitat.

and a specified number of spills on the rectangular area containing the TPP (Jager et al., 2005). A 2D Poisson model is used to locate spill centers on the landscape, and spill sizes were drawn from a Dirichlet distribution for the proportion of total spill area. A random walk algorithm simulates diffusion of the spill area outward from the spill center.

The habitat quality of a model cell influences whether it will be part of an individual's breeding territory. If a cell becomes incorporated into a territory,

its quality influences the individual's chances of survival while visiting the cell. In the model, we assign a habitat suitability index (HSI) to each vegetation category in the landscape based on qualitative information describing badger habitat preferences, which reflect its burrowing lifestyle and dependence on small fossorial mammals as prey (Messick and Hornocker, 1981). Tallgrass and mid-grass prairie, which is considered ideal habitat for the American badger, is assigned the maximum quality (HSI = 1.0). We assign croplands,

pasturelands, savanna forest and woodland habitats as intermediate quality ($HSI = 0.5$). Cells containing lakes, reservoirs, residential areas, industrial areas and brine spills are considered unsuitable ($HSI = 0.0$).

4. Population model description

Three processes that define the dynamics of spatially structured populations are reproduction, survival and movement. Each of these is represented in our model and described in the sections below. Parameter values used in the model are given in Table 1.

The population model is spatially explicit and tracks individual badgers using an object-oriented approach.

We adopted an individual-based approach to simplify simulation of Allee effects, formation of territories and aggressive interactions (which are important for mustelids). Each animal can belong to one of five distinct phases at one time: (1) pre-breeding, (2) mating, (3) post-mating, (4) birthing and (5) rearing of young. However, different individuals may be in different phases at a given time and individuals may enter some phases multiple times during their lives. Its phase determines what activities the animal engages in. Species-specific beginning and ending dates are provided for these phases, but they may also depend on attributes of the individual. For example, adults do not enter the mating phase until they establish a territory.

Table 1
Description of model parameters and values used in simulations

Parameter description	Name	Parameter value	Reference
Age of infant to juvenile transition	AgeJuv	84 days	Blood (1995)
Age of juvenile to adult transition	AgeAdult	365 days	Blood (1995)
Duration of incubation	BirthDays	10.0 days	Blood (1995)
Initial population size	N_0	250	Fixed
Fraction of female juveniles breeding	JuvBreed	0.40	Messick and Hornocker (1981)
Average dispersal distance	AvgDisp	10 cells	Calibrated
Average within-range movement distance	InRangeDist	0.4 km	Minta (1993)
Minimum acceptable territory quality	Q_{min}	0.75	Fixed
Min. territory size male, female	TerrSizeMin	2.70, 1.37 km ²	Messick and Hornocker (1981)
Max. territory size male, female	TerrSizeMax	6.27, 3.04 km ²	Messick and Hornocker (1981)
Number of sub-grids per side	N_{sub}	7	Fixed
Limit on within-range movement attempts	N_{tries}	50	Fixed
Max. number of offspring	MaxBorn	5	Minta (1993)
Movement wait in summer	SummerWait	1 day	Messick and Hornocker (1981)
Movement wait in winter	WinterWait	10 days	Messick and Hornocker (1981)
Interval between attempts to establish territories	DispWait	7 days	Fixed
Probability of emigration at boundaries	P_{emig}	0.0	Fixed
Probability of staying put	P_{stay}	0.40	Fixed
Probability of moving (eight directions sum to $1 - P_{stay}$)	P	0.15, 0.05, 0.05, 0.05, 0.05, 0.05, 0.05, 0.15	Fixed
Male cell quality factor (#other males)	QN(0), QN(1), QN(2)	1.0, 0.25, 0.0	Messick and Hornocker (1981)
Female cell quality factor (#females)	QN(0), QN(1), QN(2)	1.0, 0.50, 0.0	Messick and Hornocker (1981)
Sex ratio (proportion male)	Ratio	0.50	Messick and Hornocker (1981)
Survival in poor habitat	S_{qm}	0.99600	Calibrated
Survival of movement inside/outside home range	S_{in}, S_{out}	0.99999, 0.99990	Calibrated
Survival of fight (resident, non-resident)	$S_{fight.res}, S_{fight.nres}$	1.00000, 0.99990	Fixed
Survival to birth	S_{birth}	0.45400	Messick and Hornocker (1981)
Survival – baseline age 0	$S_{age}[0]$	0.99965	Messick and Hornocker (1981)
Survival – baseline age 1	$S_{age}[1]$	0.99965	Messick and Hornocker (1981)
Survival – baseline age 2	$S_{age}[2]$	0.99982	Messick and Hornocker (1981)
Survival – baseline age 3	$S_{age}[3]$	0.99995	Messick and Hornocker (1981)

4.1. Movement

Like most terrestrial mustelid predators, American badgers defend territories (Johnson et al., 2000). Although badgers territories are not completely exclusive, we consider the term “territory” to be a useful descriptor of badger home ranges and use the two terms interchangeably. Messick and Hornocker (1981) found no evidence of individuals relocating their territories between seasons or years. We simulate this by allowing individuals to establish a permanent home range, which also serves as its breeding territory. Two types of movement represented by the model are dispersal and territory establishment and within-range movement (described below).

4.1.1. Dispersal and territory establishment

Juveniles disperse in the spring of their first year between the ages of 3 and 6 months. Juveniles (and adults lacking territories) disperse and attempt to establish territories between mid-June and mid-August.

To establish a breeding territory, individuals assess the suitability of habitat cells for reproduction. We define an index for breeding quality, QB, which combines a density-dependent quality index, QN, with the habitat suitability index, HSI, associated with vegetation type (Eq. (1)). We assume areas impacted by brine spills are not suitable, HSI = 0. Density-dependent cell quality, QN in Eq. (1) decreases as the number of same-sex conspecifics, N , increases. Thus, contest competition is simulated through the influence of density on the establishment of territories by individual animals. The inability of individuals that fail to establish a territory to reproduce ultimately regulates population size.

$$QB = QN \times HSI \quad QN_{\text{male}} = \begin{cases} 1, & N = 0 \\ 0.25, & N = 1 \\ 0, & N > 1 \end{cases} \quad QN_{\text{female}} = \begin{cases} 1, & N = 0 \\ 0.5, & N = 1 \\ 0, & N > 1 \end{cases} \quad (1)$$

Solitary, sparsely distributed mammal species, such as the American badger, are stereotyped as having little tolerance for conspecifics of the same gender, particularly among males (Sandell, 1989). However, further study has shown that the American badger is

more tolerant of overlapping territories than previously believed. Two studies reported overlap among female territories (Messick and Hornocker, 1981; Minta, 1993), and another reported overlap among male territories (Goodrich and Buskirk, 1998). Our choices for the two QN vectors permit overlap with one other animal of the same gender and assign lower tolerance of overlap to males than females (Table 1).

Individuals typically have larger territories in areas with poor habitat than in areas with good habitat. For example, average territory sizes reported in the Utah desert (5.8 km² for males, 2.4 km² for females, Lindzey, 1978) are much larger than those reported in more productive habitat in Idaho (2.4 km² for males, 1.6 km² for females, Messick and Hornocker, 1981). Males establish larger territories than females, presumably in order to ensure overlap with female partners (Minta, 1993). We therefore assign larger territory sizes to males than females (Table 1).

Our algorithm results in larger territories in poor habitat. Each individual begins to search for a territory at a suitable starting location, and then expands the search outward until the territory reaches a minimum size. If, at this point, the candidate territory meets a minimum average quality, it is adopted. Otherwise, the individual will continue dispersing and try to establish a territory later, starting at a different cell. Because territory acquisition during the dispersal period is computationally demanding, the time interval between attempts to form a territory from a new starting location, DisperseWait, can be specified.

The initial starting location is defined by choosing a distance and direction. The distance is drawn from an exponential distribution (Eq. (2)) with mean AvgDisp = 3.43 km (Hornocker et al., 1983). The direction is selected by dividing the area around the individual into eight pie-shaped wedges with the individual facing one of those wedges. A vector of movement propensities for eight directions, P , control the tendency for an individual to keep moving in the same direction, $P(0)$, or to deviate by moving toward one of the seven other directions.

$$\text{AvgDisp} = E[x] = \int_0^{\infty} \lambda e^{-\lambda x} dx, \quad \lambda > 0. \quad (2)$$

A hierarchical approach is used to expand from this initial starting location. First, a large square with area TerrSizeMax is centered there, where TerrSizeMax

should be large enough to contain the largest territories observed in the field. This large square is divided into a coarse $N_{\text{sub}} \times N_{\text{sub}}$ -grid of sub-squares, and the average quality of each sub-square is evaluated from the QB values of its cells (Eq. (1)). The center sub-square is first added. The algorithm continues by evaluating the quality of all adjacent sub-squares and adding the sub-square with the highest quality. Range expansion continues until the candidate territory reaches a minimum territory size, TerrSizeMin . Once this minimum size is attained, additional sub-squares are added only if they increase the average quality of the candidate territory and do not allow the territory to exceed the maximum size, TerrSizeMax . Whether the candidate territory is finally accepted or rejected depends on whether its average quality exceeds Q_{min} . We assume that badgers retain territories that they establish for life.

4.1.2. Within-territory movement

Adults with territories move among cells that are within the territory. Badger movements are widely reported to be less frequent in winter than summer (Lindzey, 1978; Messick and Hornocker, 1981). In summer, we simulate movements daily; in winter (November–March), individuals wait 10 days between moves (see parameters SummerWait and WinterWait in Table 1). At each movement opportunity, the movement algorithm draws up to $N_{\text{tries}} = 50$ candidate locations at random from cells in the territory. The likelihood of accepting a candidate cell is higher for closer cells, and is calculated using the exponential density function with mean InRangeDist .

Gestating females do not move during the birthing period. After birth and during nesting, the mother typically moves her litter to a new den from time to time, allowing her access to new hunting grounds and providing the family access to a new latrine area (Messick and Hornocker, 1981). We do not simulate independent movement of offspring until they disperse. Instead, individuals in the litter are moved whenever the mother moves.

4.2. Reproduction

Understanding the social relationships among related females and their tolerance of shared breeding space allows more accurate predictions of the reproductive potential for a given area of habitat for mammal

species that have non-mobile, altricial young (Wolff, 2001). Badgers mate in the summer when they are moving about and more likely to encounter a mate. The mating period extends from mid-July to mid-August. Mated females delay implantation of their embryos until late winter and give birth in spring. The mother provides parental care from birth, in early April, to mid-July, when juveniles disperse to establish a home range (Minta, 1993). Earlier dispersal has also been reported (Messick and Hornocker, 1981).

Our model assumes that any mature female with a home range successfully mates if her home range overlaps with that of at least one mature male. Because badger births are synchronized, they occur during a brief period, BirthDays , in early spring. For each mated female that survives until spring, we simulate the number of offspring born as a Poisson random variable with a mean value of $\text{MaxBorn} \times S_{\text{birth}}$, where MaxBorn is the maximum litter size and S_{birth} is the average survival of young (Table 1). The gender of each offspring is determined by assuming that those offspring who draw a uniform random number, $U \leq \text{ratio}$ (Table 1) are male.

4.3. Survival

The model simulates six general sources of mortality that affect terrestrial animals. These include: (1) habitat-related mortality, (2) risk associated with movement, (3) mortality caused by fighting with conspecifics, (4) age-related mortality, (5) mortality caused by losing a parent during rearing and (6) emigration. The order in which risks are encountered is scrambled each day to ensure that the risks do not compete. For each risk, a uniform random deviate, U , is drawn on the interval $[0,1]$ and compared to the probability of survival, $S = 1 - \text{risk}$. A particular individual survives if $U \leq S$. We distinguish between event-based risks and non-event-based risks. Simulated badgers are exposed to non-event-based risks daily, whereas event-based risks are triggered by specific events like the loss of a parent.

The relative importance of these risks is not known, but can be controlled by varying survival parameters S_{in} , S_{out} , S_{qmin} and $S_{\text{fight_nres}}$, which are defined below. Badger mortality is dominated by human causes (Hornocker et al., 1983; Van Apeldoorn et al., 1998). In Southwest Idaho, road-related mortalities accounted

for 59% of deaths and hunting and trapping accounted for 30%. Messick and Hornocker (1981) reported that starvation was also a factor in Idaho badger populations. Road mortality at the TPP is less important because there are few roads, mostly dirt, that are traveled slowly. More detail about the simulation of each risk is described below.

4.3.1. Survival of movement risk

We simulate movement-related mortality as a simple representation of risks associated with traveling. Movements outside the home range are assumed to be more risky than those within the home range. We specify a probability of surviving movement between adjacent 30-m cells within the home range, S_{in} , and outside the home range, S_{out} . An individual's probability of surviving movement in a given day, S_{move} , is:

$$S_{move} = S_{in}^{(D_{in})} + S_{out}^{(D_{out})} \quad (3)$$

S_{move} decreases with the distance (#cells) traveled both inside, D_{in} , and outside, D_{out} , of the home range. Movements outside the home range occur during dispersal.

4.3.2. Habitat-related survival

Habitat-related mortality simulates the increased risk of starvation associated with spending time in poor quality areas; i.e., those with an inadequate supply of small mammal prey. Daily survival of habitat-related mortality, QS , is linked to the quality of the cell in which the simulated badger resides through a function that increases from a minimum value, S_{qm} , in unsuitable habitat to a maximum value of one in optimal habitat.

$$QS = S_{qm} + HSI(1 - S_{qm}) \quad (4)$$

4.3.3. Survival of intraspecific aggression

Badgers are known to fight, especially during encounters between individuals of the same gender. Many individuals have scars (Messick and Hornocker, 1981), and the incidence of scars increases with age (Minta, 1993). However, we did not find estimates of mortality due to fighting.

In the model, each individual is checked daily to see whether it occupies the same location as a conspecific individual of the same gender. If so, we apply a survival probability that is higher for residents (i.e.,

the cell belongs to its territory; $S_{fight.res}$) than for non-residents ("marginal" individuals; $S_{fight.nres}$, Table 1).

4.3.4. Age-dependent survival

Messick and Hornocker (1981) reported annual survival estimates that increased with age from 0.788 during the first year of life to 0.981 for older adults. These values were converted to daily rates for use in the model (S_{age} vector in Table 1), which uses a daily timestep.

4.3.5. Orphan survival

When a female parent simulated in the model dies for any of the reasons above, we assume that its offspring are vulnerable to predation and starvation, and therefore die.

5. Simulation experiment

We compared simulation results for a baseline landscape with no brine spills against results for landscapes with different percentages and numbers of spill area. Thus, we first established a baseline set of parameters and then compared simulated population responses to landscapes with varying degrees of habitat loss (i.e., percentage of spill area) and habitat fragmentation (i.e., number of spills).

5.1. Experimental design

Two goals of this study are to estimate the separate effects of habitat loss and fragmentation caused by brine spills on badger populations. To evaluate the effect of habitat loss, we compare results for populations simulated on a landscape with no brine spills with results for populations simulated on landscapes with different target percentages of brine spill: 1%, 10%, 20%, 30%, 40% and 50% of area. To evaluate the effect of habitat fragmentation, we compare results for landscapes with less-fragmented (100 spills) and more-fragmented disturbances (1000 spills), holding target spill area constant. Note that access of badgers to the remaining areas of suitable habitat is an emergent property of the model that depends on simulated movement and territory acquisition. For each treatment, we generated 30 replicate landscapes (Fig. 2) used to simulate one of 30 replicate populations for 100 years.

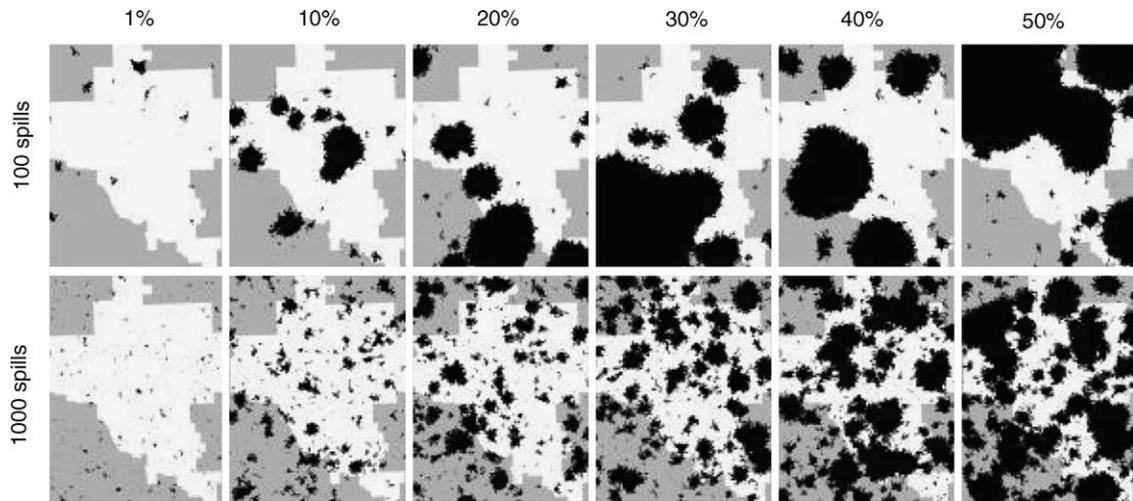


Fig. 2. Example landscapes generated by the Poisson-gamma model. Landscapes in the 1st and 3rd row have 100 spills and those in the 2nd and 4th row have 1000 spills. The target spill percentages shown are 1%, 10%, 20%, 30%, 40% and 50% of total area.

5.2. Simulated population responses

Model responses include average final population size, the fraction of populations that persist to 100 years and cumulative mortality for each of five causes. Another response of interest is the proportion of potential female breeders (territory owners) that successfully mated, P_{fmate} . P_{fmate} contributes to an Allee effect, or inverse density dependence that leads to faster population decline at low density (Allee, 1938). Error bars presented with treatment means reflect the combined uncertainty due to demographic stochasticity and landscape variation.

5.3. Sensitivity analysis and parameter exploration

Many parameter values used in our baseline simulations were obtained from studies reported in the literature, but others were not (Table 1). Sensitivity analysis was used to evaluate the effects of parameter choices for parameters not well supported by data on model results. We conducted a sensitivity analysis using the PRISM Monte Carlo method (Gardner et al., 1981). Ten model parameters were sampled using the Latin-hypercube method from independent normal distributions with nominal values given in Table 1 and a 25% coefficient of variation. As an index of sensitiv-

ity, we report the standardized regression coefficient in the multiple regression models between each of two response variables, final population size and the percent of females mating and the 10 model parameters. Populations were simulated on a single habitat map with 10% of spill area and 1000 brine spills (i.e., high fragmentation).

Two sources of uncertainty were the relative importance of mortality sources and the minimum quality required to form a territory. We conducted parameter explorations to better understand how these two sources of uncertainty influence the model's response to habitat loss and fragmentation. In addition, we explored parameters that might control the simulated build-up of marginal individuals (those lacking a territory).

We varied parameters that control the relative importance of movement-related mortality and habitat-related mortality to see whether both types of risk produce the same response to habitat loss. We chose two sets of parameters that produced similar final population sizes in landscapes with no habitat loss. One set assigned a lower survival of movement (S_{out}) and higher survival in poor habitat (S_{qm}) than the other (sets one and two in Table 2). Simulation results were compared for landscapes with 1% and 30% habitat loss (100 spills).

We also simulated different levels of minimum habitat quality to compare with the value we used for

Table 2

Parameter sets designed to evaluate the influence of parameter choices on model results

Set	Scenario	P_{emig}	S_{fight_nres}	S_{qm}	S_{out}	Q_{min}
1	Nominal	0.00	0.9999	0.9960	0.9999	0.75
1.1	No fighting	0.00	1.0000	0.9960	0.9999	0.75
1.2	Emigration and no fighting	0.05	1.0000	0.9960	0.9999	0.75
2	Movement	0.00	0.9999	0.9990	0.9995	0.75
3.1	Quality	0.00	0.9999	0.9960	0.9999	0.10
3.2	Quality	0.00	0.9999	0.9960	0.9999	0.50
3.3	Quality	0.00	0.9999	0.9960	0.9999	0.90

landscapes with 100 spills and 10% habitat loss (set three in Table 2). Our goal was to evaluate whether this threshold has a strong effect on the number of territories formed. We expected to find that an intermediate value of Q_{min} would be optimal for the population. In theory, low values should increase habitat-related mortality (badgers spend more time in poor habitat within their territories). High values of Q_{min} should make it difficult for individuals to form an acceptable territory, which should reduce the number of breeding individuals.

Finally, we explored processes that control the build-up of marginal individuals in simulated populations. In preliminary simulations, we noticed the rare occurrence of large populations dominated by marginal adults lacking territories. This model behavior is unrealistic for badger populations, but it is interesting because it is realistic for other species. We hypothesized that individuals lacking territories would be eliminated from the population if emigration were permitted, or if aggressive encounters with badgers with territories resulted in mortality. Parameter set 1.1 (Table 2) was designed to see whether the number of marginal individuals would increase in simulations without mortality due to fighting. Parameter set 1.2 (Table 2) was designed to see whether adding emigration (with no fighting) would prevent a build-up of marginal individuals.

6. Results

6.1. Response to habitat loss

For landscapes with 100 and 1000 spills, average final population size decreased with increasing habitat loss (Fig. 3a). The fraction of replicate populations

that persisted to the end of the simulation also declined (Fig. 3b).

Simulated population declines associated with habitat loss were caused by a combination of fewer births and higher proportional mortality (Fig. 4). Total

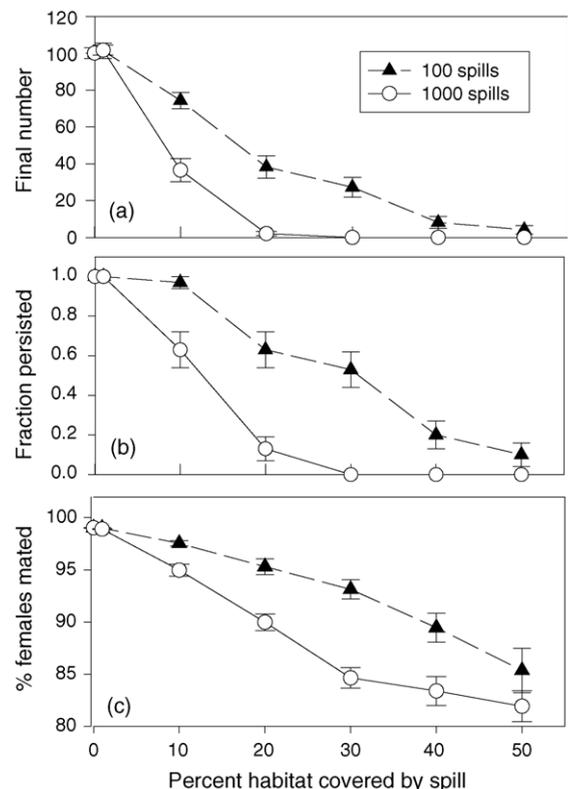


Fig. 3. Simulated population responses to habitat loss: (a) final population size, (b) fraction of replicate populations that persist and (c) fraction of females eligible to breed that find mates. Error bars show 1S.E. surrounding the mean of 30 replicate simulations for landscapes with 100 and 1000 spills.

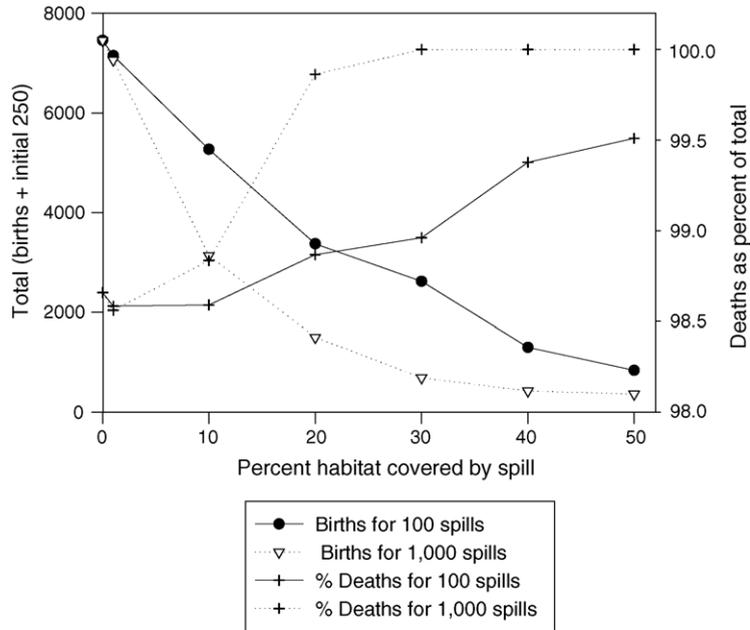


Fig. 4. Simulated population responses to habitat loss illustrating the decrease in total animals due to fewer births (left axis) and the proportional increase in mortality (right axis) for simulations with 100 (solid line) and 1000 (dotted line) brine spills.

mortality was higher in the baseline landscape scenario and declined with the fraction of habitat loss, as did the number of mortalities attributed to each of the five individual causes, because there were fewer births. However, the death rate increased (Fig. 4), and the proportion of deaths attributed to the various causes shifted. As habitat loss increased, the proportion of habitat-related deaths increased and the proportions of age-related mortality and orphan mortality decreased (Fig. 5).

On the other side of the demographic equation, reproductive success declined with habitat loss due to Allee effects in populations after they were reduced by habitat-related mortality. The proportion of juveniles that eventually formed territories did not decrease with increasing habitat loss suggesting that failure to establish a territory was not a problem. However, the fraction of females that found mates declined with increasing habitat loss (Fig. 3c). In simulations of landscapes with 50% habitat loss, more than 10% of females eligible to breed failed to find a mate because territories of potential mates did not overlap. In contrast, on intact landscapes, virtually every female of breeding age that

owned a territory overlapped with the territory of one or more breeding males.

6.2. Response to habitat fragmentation

Habitat fragmentation decreased the viability of badger populations in simulations with habitat loss of 10% or more (Fig. 3). Fragmentation reduced final population size (Fig. 3a), persistence (Fig. 3b) and the ability of females to find mates (Fig. 3c).

The percentage of deaths increased more sharply with habitat loss in landscapes with 1000 spills than in those with 100 spills (Fig. 4). In fragmented landscapes, it was more difficult for badgers to form high-quality territories by avoiding spill areas. Consequently, average territory quality was lower in fragmented landscapes, which increased habitat-related mortality. Fragmentation also resulted in higher levels of movement- and aggression-related mortality (compare Fig. 5a and b). Average dispersal distance was higher in the fragmented landscapes, with distances 0.15–0.55 km farther in 1000 spill landscapes than in their 100-spill counterparts.

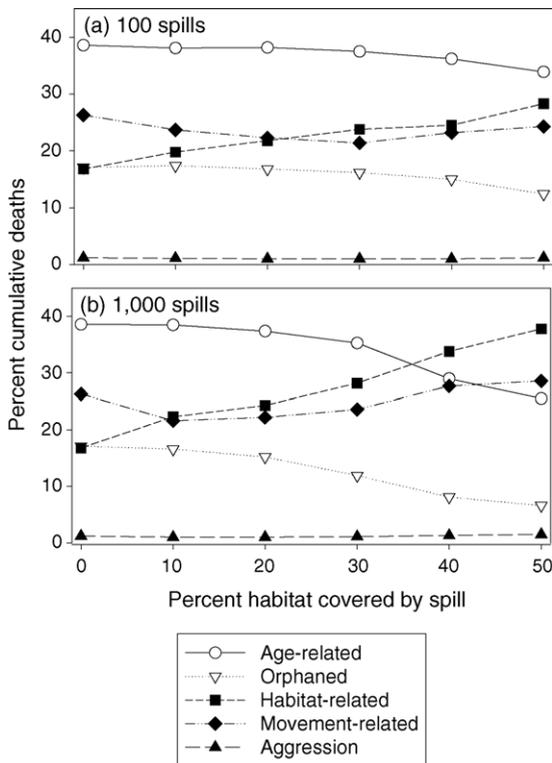


Fig. 5. Change in the relative importance of six sources of mortality in response to higher levels of habitat loss. Cumulative mortality results are shown for simulations of landscapes with (a) 100 and (b) 1000 spills.

Once numbers were reduced by these risk factors in fragmented landscapes, it became more difficult for badgers to find mates (Fig. 3c). The number of births declined much more sharply with habitat loss in landscapes with 1000 spills than in those with 100 spills (Fig. 4). Fragmentation caused a steeper decline in persistence with increasing habitat loss (decreasing suitable habitat) (Fig. 3b).

6.3. Sensitivity analysis and parameter exploration

Sensitivity analysis showed that final population size was most sensitive to the minimum size of female territories, $TerrSizeMin$ (Fig. 6). Dispersal distance, $AvgDisp$, was second in importance, followed by survival of fighting by non-residents, S_{fight_nres} . The percentage of females that mated was most sensitive to the

minimum quality habitat included in territories, Q_{min} (Fig. 6).

Parameter sensitivities of our model highlighted the same parameters as those reported by Rushton et al. (2000) in a sensitivity analysis of a model for water vole. On intact landscapes, Rushton et al. found that predictions of vole persistence were most sensitive to territory size, but on fragmented landscapes, they were most sensitive to dispersal distance. Although our sensitivity analysis simulations used a map with relatively high fragmentation (1000 spills), our results are more consistent with those obtained by Rushton et al. for a patchy population on a less-fragmented landscape.

Next, we explored the influence of specific parameters. Our first comparison showed that habitat-related mortality produces a steeper decline in response to habitat loss than movement-related mortality. Parameter set two (Table 2) increased survival in marginal habitat, S_{qm} , and lowered survival associated with dispersal or out-of-range movement, S_{out} , compared with the values in set one. Final population sizes simulated using set two were less sensitive to habitat loss, but more sensitive to fragmentation (Fig. 7). The relative importance of these two risks is poorly understood, and further field quantification would improve our understanding of this species and its expected response to habitat loss and fragmentation.

Our second comparison showed a monotonic decrease in final population size and persistence as parameter Q_{min} increased. As Q_{min} increased from 0.75 to 0.9, both the final number of females with territories (36–24) and the proportion of final females with territories (0.72–0.36) decreased, resulting in a smaller average final population size and lower persistence. This result ran counter to our expectation, which was that final population size would be highest at an intermediate value of Q_{min} . As we expected, badger populations formed fewer territories with higher average quality and experienced lower habitat-related mortality when Q_{min} was high. However, badgers also experienced higher levels of movement- and aggression-related mortality because they were forced to travel farther during dispersal. Dispersal costs and failure to acquire territories reduced population viability in simulations with high Q_{min} , despite the higher quality of territories.

Our third parameter exploration sought conditions that permit a build-up of individuals lacking territo-

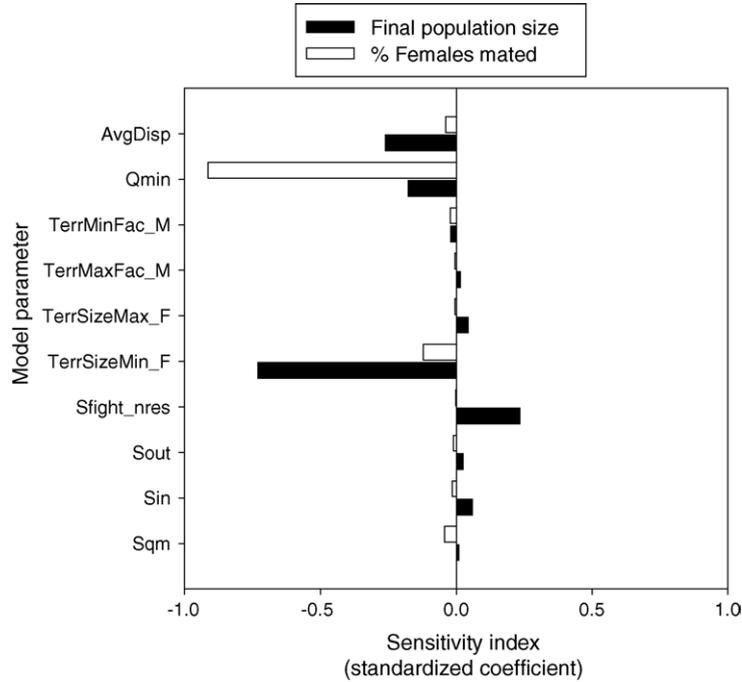


Fig. 6. Sensitivity of two model responses, final population size and percent of females mated, to each of 10 model parameters.

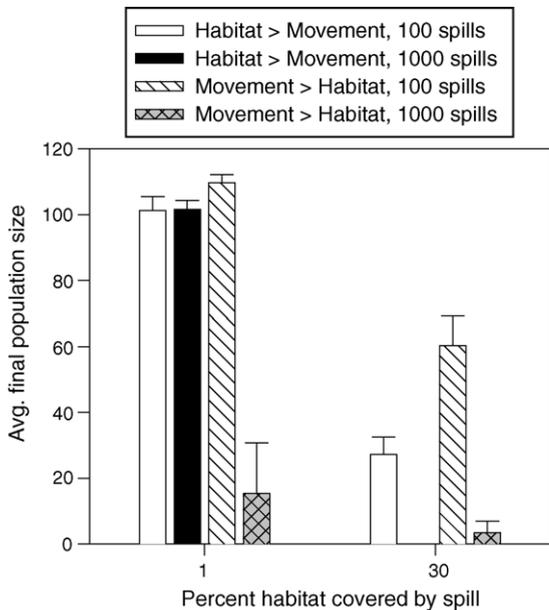


Fig. 7. Comparison of the response to habitat loss and fragmentation for parameters with higher habitat-related mortality vs. higher movement-related mortality.

ries. When we disallowed emigration and imposed no penalty for wandering into another badger’s territory (set 1.1 in Table 2), the population increased to >1000 individuals in seven of 30 replicate simulations (Fig. 8a). At the end of these 7 simulations, more females had territories than in the remaining 23 simulations, but a large majority of females did not establish territories (Fig. 8b) or, therefore, reproduce. The build-up of marginal individuals did not occur in simulations that permitted emigration or in simulations that applied a penalty for encountering a resident badger of the same gender (Fig. 8b).

7. Discussion

Our simulations suggest that habitat loss and fragmentation both have adverse affects on badger populations. Because badger territories incorporated poorer habitat on landscapes that were either fragmented or had a large percentage of spill area, elevated habitat-related mortality contributed to population decline. On fragmented landscapes, efforts to find a suitable territory also resulted in higher levels of movement- and

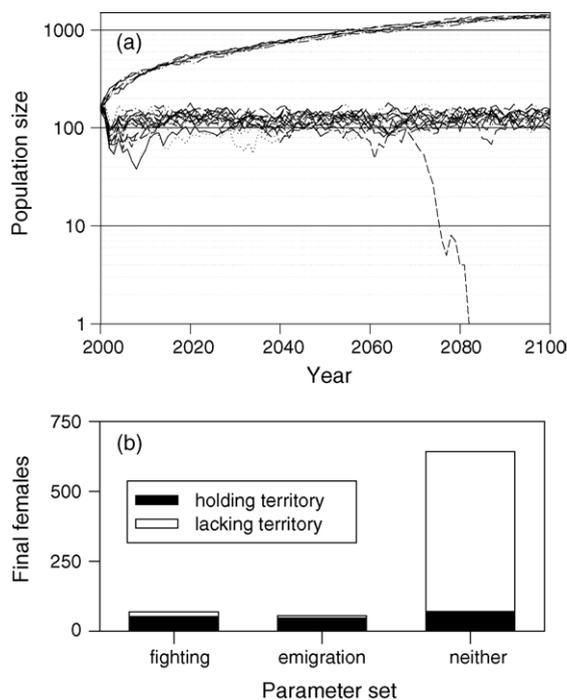


Fig. 8. Parameter exploration of conditions leading to marginal breeders. (a) Trajectories for 30 replicate simulations with no emigration or fighting. (b) Average number of females with and without territories for the seven replicates that increased to >1000 individuals for simulations that permitted losses due to fighting between conspecifics, for simulations that permitted emigration but no fighting and for simulations that permitted neither.

aggression-related mortality. As numbers declined, simulated females with territories became less likely to find mates, which further decreased populations.

Gough and Rushton (2000) reviewed modeling approaches to understanding the influence of habitat characteristics on mustelids. They concluded that an individual-based approach offers considerable potential for modeling the majority of mustelids that exhibit solitary behavior and occupy space to the exclusion of conspecifics of the same sex. The types of behavioral information available were also well suited for this approach, as first suggested by DeAngelis and Rose (1992). For example, we used field information about the size and overlap of territories and statistical summaries of radio-telemetry data collected on individuals to characterize the spatial life history of this species. An individual-based approach provided the flexibility needed to quantify mechanistic causes of death (e.g.,

the event-based mortality of juveniles when the parent providing care dies). Additional data would improve our ability to represent these risks; for example, this model would benefit from better estimates of mortality risks experienced by badgers that fight and those in poor habitat.

Allee effects are increasingly recognized as important factors to understand in population viability analysis (Dennis, 2002). In this study, we found that an important advantage of using a spatially explicit individual-based model was its ability to naturally simulate behavioral interactions leading to depensatory population growth, such as failure to find mates when local densities are low or when sex ratios are skewed. We note that the level of habitat loss and fragmentation at which some fraction of eligible females with territories fail to mate might serve as an early warning that densities are too low, and may be approaching an Allee threshold.

Our population viability analysis for this species included demographic stochasticity naturally by simulating individual variation in survival and reproduction (Henle et al., 2004), but it did not include environmental stochasticity. Environmental stochasticity can be used to forecast year-to-year variations in risk that are tied to rainfall, river flow, or other environmental drivers. However, extinction risk is not temporally variable for all species or in all habitats (Kendall, 1998), and the effects of environmental variation may already be included in the estimates of vital rates from historical data (Brook, 2000). It is not clear what environmental drivers are important for this species, but if we have overlooked a pattern, then our predictions of the likelihood of persistence should be considered optimistic.

7.1. Habitat loss

We observed that fragmentation contributed to steeper population declines that resulted in local extinction on most landscapes with more than 10% habitat loss. In addition to fragmentation, our experiments with parameter values suggest that steeper declines occur in situations when mortality risk in poor habitat is high (low S_{qm}) and when poor habitat is not excluded from territories (low Q_{min}). However, given the uncertainty surrounding some of our parameters, the extinction thresholds presented here should not be taken out of context before our results are validated in the field.

As demonstrated by Tilman et al. (1997), predicted extinction thresholds are highly dependent on model assumptions.

The total footprint of infrastructure associated with petroleum extraction may be considerably larger than that of brine spills alone. For example, Weller et al. (2002) used a 30–152 m zone of ecological effect to estimate that roads associated with oil and gas development affected 28–73% of area in a 430-km² Wyoming gas field. This study focused on brine spills, and did not attempt to simulate changes in road density or other landscape changes associated with petroleum exploration and production. Consideration of these additional impacts could be done, but first it would be necessary to quantify relationships between the density of wells and road density on landscapes dominated by petroleum-related activities.

Our results suggest that habitat loss is a threat to solitary, territorial predator like the badger. Population densities of such species are mediated by space through territory ownership. Our simulations also suggest that an inability to find mates becomes important in disturbed habitats that support a sparse distribution of territories. Sensitivity results suggest that species that, unlike badgers, avoid moving into the matrix of poor habitat may be less susceptible to adverse effects of habitat loss, a result also suggested by Fahrig (2002).

7.2. Habitat fragmentation

On landscapes with an intermediate proportion of unsuitable habitat, fragmentation made the difference between persistence and extinction of simulated badger populations. Longer dispersal distances to find territories increased movement-related mortality, territories included lower quality habitat, which elevated habitat-related mortality and Allee effects (failure to find mates) reduced births. These factors contributed to the negative effects of fragmentation in our simulations.

Studies on fragmentation effects on badgers in the literature focus mainly on roads. A study that evaluated road development impacts on the social Eurasian badger (*Meles meles*) in the Netherlands found simulated adult road-kill mortality to be most harmful, followed by disrupted dispersal (Van Apeldoorn et al., 1998). A study in southern California, USA found that badgers, which were rare, only occurred in three large, inte-

rior habitat blocks (11.9, 44.5 and 44.5 km²) (Crooks, 2002). The spotted skunk and long-tailed weasel also occurred only in larger patches. Patches in the Crooks study were defined by road boundaries. Fragmentation caused by brine spills probably has a smaller impact on populations than fragmentation by roads, which is not of primary interest here. In addition to causing direct road-kill mortality, roads are linear features and are more likely to disrupt dispersal than brine spills are (Carr and Fahrig, 2001; Jager et al., 2001).

We believe that the effects of habitat loss and fragmentation on the badger are of interest because mustelids represent one extreme of a continuum of social systems followed by mammals, with strong site attachment and aggression toward conspecifics. At first glance, the American badger fits the profile of a fragmentation-tolerant species because it is a wide-ranging generalist with an extended breeding season. However, the results of this simulation study suggest that species like the badger are sensitive to the combined effects of risks related to poor habitat, movement and aggression, amplified by Allee effects, on fragmented landscapes and those with a small fraction of suitable habitat.

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