Source-Sink Models and the Problem of Habitat Degradation: General Models and Applications to the Yellowstone Grizzly

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Abstract: *I used source-sink population models to explore the consequences of habitat degradation for populations living on good and degraded habitats linked by movement. In particular, I modeled the conversion of land from good habitat quality supporting positive population growth to a degraded condition in which there was population decline. I found that with high rates of movement between good and bad quality areas populations require relatively large amounts of good habitat to remain stable. However, low movement rates resulted in greater sensitivity of population growth to habitat loss. Even small amounts of habitat degradation could result in rapid changes in overall population growth rates depending upon the rates of population increase and decline in the two habitat types. I also developed and simulated an age-structured model for grizzly bears (Ursus arctos horribilis) existing in good and degraded habitats and fit this model to data from the Yellowstone grizzly population. I used this model to predict the ability to detect crucial amounts of habitat degradation from census data and found that when degradation is slow (e.g., 1% conversion of good to poor habitat per year), more than a decade may pass between crucial amounts of degradation—beyond which populations begin long-term decline—and its detection, even if census data were unrealistically good. Thus these simple models indicate that, at least in some circumstances, habitat degradation can have rapid and severe impacts on population dynamics and traditional monitoring programs may not be adequate to detect the consequences of degradation.*

Los modelos de fuente-sumidero y el problema de la degradación del hábitat: Modelos generales y aplicaciones al oso gris de Yellowstone.

Resumen: *En el presente estudio se utilizaron modelos a les poblacion fuente-sumidero para explorar las consecuencias de la degradación del hábitat en las poblaciones que viven en hábitats buenos y en hábitats degradados conectados por el movimiento de individuos. En particular, modelé la conversión de tierras que pasaron de ser hábitats de buena calidad, que sustentaban un crecimiento poblacional positivo, a ser hábitats degradados en los cuales existía una declinación poblacional. Encontré que con altas tasas de movimiento entre áreas buenas y malas, las poblaciones requieren altas cantidades relativamente de hábitats buenos para permanecer estables. Sin embargo, tasas de movimiento bajas resultaron en una mayor sensibilidad del crecimiento poblacional a la pérdida del hábitat. Una degradación limitada del hábitat puede conducir a rápidos cambios en la tasa de crecimiento poblacional total dependiendo de las tasas de crecimiento poblacional y de la declinación en los dos tipos de hábitat. También desarrollé y simulé un modelo estructurado por edades para osos grises (Ursus arctos horribilis) residentes de los hábitas buenos y degradados y ajusté este modelo a datos obtenidos de la población de osos grises de Yellowstone. Usé este modelo para predecir la capacidad de detectar cantidades cruciales de degradación del hábitat a partir de datos censales y encontré que cuando la degradación es baja (por ejemplo una conversión de los hábitats buenos a pobres de un 1% por año) puede pasar más de una década entre el momento en que las cantidades cruciales de degra-*

dación (por encima de las cuales las poblaciones comienzan una declinación a largo plazo) se hacen presentes y el momento en que son detectadas, aún si los datos sensales son, en un sentido irreal, buenos. Por consiguiente estos simples modelos indican que por lo menos en ciertas circumstancias la degradación del hábitat puede tener efectos rápidos y severos sobre la dinámica poblacional y que los programas tradicionales de monitoreo pueden no ser adecuados para detectar las consecuencias de la degradación.

Introduction

Habitat destruction and degradation are often cited as the most important causes of species endangerment and extinction. Although habitat destruction is a far more dramatic conservation problem, the degradation of habitat, an often slow transformation from optimal to suboptimal to unsuitable conditions for a species' survival and reproduction, is perhaps the more serious conservation concern in many areas today. Throughout North America and in many other parts of the world, large amounts of natural or semi-natural habitat already are protected at least at some level but are still subject to widespread and ongoing degradation (e.g., national forests and Bureau of Land Management lands). In spite of its prevalence the problem of habitat degradation has proven difficult to address; degradation is usually diffuse and often occurs very gradually through time, thus being quite difficult to measure.

The simplest demographic models linking habitats of differing quality are source-sink difference equations (Pulliam 1988). These models have included birth, death, and movement rates for a source population (in good habitat) and a sink population (in poor habitat). Both Pulliam (1988) and others (Pulliam & Danielson 1991; Howe et al. 1991; Davis & Howe 1992; Wootton & Bell 1992) use source-sink models to illustrate the possible importance of marginal habitats in maintaining overall population numbers and hence long-term viability. However, this simple model structure has not to my knowledge been used to address the dangers gradual habitat degradation poses.

I address the general demographic changes that occur in isolated populations living in two linked or adjoining types of habitat: good habitat and poor or degraded habitat. In particular, I ask how habitat conversion (from good to poor) changes the population growth rate of a species and how difficult it is to detect the effects of conversion on population viability. I first use a general model to explore how movement rates between the two habitat types and the rates of population growth and decline in the good and bad habitats (i.e., the severity of habitat degradation) will affect population responses to degradation. To make this exploration less abstract I then fit a simple age-structured version of the model to data on the Yellowstone grizzly bear (*Ursus arctos horribilis*) population. The Yellowstone grizzlies have been the subject of extensive field investigations (Mattson et al. 1987; Craighead et al. 1988; Knight et al. 1988; Blanchard & Knight 1991; Mattson & Knight 1991a), modeling efforts (Shaffer 1983; Knight & Eberhardt 1984, 1985; Shaffer & Samson 1985; Dennis et al. 1991; Eberhardt et al. 1994) and a recently released recovery plan (U. S. Fish and Wildlife Service 1993). Further, the ways in which human use decreases the quality of grizzly habitat are relatively well-understood (Knight et al. 1988; Mattson & Knight 1991b; Mattson & Reid 1991). Thus, this is a good population for which to examine the effects of habitat degradation on population health.

A Simple Model of Habitat Degradation

Structure

The simplest model of the effects of habitat degradation on the demography of a species involves only two types of habitat, good and bad, and assumes that the total habitat area remains constant. Therefore, the amount of good and bad habitat can be expressed as fractions of the total habitat area. This scenario corresponds to an isolated habitat patch, such as a national forest, in which some of the area is degraded and hence of lower quality to the species in question, and the rest is still relatively pristine and hence of high habitat quality.

To create the simplest model possible to show the effects of habitat degradation, I assumed that population growth is density independent in good and bad habitat areas and that neither population growth nor movement rates have stochastic variance. Inclusion of these or myriad other complexities could, of course, result in significant quantitative changes in the model results. However, I choose to make these simplifying assumptions because my goal is not to make accurate long-term predictions but rather to provide an initial exploration of the short-term, qualitative effects of degradation.

Two different equations describe the populations living in the two habitat areas:

$$N_g(t+1) = \lambda_g \left[N_g(t) + \frac{M}{2} \left(\frac{N_b(t)}{(1-p)A} - \frac{N_g(t)}{pA} \right) \right] \quad (1)$$

$$N_b(t + 1) = \lambda_b \left[N_b(t) + \frac{M}{2} \left(\frac{N_g(t)}{pA} - \frac{N_b(t)}{(1 - p)A} \right) \right] \quad (2)$$

Here, $N_g(t)$ and $N_b(t)$ represent the population sizes in the good (g) and bad (b) habitats in year t, and, similarly, λ_g and λ_b are the annual multiplication rates of the population in the good and bad habitats, respectively. The total area of all habitat types is A, and the fraction of this area that is good habitat is equal to p.

The last parameter, the movement coefficient M, requires more explanation. This parameter scales the rate of net movement between the good and bad habitats. The model allows individuals to move in either direction between the habitat types, although if $\lambda_g > 1$ and $\lambda_b < 1$ as in the results I present, net flow will always be out of the good habitat type. The terms N_g/pA and $N_b/((1-p)A)$ are the population densities in the good and bad habitats, and thus one-half their difference is the amount by which both densities would have to change in order to be equal. Looked at another way, this difference, $0.5(N_g/pA - N_b(1-p)A)$, is the density "pressure" that exists between the two habitat types. The movement coefficient is thus a parameter that determines the ease with which movement occurs as a result of this pressure. At a minimum, $M = 0$ and the two habitat types are completely isolated (no movement), and at a maximum, $M = 2Ap(1-p)$ (the movement in each year is exactly enough to equalize the densities in the two habitat types). Between these two extremes the value of M determines the relative ease of movement between the two habitat types, with the absolute amount of movement also being determined by the two densities. The movement coefficient M can also be thought of as the amount of area in each habitat in which the population density will equalize each year with the population in the same amount of area of the other habitat, thus making it the amount of area over which effective movement occurs near to the boundary of the two habitat types.

Importantly, I assumed in this model that individuals do not perceive differences in habitat quality and thus move solely on the basis of relative densities in the two habitat types. This is quite different from the assumptions made in constructing previous source-sink models (Pulliam 1988; Davis & Howe 1992) but is consistent with the dispersal and movement behavior of many species encountering human-altered habitats. Habitat degradation usually results from factors such as mortality on highways, eggshell thinning from pesticide residues, or mortality from shooting, the dangers of which are not adequately perceived or avoided by many species (e.g. grizzly bears [Mattson 1990; Mattson & Reid 1991] and Northern Spotted Owls *Strix occidentalis caurina* [Thomas et al. 1991]). Thus it is reasonable to assume in this simple model that individuals do not perceive degraded areas as such and therefore do not actively avoid these areas as they naturally would poor habitats. Additionally, the model does not incorporate the effects of boundary/area ratios on movement rates, which drive the behavior of diffusion models for minimum patch size (Okubo 1980).

Interpretation and Results

Because equations (1) and (2) describe a set of simple liner difference equations, constant overall population growth rates (λ_T) exist for the total population for any set of parameter values. Figure 1 shows the effects of movement rate (determined by different values of the movement coefficient, M) on the relationship between the fraction of good habitat and overall population growth and decline for different combinations of λ_g and λ_b and for three different movement coefficients ($M = 160$, 40, or 10). I varied the rates of population change from 2.5 to 10% increase or decline per year to simulate low to high rates of population growth in the good habitats and large to small degrees of habitat degradation in the bad habitats.

Overall population growth is strongly influenced by both the absolute and relative rates of growth and decline in good and bad habitat areas (Fig. 1). The larger the values of λ_g and λ_b, the smaller the fraction of good habitat (p) needed for overall population stability ($\lambda_T = 1$). I refer to this value of p as the critical amount of good habitat. Conversely, when λ_g and λ_b are both small, ($\lambda_g = 1.025$ and $\lambda_b = 0.90$), p must be large in order for a population to remain stable. A more interesting result is that the values of λ_g and λ_b strongly determine the shape of the relationship between λ_T and p. High rates of population growth in good habitat and rapid rates of population decline in bad habitat ($\lambda_g = 1.10$ and $\lambda_b = 0.90$) lead to extreme sensitivity of λ_T to changes in p, with small changes in p translating into large differences in overall population growth. Conversely, slow rates of growth and decline in the two habitats result in a weak dependence of λ_T on changing amounts of good habitat ($\lambda_g = 1.025$ and $\lambda_b = 0.975$).

To clarify the effects of λ_g and λ_b on population growth I plotted λ_T versus p for three combinations of λ_g and λ_b, holding $m = 40$ (Fig. 2). For all three pairs of λ_g and λ_b values plotted the mean of λ_g and λ_b is approximately 1. That is to say, if $p = 0.50$ and mixing between the two habitat types were complete each year, these pairs of λ_g and λ_b values would all result in stable population sizes ($\lambda_T = 1$), although they vary in the magnitude of the difference between growth and decline in the two habitat types. Large differences between λ_g and λ_b result in lower, critical values of p but also in greater sensitivity of λ_T to changes in p. Conversely, when λ_g and λ_b are both near 1, critical values of p are high but sensitivity of λ_T to changing amount of good habitat is fairly low.
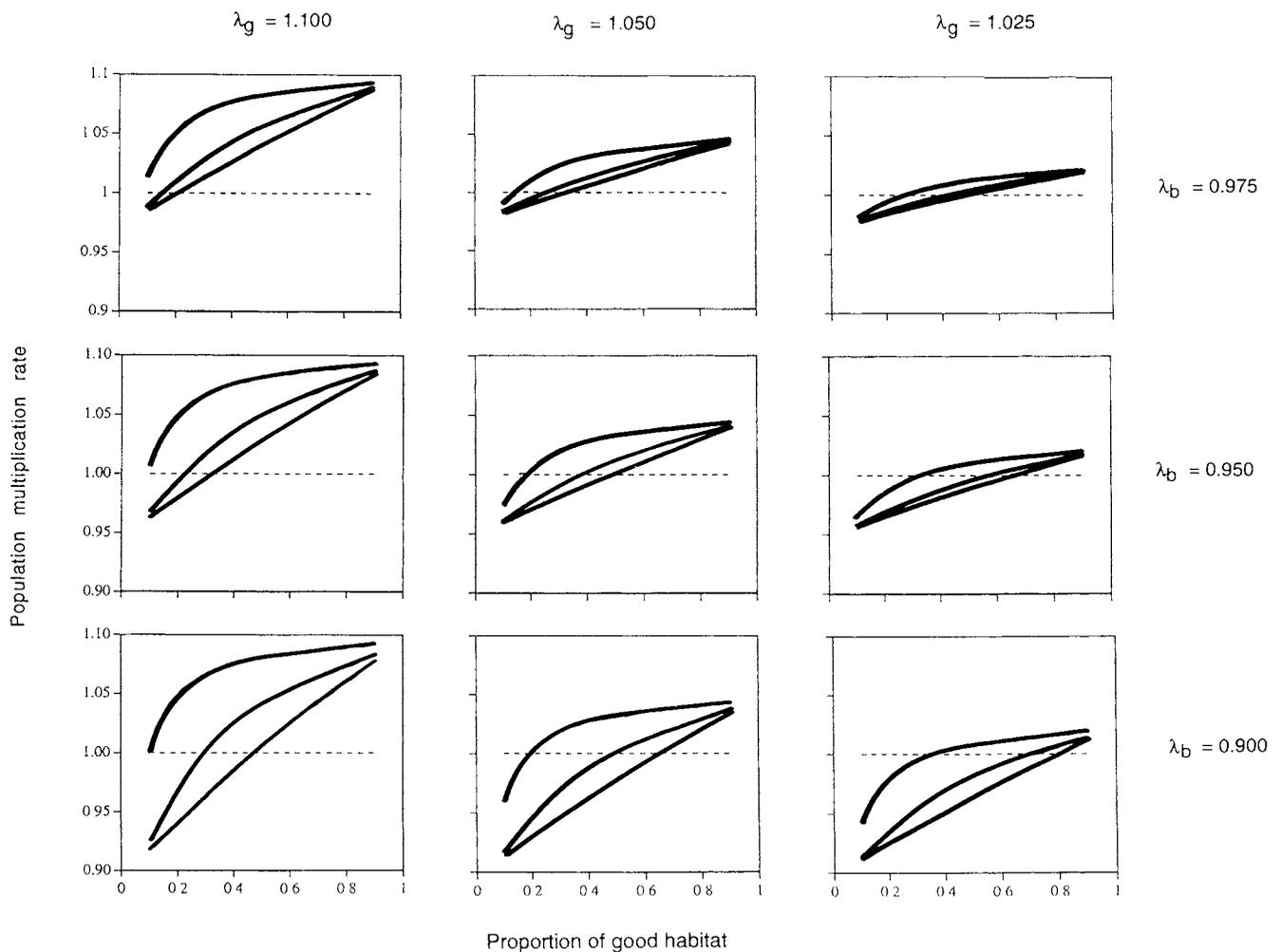
Figure 1.   Annual population growth rates plotted as functions of the proportion of good habitat. Each graph shows results for one combination of good and bad habitat qualities (λ_g, good habitat growth rate; λ_b, bad habitat growth rate). In each graph the lowest curve corresponds to the highest movement coefficient (160) and the highest curve to the lowest movement coefficient (10). The middle curve corresponds to a movement coefficient of 10. (If the proportion of good habitat is 0.20, the highest movement coefficient 160, completely equalizes population density in the good and bad habitats each year.) The horizontal, dashed lines indicate a growth rate of one, equivalent to a stable population size. Total area is always equal to 500.

Movement rate, determined by the movement coefficient, has two striking effects on population growth (Fig. 1). First, high movement rates raise the critical value of p, at which overall population growth changes to population decline. This is not surprising because higher movement rates result in faster leakage of individuals from the good into the bad habitat, essentially reducing population growth in the good habitat. The strength of this effect varies with λ_g and λ_b, with the critical values of p being most sensitive to movement when population growth in good habitat is low and population decline in bad habitat is rapid (e.g. λ_g = 1.025 and λ_b = 0.90). However, movement exerts a significant effect over all values of λ_g and λ_b shown—the strength of this effect is worth noting if only because accurate knowledge of movement rates is extremely rare.

More interesting is the effect of movement on the shape of the relationship between population growth and the fraction of good habitat. When the movement rate is high, overall population growth is an approximately linear function of p, the fraction of good habitat. However, with lower movement rates this relationship becomes convex and rapid changes in population growth result from small changes in p. This effect is particularly strong when the degraded habitat is quite inhospitable and population growth is rapid in good habitat, although it occurs for all combinations of λ_g and λ_b (Fig. 1).

The important point for conversation that emerges from this simple model is that very small amounts of habitat degradation can lead to dramatic changes in population growth rate, depending upon the severity of degradation and the ease or rate of movement between de-
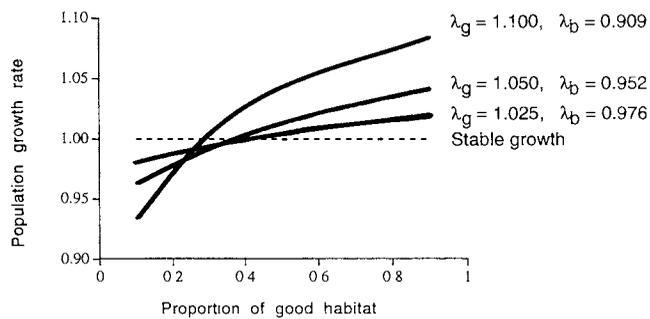
Figure 2. Annual population growth rates for three combinations of good and bad habitat qualities (λ_g, good habitat growth rate; λ_b, bad habitat growth rate) in relation to proportion of good habitat. For all curves plotted the movement coefficient (M) is 40.

graded and undisturbed habitat areas. For example, the additional conversion of 15% of an area from good habitat to bad can shift a population from stability to a 4% annual decline ($\lambda_g = 1.10$, $\lambda_b = 0.90$, $M = 40$). This result raises serious questions about our ability to predict the consequences of habitat degradation. The magnitude of differences between λ_g and λ_b and the absolute values of p and M modeled here are in practice very difficult to resolve with field data. Thus, even what is seen as very mild and incremental degradation (e.g., the building of roads or selective forestry) must be viewed with caution and with the knowledge that severe consequences could result from incremental changes in the proportion of good and bad habitat. Although this concept is not new, my results quantify the risks posed by degradation and emphasize that arguably insignificant changes may have serious results.

A Stage-Structured Model for Grizzlies

To illustrate how this modeling approach can be used to address real species and cases of habitat degradation, I present an age-structured version of the model for a species living in good and bad habitats and fit the model with parameters for grizzly bears inhabiting the Greater Yellowstone Ecosystem (GYE). Although Yellowstone grizzly populations have been modeled in several ways (Shaffer 1983; Knight & Eberhardt 1984, 1985; Shaffer & Samson 1985; Dennis et al. 1991; Eberhardt et al. 1994), previous models have not explicitly linked human degradation of habitat to changes in the population's health. For grizzlies degradation is largely the result of human access to bear habitat, which in turn leads to greatly increased mortality rates due to increased human-bear encounters; this mortality is due both to deliberate (shooting deaths) and accidental (road kills) human action (Knight et al. 1988; Mattson & Knight 1991b; Mattson & Reid 1991).

As with the first model, I take the approach of developing the simplest possible formulation needed to describe the species and its habitat conditions and hence ignore many aspects of bear biology, habitat geometry, and specific threats to bears in the Yellowstone area. Given that the grizzly is a highly intelligent species with diverse and flexible habitat needs and behaviors, the model presented here is best thought of as a cartoon of grizzly populations. This is not to say that the model is useless but rather an extremely simplified depiction of a complicated situation; like other simple models, it can provide insight into reality but should not be interpreted as providing quantitatively robust answers to the concerns it addresses.

The age-structured model is a direct extrapolation of my general model. Again, there are two habitat types linked by movement. In each habitat individuals are now divided into 8 age classes, all of which except the last are one-year age classes (the last class lumps together all individuals 13 or more years of age). The model includes only female bears. In presenting the equations that describe the population the net movement from the good to the bad habitat for a class i is conveniently defined as:

$$m_i(t) = \frac{M}{2}\left(\frac{N_{g,i}(t)}{pA} - \frac{N_{b,i}(t)}{(1 - p)A} \right) \qquad (3)$$

where $N_{g,i}(t)$ and $N_{b,i}(t)$ are the number of age i bears in year t in the good and bad habitat types, respectively. As in the simple model, A is the total area of habitat, p is the fraction of good habitat, and M is the movement coefficient. From this definition the population in each year is determined by three equations for each type of habitat.

For the good habitat:

(1) age 0 (cubs)

$$N_{g,o}(t + 1) = \sum_{i = 1}^{13} f_{g,i} s_{g,i - 1} [N_{g,i - 1}(t) - m_{i - 1}(t)]$$

(2) ages $j = 1$ to 12

$$N_{g,j}(t + 1) = s_{g,j - 1} [N_{g,j - 1}(t) - m_{j - 1}(t)]$$

(3) ages ≥ 13

$$N_{g,13}(t + 1) = s_{g,12} [N_{g,12}(t) - m_{12}(t)]$$
$$+ s_{g,13} [N_{g,13}(t) - m_{13}(t)]$$

For bad habitat:

(1) age 0 (cubs)

$$N_{b,o}(t + 1) = \sum_{i = 1}^{13} f_{b,i} s_{b,i - 1} [N_{b,i - 1}(t) + m_{i - 1}(t)]$$

(2) ages j = 1 to 12

$$N_{b,j}(t+1) = s_{b,j-1}[N_{b,j-1}(t) + m_{j-1}(t)]$$

(3) ages $\geq$ 13

$$N_{b,13}(t+1) = s_{b,12}[N_{b,12}(t) + m_{12}(t)] +$$
$$s_{b,13}[N_{b,13}(t) + m_{13}(t)].$$

Here, $s_{g,i}$ and $s_{b,i}$ are the annual survival probabilities from age class i to age class $i + 1$ in the good and bad habitats, respectively. Similarly, $f_{g,i}$ and $f_{b,i}$ are the annual fecundities (average number of female offspring) for females in the good and bad habitat areas, respectively.

These equations describe a population divided between two habitats, good and bad. They assume that in each year movement occurs first, followed by survival, growth, and reproduction and then by censusing. I also assumed that only the densities of a given age class determined the movement rate between habitat areas for that age class; that is, that individuals only move in response to densities of bears in their own age class rather than the total densities of bears in the good and bad habitats. Although this assumption is clearly unrealistic (Mattson 1990; Mattson et al. 1987, 1992) because of other assumptions I make in using the model (equal movement rates for all ages and no density dependence in survival and reproduction), it is equivalent, with rescaling, to the assumption that density effects are felt across all age classes. As with the more general model, these equations are linear and hence yield exponential growth or decline for the population as a whole.

Parameter Estimates

I use empirical data from three primary sources to parameterize the model for Yellowstone Grizzlies. First, Knight et al. (1991) provide estimates for natality rates. Second, Knight et al. (1993 and cited in U. S. Fish and Wildlife Service 1993 Appendix D) provide a complete set of survival rate estimates calculated for the entire Yellowstone grizzly population (Table 1). Third, to use these survival data in the model I derive separate estimates of demographic rates for good (undisturbed) and bad (degraded or disturbed) habitats using information in Mattson and Knight (1991b).The first step in this process is the definition of good and bad areas. Various authors (Knight et al. 1988; Mattson & Knight 1991b) argue that otherwise suitable habitats that are close to roads or developments are sinks for grizzlies because of increased human encounters and hence increased mortality rates. I use the classification of disturbance types presented in Mattson and Knight (1991b) who define bad habitat as those areas within 6 km of developments, 3 km of primary roads, or 1.5 km of secondary roads. These areas account for 32.9% of the area of the GYE

(Mattson & Knight 1991b) but from 1983 to 1990 account for 70.3% of all known mortalities occurring in the GYE. In calculating demographic rates for the model I lump together these three types of area as bad habitat and consider all other areas (the backcountries of all national forests and national parks in GYE) as good habitat.

Mattson et al. (1992) provide data showing no or relatively small differences in the densities of grizzlies in areas adjacent to or far from roads and human developments (but see this paper and Mattson et al. 1987 and 1992 for evidence that some density differences do arise from human impacts). Based upon this analysis I assume that the relative areas of good and bad habitat reflect the numbers of bears in these habitats. Given this assumption Mattson and Knight's (1991b) data on the fraction of good and bad habitat (0.329 and 0.671, respectively)—or equivalently the fraction of the total bear population in each habitat type—can be used with the fraction of known mortalities that occurred in good and bad habitats (0.703 and 0.297, respectively) to calculate that the per capita mortality rate in bad habitat is 4.83 times the mortality rate in good habitat. Total mortality should equal the average of the mortality rates in the two habitat types, weighted by area, or $m_t = p_g m_g + (1 - p_g)m_b$. Here m_t is the total mortality rate for an age class throughout the GYE, p_g is the fraction of the ecosystem that is good habitat, and m_g and m_b are the mortality rates in the good and bad habitats, respectively. By substituting in the ratio of mortality rates and using the total annual mortality rates calculated from the total survivorship data (mortality = 1 − survivorship), one can calculate habitat-specific mortality, and hence survivorship, values for the good and bad habitat areas for each age class. Table 1 provides the survival estimates based upon this procedure. I assume that reproductive rates are identical everywhere.

I emphasize that the demographic rates calculated here may not be highly accurate because they are based on a series of simplistic assumptions. However, I am us-

Table 1. Parameters used in simulations of Yellowstone grizzly bears living far from and near roads and developments.[a]

Age class (years)	Annual survival rates[b]			Female cubs produced per year[c]
	Observed	Far	Near	
0	0.89	0.95	0.76	0
1	0.85	0.93	0.68	0
2	0.83	0.92	0.64	0
3	0.88	0.95	0.74	0
4	0.88	0.95	0.74	0
5–12	0.93	0.97	0.85	0.41
13 and up	0.90	0.96	0.79	0.41

[a] *Total area (A) = 23,000 km and movement coefficient (M) = 4140, 2070, 1035, and 517.5 km.*
[b] *Survival rates from Knight et al. (1993) for females only. Because of sample sizes, the average survival rates for females ages 5 through 12 years and for all bears of 13 years and older are used.*
[c] *Reproductive rates from Knight et al. (1991) for 1981–1990.*

ing data for the Yellowstone grizzly to reach general conclusions about the ways in which bears will respond to habitat degradation; somewhat different sets of demographic data will not change the general conclusions, provided that bears on average replace themselves in good habitat and do not do so in bad habitat. I expect my results to be quite optimistic because they rely on very recent demographic estimates that show far higher survival rates, and hence population growth rates, than do slightly older summaries of data for Yellowstone grizzlies (e.g., Knight & Eberhardt 1984).

I found no data that could be used to estimate the movement coefficients for each age class of bears. For bears in the GYE these values reflect both the rate at which bears may change their home ranges on a large scale to overlap with or avoid areas close to humans and more subtle behavioral changes leading to avoidance or attraction to human-impacted areas. A better understanding of the ways in which habituation behavior operates in bears of different ages and sexes would be essential to realistically estimate movement rates and how they vary with density. However, in my model all these effects are lumped into a simple density-driven rate of movement. Data on home range sizes and locations indicate that most bears may regularly travel near roads and developments (Knight et al. 1988), translating into very high movement coefficients in the model. Lacking any quantitative estimates for the movement coefficients, I elected to, first, assume that movement coefficients are identical for bears of all ages and, second, to examine model results under a range of plausible movement coefficients (Table 1). The highest value I used (M = 4140) corresponds to complete equalization of densities each year when 10% of the total area is good habitat and when the total area of the GYE is 23,000 km.

Predicting Population Response to Human Encroachment

If no movement were possible between the good and bad habitat areas, given current survival and reproductive rates annual population growth would be 1.123 in the good area and 0.920 in the bad habitat. If one assumes a static landscape with a range of movement rates, this stage-structured model makes similar predictions to that of the simple model (Fig. 3). In particular, lower movement rates allow population stability or growth with smaller fractions of good habitat, but lower movement rates also lead to nonlinear responses of population growth to decreasing amounts of good habitat near the critical point at which annual growth changes into annual decline.

The model can also be used to examine population change in a varying landscape and in particular the ability of population size to indicate long-term population health when habitat degradation is ongoing. I choose to look at the two intermediate movement rates (M = 1035
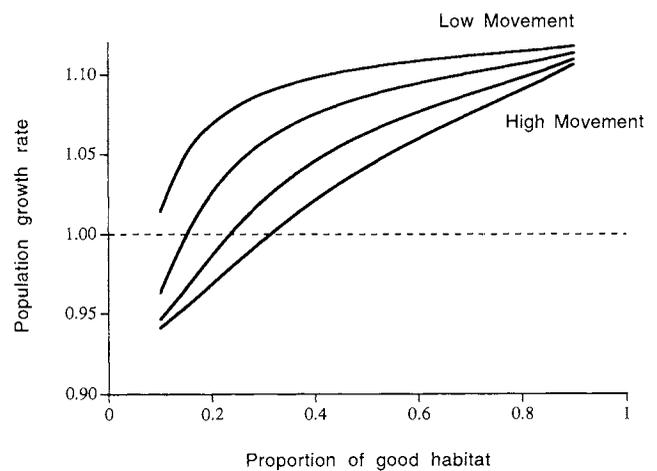
Figure 3. Population growth rates for simulated grizzly bear populations living in connected good and degraded habitat areas. Each curve indicates population growth rates for one movement coefficient value, with curves for four movement coefficients shown (M = 4140, 2070, 1035, and 517.5). The dashed line indicates a growth rate of one, equivalent to a stable population size. See Table 1 for parameter values.

and 2070) and at two rates of habitat degradation: conversion of either 0.5% or of 1% of the total area from good to bad habitat per year. For the lower movement rate the population is in equilibrium when p = 0.152, and for the higher rate the population is stable when p = 0.235. I started simulations with 1000 total bears (arrayed between habitats and ages in a stable distribution) and with slightly more good habitat than needed for population stability (0.162 and 0.245 for the lower and higher movement rates, respectively).

Figure 4 shows the results of these simulations. As expected, ongoing habitat degradation leads to accelerating declines in population size, even though degradation rates are constant in these simulations. Thus, even very slow rates of degradation—conversion of only 0.5% of the total habitat per year—can lead to rapidly worsening population dynamics.

Compounding this problem is what the results imply about the ability to detect changing population health under conditions of slow habitat degradation. Because directly measuring habitat degradation or its immediate effects on individual animals is difficult, most studies gauge the health of populations impacted by habitat degradation by monitoring trends in total population size. This is particularly the case with grizzlies; the recovery plan (U. S. Fish and Wildlife Service 1993) uses measure of population size (unrepeated adult females with cubs) as its primary metric of population health. Therefore, using the model to predict the usefulness of census data in measuring the effects of ongoing habitat degradation is interesting.
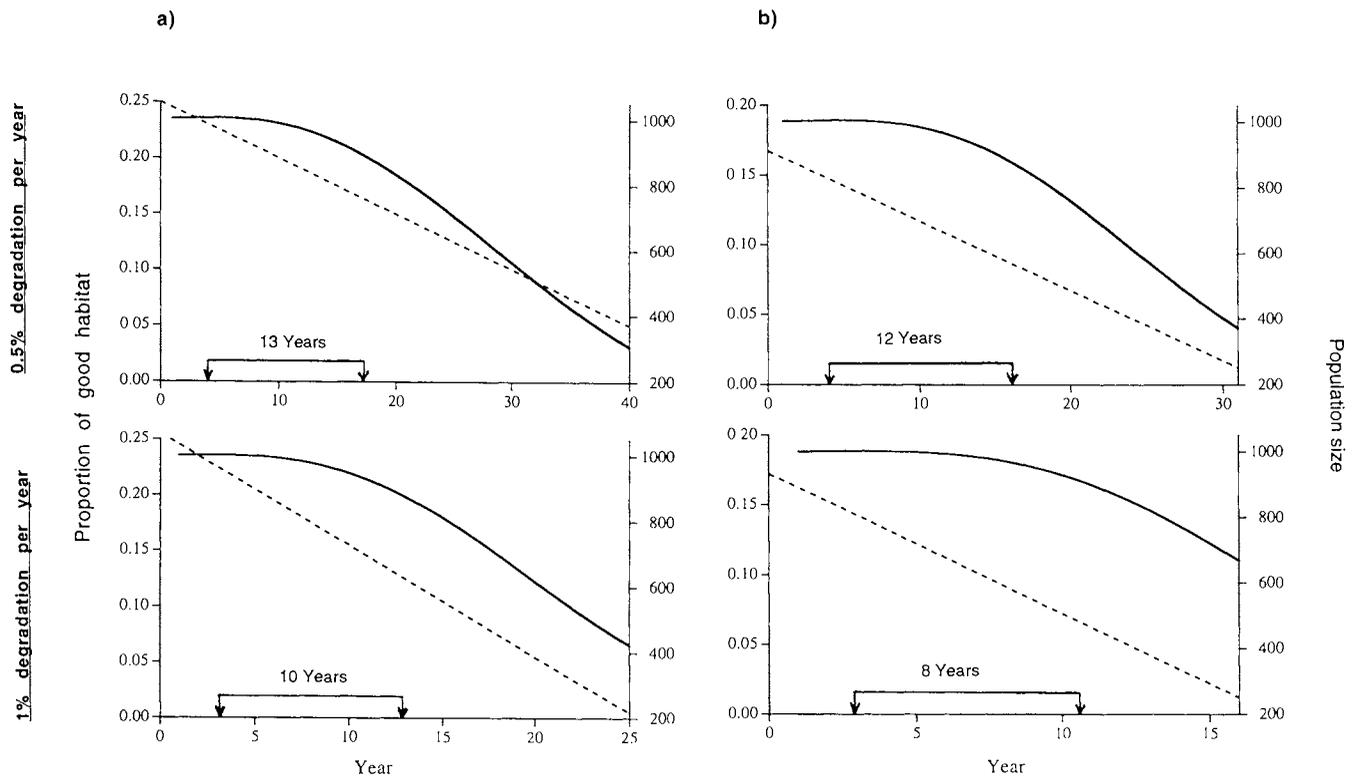
Figure 4. Population trajectories for simulated bear populations subjected to ongoing habitat degradation. Each plot shows population size (solid curve) and the proportion of good habitat remaining (dashed line) through time. Trajectories are shown for 0.5 and 1% rates of habitat conversion per year and for movement coefficients of M = 2070 (a) and M = 1035 (b). Connected arrows indicate the year when the amount of good habitat first falls below that necessary to maintain a stable population and the year in which population size first falls below 900, a 10% decrease from the starting populations of 1000.

Consider the situation in which a 10% change in population size can be detected from field census data. For species that can be very accurately censused, detecting a 10% decrease in population size may sometimes be possible; it is highly unlikely that so small a change in a grizzly population could ever be detected. Therefore, this detection criterion will give quite optimistic predictions for the particular case of the grizzly. In each graph in Fig. 4 the pair of connected arrows indicate the year in which *p* is first below that needed for a stable population and the year in which the population size has declined to 90% of its initial value. The difference between the two arrows indicates the lag time between the crucial point in degradation from which population decline will begin and when degradation effects might first be detected. For the four scenarios simulated this lag time ranges from 8 to 13 years. By the time population decline would be detectable, the remaining amount of good habitat—even if no more degradation occurred past that point—would result in annual declines of from 3 to 6%. Thus, the general conclusion is that census data may provide extremely poor measures of population safety or health under conditions of ongoing habitat degradation. As Taylor and Gerrodette (1993) forcefully argue,

statistical problems will often make detection of population declines from census data very unlikely. My results extend their argument by showing that by the time declines are detected, it will probably be too late to prevent critical amounts of habitat degradation from occurring.

Note that the model assumptions I make are biased against finding lag effects in population response to degradation. In particular, assuming that bears of all age classes move between habitats at the same rate reduces time lag effects because of the delayed reproduction. Further, the very slow rates of habitat degradation I simulate here allow the population to track the changing proportions of good and bad habitat. Thus, even species with quite different life history characteristics from bears will probably show similar population level responses to slow degradation.

I emphasize that while generalizations about the sensitivity of population growth to habitat loss and about the timelags expected in our detection degradation of effects are quite robust for different parameter estimates, the absolute value of the critical amount of good habitat is not. In particular, use of other estimates of demographic rates (e.g. Knight & Eberhardt 1985) leads to very different estimates of the minimum amount of good habitat

needed to sustain a grizzly population. Thus, given that demographic estimates for Yellowstone grizzlies have changed considerably over the past three decades and that all estimates come from very small sample sizes, the particular critical amounts of good habitat derived from the analyses I show here should not form the basis of any conclusions about how much absolute amount of degradation is in fact safe.

Discussion

This exercise in simple modeling provides several insights into the phenomenon of habitat degradation in general and the current management of grizzly bears in particular. First, habitat degradation can have highly nonlinear effects on population growth rates, with small amounts of degradation leading to large decreases in overall population growth. Thus to assume the safety of incremental degradation is not possible, very small losses could result in rapid declines of previously stable populations.

Second, our ability to detect crucial degrees of habitat degradation are imperfect at best (Taylor & Gerrodette 1993). The usual test of population health is change in numbers, and political compromises over human development (habitat degradation and loss) often result in ongoing degradation with monitoring of population sizes to gauge effects on threatened species. The statistical power of monitoring to detect population declines is often weak and thus provides little safety for threatened populations (Taylor & Gerrodette 1993). My results show another fallacy of this approach: If degradation is slow, long lag times can exist between critical levels of habitat degradation and any detectable change in population sizes, even when monitoring data are excellent. This point has also been made in the case of habitat destruction for the Northern Spotted Owl (Thomas et al. 1990; Lamberson et al. 1992). Thus, an assurance of even rigorous population monitoring while degradation continues is not a justifiable substitute for an a priori analysis of the probable consequences of development.

Third, the models point out that movement rates and habitat-specific demographic rates are crucial variables to understand and measure if we are to predict the critical amounts of degradation that a population can tolerate. These data are rarely available; the model therefore suggests a very conservative approach in assessing the dangers of habitat degradation. This result is particularly relevant to the management of the remaining grizzly populations of the lower 48 States. The Recovery Plan (U. S. Fish and Wildlife 1993) sets criteria that are either indirectly based on population numbers (e.g., number of females with cubs seen per year) or rely on population size estimates (i.e., human-caused mortality as a percent-

age of estimated population size) and uses census data as the primary measures of continuing population health (Shaffer 1992). Although the plan is careful to state that the recovery criteria are not explicitly population number goals, all the criteria are in fact directly related to population size. At the same time, no clear plans are set forth to assess the impacts on bear populations of further development in the national parks and forests that comprise most of the grizzly ecosystems in the lower 48 states. Thus, population monitoring data appear to be the only measures of the continuing, incremental effects of road building for mineral exploration, logging, and tourism.

My analysis indicates that the planned data collection will not adequately safeguard bear populations from this habitat degradation. Rather, analyses of how much degradation is too much and how best to monitor for degradation effects must be completed before degradation proceeds. These analyses could consist of behavioral and demographic modeling of bear populations living in complex sets of interspersed habitat types, similar to the spatially explicit models that have been used to assess the health of Northern Spotted Owl populations (Thomas et al. 1990; Lamberson et al. 1992). In the case of grizzlies and many other species changes in population densities in particular habitat types or change in specific demographic rates may be more effective measures of population status than are overall population numbers. Specific analyses are necessary to determine the most effective monitoring strategy for each species and situation.

By demonstrating the great effects that slow degradation can have on threatened populations and the difficulty in accurately detecting these effects with simple population monitoring, my results bolster the concerns about continuing habitat loss and degradation. Nevertheless, many management plans still rely exclusively on census data to measure effects of ongoing human impacts, even in cases where degradation is essentially irreversible. Little evidence exists to justify such a wait-and-see approach, especially for species such as the grizzly for which relatively complete demographic and behavioral data are already available. Rather, careful analyses to predict future viability should be carried out before allowing habitat degradation and loss to continue and certainly before populations can justifiably be declared recovered.

Acknowledgments

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