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The Relative Influence of Habitat Quality on Population Extinction

by

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Abstract

The current paradigm for species conservation emphasizes the roles of habitat quantity and configuration in influencing extinction risk. Spurred by the theories of island biogeography and metapopulation biology, studies often assume habitat quality to be homogeneous across habitats and rarely consider its influence. Yet the variation in the density or value of resources within habitats may influence population extinction. Thus, it is unclear which habitat variable has the greatest effect on extinction. The aim of my dissertation was to examine the merit of including habitat quality in habitat assessments and estimations of regional population persistence.

To determine the relative importance of habitat quantity, quality and configuration, I undertook a series of simulation modeling studies. Within a spatially-explicit individual-based model, landscapes varied in their degree of habitat loss, degradation, and fragmentation, and were linked with population dynamics to simulate extinction risk. Habitat quality affected persistence through a broad range of conditions, resulted in substantial extinction risk sensitivities, and outweighed the influences of quantity and configuration. Strong interactive effects suggested that combined habitat influences may strongly affect persistence. Quality improvements were more effective than habitat additions in meeting persistence goals, except in highly fragmented landscapes. While management often focuses on habitat additions and patch arrangements, quality improvements may be valuable in compensating for landscape change.

Using habitat removal simulations, the relative importance of habitat quality on the regional extinction of Ord's kangaroo rats (*Dipodomys ordii*) was assessed and results

supported theoretical conclusions. An approach to assessing critical habitat by integrating habitat quality and population dynamics was developed. Quality strongly influenced the relative contribution of habitats to persistence, suggesting that assessments that do not include these variables may undermine under- or over-estimate the value of patches.

The influence of habitat quality can be integral to assessing habitat and predicting population extinction, perhaps more so than quantity and configuration. Despite the widespread acceptance of quantity-configuration models, this emphasis is likely not appropriate in landscapes of heterogeneous quality. A more inclusive paradigm is required to elucidate the influence of habitat quality and accurately predict the effects of landscape change on population extinction.

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CHAPTER 1 - INTRODUCTION

Habitat loss and fragmentation are the most prominent concerns under the current paradigm for species conservation (Ehrlich and Ehrlich 1981, Schmiedel and Monkkonen 2002, Prugh et al. 2008). Spurred by the theories of island biogeography and classical metapopulation biology, landscape ecology and conservation biology research emphasize the roles of habitat quantity and configuration in influencing the distribution, abundance, and persistence of wildlife populations, and tend to overlook or generalize the influence of habitat quality (e.g., degradation). Central to the theory of island biogeography (MacArthur and Wilson 1967) is the premise that the probability of species occurrence in habitat patches is a function of patch size and isolation. Similarly, classical metapopulation theory (Levins 1969, Gilpin and Hanski 1991, Hanski et al. 1997, Hanski 1999) states that metapopulation dynamics and persistence are the result of a balance between the processes governing the extinction of local populations (affected by patch size) and colonization of empty patches (influenced by patch isolation). Patch area is often used as a surrogate for local population size as the amount of habitat imposes limits on resources and hence, local population capacity and size. The colonization probability of a given patch is related to its isolation from other patches as well as the size of nearby patches, which is assumed to correlate with the number of potential dispersers. As smaller populations tend to be subject to greater risk of extinction due to stochastic events (Gaggiotti and Hanski 2004), metapopulation theory predicts that local populations inhabiting smaller and/or more isolated patches are at greater risk of extinction.

Building upon the theories of island biogeography and metapopulation biology, much research has been devoted to assessing the relative influence habitat quantity and configuration on regional population dynamics and persistence in heterogeneous landscapes (e.g., Andrén 1994, Fahrig 1997, With and King 1999, Flather and Bevers 2002). Simulation modeling studies suggest that populations inhabiting landscapes of greater habitat amount or high spatial aggregation of habitat will exhibit greater regional population persistence than in landscapes with little or fragmented habitat. Such hypotheses have been applied in an array of terrestrial landscapes to predict population dynamics and persistence (e.g., Carlson 2000, Ferraz et al. 2007, Prugh et al. 2008). However, these theories and hypotheses make the simplifying assumption that the density or value of resources within or among habitats is homogeneous. Natural environments are typically heterogeneous, wherein populations encounter variation in both abiotic and biotic conditions (Kawecki 1995). Coarse-grained differences in the resources required for survival and reproduction may translate into differences in the performance of individuals in different habitats (Kawecki 1995), and ultimately local and regional population persistence. Heterogeneous habitat quality may also result in source-sink population dynamics (Pulliam 1988) wherein population growth rates are positive in source patches and negative in sinks (With 2004), potentially obscuring the expected relationship between habitat attributes and population response.

In general, the influence of habitat quality on regional population persistence has received little attention (Klok & de Roos, 1998). However, an emerging number of empirical studies that include habitat quality variables (e.g., food availability, habitat-specific survival or reproduction rates) have suggested that habitat quality, or the ability

of habitat to provide conditions appropriate for individual and population persistence (Hall et al. 1997), plays a crucial role in population dynamics and local population persistence (e.g., Dennis and Eales 1997, Thomas et al. 2001, Fleishman et al. 2002, Franken and Hik 2004, Ozgul et al. 2006). Similarly, the results of a theoretical landscape-level study that included habitat quality indicated that quality was important for predicting regional population size (Wiegand et al. 2005). Using mathematical models, Klok and De Roos (1998) contrasted the relative efficacy of increasing population size (which, in theory, is analogous to habitat amount) versus reproductive success (which is analogous to habitat quality) on the extinction risk of *Sorex araneus* populations. They concluded that reproductive success (i.e., habitat quality) had a greater influence on extinction risk; however, these conclusions were based on a spatially-implicit model, devoid of spatial structure and individual interactions with the structure and composition of the landscape which can influence dispersal, territory selection, and ultimately population persistence. Thus, despite emerging interest in quality-related studies, the relative influence of habitat quality on regional population persistence remains unclear.

Habitat quality considerations are often of lesser interest than habitat quantity or configuration, owing in part to the relative ease of measuring habitat area and isolation and the challenges associated with assessing habitat quality. In field studies, measurements of habitat quality can be difficult to obtain, as identifying the habitat attributes that are associated with habitat quality ideally requires the effort-intensive collection of habitat-specific vital rates. In a review of papers published in *Conservation Biology*, Armstrong (2005) concluded that while most studies examined habitat variables

relating to habitat quantity, quality, or configuration, few papers included data related to vital rates. Further, most studies took a shotgun approach to analyzing habitat quality, with few assessing quality using site-specific vital and movement rates or attempting to disentangle potentially confounding effects (Armstrong 2005). Given the effort required to obtain robust habitat quality data, the question is: how important is it to explicitly consider habitat quality in population persistence predictions? If the influence of habitat quality does not out-rank measures of habitat quantity and configuration, the predictions based on classical models derived from the theories of island biogeography and metapopulation biology may be reasonable to apply to populations occupying landscapes of heterogeneous habitat quality. However, if habitat quality ranks highly relative to habitat quantity and configuration, hypotheses generated from habitat quantity-configuration models may not sufficiently explain population distribution, abundance, and persistence in real landscapes of variable quality. Further, habitat and species management based on the habitat quantity-configuration paradigm may inadvertently compromise habitat conservation and species recovery efforts by misdirecting conservation resources to less effective or even detrimental conservation projects. For example, prioritizing patches for conservation based solely on size may promote the preservation of large, low quality or attractive sink habitats, rather than smaller, more productive, higher quality patches. Subsequent occupancy or relocation of animals to sink habitats may jeopardize population persistence, particularly for species at risk.

The overarching goal of my dissertation was to assess the relative influence of habitat quality on regional population persistence, and to provide general insight into the relationships between habitat attributes (quantity, quality, and configuration) and

extinction risk. In doing so, I sought to evaluate the basis for explicitly considering habitat quality in theoretical and empirical models used to predict population responses to the composition and structure of the landscape. In addition, I aimed to assess from a conceptual perspective, the adequacy of habitat quantity-configuration models to generate meaningful predictions for populations inhabiting landscapes of variable habitat quality. To this end, I undertook a series of simulation modeling investigations.

Simulation modeling is commonly used to explore population responses to habitat composition and configuration and has been instrumental in evaluating the relative effects of habitat loss and fragmentation on population persistence (e.g. Fahrig 1997, With and King 1999, Wiegand et al. 2005). This approach is of particular assistance in landscape-level investigations wherein the challenges of experimental manipulation, control, and replication largely preclude the use of real landscapes, as well as for species of conservation interest where simulations may be the only means of investigating the outcome of interest (i.e., population persistence). In this dissertation, I undertook both theoretical and applied simulation modeling investigations. Theoretical projects simulated the population extinction responses of hypothetical organisms occupying realistic landscapes of varying quantity, quality, and configuration. Applied projects were based on habitat and population data from a small mammal case study in southeastern Alberta, Canada, and aimed to evaluate the importance of including quality and population dynamics in habitat assessments and in extinction risk predictions. The following describes the overall structure of the dissertation and outlines the key questions examined in subsequent chapters.

Theoretical Projects

Population responses to habitat loss and fragmentation have been well studied in the literature. The aim of Chapter 2 was to relax the common assumption of homogeneous habitat quality and expand existing conceptual models to describe population extinction responses to habitat quality. The relative importance of habitat variables (amount, quality, fragmentation) was assessed using simulation modeling and the consistency of generalizations was evaluated among a number of hypothetical species with specific habitat requirements. Another goal was to identify the conditions under which interactions between habitat variables are likely to produce dramatic non-linear extinction responses. An understanding of such non-linear relationships may be of value in species conservation in attempting to avoid threshold extinction responses to landscape change. Similarly, an understanding of the relative influence of habitat quality may be useful in developing general guidelines regarding the role of quality in habitat monitoring and landscape change studies, and in informing habitat conservation strategies. Thus, in addition to exploring the relative importance of habitat variables and threshold responses, I discuss the utility and application of such generalizations for species conservation

Chapter 3 expands on the data and analyses from the previous chapter to examine the influences of habitat quantity and quality from a habitat restoration perspective. A greater range of landscape conditions were explored in order to estimate the amount or quality of habitat required to meet population persistence goals. I hypothesized that if the influences of landscape change processes such as habitat loss and degradation have similar effects on extinction risk, it may be possible to mitigate the population viability impacts of one process by improving the condition of the other. Thus, the aim of Chapter

3 was to examine the degree to which habitat quality and quantity could potentially be substituted to compensate for the population persistence consequences of habitat loss or degradation, respectively. In doing so, this research sought to assess the conditions under which quality-quantity trade-offs are likely to be effective, estimate the magnitude of improvement that would be required to meet various population persistence goals, and assess the relative effectiveness of habitat quality improvements.

Applied Projects

While generalizations such as those generated from Chapters 2 and 3 are useful for developing and extending theory, predictions arising from general models may not correspond well with landscape and species-specific population responses. For example, real landscapes are often more complex, with more types and qualities of habitat and greater variation in patch size and isolation. Similarly, real species often have more complex life cycles and behaviours which may obscure the expected theoretical relationships. To assess the congruence of theoretical predictions with those from an applied system, I undertook a case study highlighting the endangered Ord's kangaroo rat (*Dipodomys ordii*) population in Alberta. This relatively well studied population occupies a complex landscape of discrete sandy habitat patches that vary in size, isolation, and quality. The population is highly dynamic, experiencing substantial seasonal and inter-annual fluctuations in abundance (COSEWIC 2006) and local extinctions in habitat patches (e.g., individual sand dunes or road segments) are common (Kenny 1989, Gummer and Robertson 2003c). The goal of Chapter 4 was to use field data within a simulation modeling framework to assess the relative influence of patch- and landscape-level quantity, quality, and configuration on regional population

persistence in this complex study system. To accomplish this, I simulated the removal of habitat patches based on their patch characteristics, and assessed the resulting risk of regional population extinction. The results were used to identify important patch attributes for use in directing habitat conservation and restoration efforts. This chapter follows naturally from the preceding theoretical projects; however, it was written out of order and portions of the species background and methods refer to the subsequent chapter. Thus, interested readers may benefit from reading Chapter 5 prior to Chapter 4.

A principal challenge of species conservation is to identify the specific habitats that are critical for the long-term persistence or recovery of imperilled species. However, many commonly used approaches to identify important habitats do not include habitat quality information or consider emergent population dynamics. Further, most approaches, such as those based on occurrence data or models are unable to provide direct insight into the contribution of habitats to population persistence. If habitat quality is an important variable influencing population persistence, identifying important habitats for conservation using approaches that do not integrate information on habitat quality and population dynamics may be ineffective or even perilous, particularly for species at risk. Chapter 5 incorporates the ideas of preceding chapters and presents a novel approach for including habitat quality and population dynamics in habitat assessments and extinction risk predictions. Using a spatially-explicit simulation modeling framework, I integrated the details of habitat composition (including habitat quality) and structure with movement behaviour and population dynamics. Using habitat removal simulations, I quantified the relative contribution of specific habitats to regional population persistence, thereby identifying the specific habitats that were likely important for regional persistence. I

demonstrated the utility of explicitly including habitat quality in conservation assessments using Alberta's Ord's kangaroo rat population as a case study.

CHAPTER 2 - THE RELATIVE INFLUENCES OF HABITAT LOSS, FRAGMENTATION, AND DEGRADATION ON POPULATION EXTINCTION

Abstract

It is unclear which process of habitat change has the greatest effect on population extinction. While the most prominent conservation concerns are habitat loss and fragmentation, the role of habitat degradation has received comparatively little attention. To examine the relative influence of landscape-level habitat loss, fragmentation, and degradation on regional population persistence, I used a spatially-explicit individual-based model to incorporate several hypothetical species profiles, representing a spectrum of dispersal abilities, resource requirements, and life history strategies. Population dynamics were simulated in landscapes which varied in habitat amount, fragmentation, and quality according to a factorial design. Landscapes were composed of a range of proportions of high quality habitat, independent of variation in habitat amount (10-50%). Landscape configurations varied from contiguous to highly fragmented. Probability of extinction was measured and the relative importance of habitat quantity, quality, and fragmentation were statistically assessed using generalized linear models. In general, habitat quality outweighed the influence of habitat quantity and fragmentation. Habitat quality affected persistence through a broad range of conditions and resulted in substantial extinction risk sensitivities. The most severe extinction responses were observed in scenarios of combined habitat loss and degradation, suggesting that the interactive effects of these variables may greatly affect persistence. Habitat degradation

may also exacerbate the effects of fragmentation *per se* by reducing the capacity of habitat fragments to support individuals or populations. Results indicate that restoring sub-optimal to high quality habitat is generally likely to be more effective in reducing extinction risk than improving habitat quantity or configuration. While the current paradigm for the conservation of spatially structured populations often emphasizes habitat amount and fragmentation, these results indicate that habitat quality may be of greater concern. Extinction risk predictions based on population responses to habitat amount and fragmentation alone may be inaccurate in landscapes affected by habitat degradation or those with heterogeneous habitat quality. As such, a more inclusive paradigm is required to elucidate the influence of habitat quality on population extinction. Habitat degradation, along with habitat loss and fragmentation, should be explicitly considered when assessing the implications of landscape change on population extinction.

Keywords: Extinction; Fragmentation; Habitat degradation; Habitat loss; Habitat restoration; Habitat quality; Simulation; Species conservation

Introduction

Habitat loss and fragmentation are often cited as the primary threats to population persistence (e.g., Fahrig 1997). As such, much research has sought to determine the relative importance of habitat amount and landscape fragmentation on population size or extinction risk (e.g., Andren 1994, Fahrig 1997, With and King 1999, Flather and Bevers 2002). Despite variation in results due to modeling approaches and population viability measures, it is generally agreed that habitat amount better predicts population persistence (Fahrig 1997, Fahrig 2003, With 2004). Habitat loss reduces the total amount of suitable habitat, and if all else is equal, decreases the population size by limiting the capacity of the landscape to support individuals. However, the effects of fragmentation *per se* (which involve the breaking apart of habitats) have been shown to influence the risk of population extinction, particularly in landscapes composed of low habitat amounts (e.g., < 20%, Fahrig 1997, Fahrig 2003).

While less prominent, habitat degradation may be a more serious conservation concern for some species and systems (Doak 1995). Habitat degradation is often a slow transformation from optimal to sub-optimal habitat, wherein habitat quality is reduced and habitats are less able to provide the appropriate conditions (i.e., resources) for individual survival and population persistence (Hall et al. 1997). Coarse-grained differences in the density or value of resources among habitats or landscapes may translate into differences in capacity and ultimately, extinction risk. All else being equal, lower quality habitats have fewer or less valuable resources (e.g., food, shelter, cover) than higher quality habitats. Thus, lower quality habitats or landscapes should exhibit reduced population densities and sizes, and increased risks of extinction. Many studies

have concluded that the quality of habitat patches plays a role in population dynamics and local population persistence (e.g., Dennis and Eales 1997, Thomas et al. 2001, Fleishman et al. 2002, Franken and Hik 2004, Ozgul et al. 2006). Similarly, the results of landscape studies that include habitat quality indicate that this variable is important in predicting regional population size (Wiegand et al. 2005) and extinction risk (Klok and De Roos 1998). Despite this, the relative importance of habitat degradation in affecting population extinction has received little attention and has yet to be studied from a spatially-explicit perspective that simultaneously examines a broad range of variation in habitat quality and a diverse range of organisms.

Documentation of the relative influence of habitat amount, quality, and fragmentation on population extinction is lacking. As both habitat quantity and quality affect the potential capacity of the landscape to support individuals, I expect their influences on extinction risk to be evident over a wide range of habitat amounts and qualities and their effects to be greater than that of fragmentation. Habitat amount and quality may also interact such that landscapes with low quantities and qualities of habitats result in disproportionately large risks of extinction. In such landscapes, greater than expected risks of extinction may arise from mechanisms that result in the under-occupancy or reduced productivity of habitat patches. For example, the combined effects of habitat loss (which results in larger inter-patch distances and reduced dispersal success), and degradation (which limits resources and may trigger density-dependent emigration or reduced vital rates) may limit population size, distribution, and persistence beyond predictions based on the overall capacity of the landscape alone. Habitat fragmentation *per se* can affect the capacity of the landscape if habitat fragments become too small to

support individual or group ranges and may also affect population size if the configuration of habitats (independent of habitat loss) limits the distribution of the population. However, fragmentation effects are only anticipated to emerge in landscapes of low habitat amounts (Fahrig 1998, Flather and Bevers 2002), where habitat loss and fragmentation interact to produce smaller more isolated patches (with greater edge), resulting in greater rates of local extinction (Fahrig 2002, Fahrig 2003).

The aim of this study was to assess the relative importance of habitat amount, quality, and fragmentation in influencing population extinction risk. In doing so, I sought to provide general insight into the relationships between habitat variables and extinction risk and assess the consistency of these generalizations among various ecological profiles. An understanding of the general relationships between habitat variables and extinction risk may be of value in species conservation in attempting to avoid non-linear extinction responses to landscape change and in habitat restoration planning. If the influences of landscape change processes have similar effects on extinction risk, it may be possible to mitigate the population viability impacts of one process by improving the condition of another. Thus, in addition to exploring the relative importance of habitat variables, I discuss the utility and broad application of such generalizations for species conservation.

Methods

Approach

To determine the relative influence of landscape-level habitat loss, fragmentation, and degradation on regional population persistence, a spatially-explicit individual-based population model was used to incorporate several ecological profiles, representing a

spectrum of dispersal abilities, resource requirements, and life history strategies.

Population dynamics were simulated in landscapes which varied in their degree of habitat amount, fragmentation, and quality according to a factorial design. The probability of extinction (PE), wherein no animals were surviving in the landscape, was recorded and the relative importance of habitat quantity, quality and fragmentation was assessed using generalized linear models.

Simulation models have been a popular tool to assess the relative importance of habitat loss and fragmentation; however, they often contain simplifying assumptions such as binary (i.e., habitat/non-habitat) landscapes, random walk dispersal, or a single type of organism life history (e.g., Bascompte and Sole 1996, Fahrig 1997, Flather and Bevers 2002), which may not be generalizable to many species. The model I developed sought to relax these assumptions and to provide a greater degree of biological realism by introducing variation in habitat quality, a range of ecological profiles, and more realistic behavioural rules that allowed simulated animals to respond to the composition and structure of the landscape (e.g., Wiegand et al. 2005). Building upon previous studies, I sought to examine the relative effects of a broad range of habitat qualities on population extinction.

Landscapes

One-hundred and twenty-five fractal landscapes (128 x 128 pixels) were generated within QRULE (Gardner and Urban 2007) according to a factorial design. The landscapes (e.g., Fig. 2.1) represented proportions of habitat amounts that are likely to be in the range of conservation concern (0.1, 0.2, 0.3, 0.4, and 0.5). Landscape structures varied from contiguous to highly fragmented habitat. Spatial contagion (0.1, 0.3, 0.5, 0.7,

0.9) describes the tendency of habitat to be spatially aggregated or clumped (Leitão et al. 2006) and was used to characterize habitat fragmentation, which can be interpreted as its inverse. Landscapes were composed of both higher and lower quality habitat embedded in uninhabitable matrix, wherein individuals could move through non-habitat areas but could not establish a residence. Independent of habitat amount, the proportion of habitat in the landscape that was high quality (0.1, 0.3, 0.5, 0.7, 0.9; the reciprocal proportion was low quality) was varied. Low quality sites arbitrarily contained half the resources (i.e., 50 resource units) of high quality sites (100 resource units). As the relative importance of habitat quality may be sensitive to the resource level of low quality habitat (i.e., 50 units), an additional resource level (25 units) was explored to assess the sensitivity and stability of the influence of habitat quality on extinction risk. The landscape generation process was replicated once for each factorial scenario using another random seed to ensure that results were independent of the initial conditions of landscape generation.

Populations

Landscape composition and structure were linked with population extinction risk in the spatially-explicit individual-based model HexSim (version 1.5.0.19, previously PATCH; Schumaker 1998, 2009) by employing behavioural rules that allow simulated animals to respond to the amount, quality and fragmentation of the landscape. As dispersal and the establishment of territories are cited as the key factors linking population demography to the landscape (Wiegand et al. 2005), four ecological profiles were created to compare the relative influence of habitat variables among species. Species characteristics were chosen to represent a spectrum of territorial species with

specific habitat requirements, but with different movement abilities, resource requirements, and life history strategies. K strategists had high resource requirements, delayed reproductive maturity, low reproductive and high survival rates. r strategists required fewer resources, reached reproductive maturity sooner, and had higher reproductive and lower survival rates (see Table 2.1). Juvenile dispersal ability varied within each life strategy, with short (Ks and rs) and long dispersers (Kl and rl).

Following adult (territory holder) reproduction, juveniles dispersed in search of their own territories (Fig. 2.2). Movement was directed such that individuals had forward momentum and a preference (that increased linearly with habitat quality) to move into adjacent higher quality pixels. Individuals were able stop before they reached their maximum path length if they came across a suitable territory. Movement did not incur mortality; however, individuals that required longer dispersal distances or multiple movements to locate an unoccupied territory (e.g., during times of high population density) were less likely to acquire the necessary resources for survival. After dispersing, the immediate area (4 times the maximum territory size) was searched and the highest resource territory (above a minimum resource level) was occupied until death. Those unable to establish a territory had a 0.1 probability of survival.

To receive the maximum possible survival and reproductive rates, individuals had to occupy territories that met or exceeded the target resource level (Table 2.1). High quality habitats contained a greater density of resources; therefore, individuals required fewer pixels to meet the target level. In low quality habitats, individuals had to occupy larger territories to include a greater amount of habitat with lower resource density to reach the same target. Territories were required to include at least some high quality habitat to

reach the target resources level to impose a cost for defending a larger area. Individuals unable to reach the target resource level received reduced survival and reproductive rates that declined linearly as acquired resources declined from a maximum value.

Environmental stochasticity was incorporated using variation in survival rates. Each year one survival rate was selected at random (with replacement) from a normal distribution and used as the maximum rate for that time step. Juvenile maximum rates were decremented 0.05 from adult rates. As there was no sex structure, all individuals reproduced, but at half the rate expected of females. The values for vital rates were chosen for each profile to yield an overall population rate of increase of > 1 for species in landscapes composed of all high quality habitat, and < 1 for those in landscapes of all low quality habitat.

Analysis

Simulations were initialized with 1000 individuals randomly distributed within habitat. 500 years of data were collected for each scenario, with 100 repetitions. In total, the simulations required ~24000 computer processing hours. As the initial random number seed did not significantly influence extinction risk (t test for 50 units: $t = -1.0969$, (1, 248), $P = 0.2737$, $n = 250$; 25 units: $t = -0.4128$ (1, 248), $P = 0.6801$, $n = 250$; similar results were obtained with non-parametric tests), the results of landscape replicates were averaged. Habitat amount, quality, fragmentation, as well as all two-way interactions were included in fixed effects multiple regression models. Generalized linear models (binomial distribution) were used to evaluate relative importance and habitat variables were ranked according to their Chi-square values. To investigate the general importance of habitat variables on extinction risk, I pooled profile-specific data. Subsequent analyses

compared the relative importance of habitat variables among species profiles using averaged low quality sensitivity results (i.e., 50 and 25 resource unit scenarios). Extinction risk sensitivities were examined in plots of both moderate and maximal effects, wherein variables were held constant at intermediate and low values, respectively.

Results

Relative Importance

Habitat quality had the greatest influence on the probability of extinction (whole model Chi-square 6676.823, $df = 6$, $P < 0.00001$; Pearson Chi-square = 0.7644, $n = 125$; Table 2.2). Habitat amount and the interaction between habitat quality and amount followed in terms of their relative importance. Habitat fragmentation (arrangement), conceptualized as the inverse of spatial contagion, was important in influencing extinction risk, but less so than habitat quality or amount. A negative relationship between all variables and extinction risk was expected and observed. All interactive effects were significant; however, with the exception of amount*quality, were less important than single-variable effects. The relative importance of habitat quality did not differ among low quality sensitivity scenarios (whole model Chi-square 4557.202, $df = 6$, $P < 0.00001$; Pearson Chi-square 1.000, $n = 125$).

Moderate Effects

As the amount of habitat decreased (with spatial contagion held constant at an intermediate level, 0.5), the probability of extinction largely depended on the proportion of high quality habitat in the landscape (Fig. 2.3 - A). Landscapes comprised of low

habitat amounts (e.g., 0.1) had extinction risks ranging from 1% for landscapes with 0.9 high quality habitat (and 0.1 low quality), to 89% for those with only 0.1 high quality. When habitat quality fell below 0.3 (Fig 2.3 - B), dramatic increases in the probability of extinction were observed in habitat amount scenarios.

As habitat quality declined, a narrower range of variation was observed among habitat amount scenarios (Fig. 2.3 – B, compared to A), with probabilities of extinction ranging from 30 – 89 % for landscapes composed of 0.5 - 0.1 proportions of habitat. In general, scenarios with habitat amounts of less than 0.2, exhibited a marked increase in extinction risk (A, C).

Extinction risk was insensitive to the degree of fragmentation in landscapes with moderate to high habitat quality or proportions of habitat. There was little difference in extinction risk among spatial contagion scenarios above habitat amounts of 0.2 and qualities of 0.3 (when habitat quality and amount, respectively, were held constant at intermediate values; Fig. 2.3 – C, D). However, in scenarios with low habitat amounts, notable differences among fragmentation scenarios were observed.

Maximal Effects

The habitat amount and quality trends observed in plots of moderate effects were also observed when contagion was held constant at the lowest (0.1), rather than an intermediate level (Fig. 2.4). For example, a wider range of variation was observed among habitat quality scenarios (E), than was observed for amount scenarios (F), albeit the magnitude of difference was less than observed in plots of moderate effects. However, extinction responses to habitat fragmentation in low resource landscapes (i.e., quality – G, or amount – H, held constant at 0.1) differed from those observed in

moderate resource landscapes. When quality was held at a low level (G), the previously observed threshold effect was not evident and little difference was observed among contagion scenarios at low habitat amounts. In contrast, when habitat amount was low, extinction risk was influenced by contagion through a range of moderate to high levels of qualities (H), and dramatic increases in extinction risk were observed in most contagion scenarios as quality was reduced below 0.5.

Relative Importance: Ecological Profiles

Among ecological profiles, habitat quality consistently ranked as the most important variable influencing population persistence, followed by habitat amount (Table 2.3). Spatial contagion ranked as the third most important variable for K strategists, while the interaction between amount and quality ranked third for r strategists. The relative importance of other variables differed among profiles. While profiles with greater dispersal abilities exhibited fewer extinctions (mean number of extinctions was 16.5 and 26.3 for long and short dispersers respectively; Welsh's test $F = 11.9843$ (1, 497.9), $P = 0.0006$, $n = 500$), little difference was observed among long and short dispersers in terms of the relative importance of habitat variables (Table 2.3).

In plots of moderate effects, the responses of K and r populations to the amount and quality of habitat, and level of spatial contagion in the landscape were similar to those detected in the generalized results (Fig. 2.5). As habitat amount declined below 0.2, marked increases in extinction risk were observed in habitat quality (A, E) and contagion scenarios (C, G), particularly in lower quality scenarios. Similarly, sensitivities in extinction risk were apparent among habitat amount (B, F) and contagion scenarios (D,

H) when the proportion of high quality habitat fell below 0.3. The effects of spatial contagion were generally only observed below these thresholds.

Discussion

Relative Importance: General

A goal of this study was to provide insight into the relative importance of habitat quality and to contrast its influence on population extinction with that of habitat quantity. In this model, habitat amount presumably influenced the minimum population size, while habitat quality influenced population density. In combination, they were the primary factors constraining the capacity of the landscape to support individuals. Thus, it is not surprising that populations in scenarios with combined habitat loss and degradation exhibited the greatest risks of extinction. The strong interaction between habitat amount and quality indicates that populations inhabiting landscapes of low amount and quality are likely to have disproportionately higher extinction rates, well beyond the sum of their independent effects. While a detailed investigation of the mechanisms giving rise to these responses was beyond the scope of this study, such an examination should be a topic of further investigation.

Within the explored parameter space, habitat quality was more influential than the quantity of habitat in the landscape. Throughout the range of habitat amounts (0.1- 0.5), extinctions were observed in some habitat quality scenarios regardless of the amount of habitat in the landscape. This suggests that generalizations or ‘rules of thumb’ arising from habitat amount versus fragmentation studies may not hold true in landscapes with sub-optimal habitat quality. For example, previous modeling studies suggest that

appreciable risks of extinction only emerge when the amount of habitat is reduced below a threshold of 20% (Fahrig 1997, Fahrig 1998, Flather and Bevers 2002). While these results support sensitivity in extinction risk around 20% habitat amount, the magnitude of risk differed considerably among habitat quality scenarios below this threshold. In addition, some scenarios exhibited substantial risks of extinction well above the threshold. Particularly in scenarios of low habitat quality (i.e., 0.1 high quality habitat), extinctions were observed in high habitat amount landscapes (Fig. 2.3 – A). These results suggest that when the value and density of resources in the landscape are explicitly considered, population extinctions are likely to be observed in a broader range of landscape conditions than hypothesized by models that only account for habitat quantity and fragmentation (e.g., Fahrig 1997, Flather and Bevers 2002).

The importance of habitat quality is also supported by previous research. Fahrig (2001) and With and King (1999) modeled a range of reproductive outputs as a means of exploring the influence of species characteristics on extinction thresholds. However, if reproductive outputs are re-interpreted as resulting from habitat quality rather than species-specific traits, results support the primacy of habitat quality. Reproductive output greatly affected extinction risk in a range of landscapes (With and King 1999), and Fahrig (2001) concluded that reproductive rate had a larger effect on population extinction than habitat amount or fragmentation.

Population extinction thresholds were expected to emerge in low habitat amounts based on previous literature (e.g., Fahrig 1997, With and King 1999, Fahrig 2001, Flather and Bevers 2002); however, similar extinction sensitivities in landscapes of low habitat quality have not previously been modelled. As the proportion of high quality habitat

(independent of habitat amount) was reduced below 30%, extinction risk dramatically increased in the majority of habitat amount and fragmentation scenarios. In low quality landscapes, fewer or less valuable resources were available, forcing individuals to expand their territories to include additional resources, or else experience lower survival and reproduction rates. Limits to expansion were imposed by both the amount of habitat and its spatial configuration. Lesser amounts of habitat translated into less potential area for expansion. Similarly, in highly fragmented landscapes, patch sizes decreased and it became increasingly difficult for individuals to piece together enough resources to meet their requirements. In both cases, reductions in population density or vital rates likely resulted in small unstable populations, at greater risk of extinction by stochastic events. This threshold indicates that dramatic non-linear extinction responses should be expected in low quality landscapes, even in those with moderate amounts of habitat availability and levels of fragmentation. The significant interaction between habitat quality and fragmentation (Table 2.2) also suggests that the effects of habitat fragmentation are likely to be exacerbated in low quality landscapes, particularly in those with little habitat (Fig. 1.4 – H).

The results of this study suggest that the influence of landscape composition outweighs that of fragmentation. As the former determined to a greater extent the capacity of the landscape and therefore population size, this result is not unexpected. In contrast to habitat quantity and quality which influenced the risk of extinction through a wide parameter space, the effect of habitat fragmentation was only observed in landscapes composed of little and/or low quality habitat. This supports previous conclusions that the effects of habitat loss are not likely to be mitigated by optimizing the

configuration of habitat patches, except possibly within a narrow range of habitat compositions (Andrén 1994, Fahrig 1997, With and King 1999, Fahrig 2001, Flather and Bevers 2002). In addition, my results suggest that altering the arrangement of habitats is generally unlikely to compensate for the effects of habitat degradation.

Relative Importance: Ecological Profiles

Extinction responses to landscape change were expected to differ among ecological profiles as a result of both their varying dispersal and resource requirements. However, the relative importance of habitat amount, fragmentation, and quality was more greatly affected by resource requirements and life strategies than by dispersal ability. In particular, habitat fragmentation ranked more highly in terms of relative importance for K, than for r strategists. With greater requirements for resources, K strategists sought to build larger territories and hence required larger contiguous habitats to do so. As the degree of fragmentation limits patch sizes, it follows that species with greater requirements for resources would be more responsive to habitat fragmentation.

Species with short dispersal distances were expected to be more sensitive to habitat amount and fragmentation than those with longer dispersal abilities. However, this was not apparent in the modelling results as the importance of habitat amount and fragmentation (as single variables) did not differ among long and short dispersers. This may be due to the more realistic and efficient movement and habitat selection behaviours implemented in this model, enabling short dispersers to increase their chances of successful dispersal and territory acquisition in low amount and connectivity landscapes. These results imply that when more realistic movement and habitat selection behaviours exist (e.g., as opposed to unrealistic but commonly implemented random walk models),

the effects of coupled habitat loss and fragmentation may be less important for population persistence than models with simplistic movement and range establishment assumptions would suggest, particularly for species with relatively short dispersal capability.

In species conservation, the aim is often to predict how a particular type of organism will respond to landscape change. In this study, the hierarchy of the most important habitat variables (1- quality, 2- amount) influencing extinction risk was consistent among all species profiles, suggesting that generalizations regarding the relative importance of these variables are likely to be robust among species. Beyond this, species-specific considerations are likely to become important. In this study, the third-most important variables were either habitat fragmentation or the interaction between quality and amount, depending on the resource requirements and life history strategy. As the order of this short-list is largely consistent with that of the generalized relative importance results (which does not distinguish among the ecological profiles), the general interpretations gleaned from this analysis are likely to be applicable to a spectrum of species with specific habitat requirements, divergent life strategies, dispersal abilities, and resource requirements.

Conclusions

Recent literature examining the relative importance of habitat variables on population extinction risk emphasizes habitat loss and fragmentation, and generalizes or ignores the influence of habitat degradation (e.g., Andrén 1994, Fahrig 1997, 2001, Flather and Bevers 2002). However, this research suggests that this emphasis may be misplaced. The effects of habitat quality can affect persistence through a broad range of conditions and can result in substantial extinction risk sensitivities. Habitat degradation may also

exacerbate the effects of habitat loss and fragmentation such that populations exhibit much greater than expected risks of extinction. As such, extinction risk predictions based on population responses to habitat quantity and fragmentation alone may be inaccurate in landscapes affected by habitat degradation or those with heterogeneous habitat quality. Further, binary (habitat vs. non-habitat) landscapes are likely to be inappropriate for habitat modelling and analysis, unless habitat quality is relatively homogenous across the study area.

Beyond theoretical investigations, the amount – fragmentation emphasis pervades much of the applied habitat conservation research. For example, habitat monitoring and landscape change studies commonly limit their investigations to easily quantifiable metrics describing habitat amount and fragmentation. Similarly, habitat restoration efforts commonly focus on habitat additions or improving connectivity among existing habitat patches, and rarely consider the explicit trade-offs between improving habitat quality and augmenting existing habitat (Klok and De Roos 1998). While conserving or restoring habitats to meet specific theoretical landscape targets (e.g., > 20% habitat amount or > 30% high quality) is unlikely to be appropriate for all species and circumstances (see Fahrig 2001), these simulations suggest that restoring sub-optimal to high quality habitat is likely to be effective in reducing the risk of population extinction. The greater degree of variation in extinction risk among quality scenarios than among habitat amount scenarios suggests that improvements to habitat quality are generally more likely to be successful in reducing extinction risk than increases in habitat quantity; however, quality and quantity may be substitutable to a greater degree in landscapes with low resource availability. Although habitat quality can be comparatively more difficult

to measure than habitat quantity and fragmentation (Armstrong 2005, Johnson 2007), this study suggests that applied research is likely to benefit from explicitly considering quality in habitat and population assessments.

In conclusion, the influence of habitat degradation is likely to be integral to understanding and predicting population responses to landscape change, perhaps even more so than loss and fragmentation. Spatial considerations such as habitat fragmentation are likely to be important in low quality and/or quantity landscapes; however, this relatively narrow range of conditions suggests that a shift away from the commonly utilized habitat amount-fragmentation paradigm is warranted. These results indicate that the focus should lie foremost in examining the effects of habitat quality and quantity on population extinction, and to a lesser extent on habitat fragmentation. Despite the wide-spread recognition and application of the amount-fragmentation paradigm, a more inclusive conceptual framework is required to elucidate the influence of habitat quality and accurately predict the effects of landscape change on population extinction.

Table 2.1. Population parameters for ecological profiles.

Parameter	Profile	
	K	r
Dispersal distance	KS: 32 pixels KL: 128 pixels	RS: 32 pixels RL: 128 pixels
Early stopping triggered if find	7 high quality pixels	3 high quality pixels
Target resource level	4000	1000
Min. resource level	2000	500
Max. territory size	60 pixels*	15 pixels*
Age at reproductive maturity	2	1
Max. number of offspring	1	4
Max. reproductive rate	Mean 0.5; SD 1**	Mean 2; SD 1**
Max. survival rate	Mean 0.9; SD 0.1**	Mean 0.5; SD 0.1**

*Values doubled in low quality sensitivity scenarios

**Values are normally distributed

Table 2.2. Relative importance rankings of habitat variables in influencing the probability of population extinction, generalized across ecological profiles, including parameter coefficients (β), standard errors (SE), and Chi-square values from the generalized linear (binomial) model.

Rank	Variable	β	SE	Chi-square	<i>P</i>
1	Quality	-27.31	1.1234	4983.75	<0.00001
2	Amount	-44.17	2.2373	1551.75	<0.00001
3	Quality*Amount	-92.08	5.5584	705.15	<0.0001
4	Contagion	-5.35	0.3520	280.41	<0.0001
5	Quality*Contagion	-11.94	0.9730	173.64	<0.0001
6	Amount*Contagion	-1.49	1.1190	1.78	0.1822

Table 2.3. Relative influence of habitat variables on the probability of extinction, reported separately for each ecological profile (as described in the text), ranked according to their Chi-square values in each generalized linear (binomial) model.

Rank	Kl	Ks	rl	rs**
1	Quality	Quality	Quality	Quality
2	Amount	Amount	Amount	Amount
3	Contagion	Contagion	Amount*Quality	Amount*Qual.
4	Amount*Quality	Quality*Contagion	Quality*Contagion	ns
5	Quality*Contagion	Amount*Quality	Contagion	ns
6	Amount*Contagion	Amount*Contagion	Amount*Contagion	ns

All models: Whole model df = 6; $p < 0.00001$; $n = 125$ scenarios

Whole model Chi-square: Kl 4884.85; Ks 3229.67; rl 9953.85; rs 69.03

Pearson Goodness of Fit P : Kl 0.8472; Ks 0.9920; rl 0.6628; rs 1.0000

ns = variables were not significant in the statistical model

**used exponential distribution

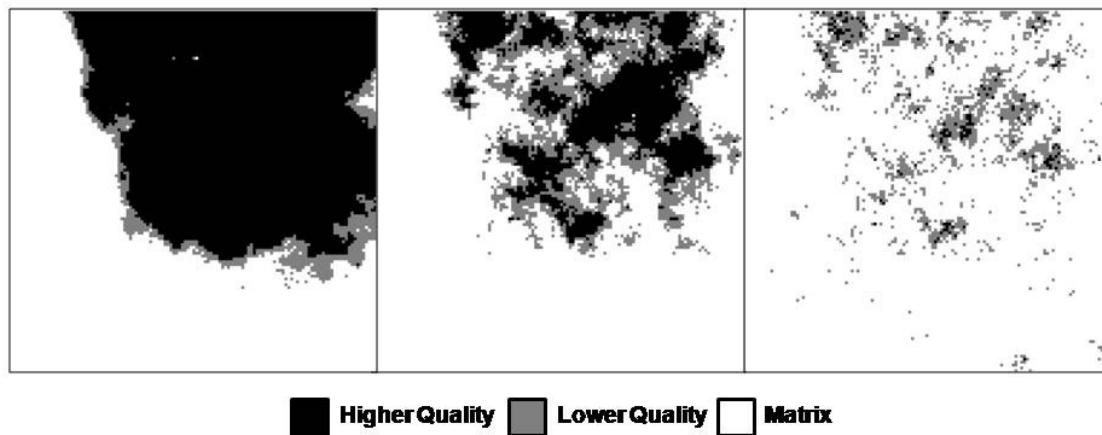


Fig. 2.1. Example landscapes spanning the experimental parameter space. Landscape ranged from those with large proportions of habitat amounts, high quality, and contiguous habitat (first frame) to those with low habitat amount, quality, and contagion (last frame).

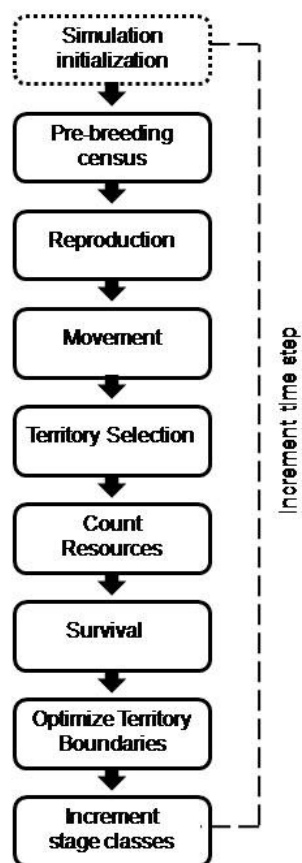


Fig. 2.2. Population cycle as implemented in HexSim.

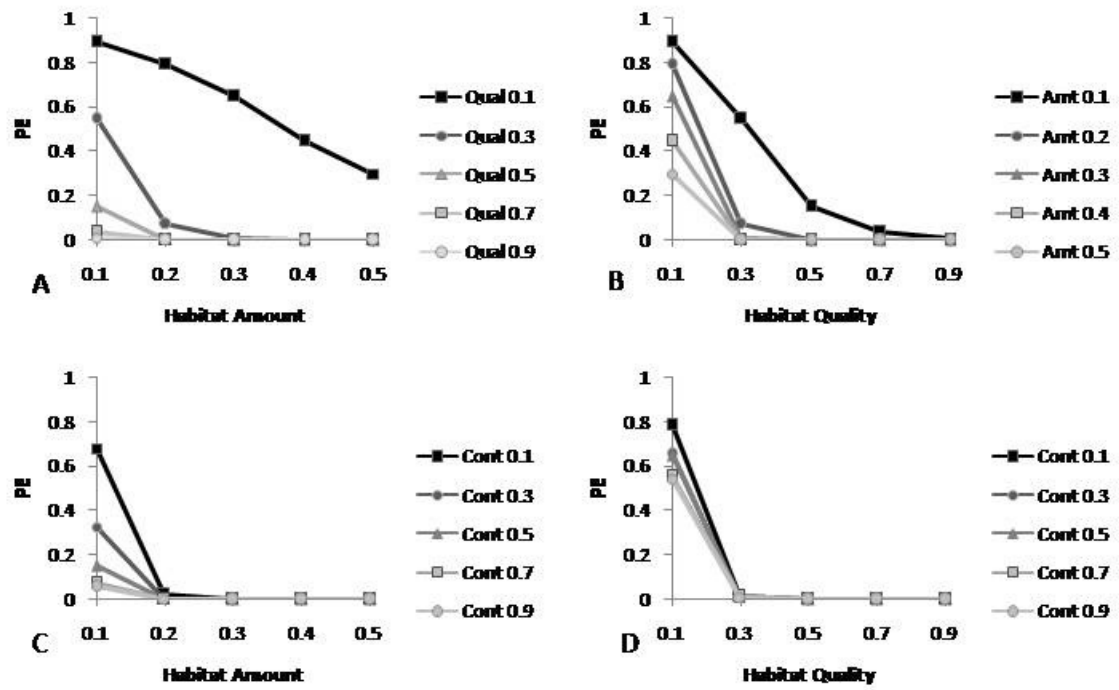


Fig. 2.3. The effect of habitat amount, quality, and fragmentation on the probability of population extinction. In each frame, the un-plotted variable was held constant at an intermediate level (0.5 for quality and contagion, 0.3 for amount).

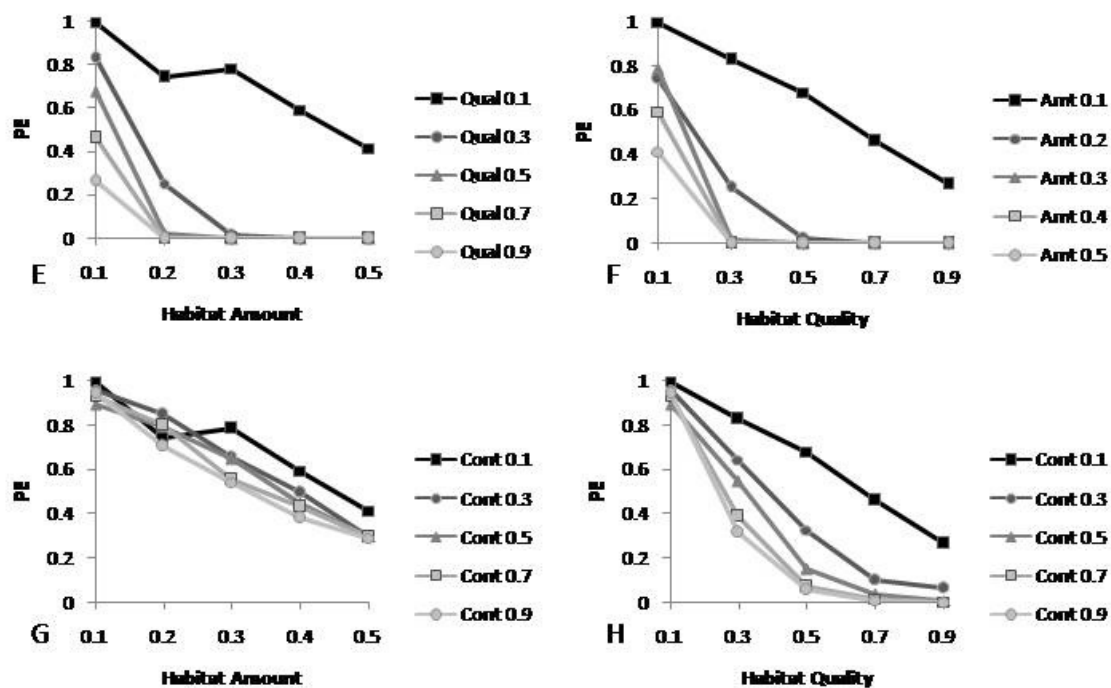


Fig. 2.4. The maximal effects of habitat amount, quality, and fragmentation on the probability of population extinction. In each frame, the un-plotted variable was held constant at the lowest level (0.1).

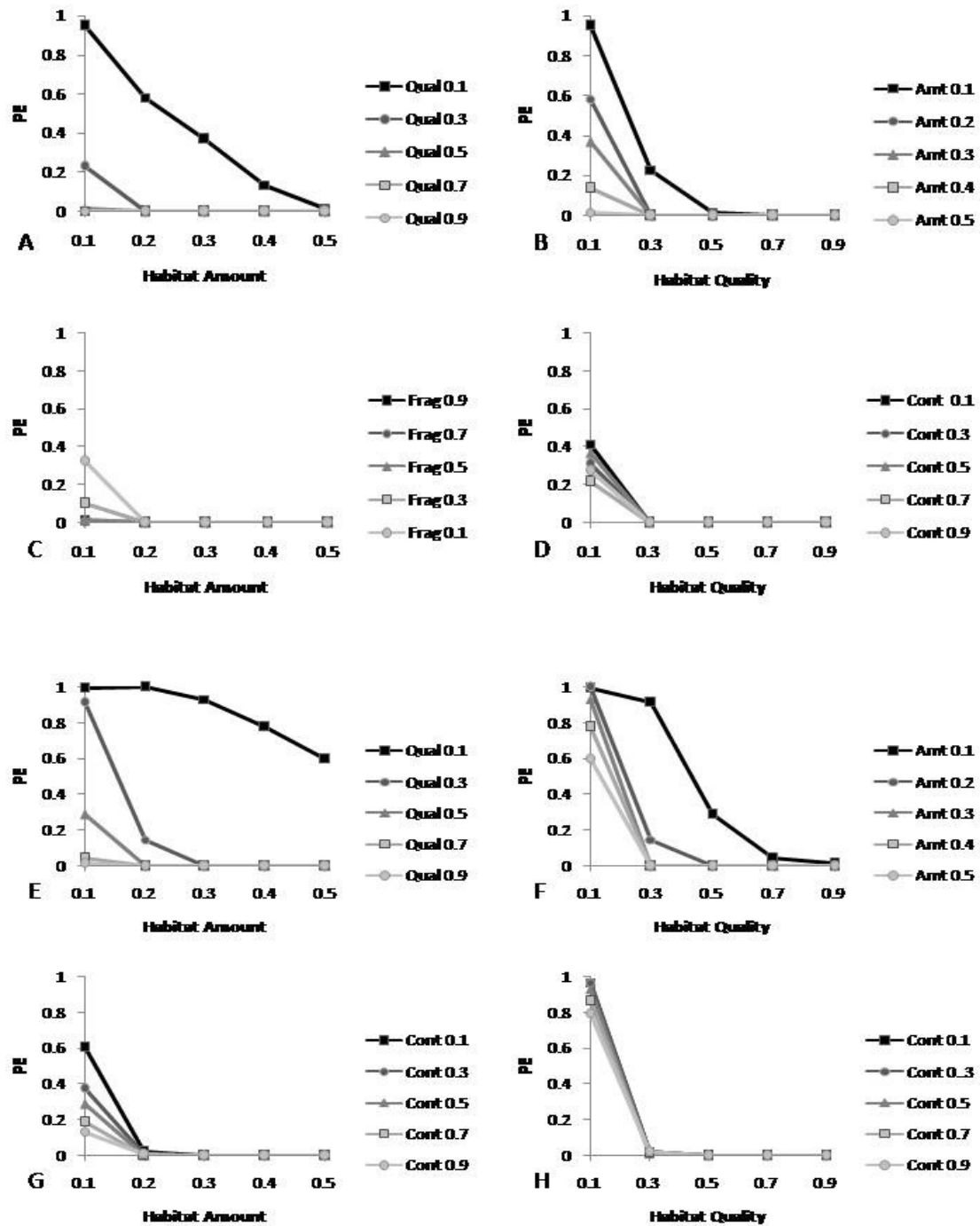


Fig. 2.5. The effect of habitat amount, quality, and fragmentation on the probability of population extinction for ecological profiles KI (A-D) and rl (E-H). In each frame, the un-plotted variable was held constant at an intermediate level (0.5 for quality and contagion, 0.3 for amount).

CHAPTER 3 - HABITAT QUANTITY VERSUS QUALITY: EXAMINING THE EFFICACY OF HABITAT TRADE-OFFS FOR SPECIES CONSERVATION

Abstract

Management practices for species conservation have been profoundly influenced by the theories of island biogeography and metapopulation biology, wherein species or population persistence is related to habitat quantity and configuration, and habitat quality effects are generalized or disregarded. As such, habitat restoration strategies typically focus on habitat additions and improving the spatial arrangement or connectivity of habitat patches and often overlook habitat quality improvements. However, habitat quality can play an integral role in population dynamics and persistence, and may outweigh the influences of habitat amount and configuration. My aim was to examine the degree to which habitat quality and quantity could potentially be substituted to compensate for the population persistence consequences of habitat loss or degradation, respectively. A spatially-explicit individual-based model was used to simulate population dynamics in landscapes that varied, according to a factorial design, in the proportion of high quality habitat (0.1- 0.9), independent of habitat amount (0.1- 0.9), and fragmentation *per se* (spatial contagion of 0.1, 0.5, 0.9). The probability of persistence was measured and the proportion of habitat or high quality required to meet population persistence thresholds (0.5- 0.9) was estimated for each landscape. Results suggest that within limits, habitat quality and quantity could potentially be substituted to meet or maintain a range of population persistence goals. However, the equity of trading habitat quality for quantity, or vice versa, appears to vary with the species and landscape.

Habitat quality improvements were more effective than habitat additions in meeting population persistence goals in clumped or moderately fragmented landscapes, although results imply that there are limits to the efficacy of quality to compensate for low habitat amounts in highly fragmented landscapes. In such landscapes, habitat additions were more effective than quality improvements. While habitat quality is often difficult to assess in the field, quality improvements are likely to be valuable in recovering populations under a wide range of landscape conditions. Habitat quality improvements may be valuable and feasible options to compensate for habitat loss and should be considered alongside habitat quantity and configuration in evaluating habitat restoration and species recovery options.

Keywords: Extinction risk; Fragmentation; Habitat degradation; Habitat loss; Habitat quality; Habitat restoration; Individual-based model; Simulation

Introduction

Habitat alteration and destruction are often cited as the primary factors responsible for population decline and species extinction (Ehrlich and Ehrlich 1981, Tilman et al. 1994). Beyond habitat conservation, there is often a need to reclaim or restore landscapes in order to recover populations. However, restoring landscapes to their previous states may not be feasible. Additionally, the need to identify effective strategies to offset the population consequences of landscape change is increasingly recognized (Hobbs 2005).

Shaped by the theories of island biogeography and metapopulation biology (MacArthur and Wilson 1967, Levins 1969, Gilpin and Hanski 1991, Hanski et al. 1997, Hanski 1999), the current paradigm for species conservation emphasizes the influences of habitat amount and fragmentation *per se* on population performance and persistence. As such, management practices are often based on the assumption that modification of habitat quantity and configuration are the primary habitat factors threatening species survival, and much of conservation and habitat restoration practice is focused on habitat additions and improving the spatial arrangement or connectivity of habitat patches. This emphasis has lessened the interest in investigations of habitat quality improvements (Klok and De Roos 1998).

Studies at both the patch and landscape extents have concluded that habitat quality can play an integral role in influencing population dynamics, local persistence, and regional population size (Dennis and Eales 1997, Thomas et al. 2001, Fleishman et al. 2002, Franken and Hik 2004, Wiegand et al. 2005, Ozgul et al. 2006) and habitat quality may even outweigh the influence of habitat amount and configuration (Chapter 2). Using

mathematical models, Klok and De Roos (1998) contrasted the relative efficacy of increasing population size (which may be theoretically analogous to habitat amount) versus reproductive success (which may be analogous to habitat quality) on the risk of population extinction. They concluded that extinction risk for *Sorex araneus* populations (resulting from demographic stochasticity) can most effectively be reduced by increasing individual reproductive success (i.e., increasing habitat quality). However, these conclusions were based on a spatially-implicit model, that did not include individual interactions with the structure and composition of the landscape which can influence dispersal, territory selection, and ultimately population performance and persistence.

In Chapter 2 I used a spatially-explicit individual-based model to simulate population extinction responses across a gradient of landscapes, varying in amount, quality, and configuration of habitat. The results indicated that the influence of habitat quality outweighs that of habitat amount, suggesting that habitat quality improvements may generally better promote population persistence than increases in the amount of habitat in the landscape. However, in low resource landscapes (i.e., low amount or quality) which are likely to be of particular conservation concern, the influences of habitat quality and quantity were predicted to be more similar. In such landscapes, a greater degree of substitutability among habitat quality and quantity variables may exist, providing more options for habitat restoration and population recovery. However, there is a lack of general understanding regarding the degree to which habitat quality could be improved to compensate for the population persistence consequences of habitat loss or fragmentation. Insight into the efficacy of habitat trade-offs to compensate for the impacts of habitat loss

and degradation is likely to be valuable in habitat conservation and restoration planning and in implementing effective species recovery actions.

The aim of this chapter is to examine, from a theoretical perspective, the degree to which habitat quality and quantity could potentially be substituted to compensate for the population persistence consequences of habitat loss or degradation. In doing so, I sought to assess the conditions under which quality-quantity trade-offs are likely to be effective, estimate the magnitude of improvement that would be required to meet various population persistence goals, and assess the relative effectiveness of habitat quality improvements.

Methods

Approach

Population dynamics were simulated in landscapes of varying habitat amount, quality, and fragmentation to assess the degree to which habitat quality and quantity could be substituted to compensate for the population persistence consequences of habitat loss and degradation, respectively. Two different ecological profiles were implemented in a spatially-explicit individual-based model, and the quality or quantity of habitat necessary to meet population persistence goals under different scenarios of habitat loss and degradation was estimated.

Landscapes

One hundred and five fractal landscapes (128 x 128 pixels) were generated within QRULE (Gardner and Urban 2007) according to a factorial design. Landscapes were composed of both high and low qualities of habitat embedded within uninhabitable

matrix, wherein individuals could move through non-habitat, but could not take up residence. Habitat quality represented the density or value of resources within habitats, with low quality habitats containing half the resources available in high quality habitats. Landscapes varied in their proportion of high quality habitat (five levels: 0.1, 0.3, 0.5, 0.7, 0.9) independent of habitat amount (seven levels: 0.1, 0.2, 0.3, 0.4, 0.5, 0.7, 0.9). The structure of habitats varied from highly clumped to highly fragmented habitat. Three levels of spatial contagion (0.1, 0.5, 0.9), which describe the tendency of habitat to be spatially aggregated (Leitão et al. 2006), were included to assess the influence of habitat configuration on the efficacy of habitat quality-quantity trade-offs. For convenience, landscapes were characterized as possessing low, moderate, or high levels of fragmentation (which can be interpreted conceptually as the inverse of spatial contagion). Two landscape replicates of each factorial combination of quality, quantity, and configuration were generated for a total of 210 distinct landscapes.

Population Model

Landscape structure and composition were linked with population persistence using behavioural rules governing individual movement and territory selection within the spatially-explicit individual-based model HexSim (previously known as PATCH, Schumaker 1998, 2009). Two previously developed population scenarios (Chapter 2) were used to represent a spectrum of territorial species and their responses to landscape structure and composition. The ecological profiles emulated a K life strategist with large resource requirements and the ability to disperse long distances (equivalent to the full width of the landscape). K strategists also displayed delayed reproductive maturity, low reproductive and high survival rates. In contrast, the r strategist required fewer resources

and could only move short distances during dispersal (maximum distance equivalent to 25% of the landscape width). *r* strategists reached reproductive maturity sooner, and were given high reproductive and low survival rates. The following outlines how habitat amount and quality affect individual fitness and population dynamics (but see Chapter 2 for more details).

The quantity and quality of resources acquired by individuals determined their probability of survival and reproduction. Individuals attempted to build a territory that contained a target resource level (4000 or 1000) out of a maximum of 60 or 15 unoccupied pixels (for *K* and *r* profiles, respectively). Those that met the resource target received the maximum possible survival and reproductive rates. High quality habitats contained a greater density of resources; therefore, individuals required fewer pixels of habitat to meet the target level. In low quality habitats, individuals had to occupy larger territories to include a greater amount of habitat with lower resource density to reach the same target. Territories were required to include at least some high quality habitat to reach the target resource level to impose a cost for defending a larger area. Individuals unable to reach the target resource level received reduced survival and reproductive rates that declined linearly as the acquired resources declined from a maximum value. Those unable to meet the minimum requirement to establish a territory were termed floaters and had a low probability of survival and were unable to reproduce. Environmental stochasticity was incorporated by selecting at random (with replacement) a maximal survival rate from a normal distribution. The mean values for the maximum vital rates were chosen for each ecological profile to yield an overall population rate of increase of > 1 for species in landscapes consisting of completely high quality habitat, and < 1 in low

quality habitat (e.g. Wiegand et al. 1999, Wiegand et al. 2005). Simulations were initiated with 1000 individuals distributed within the habitat. As the long-term population response to landscape conditions was of interest, 100 repetitions of 500 years of data were recorded.

Analysis

The probability of extinction (PE = no surviving animals in the landscape) was recorded for each landscape simulation. Extinction risk did not differ among replicates within each landscape scenario in previous (Chapter 2) simulations (t test t ratio = -1.0969 (1, 248), $P = 0.2737$, $n = 250$; similar results were obtained with non-parametric tests; Chapter 2), and were averaged for each landscape. Probabilities of extinction were plotted as functions of both habitat amount and quality. Spline functions were fitted to interpolate the qualities and quantities of habitat required to meet specific probabilities of persistence (0.5 - 0.9) under different habitat loss and degradation scenarios (respectively). Probabilities of persistence ($1 - PE$) were then plotted as a function of the proportion of high quality or amount of habitat required to meet the thresholds.

Results

The heights of lines within plots (Figs. 3.1, 3.2) indicated the minimum habitat amount or proportion of high quality required to meet persistence targets under different landscape scenarios. Differences in the heights of lines within plots indicated the magnitude of improvement required to compensate for habitat degradation (A, C, E) or loss (B, D, F), thus, the closer the lines, the less required improvement to meet persistence targets. Comparisons of the required improvements among amount and

quality plots (e.g. proximity of lines in frame A compared to B) indicated whether habitat amount or quality improvements were more effective in compensating for landscape change at each level of fragmentation. The shape and steepness of lines indicated the sensitivity of persistence to habitat amount, quality, fragmentation, and their interactive effects.

Amount Required

The proportion of habitat required to meet population persistence targets varied among habitat quality scenarios. For the K strategist, the minimum amount of required habitat differed greatly between the 0.1 and 0.3 - 0.9 habitat quality scenarios (Fig. 3.1). Modest differences in the amounts of habitat required were generally observed among scenarios with > 0.3 high quality (and hence < 0.7 low quality) habitat. In relatively contiguous or moderately fragmented landscapes, only minimal amounts of habitat were required to meet persistence goals in landscapes where high quality was > 0.3 of the landscape (Fig. 3.1 frames A, C). In highly fragmented landscapes, there was less variation in the required proportion of habitat among habitat quality scenarios than observed in the proportion of required quality of habitat among habitat amount scenarios (e.g., Fig. 3.1, E compared to F). Figure 3.2 illustrates qualitatively similar results for the r ecological profile.

Quality Required

In contiguous and moderately fragmented landscapes, the proportions of habitat quality required to meet persistence targets in habitat amount scenarios of 0.1 and 0.3 (Fig. 3.1, frames B, D) varied to a lesser degree than the amount of habitat required for 0.1 and 0.3 quality scenarios (frames A, C). Minimal proportions of high quality habitat

were required to meet persistence targets when the amount of habitat in the landscape exceeded 0.3. In highly fragmented landscapes of amounts $\geq 0.5 - 0.7$, little habitat quality (< 0.2) was required to meet persistence targets (Fig. 3.1, frame F); however, a substantial level of quality was required when the amount of habitat in landscapes was low (0.1). In particular, for the K strategist to meet the modest persistence target of 0.5, the estimated level of required quality was approximately 0.6 (Fig. 3.1, F). This value increased to 1 for a probability of persistence of 0.9, indicating that the maximum quality level was insufficient to meet the persistence target. Similarly, most persistence targets were unattainable for the r strategist occupying highly fragmented landscapes with small amounts of habitat (Fig. 3.2, F). In general, similar trends were observed for the r strategist as were described for the K strategist (Fig. 3.2), although a greater proportion of high quality habitat was required to reach persistence targets in scenarios with intermediate levels of habitat amount (0.5).

Discussion

As most persistence goals were attained with different combinations of habitat amount and quality, the results of this study suggest that within limits, habitat quality and quantity could potentially be substituted to compensate for habitat loss or degradation. However, the equity of trade-offs and the effort required to compensate for landscape change depends in part on the degree of landscape fragmentation.

Contiguous and Moderately Fragmented Landscapes

In relatively contiguous and moderately fragmented landscapes (i.e., spatial contagion 0.5 – 0.9), the amount of habitat required to meet persistence goals in landscapes of low

quality (0.1 - 0.3) greatly differed, suggesting that a large increase in the amount of habitat in the landscape may be required to compensate for a modest reduction in habitat quality. In contrast, the level of quality required to meet persistence goals differed to a lesser degree between habitat amount 0.1 and 0.3 scenarios. This indicates that somewhat minor increases in habitat quality could compensate for habitat loss and that habitat quality improvements within this range are likely to be more effective in restoring habitats to meet population persistence goals. Populations inhabiting landscapes with high levels of quality and/or amount of habitat experienced few extinction events. As such, little difference in the proportion of habitat amount or quality required was observed in relatively contiguous landscapes where the proportion of high quality and/or amount of habitat was greater than 0.3. This suggests that the effects of habitat amount and quality are largely substitutable in this region of parameter space.

Highly Fragmented Landscapes

In highly fragmented landscapes (i.e., spatial contagion 0.1), populations experienced a greater number of extinction events, and greater proportions of habitat amount and quality were generally required to meet population persistence goals. Modest differences were observed among quality scenarios (0.3 – 0.7 and 0.3 – 0.9 for K and r ecological profiles respectively), implying that only minor increases in the proportion of habitat in landscape would be required to compensate for habitat degradation within this range. In contrast, more substantial increases in quality were generally required to compensate for habitat loss.

In low resource landscapes, where quality or quantity was low (0.1), a dramatically greater proportion of habitat or level of quality was required to counter the increased risk

of extinction. This suggests that the recovery of populations inhabiting low resource landscapes may require a great degree of habitat restoration to achieve population persistence goals, especially when habitat is highly fragmented. In particular, when habitat amount was held at 0.1, no level of quality was sufficient to meet all persistence goals for both K and r profiles (Figs. 3.1 & 3.2, F). This implies that there are limits to the efficacy of quality to compensate for very low habitat amounts in fragmented landscapes and improvements in both amount and quality may be required to meet persistence targets.

Implications for Designing Restoration Strategies

Previous research suggested that the influence of habitat quality outweighs that of habitat amount (Chapter 2), indicating that habitat quality improvements should generally be more effective than habitat additions in compensating for landscape change. Thus, I expected that quality improvements would be effective in countering the population persistence consequences of habitat loss through much of the parameter space. Not surprisingly, habitat quality improvements were more effective (i.e., required less improvement) than habitat additions at reaching population persistence goals in low- or moderately-fragmented landscapes. Klok and DeRoos (1998) similarly concluded that increases in population growth rates, as accomplished through habitat quality improvements, should be more effective in reducing the risk of extinction than increases in habitat amount. However, their study may not apply to a wide range of landscapes as spatial structure was not considered, potentially resulting the overestimation of population size (Wiegand et al. 2005) and persistence. Support for the greater efficacy of habitat quality improvements over habitat additions and spatial arrangements can be

gleaned from other spatially-explicit studies evaluating the influence of habitat amount, configuration, and species' reproductive outputs on extinction risk (e.g., With and King 1999, Fahrig 2001). If reproductive rates are re-interpreted as resulting from habitat quality rather than species-specific attributes, these studies suggest that habitat quality improvements are likely to be more influential than habitat additions (Fahrig 2001). Further, With and King (1999) note that enhancing reproductive output by improving habitat quality may be more effective than habitat configuration improvements.

Contrary to my expectation, habitat additions were more effective than quality improvements in meeting population goals in highly fragmented habitats. Habitat fragmentation decreases the average size of patches while increasing the number of patches in the landscape (Fahrig 2003). Thus, as fragmentation *per se* increases, it becomes more difficult for individuals to find patches of a sufficient size and resource level to establish a successful territory. Less of an increase in habitat amount was required to meet population goals (compared to quality improvements), likely because habitat additions compensated for fragmentation to some extent. As habitat patches were extended, inter-patch distances and patch edge were reduced, making previously uninhabitable habitat fragments more attractive and suitable to occupy. This result also suggests that the isolation or connectivity characteristics of patches may determine how useful habitat additions are likely to be. For example, habitat additions may be more effective if used to expand and coalesce existing clustered patches versus adding a number of new, small and isolated patches to the landscape.

Despite having different requirements for resources and hence different territory sizes, K and r strategists responded similarly in highly fragmented landscapes, both requiring a

lesser degree of habitat additions than quality improvements. However, habitat additions were generally more effective in compensating for the effects of habitat degradation for *r* compared to *K* profile, suggesting that species-specific responses are likely to influence the efficacy of habitat improvements. Among ecological profiles, the differences in the proportion of habitat or high quality required to meet persistence goals is likely attributable to the greater variability in population size exhibited by the *r* strategist. The high reproductive rates of the *r* strategist combined with low survival rates, which are subject to variation as a result of environmental stochasticity, resulted in greater fluctuations in population size and increased risks of extinction. Particularly when occupying low resource landscapes, *r* strategists often required a greater proportion of habitat or high quality to meet persistence goals despite having smaller territory requirements and larger population sizes. This suggests that while extinction risk as a result of stochastic events is often assumed to be strongly correlated with population size, for some populations, extinction risk may depend to a greater extent on the stability of the population size rather than the total number of individuals.

While the metapopulation literature emphasizes the role of habitat configuration on population dynamics, models arising from habitat fragmentation literature indicate that fragmentation effects are likely to influence extinction risk only within a relatively narrow range of habitat amount (Fahrig 1997, Flather and Bevers 2002, Fahrig 2003). However, when habitat quality was explicitly considered in this model, extinctions were observed in highly fragmented landscapes of moderate-high amounts of habitat, suggesting that fragmentation effects are likely to be observed in low quality landscapes, and may be more prevalent than previous models might suggest. Thus, optimizing the

spatial arrangement of habitats is likely to be of value in areas of low habitat amount as well as in low quality landscapes.

My aim was to provide general guidance, from a theoretical perspective, regarding the equity of quantity-quality substitutions. This study described where habitat trade-offs are likely to be beneficial and discussed under what circumstances different habitat restoration strategies are likely to be the most efficient. Results indicate that habitat quality and quantity could potentially be substituted, within limits, to meet or maintain a range of population persistence goals, and habitat quality improvements are generally likely to be more effective than habitat additions, except in highly fragmented landscapes. However, the specific proportion of habitat or quality required to meet persistence goals may vary widely depending on the amount, quality, and fragmentation of the landscape. Thus, beyond such broad generalizations, landscape and species-specific factors are likely to influence the degree of substitutability of habitat quality and quantity.

While I was able to describe general conditions under which habitat quality improvements are likely to be of value, my study does not address the practical costs of restoration strategies, which may largely determine their efficiency and feasibility. For example, while habitat additions may, in theory, be more effective than quality improvements in highly fragmented landscapes, it may be less costly to improve habitat quality by a large proportion than it is to add a small amount of habitat, or vice versa. Thus, case-specific factors will ultimately dictate the feasibility of habitat restoration options. Further, because the aim was to contrast habitat quality and quantity improvements, I did not emphasize the efficacy of combined improvements. In some scenarios, large changes in the amount or quality of habitat were required to meet

population persistence goals; however, smaller combined improvements in the amount and quality may be sufficient to achieve goals where the options for dramatic improvements in one variable are infeasible.

Conclusions

The current emphasis on habitat quantity and configuration has fostered management practices based on the assumption that habitat loss and fragmentation are the primary landscape factors limiting population persistence (Klok and De Roos 1998). As such, many habitat restoration strategies are focused on habitat additions and optimizing the configuration or connectivity of habitat patches. Habitat quality improvements are often of lesser interest, owing in part to the theories of island biogeography and metapopulation biology (MacArthur and Wilson 1967, Levins 1969, Gilpin and Hanski 1991, Hanski et al. 1997, Hanski 1999) that emphasize patch size and isolation. In addition, habitat quality improvements are likely of less concern as a result of the challenges associated with measuring and incorporating habitat quality in a meaningful way into habitat assessments (Armstrong 2005, Johnson 2007). From a spatial perspective, quantifying the amount of habitat in a landscape or the clustering of patches is relatively straightforward, assuming there is a reasonable understanding of what constitutes habitat for a species. However, habitat quality measurements rely on species-specific measures that describe the density or value of resources such as food items or shelter (which are often not discernable from commonly available maps), or inferences made from habitat-specific survival and reproductive rates. Without detailed study, it is often difficult to identify the key environmental factors that represent or influence habitat quality and to

characterize the relationship between habitat quality and population performance (Johnson 2007).

While the current paradigm for species conservation emphasizes habitat additions and optimizing the arrangement or connectivity of habitat patches as potential strategies to address the consequences of landscape change, my results suggest that habitat quality improvements may be more effective in restoring habitats under a range of conditions and for a variety of species, and may be particularly valuable in compensating for habitat loss in relatively contiguous or moderately fragmented landscapes. Thus, while habitat quality may be difficult to assess, an understanding of habitat quality and the influence of quality improvements on population persistence could be vital to species recovery planning, particularly in landscapes where the potential for habitat expansion is limited. In conclusion, habitat quality improvements may be valuable and feasible options to compensate for the population persistence consequences of habitat loss and should be explicitly considered alongside habitat quantity and configuration in evaluating habitat restoration and species recovery options.

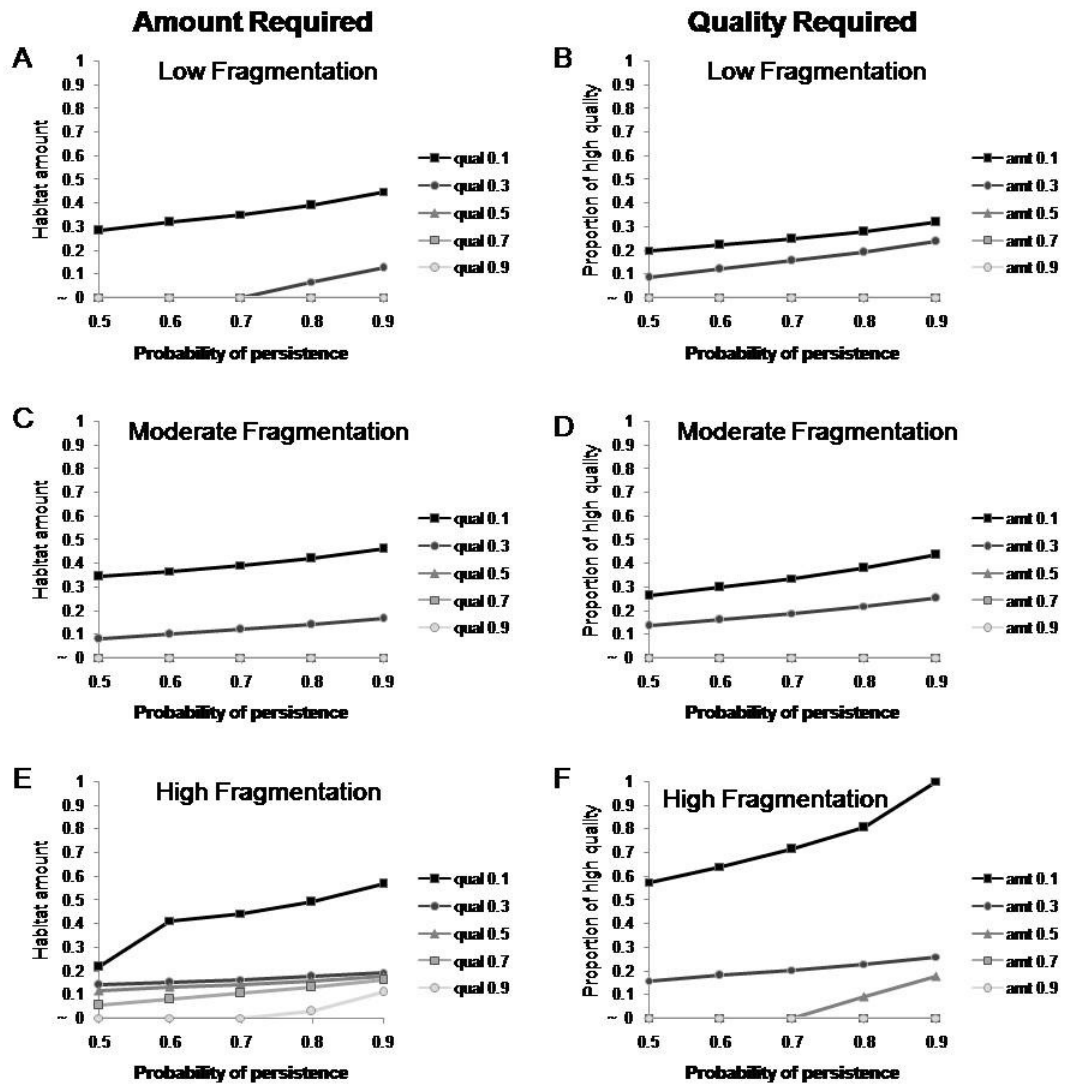


Fig. 3.1. The estimated proportion of habitat (left) or high quality habitat (right) required to attain 0.5- 0.9 probabilities of persistence for the K ecological profile in landscapes of varying combinations of habitat amount, quality and levels of fragmentation.

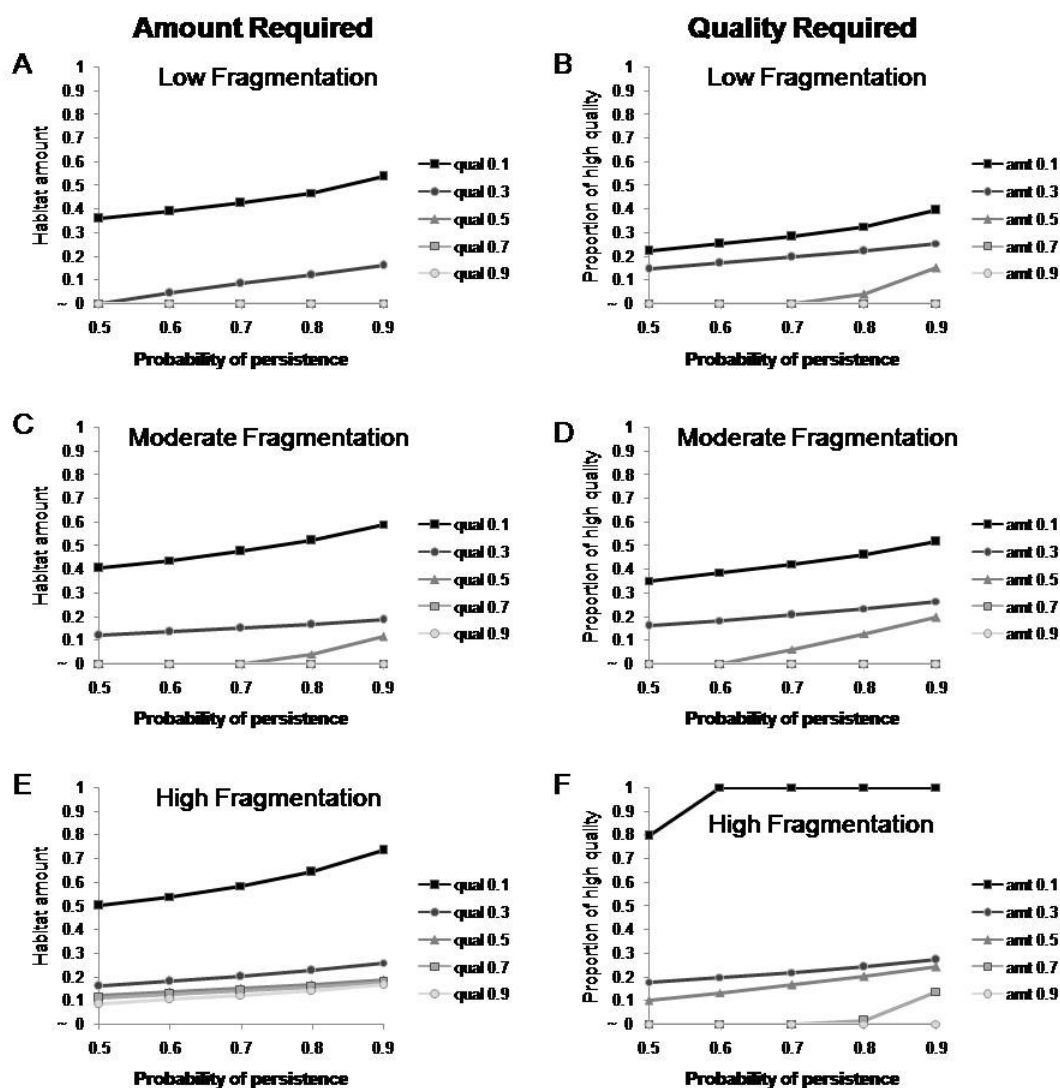


Fig. 3.2. The estimated proportion of habitat (left) or high quality habitat (right), independent of habitat amount, required to attain 0.5- 0.9 probabilities of persistence for the *r* ecological profile in landscapes of varying combinations of habitat amount, quality and levels of fragmentation.

CHAPTER 4 - IMPACTS OF HABITAT REMOVALS ON POPULATION PERSISTENCE: A SIMULATION EXPERIMENT WITH ENDANGERED KANGAROO RATS

Abstract

Habitat patch size and isolation are often described as the key habitat variables influencing population dynamics. Yet habitat quality may also play an important role in influencing the regional persistence of spatially structured populations as the value or density of resources within habitats can affect the capacity of habitats to support individuals. To examine the relative importance of patch size, quality, and isolation on the regional persistence of endangered Ord's kangaroo rats (*Dipodomys ordii*) in Alberta, I conducted habitat removal simulations using a spatially explicit population model. Groups of habitat patches were removed based on their size, quality, and isolation characteristics, and the resulting risk of regional population extinction was measured. A proportional hazards model was used to assess the relative importance of habitat variables. Patch-level variables contributed to the risk of population extinction, despite the dominant influence of landscape-level variables (particularly quality and habitat amount). The most highly ranked variables all related to habitat quantity and/or quality, suggesting that kangaroo rat persistence is heavily influenced by variables that influence habitat capacity, and less influenced by habitat configuration. Results indicate that both landscape considerations and the attributes of constituent patches should be of vital interest for kangaroo rat conservation. While linear or proportional relationships between patch area and local population size are often assumed, the influence of patch quality

outweighed that of patch area, suggesting that such assumptions may not be appropriate in landscapes of heterogeneous habitat quality. The removal of low quality habitats (road margins) actually increased persistence, suggesting that the prioritization of habitats based only on patch size and isolation may jeopardize persistence by promoting the preservation and proliferation of low quality or detrimental sinks. Conservation planning should consider the potential influence of habitat quality in landscapes where differences in resources or population density may be important.

Keywords: Alberta, Canada; *Dipodomys ordii*; extinction risk; habitat capacity; habitat quality; isolation; patch size; persistence; population viability; spatially-explicit population model

Introduction

Much of our understanding of the responses of spatially-subdivided populations to habitat characteristics was initially drawn from the theories of island biogeography (MacArthur and Wilson 1967) and metapopulation dynamics (Levins 1969, Gilpin and Hanski 1991, Hanski et al. 1997, Hanski 1999, Wilson et al. 2009). Thus it is not surprising that the current paradigm for species conservation focuses primarily on patch size and isolation as the key habitat variables influencing population dynamics and persistence. However, variation in the value or density of resources and environmental conditions in different habitat patches (i.e., patch quality) may affect occupancy, and survival and reproduction of individuals (Hall et al. 1997, Fleishman et al. 2002). A growing number of studies have reported that variation in habitat quality affects population dynamics and local population persistence (e.g., Dennis and Eales 1997, Fleishman et al. 2002, Ozgul et al. 2006, Jaquiere et al. 2008). Further, habitat quality may be equally or more important than patch size or isolation for determining where populations persist in fragmented landscapes (Thomas et al. 2001, Franken and Hik 2004). However, few studies have examined the relative influence of patch size, quality, and isolation for regional or metapopulation persistence (e.g., Day and Possingham 1995).

Extinction risk is often related to the size of the population, with larger populations being less vulnerable to extinction as a result of stochastic events. A similar effect may be observed as a result of heterogeneous habitat quality (Harrison and Taylor 1997). All else being equal, larger patches contain more space and total resources than smaller patches and should have a greater capacity to support a larger population. Similarly, the

greater the density or value of resources (i.e., food, shelter) within habitat patches, the greater the potential local population density, size, and higher predicted persistence.

Patch size and quality may also interact such that large, high quality patches contain disproportionately large populations. For example, a large amount of high quality resources within a large patch may result in greater occupancy and population abundance if these attributes result in greater immigration and less emigration. All else being equal, larger patches should receive more immigrants (Kawecki 2004), and this may be exaggerated if animals perceive habitat quality from a distance and direct their movements to locate high quality areas of the landscape. Some animals may also display greater site fidelity in high quality habitats, resulting in reduced emigration rates. In addition, animals may be more likely to leave a patch if they encounter its edge, hence larger patches may have lower emigration rates (Bowman et al. 2002). Therefore, populations in landscapes comprised of large and/or higher quality patches should have a greater likelihood of at least one local population persisting than those containing smaller and/or lower quality patches.

The isolation of patches with respect to other local populations (whose dynamics are linked by dispersal) influences the probability of patch re-colonization following local extinctions (Brown and Kodric-Brown 1977, Hanski 1999). A population occupying a landscape comprised of relatively proximate patches may exhibit a reduced risk of regional extinction, because inter-patch dispersal and re-colonization events are more likely than in landscapes with highly isolated patches. Large patches in close proximity to other populations may also have disproportionately high population sizes if patch size and isolation effects interact. For example, a patch may be more likely to be found if it is

both large and proximate to other populations, thereby boosting local population occupancy and abundance, and reducing extinction risk. A similar rationale may apply to proximate, high quality patches if territory selection or the movements of individuals are influenced by the quality of nearby patches.

My goal was to assess the relative importance of patch size, quality, and isolation, including potential interactions, on the regional persistence of a naturally fragmented population of the Ord's kangaroo rat (*Dipodomys ordii*) in Alberta, Canada. I also sought to identify the most important attributes of habitat patches for persistence and recovery of this study population. To accomplish this, I conducted habitat removal simulations based on patch characteristics, and quantified the resulting risk of regional population extinction.

Methods

Study System

The Ord's kangaroo rat is the only species of kangaroo rat that occurs in Canada and it is endangered by its small population size and dramatic fluctuations, geographic isolation, and rapid loss and degradation of natural habitat (COSEWIC 2006). The distribution of this northern population of kangaroo rats is limited to one small region (a cluster of sand dune complexes) in south-eastern Alberta and south-western Saskatchewan (COSEWIC 2006). The majority of occupied sites in Alberta are located within Canadian Forces Base (CFB) Suffield (Fig. 4.1), primarily in the Suffield National Wildlife Area (SNWA).

The Ord's kangaroo rat requires sparsely vegetated, sandy habitats to support its burrowing behaviour and salutatory mode of locomotion (Bartholomew and Caswell 1951, Armstrong 1979, Hallett 1982, Kenny 1989, Gummer 1999). Natural habitats for this species consist of actively eroding sand dunes, as well as semi-stabilized sand dunes where encroaching vegetation has limited the amount of open sand. Kangaroo rats also inhabit sandy soils exposed by human activities (Nero and Fyfe 1956, Smith and Hampson 1969, Kaufman and Kaufman 1982, Stangl et al. 1992, Gummer 1997, Gummer 1999), including the margins of sandy roads and ploughed fireguards (i.e., firebreaks; (COSEWIC 2006). Road margin habitats are characterized by greater soil compaction, colder burrow temperatures, and lower overwinter survival rates than active sand dunes (Teucher 2007). These habitats are subject to disturbance from human activities (e.g., vehicle traffic, grading), are often dominated by invasive plant species that may influence the diet composition of kangaroo rats, and pose greater risk of predation (Teucher 2007) and parasitism of kangaroo rats than natural habitats (COSEWIC 2006). These types of habitats may act as population sinks because they contain high densities during in the summer months following the influx of new juveniles to the population, but exhibit high rates of local extinction following harsh winter conditions (Gummer and Robertson 2003b, COSEWIC 2006). The results of a simulation modeling study of kangaroo rat population dynamics suggested that many road segments serve as population sinks over the long-term (Chapter 5). To a lesser extent, kangaroo rats in Alberta also inhabit other natural, exposed sandy soils (such as the steep sandy slopes of the South Saskatchewan River valley). Kangaroo rats do not typically occupy fully stabilized sand dune complexes (Kenny 1989) and hence the

discrete natural and anthropogenic habitat patches are embedded in a matrix of largely uninhabited land.

Habitat Removals

Individual habitat patches for Ord's kangaroo rat in Alberta were identified based on a previously developed habitat-occurrence model, using a resource selection function (Bender et al. 2010; Chapter 5). Habitat type-specific quality information was subsequently incorporated (see below) and the resulting model was used to quantify kangaroo rat habitat composition and configuration.

Patch Quality

Habitat patches were identified as belonging to one of four habitat types: active dune, semi-stabilized dune, road margins, and exposed sandy river valley slopes, and were classified using air photo interpretation and knowledge of features on the ground (Bender et al. 2010; Chapter 5). The relative quality of active dune and road-side habitat types was estimated using habitat-specific overwinter survival rates (derived from Teucher 2007), while the quality of the semi-stabilized sand dunes and exposed soil habitats was inferred from distribution data and expert knowledge (R. Dzenkiw, Lead Surveyor for Alberta Long-term Population Monitoring Program; see Chapter 5). Raster grid cells in the habitat map were assigned the habitat quality scores (Table 4.1) of their corresponding habitat types (Fig. 4.2). Habitat fragments of similar quality (e.g. all patches associated with dunes) that were within 30m of each other were aggregated into one functional patch for patch removals and isolation calculations. A majority rule was used to determine the habitat type. This procedure identified 8413 habitat patches within the entire range (~1800 km²) in Alberta.

Patch Size

The area of each patch was used to classify patches into four size categories based on the maximum possible number of kangaroo rats that could occupy a given habitat patch. Male and female kangaroo rats are solitary, territorial and defend burrows and food caches (Bartholomew and Caswell 1951, Eisenberg 1963, Garner 1974, Daly et al. 1984). Patch capacities were based on a kangaroo rat territory size $1750 \text{ m}^2 (\pm 1 \text{ SE})$ in high quality habitat (Gummer and Robertson 2003a). Thresholds for patch size categories were chosen to reflect a range of population sizes, while accounting for the distribution of patch sizes within the landscape (Table 4.2). Patches that were less than 3500 m^2 could only support a maximum of one kangaroo rat, but were included as they may provide stepping-stone habitats (see Baum et al. 2004) to facilitate dispersal to other populations or unoccupied patches.

Patch Isolation

I calculated a proximity index for each patch in the landscape (below). Patch proximity, which is the conceptual inverse of patch isolation, was calculated as the sum of all patch areas (a_{ijs}) within a specified neighbourhood distance of the focal patch (ij), divided by the edge-to-edge distance squared (h^2_{ijs}) between the patch and the focal patch (McGarigal et al. 2002). A neighbourhood distance of 8500 m was used in the calculation as it corresponded with the maximum observed single movement distance of an individual kangaroo rat in Alberta (Gummer, unpubl. data). Patches were classified as belonging to one of three categories of proximity by binning the patch proximity index into three equal (tertile) bins. The equation for the proximity index (McGarigal et al. 2002) is:

$$PROX = \sum_{s=1}^n \frac{a_{ijs}}{h_{ijs}^2} \quad (1)$$

Where a_{ijs} equals the area (m^2) of patch ijs within specified neighbourhood (8500 m) of patch ij , and h_{ijs} equals the distance (m) between patch ijs and patch ij , based on patch edge-to-edge distance, computed from cell center to cell center.

Habitat Removal Simulations

Groups of habitat patches were removed based on their quality, size, and isolation characteristics. A factorial design was employed to create 36 unique combinations or habitat removal scenarios, using three levels of patch quality, four patch size categories, and three levels of isolation. As exposed sandy slopes were of little conservation interest (Chapter 5), this habitat type was not included in habitat removals but remained present in the landscape to maintain realistic dynamics within the model. The landscape did not contain all possible combinations of these variables and some habitat removal scenarios were not possible. In total, 27 out of 36 possible removal scenarios were conducted. The number of patches was also unevenly distributed among the possible combinations, precluding the removal of an equal number of patches for each scenario. Therefore, all habitat patches within a given combination bin were removed in each scenario. Some habitat removals resulted in large changes in the composition and configuration of the landscape, and hence the following landscape-level measures were included in the analysis as covariates. The total amount of habitat (ha) remaining in the landscape (after the removal of the habitat patches), average habitat quality across all remaining habitat in the landscape, and landscape-level isolation (mean proximity of all patches in the

landscape), were calculated for each habitat-removal landscape. The landscape proximity index characterized the proximity of all patches in the landscape but did not include a neighbourhood distance.

Population Model

Landscape scenarios were incorporated into the spatially explicit population viability model software application HexSim (Version 1.3.6.9; Schumaker 1998, Schumaker 2008) to assess the risk of population extinction in each landscape. HexSim (formerly known as PATCH) is an individual-based model that simulates population dynamics through time, and records individual births, deaths, and movement paths through the landscape. The fate of individuals is determined by their location in the landscape and their access to resources (which is determined by both the quantity and quality of habitat in their territory). To incorporate the habitat map into HexSim, pixels from the habitat map (5 m^2) were generalized into a larger hexagonal grid (780 m^2). I used a previously developed population profile for this study population (Chapter 5). The following outlines how habitat composition and configuration affect population dynamics (see Chapter 5 for more details).

The spring/summer began with three successive reproduction, dispersal, and survival pulses to simulate the species' high reproductive potential and activity during this season. During each interval, females that held territories reproduced and the youngest stage class dispersed from their natal territory. Dispersal path lengths were assigned at random to individuals, drawn from a uniform distribution with a maximum of 8500 m, corresponding to the maximum recorded single movement distance (Gummer, unpubl. data). An intermediate level of autocorrelation in path direction was used to provide

forward momentum, and individuals were given a preference to travel along roads or higher quality habitat rather than through the matrix (with a strength that increased linearly with the habitat quality score). Movement itself did not incur mortality; however, individuals that required longer dispersal distances or more movement events to find an unoccupied territory were less likely to acquire sufficient resources for survival. Individuals were able to stop before they reached their assigned path length if they came across suitable habitat. Early stopping was triggered if an individual came across one hexagon of road-side habitat or better.

The population cycle implemented in HexSim simulated only females; hence the territory size ($1750 \text{ m}^2 \pm 1 \text{ SE}$ in active dune habitats; Gummer and Robertson 2003a) was doubled to account for the space occupied by an equal number of males in the population. When individuals reached their maximum dispersal distance or came across suitable habitat, the immediate area ($23\,400 \text{ m}^2$, representing double the maximum simulated territory size) was explored for prospective territories. The territory with the greatest total resources was then occupied until death. Individuals had to establish a territory that exceeded a minimum resource requirement (10% of the target resource level). If a suitable territory was not available, the individual continued searching during the next movement period. Mechanistic density dependence emerged as individuals spent more time searching for a territory during times of high population density.

Strong annual population fluctuations caused by environmental stochasticity were approximated using variation in overwinter survival rates of kangaroo rats. At the onset of each winter, a maximum overwinter survival rate was selected at random (with replacement) and assigned to the population. Territories had to meet or exceed the target

resource requirement ($4.49 \text{ hexagons} * 100 \text{ quality score} = 449$), using up to a maximum of 15 hexagons, for the occupant to receive the maximum possible overwinter survival rate. As habitat quality decreased, territories had to expand to include a greater area with lower resource density to reach the same target. The maximum territory size was chosen such that individuals occupying sub-optimal habitats such as in semi-stabilized dunes or road margins could expand their range to acquire additional hexagons, if available, to meet the target resource requirement and receive the maximum vital rates. Those unable to meet the resource threshold received penalized overwinter survival rates that declined linearly to zero as acquired resources declined from an optimal value. Territory expansion assumed that there were no additional costs to defending a larger area. As little variation in survival was observed in field data among habitat types during the summer, uniform survival rates (derived from Teucher 2007) were applied to each age group, regardless of their access to resources.

Simulations

To ensure that initial simulation conditions did not bias results, simulations were initialized with the landscape saturated with 25000 randomly located females. As the value of habitats for long-term population persistence may only become clear in a longer time-frame and after being subject to environmental stresses (Pelton and Manen 1996, Garshelis 2000), 500 years of data were simulated to estimate risk of extinction. Each habitat removal scenario was replicated 1000 times and the time to extinction, wherein 0 females remained in the population, was recorded for each replicate. I expected that the removal of higher quality, larger, or more proximate patches would result in increased extinction risk. Therefore, positive relationships between patch variables (quality, size,

and isolation) and risk of extinction were expected. Landscapes with less remaining total habitat, lower average quality, and lower overall proximity were expected to exhibit negative relationships with extinction risk.

Relative Importance/Statistical Analysis

A Cox proportional hazards regression model (Cox 1972) was used to assess the relative importance of habitat variables for kangaroo rat persistence. Patch-level habitat variables (patch size, patch quality, patch proximity), as well as their 2-way interactions, were included in the regression model along with the landscape-level variables (habitat amount, landscape quality, landscape proximity). The analysis approach allowed right-censoring for simulations in which no extinctions were observed and estimated an overall hazard rate. A Kaplan-Meier survival plot of the control scenario versus habitat removals was used to assess the assumption of proportional hazards (Marubini and Valsecchi 1995), wherein hazard functions are expected to express constant relative risk over time (i.e., parallel curves). All significant variables were ranked in terms of their relative influence on extinction risk using their *P* values. All analyses were conducted in JMP 8 (SAS 2008).

Results

The assumption of proportional hazards was accepted (Fig. 4.3). Within the proportional hazards model (Chi-square 1069.224; df = 12; $P < 0.0001^*$; $n = 27\,000$), all patch and landscape-level variables exerted significant ($\alpha = 0.05$) effects on the time to extinction. In addition, patch size*patch proximity and patch size*patch quality interactions had significant effects on extinction risk (Table 4.3).

Patch Variables

Based on the resulting significance (P) values, the highest ranked patch-level variable affecting regional kangaroo rat population persistence was the interaction between patch size and patch quality (Table 4.3). While visualization of interactions within the context of the statistical model was not possible in JMP (SAS Institute, Inc., pers. comm.), their relationships with extinction risk (i.e., signs of parameter estimates) were similar to those expected of non-interacting variables (Table 4.3). Separately, patch quality and patch size were ranked second and third (respectively). Removal of high quality habitat patches (i.e. active dunes compared to semi-stabilized dunes) was associated with increased extinction risk, whereas the removal of low quality road margin habitats reduced the risk of regional population extinction. Patch proximity did not rank highly, and the interaction between patch proximity and patch quality did not have a significant effect on extinction risk. The regression of patch size and proximity within the multivariate Cox proportional hazards model resulted in negative relationships with extinction risk. However, regression of these variables in univariate proportional hazards models resulted in positive relationships.

Landscape Variables

Landscape-level variables largely dominated the influence of patch variables on the risk of regional population extinction. Landscape quality was the highest ranked variable in the statistical model, followed by landscape habitat amount. Landscape proximity significantly predicted extinction risk, but did not rank highly in comparison to other variables. In contrast to patch variables (which are interpreted in the context of habitat removals), landscape variables describe the post-removal landscape and can therefore be

interpreted more directly. Negative relationships between landscape habitat amount, quality, proximity, and the hazard were observed (Table 4.3).

Discussion

Despite an increasing number of studies recognizing the importance of habitat quality in influencing population dynamics and persistence (e.g., Dennis and Eales 1997, Thomas et al. 2001, Fleishman et al. 2002, Franken and Hik 2004, Ozgul et al. 2006), the discussion of the capacity of habitats to support populations focuses primarily on the contribution of habitat quantity over quality (Ovaskainen and Hanski 2001, With 2004, Jaquiere et al. 2008). This emphasis on habitat quantity is likely the result of the ease in measuring patch sizes or amounts of habitat in a landscape, and the relative difficulty in assessing habitat quality. While Hanski & Ovaskainen (2000) suggest that patch areas within metapopulation models can be corrected to account for variation in quality, many models solely use patch area to describe local population size (Franken and Hik 2004). In the absence of edge effects, it is often assumed that the relationship between patch area and local population size is linear or proportional. In this study, the influence of patch quality outweighed that of patch area, suggesting that such assumptions may not be appropriate in landscapes of heterogeneous habitat quality. Thus, estimates of habitat capacities and population sizes in landscapes of variable quality should emphasize both the quantity and the qualities of habitats.

Landscape versus Patch Variables

Landscape-level habitat variables were predicted to rank as more important for regional population persistence than patch-level variables, as landscape attributes relate

more directly to the overall capacity of the landscape. Patch metrics such as patch size or quality describe the capacity of individual patches to support local populations and may be correlated with landscape-level attributes; however, the total availability or quality of habitat has a large effect on regional population size and is best described by landscape variables which consider the combined attributes of patches. Despite the dominance of landscape effects, the importance of patch variables implies that the details of the composition of habitat (i.e. distribution of patch sizes and qualities), and to a lesser extent configuration (patch isolation), may also significantly influence risk of regional kangaroo rat extinction. This suggests that while landscape-level habitat considerations should be of vital interest for kangaroo rat conservation, the attributes of its constituent patches may substantially influence population persistence. For example, extremes in the distribution of habitat quality among patches may give rise to source-sink population dynamics and population persistence may depend not only on the overall level of quality in the landscape, but also on the proportion of low and high quality patches.

Relative Influence of Habitat Quality, Quantity, and Isolation

Larger populations are generally thought to be less prone to extinction as a result of stochastic events (Gaggiotti and Hanski 2004). Thus, it stands to reason that habitat variables influencing habitat capacity, or the maximum number of individuals that a given habitat patch or landscape can potentially support, should be important in explaining extinction risk. This is congruent with the results of this study, wherein the five most highly ranked variables in the statistical model related to habitat quantity, which influences the minimum population size, and/or quality, which influences population density and size. The configuration of habitat patches may also influence

abundance if habitats are unequally accessible, affecting the probability of patch colonization and occupancy (Brown and Kodric-Brown 1977, Hanski 1999, Holland et al. 2005). However, isolation metrics generally ranked below habitat quantity and quality metrics in my results, indicating that habitat configuration may be less important for persistence than habitat composition. Thus, kangaroo rat persistence is likely to be more heavily influenced by variables affecting habitat capacity than habitat colonization and occupancy.

Habitat Conservation and Restoration

The relative importance of patch size and patch quality variables implies that kangaroo rat persistence could be promoted by conserving larger and/or higher quality patches such as active sand dunes. The significance of the interaction between patch size and patch quality suggests that patches that are both large and high quality are particularly valuable for kangaroo rat persistence, and underscores the importance of considering measures of quantity and quality together. The interaction of patch size and patch proximity was the most influential variable involving habitat configuration, suggesting that clusters of large patches may be particularly beneficial for regional kangaroo rat persistence.

My results suggest that the focus of habitat restoration for the Ord's kangaroo rat should be in increasing habitat capacity. While this recommendation is somewhat obvious, what is less apparent is that population persistence may depend on how one attempts to achieve this goal. For example, the tendency may be to expect that landscapes of equivalent capacities will have similar population sizes and therefore, risks of extinction. However, my findings suggest that for the Ord's kangaroo rat, population

persistence depends on how much of the capacity is contributed by low quality habitats (road margins). When the change in habitat capacity was accounted for in the statistical analysis, the removal of road margin habitats was associated with reduced risk of regional population extinction, while the removal of active dunes resulted in an increased risk of extinction. For the Ord's kangaroo rat, it is likely that many road margin habitats are operating as population sinks (COSEWIC 2006; Chapter 5), and while these sinks may serve to increase the regional population size (Pulliam 1988, Dias 1996) in favourable conditions, the risk of kangaroo rat extinction may increase as a result of the adverse conditions that make long-term survival and occupancy of these habitats difficult.

Although the simulation model was conservatively constructed such that individuals in sink habitats could expand their territories to acquire the resources needed for comparable vital rates in high quality habitats, it is possible that road margin habitats had greater densities of individuals and this precluded full expansion. Road margin habitats are likely to have a large influx of immigrants as their long, linear shape and orientation in the landscape encourages a greater rate of encounter than would be expected for more compact dune habitats (see Bowman et al. 2002). In addition, the shape of road margin habitats may restrict territory expansion to a narrow length of the road, making territory expansion more difficult than in dune habitats. These results indicate that kangaroo rat persistence is likely to increase if road margin habitats are removed and replaced with an equivalent capacity in natural sand dune habitats. In particular, the negative relationship (within a habitat removal context) between patch size*patch quality (road margin) and extinction risk indicates that replacing higher quality habitats with large road margin habitat patches is likely to be particularly detrimental for regional population persistence.

These results caution against the addition of new roads or similarly disturbed areas as a means of improving habitat capacity and kangaroo rat persistence. De-commissioning and restoring roads and their margins to uninhabitable matrix, while creating an equivalent capacity of high quality habitat (i.e., by restoring semi-stabilized sand dunes) is likely to be beneficial for kangaroo rat persistence.

Conclusions

As habitat quality can influence population density, it is reasonable to expect that patch quality is also an important variable influencing local and regional habitat capacity, and extinction risk. Yet Franken and Hik (2004) point out that studies contrasting the relative influence of patch size and isolation commonly assume that only the former is correlated with local population size, and that there is little or no difference in the density or value of resources among habitat patches. Heterogeneous patch quality was considered in this study, and the results indicated that while patch size was an important variable explaining regional risk of kangaroo rat extinction, patch quality was more so. The assumption that patch size correlates with population size, without considering habitat quality may be particularly risky for the conservation of the Ord's kangaroo rat in Alberta. My results indicate that the loss of higher quality habitats and addition of lower quality road margin habitats (and in particular large road-side patches) is likely to be detrimental to kangaroo rat persistence. If it was assumed that all large patches contain large populations that contribute to regional population persistence, low quality patches may be erroneously prioritized for conservation, and sinks may be preserved or even enlarged to increase habitat capacity and population size.

Habitat removal simulations also provided an example that it may not be appropriate to assume that landscapes of similar capacities have equally viable populations. When the change in habitat capacity was accounted for, the removal of road margin habitats was associated with increased persistence. Hence, the proportion of low quality habitats or sinks in a landscape is likely to influence regional population viability. Measures of habitat capacity (even those that include habitat quality) may not reliably predict the persistence of populations if they exhibit source-sink dynamics. In such cases, population dynamics should be explicitly considered in persistence predictions.

Most studies of the relative importance of patch attributes (size, isolation, and potentially quality) aim to elucidate the effects of patch characteristics on local population dynamics or local persistence (e.g., Dennis and Eales 1997, Thomas et al. 2001, Fleishman et al. 2002, Franken and Hik 2004, Ozgul et al. 2006). In contrast, this study provides an example that patch attributes can significantly influence the persistence of the regional population. Hence, particularly for the Ord's kangaroo in Alberta, conservation planning would benefit from considering both landscape and patch characteristics. Further, many studies describing the relative importance of habitat variables for population dynamics or persistence do not emphasize the interactive effects of habitat variables. This case study demonstrates that extinction risk may be significantly explained by these interactions and suggests that information regarding the interactive effects of habitat variables can be meaningful for species conservation. For example, the preservation or proliferation of large and low quality sink patches may jeopardize rather than support persistence, while adding or expanding large and high quality patches may result in disproportionate rewards for the effort invested.

In conclusion, the research exploring the relative importance of patch variables on population dynamics and persistence commonly focuses on the influence of patch size and isolation, and tends to overlook other variables. However, the results of this study suggest that this emphasis may be misplaced. In addition to considering habitat quantity, conservation planning should consider the potential influence of habitat quality in landscapes where differences in resources or population density exist.

Table 4.1. Habitat types and their relative habitat quality values

Habitat type	Quality value
Active sand dune	100
Semi-stable sand dune	60
Road margin	56
Exposed, sandy river valley slope	30

Table 4.2. Patch size classification used in habitat removal simulations, based on the maximum estimated carrying capacity, using a minimum territory size of 1750m² per kangaroo rat

	I	II	III	IV
Area (m ²)	<3500	3500 - <10500	10500 - <87500	87500 – 495000
Maximum k-rats	1	2-5	6-49	50-250+

Table 4.3. Parameter coefficients (β_i), standard errors (SE), Chi-square (χ^2), degrees of freedom (df), and significance (P) values for the proportional hazards extinction risk model using simulated habitat removals and times to extinction (n = 27000) for the Ord's kangaroo rat in southeastern Alberta.

Rank	Variable	β_i	SE	χ^2	df	P
1	Landscape Quality	-0.3620	0.0222	241.0114	1	2.37e ^{-54*}
2	Landscape Habitat Amount	-0.0039	0.0003	213.4159	1	2.47e ^{-48*}
3	P.Size*P.Quality – Active	0.0333	0.0081	85.0069	2	3.48e ^{-19*}
	P.Size*P.Quality – Road	-0.1030	0.0136			
4	Patch Quality – Active	0.2187	0.0370	56.4696	2	5.47e ^{-13*}
	Patch Quality – Road	-0.2913	0.0399			
5	Patch Size	-0.0486	0.0075	42.6474	1	6.55e ^{-11*}
6	P.Size*P.Proximity	3.5298e ⁻⁵	8.474e ⁻⁶	17.6600	1	2.641e ^{-5*}
7	Landscape Proximity	-0.0132	0.0038	12.3044	1	4.519e ^{-4*}
8	Patch Proximity	-0.0002	9.1574e ⁻⁵	4.1156	1	4.249e ^{-2*}
9	P.Prox* P.Quality – Active	0.0002	0.00009	5.8950	2	5.247e ⁻²
	P.Prox*P.Quality – Road	-3.0428e ⁻⁵	0.00006			

*Significant



Fig. 4.1. Range of Ord's kangaroo rats in Alberta, Canada (adapted from Alberta Ord's Kangaroo Rat Recovery Team 2005).

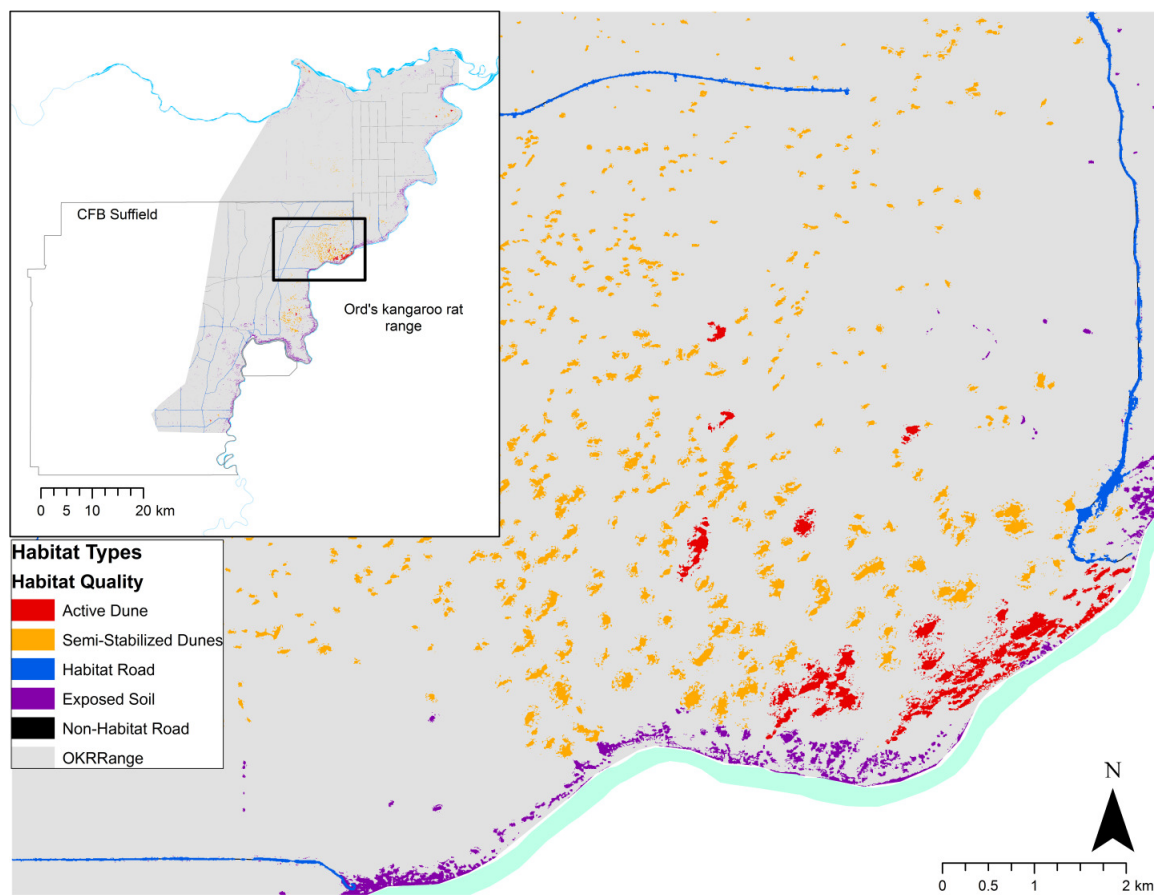


Fig 4.2. Location and extent of habitat types for the Ord's kangaroo rat in southeastern Alberta

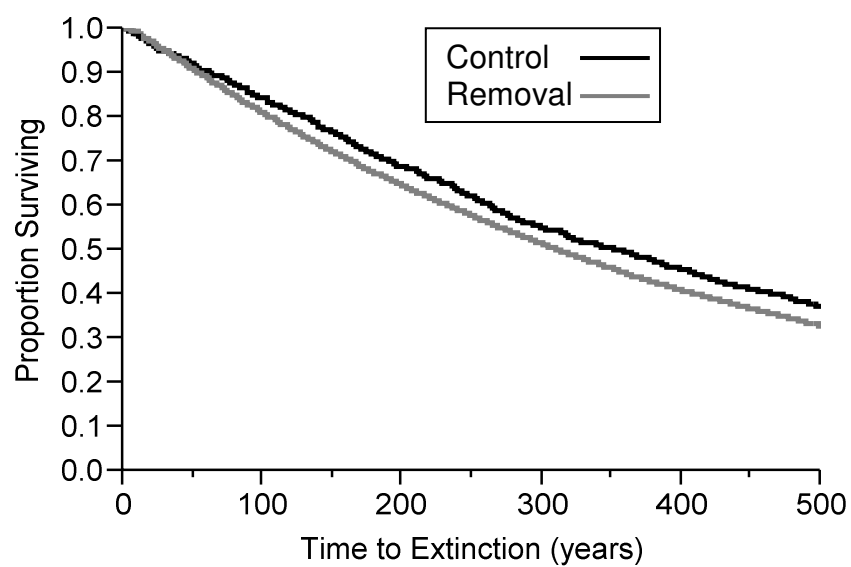


Fig. 4.3. Kaplan-Meier survival plot of the effect of habitat removals versus the control scenario (no habitat removals) on the proportion of surviving kangaroo rats through time

CHAPTER 5 - ASSESSING CRITICAL HABITAT: EVALUATING THE RELATIVE CONTRIBUTION OF HABITATS TO POPULATION PERSISTENCE

Abstract

A principal challenge of species conservation is to identify the specific habitats that are essential for long-term persistence or recovery of imperilled species. However, many commonly used approaches to identify important habitats do not provide direct insight into the contribution of those habitats to population persistence. To assess how habitats contribute to overall population viability and characterize their relative importance, a spatially-explicit population viability model was used to integrate a species occurrence model with habitat quality and demographic information to simulate the population dynamics of the Ord's kangaroo rat (*Dipodomys ordii*) in Alberta, Canada. Long-term productivity (births-deaths) in each patch was simulated and iterative patch removal experiments were conducted to generate estimates of the relative contribution of habitat types to overall population viability. My results indicated that natural dune habitats are critical for population viability, while disturbed/human-created habitats make a minor contribution to population persistence. The results also suggest that the habitats currently available to Ord's kangaroo rats in Alberta are unlikely to support long-term persistence. This approach was useful for identifying habitats that did not contribute to population viability. A large proportion of habitat (39%) represented sinks and their removal increased estimated population viability. The integration of population dynamics with habitat quality and occurrence data can be invaluable when assessing

critical habitat, particularly in regions with variable habitat quality. Approaches that do not incorporate population dynamics may undermine conservation efforts by under- or over-estimating the value of habitats, erroneously protecting sink habitats, or failing to prioritize key source habitats.

Key Words: Alberta, Canada; *Dipodomys ordii*; habitat quality; occurrence; persistence; population viability; source-sink dynamics; spatially-explicit population model; species at risk

Introduction

A principal challenge of species conservation is to identify the specific habitats that are essential for long-term persistence or recovery of endangered species. Habitat destruction as a result of loss, degradation, and fragmentation often increases the heterogeneity and complexity of landscapes, and complicates decisions as to which habitats should be protected or restored. Several approaches for identifying important habitats have been used, yet they often do not provide clear insight into the population viability consequences of protecting one habitat versus another.

Many studies have assessed habitat use by evaluating occurrence data or associating the presence/abundance of a species with local resources (e.g. Carroll et al. 2001, Boyce et al. 2003, Johnson et al. 2004). However, there are several limitations of using species occurrence data and associated models for identifying essential habitats. Such approaches often assume that short-term data represent the typical state of the population, which may be inappropriate particularly if populations cycle or fluctuate through time (Garshelis 2000, Armstrong 2005). Patterns of occurrence, particularly abundance, may also be misleading indicators of local habitat productivity (Garshelis 2000) and habitat quality (Van Horne 1983, Battin 2004). Aldridge and Boyce (2007) caution of a potential situation where habitat models identify high levels of species occurrence within sink habitats, wherein mortality exceeds survival and/or reproductive rates (Pulliam 1988). In such cases, high species occurrence is sometimes interpreted to mean ‘important’ habitat for the species, yet these habitats may not contribute to population persistence or may even jeopardize long-term population viability.

The integration of population data, such as site-specific mortality or reproduction rates with occurrence models, provides a means of assessing relative habitat quality and refining habitat conservation priorities (e.g. Nielsen et al. 2006, Aldridge and Boyce 2007, Falcucci et al. 2009). Yet such approaches cannot directly link local habitat attributes or population performance with regional population viability and therefore do not necessarily identify habitats that have key roles in population persistence.

Local population dynamics, productivity, and persistence may be influenced by patch quality and quantity (e.g. patch size), as well as the spatial effects resulting from patch shape, orientation, and isolation (Bowman et al. 2002, Fleishman et al. 2002, Franken and Hik 2004). Thus, in heterogeneous landscapes it is likely that individual habitat patches make unequal contributions to regional population persistence. Therefore, the process of assessing which habitats are biologically critical may require the integration of species occurrence mapping, habitat quality studies, population studies, and spatially-explicit population viability analysis.

I present a habitat- and demographic-based approach for identifying and prioritizing habitats that are essential for the persistence of populations. In this approach, habitat characteristics and population dynamics are integrated using population simulation, and the outcomes of the model are used to assess the contribution of individual or aggregate habitat patches to regional population persistence. This approach may be particularly useful when identifying important habitats for dynamic populations in heterogeneous landscapes, especially when habitat quality is variable. The long-term importance of currently unoccupied habitat patches can also be assessed using a population viability modeling approach, allowing a more comprehensive landscape assessment than would be

possible using demographic rates alone. Where long-term field data are lacking, simulations also allow the investigation of the effects of environmental stochasticity or directional landscape change on cumulative patch occupancy and productivity. I demonstrate this approach using the Ord's kangaroo rat as a case study.

Case Study

The Ord's kangaroo rat (*Dipodomys ordii*) is the only species of kangaroo rat to occur within Canada and its distribution is limited to one small region (a cluster of active sand dune complexes) in south-eastern Alberta and south-western Saskatchewan (COSEWIC 2006). This is a disjunct population at the northernmost periphery of the species' range (Kenny 1989, Gummer 1997), isolated from the nearest conspecifics in Montana by a distance of approximately 270 km (COSEWIC 2006). Small population size, geographic isolation, extreme fluctuations in population size, and rapid loss and degradation of natural habitat have led to the identification of this species as *endangered* in Canada (COSEWIC 2006). The majority (76%) of kangaroo rat habitats in Alberta are located within Canadian Forces Base (CFB) Suffield, primarily (68%) in the Suffield National Wildlife Area (SNWA). The range of the Alberta population extends northward from CFB Suffield into surrounding agricultural lands which comprise 24% of kangaroo rat habitats in Alberta (Fig. 5.1; Alberta Ord's Kangaroo Rat Recovery Team 2005, COSEWIC 2006).

The Ord's kangaroo rat has specific habitat requirements for open, sparsely vegetated, sandy habitats to support its burrowing and hopping style of locomotion (Bartholomew and Caswell 1951, Armstrong 1979, Hallett 1982, Kenny 1989, Gummer 1999). In Canada, natural habitats consist of discrete sandy features such as actively eroding sand

dunes or blowouts. Kangaroo rats also occupy semi-stabilized or stabilized sand dunes where encroaching vegetation has limited the amount of open sand. However, in Canada the species has not been found in fully stabilized sand dune complexes (Kenny 1989). To a lesser extent, kangaroo rats also inhabit exposed sandy soils not associated with sand dunes, often in areas where sand has been exposed by human activities (Nero and Fyfe 1956, Smith and Hampson 1969, Kaufman and Kaufman 1982, Stangl et al. 1992, Gummer 1997, Gummer 1999). Such anthropogenic habitats include sandy roads, trails, ploughed fireguards, bare ground associated with oil and gas fixtures, and the margins of cultivated agricultural lands (COSEWIC 2006). These areas are subject to human disturbances (e.g. traffic, grading), have higher rates of predation risk and parasitism than natural sites, and are often dominated by invasive plant species that may alter the diet composition of kangaroo rats (COSEWIC 2006). Road-side habitats are also characterized by greater soil compaction, colder burrow temperatures, and lower overwinter survival rates than active sand dunes (Teucher 2007).

This case study is based on the Alberta population of the Ord's kangaroo rat for which there is approximately 15 years of recent population information. This population can be characterized as highly dynamic, experiencing substantial seasonal and inter-annual fluctuations (COSEWIC 2006). Intra-annual population declines of an order of magnitude (i.e. $\leq 10\%$ survival) during winter have been observed (Kenny 1989, Gummer 1997, Gummer and Robertson 2003c) and local extinctions in habitat patches (e.g., individual sand dunes or road segments) are common (Kenny 1989, Gummer and Robertson 2003c). Environmental fluctuations as well as high seasonal reproductive rates could lead to opportunistic increases in population density in marginal habitats,

especially during the summer months when the environment becomes temporarily favourable (Van Horne 1983). Thus, local occurrence or animal density may represent a poor indicator of the importance of occupied habitats to population persistence.

Recent research examining habitat selection by kangaroo rats in Alberta (Bender et al. 2010) produced an occurrence-based model of habitat use. The model was based on 2 years of standardized population monitoring data (see Bender et al. 2007), a resource selection function (RSF) approach (Boyce and McDonald 1999, Manly et al. 2002), and its main output was a predicted occurrence map. While the model was robust, highly selective, and performed well in validation tests, the majority of habitats identified by the model are anthropogenic habitat features (roads) where kangaroo rats are known to exhibit high mortality and low productivity. In contrast, natural features (active sand dunes) that represent more productive habitats comprised a relatively small proportion of the habitat predicted to have high occurrence. The researchers remarked that it could not be used to directly assess critical habitat for the species as many locations with high probability of occurrence were low quality habitats, possibly serving as population sinks (Bender et al. 2010). Here I demonstrate how a predicted occurrence model can be integrated with information on habitat quality and population dynamics to identify specific habitat components (e.g., map pixels or habitat patches) that are expected to contribute to the long-term productivity and persistence of a population. For the purposes of assessing critical habitat from a biological perspective, such information should be more useful for evaluating and prioritizing habitat than simple maps that predict occurrence alone.

Methods

Overview

A spatially-explicit, individual-based population model was used to link landscape structure from the habitat model with habitat quality and population dynamics. This approach provides a general method for identifying some of the biologically important elements of critical habitat such as individual or groups of breeding habitat patches that make a substantive contribution to long-term regional population persistence. This use of the term critical habitat is consistent with its biological origins; however, this approach may also be useful for the identification of critical habitat within a legal context, for example under the Canadian Species At Risk Act or US Endangered Species Act. This approach is based on knowledge of species-habitat relations (e.g., from a resource selection model) and demographic information (e.g., fecundity and habitat-specific survival). The process is entirely spatially-explicit such that information about landscape composition and configuration, including effects of patch size, inter-patch distance, and barriers to movement, can be incorporated in the assessment. The outcomes of the process are spatially-explicit vital rates, namely the long-term productivity of habitats, which indicate the contribution of each unit of habitat within the model. Thus, a direct comparison of habitat units (e.g., patches) can be made for diagnostic purposes or to rank and prioritize habitats. Scenarios of landscape change, such as habitat patch removals or additions, can be used to further investigate the importance of habitats (e.g., to generalize about the contribution of specific habitat types). As the modeling process incorporates elements of population viability analysis to provide estimates of extinction risk for each modeling scenario, this approach allows one to explore the implications of habitat

modification and make inferences about the general roles of habitat types in affecting population persistence. I illustrate this approach and the useful information it generates in a case study of the Ord's kangaroo rat in Alberta, Canada.

Habitat model

An RSF-based habitat-occurrence model was developed for the Ord's kangaroo rat in Alberta as part of the recovery planning process (Bender et al. 2010). From this starting point, I sought to incorporate demographic information, such as fecundity and habitat-specific survival with the RSF-derived habitat map. A threshold probability of occurrence value representing 2/3 of the kangaroo rat occurrences (validated from an independent dataset collected in 2004-2005; Teucher 2007) was used to classify the occurrence map into regions of either breeding habitat or non-habitat. Habitat was further classified into four types: active dune, semi-stabilized dune, road margins, or exposed sandy soils (generally the steep valley slopes of the South Saskatchewan River) using air photo interpretation and knowledge of features on the ground. The relative quality of active dune and road-side habitat types was estimated using habitat-specific overwinter survival rates (derived from Teucher 2007), while the quality of the semi-stabilized sand dunes and exposed soil habitats was inferred from distribution data and expert knowledge (R. Dzenkiw, Lead Surveyor for Alberta Long-term Population Monitoring Program). Values for relative habitat quality of the different habitat types are provided in Table 5.1. A range of semi-stabilized dune quality values was explored in a sensitivity analysis as a means of exploring the influence of parameter uncertainty on model outcomes. Habitat fragments of similar quality (e.g. natural versus road) that were

within 30 m of each other were combined into one functional patch, resulting in 8413 habitat patches.

Population Model

The spatially-explicit population model HexSim (PATCH version 1.3.6.9; Schumaker 1998, Schumaker 2008) was used to integrate the occurrence model with kangaroo rat population dynamics and estimate long-term habitat productivity and population viability. HexSim is an individual-based model which simulates population dynamics through time, recording individual births, deaths, and reproduction, as well as explicit movement paths throughout the landscape. The fate of individuals is determined by their location in the landscape as well as their access to resources (the quantity and quality of habitat in their territory). Habitat quality pixel values from the habitat map (5 m²) were generalized into a hexagonal grid (780 m²) by HexSim.

The population cycle implemented in HexSim simulated females only and used discrete-time events. Following a winter survival event, all individuals were transitioned to adult status and adjusted the bounds of their territories to include more or greater quality habitat if available. In the summer, three successive breeding, movement, and survival events occurred. During each of the three summer intervals, kangaroo rats reproduced, the youngest stage class dispersed from their natal territory, mortality was imposed, and boundaries of territories were adjusted (Fig. 5.2).

Strong annual population fluctuations caused by environmental stochasticity were approximated using variation in overwinter survival rates. Mark-recapture studies estimating overwinter survival rates in active dune habitat in favorable (Teucher 2007) and harsh winters (Gummer 1997) were used to estimate a normal distribution of

overwinter survival rates (mean of 0.48; standard deviation of 0.13). One hundred rates were selected at random from the distribution and supplied to the population model. At the onset of each winter, an overwinter survival rate was selected at random (with replacement) and assigned to the population.

Short gestation, lactation, and maturation periods allow juveniles to produce one or two litters during their first year (Duke 1944, Day et al. 1956, Smith and Jorgensen 1975, Jones 1993, Gummer 1997). Reproduction was modeled as occurring in three distinct pulses wherein juveniles born in the first two breeding pulses were able to mature and produce offspring in the subsequent breeding period. Adult (1.46; 95% CL 1.44 -1.48) and juvenile-specific (1.14; 95% CL 1.09 -1.21) reproduction rates were estimated using a mean litter size of three (derived from counts of embryos and placental scars from museum specimens; Gummer 1997), the proportion of reproductively active females (adult 97%; 95% CL 96-98% and juveniles 76%; 95% CL 71-81%; Gummer unpublished data), and assuming an equal sex ratio. Only individuals that held territories were able to reproduce.

Kangaroo rats are solitary, territorial and defend burrows and food caches (Bartholomew and Caswell 1951, Eisenberg 1963, Garner 1974, Daly et al. 1984). After birth, the youngest class of juveniles disperse in search of their own territories. The distribution of dispersal distances for Alberta's kangaroo rats is highly skewed (median of 100 m; Gummer 1997) with a maximum of ~8.5 km recorded for a single movement. Roads may facilitate kangaroo rat movement (COSEWIC 2006). Therefore, an intermediate level of autocorrelation in path direction was used to provide forward momentum and simulated individuals were given a slight preference to travel along roads

or within habitat rather than through the matrix. Dispersal path lengths were assigned at random to individuals, drawn from a uniform distribution with a maximum of 8.5 km. Individuals stopped before they reached their assigned path length if they came across one hexagon of marginal quality (e.g. road-side habitat) or better. Early stopping truncated movement distances and produced an overall simulated path length distribution that approximated that of the field data. Mechanistic density dependence emerged as individuals spend more time searching for a territory during times of high population density. Movement itself does not incur mortality; however, individuals that require longer dispersal distances to find an unoccupied territory are less likely to acquire sufficient resources for survival.

When individuals reached their maximum dispersal distance or came across suitable habitat, the immediate area (23,400 m² representing double the maximum possible territory size) was explored for prospective territories. The territory with the greatest resources was then occupied until death. Individuals had to establish a territory that exceeded a minimum resource requirement (10% of the target resource level). If a suitable territory was not available, the individual continued searching during the next movement event. Territories had to meet or exceed the target resource requirement for the occupant to receive the maximum possible overwinter survival rates. As high quality habitats contain the greatest density of resources, little area is required to meet the resource target and territory sizes can be comparatively small. The average home range of radio-collared kangaroo rats is $1750 \pm 620 \text{ m}^2$ ($\pm 1 \text{ SE}$; Gummer and Robertson 2003a) in active dune habitats; this home range size was doubled to account for the space occupied by an equal number of males in the population. Thus, ideal territory sizes were

at least 3500 m² (4.49 hexagons) in high quality habitat (100%). Individuals that occupied territories that met the threshold resource target (4.49 hexagons * 100 quality score = 449), using up to a maximum of 15 hexagons, received the maximum possible overwinter survival rates. As habitat quality decreases, territories must expand to include a greater amount of habitat with lower resource density to reach the same target. Those unable to meet the resource threshold received penalized survival rates that declined linearly to zero as acquired resources declined from an optimal value.

Summer survival rates were provided by Teucher (pers. comm.), based on unreported data from his 2007 study (0.80 for adults, 0.64 for juveniles), and were applied to all individuals occupying territories in each of the summer survival intervals.

Simulations

Habitat patches were predicted to differ both in their local productivity and contribution to regional population persistence. If so, these differences would provide the basis for the prioritization of habitats for conservation. In these simulations, the productivity of local populations (births – deaths) resulted from the interaction of individual behavior with patch characteristics including size, distribution of quality, isolation, shape, and orientation. As such, productivity provides a measure of the contribution of specific patches to regional population abundance. Long-term habitat productivity was calculated by subtracting the total number of deaths from births (and dividing by 100 simulation repetitions). Habitat patches with productivity scores greater than 0 (i.e., sources) were considered to be of greater conservation value than unproductive patches (i.e., sinks).

The relative contribution of habitat components to regional population persistence was assessed by simulating the risk of population extinction under alternative habitat removal scenarios. Due to the large number of patches in the case study landscape, iterative removal of individual patches was not feasible. Instead, groups of habitat patches were iteratively removed based on their habitat quality classification or their productivity (sources versus sinks). The latter quantified the impacts of local productivity on regional population viability. The relative contribution of habitat components to extinction risk was assessed by comparing the amount of habitat that was required to be removed for a 1% change in the probability of extinction (PE), or the proportion of simulations in which there were no females at some point in time. While many uses of population viability modeling are focused on predicting the future trajectory of a species, this approach is aimed at evaluating the relative potential of existing habitats to support persistence. Therefore, simulations were initialized with the landscape saturated with 25,000 randomly seeded females. Before data were recorded, the population was allowed to stabilize (50 years) and approach a realistic population size of 250 females in the early spring, pre-breeding census. As the demographic value of a habitat may only become clear in the long-term after being subject to environmental stresses (Pelton and Manen 1996, Garshelis 2000), 100 years of data were simulated to estimate productivity and risk of extinction. Extinction risk simulations were replicated 1000 times, however the replication of habitat productivity data was limited to 100 iterations due to computational constraints.

I also sought to investigate whether sufficient habitat (of any quality) was available for the long-term persistence of the regional population. A range of population parameters

(including dispersal distances, summer survival and reproduction rates) were evaluated in a sensitivity analysis to assess the reliability of conclusions generated from model outcomes. The sensitivity analysis also explored a range of habitat quality values for secondary habitat types as a means of exploring the influence of parameter uncertainty on model outcomes. The population model did not include genetics, sex structure, or allee effects; therefore, predictions at low population sizes may be unreliable (Akçakaya 2000, IUCN 2008). To account for this, extinction risk was also expressed as the probability of the regional population falling below the population size thresholds of 50 and 25 female kangaroo rats at least once during the 100 year simulation (Ginzburg et al. 1982, Akçakaya 2000). As little is known about kangaroo rat population dynamics at very small population sizes, several arbitrary extinction thresholds were examined *a posteriori*. The results of thresholds above 50 females differed little from those at this threshold and were therefore excluded from the analysis. Scenarios that resulted in a probability of extinction (PE) of >10% in 100 years (criteria for a risk status of near threatened; IUCN 2008) and >20% probability of the population falling below 50 or 25 females were deemed as unlikely to ensure long-term population persistence.

Results

Productivity

Source habitats were generally found within the sand hills regions and consisted primarily of natural habitats (80%). Virtually all of the active dunes performed as highly productive sources and the largest dune in the study area was also the most productive patch in the landscape (Fig. 5.3). Sink habitats were located throughout the range and

consisted primarily of exposed soils (82% by area), as well as semi-stabilized dunes and road-side habitats. Exposed sandy soils accounted for all of the most severe sinks (productivity ≤ -100). As kangaroo rat habitat comprised only a small fraction of the study area (<2%), the majority of the landscape remained unoccupied.

Habitat Removals

In order to predict the relative contribution of habitat types to population persistence, all habitat patches of active dune, semi-stabilized dune, road-side habitats, as well as source and sink habitats were iteratively removed. Probability of extinction in the model was most sensitive to the removal of natural habitat (i.e. actively eroding sand dunes) with the PE increasing by 1% for every 1.7 ha removed (Table 5.2). The removal of comparatively larger areas (7.4 ha for semi-stabilized dunes and 15.3 ha for road-side habitats) were required to achieve a similar 1% increase in the probability of extinction. Extinction risk was relatively insensitive to the removal of exposed slopes, requiring approximately 37 times the amount (63.7 ha) as actively eroding dunes to produce a 1% increase in the probability of extinction. A large proportion of habitat (39%) was comprised of sinks, and their removal reduced the risk of extinction from a baseline PE of 23.4 to 20.7%.

Extinction Risk and Sensitivity Analysis

In the baseline landscape (i.e., no patch removals), extinction risk was high with a PE > 10% and with the regional population size falling below 50 and 25 females in 100% and 95% of the simulations respectively (Fig. 5.4). The overall extinction risk outcomes were largely insensitive to a range of population and habitat quality parameter variations. Extinction risk was most sensitive to decreases in survival and reproductive rates, as

measured by the absolute value change in PE /percent change in the parameter value (Table 5.3). Increases in vital rates were not as influential; however, some scenarios resulted in probabilities of extinction less than 10% although the probabilities of falling below 25 and 50 females remained high (67.4-98.4%). Extinction risk was relatively insensitive to changes in maximum dispersal distance.

The model outcomes were relatively insensitive to changes in secondary and semi-stabilized sand dune quality with all scenarios resulting in extinction risk probabilities for thresholds of 50 and 25 females ranging between 88% and 100%, and probabilities of extinction exceeding 10%.

Discussion

This approach for integrating a habitat map (i.e., RSF-based occurrence model) with population dynamics proved effective for identifying the relative contribution of each habitat type to population viability, thereby providing a straightforward method for ranking and prioritizing habitats. Predictably, the results of habitat removal and productivity simulations suggest that the highest quality habitats in this case study, natural sand dunes, provide the greatest contribution towards long-term persistence and recovery of the Ord's kangaroo rat. In this model, the removal of active dunes produced the greatest effect on regional extinction risk. While these patches represented only a small fraction of the landscape, they contained the most productive habitat patches in the landscape and appeared to drive the dynamics of this population. Semi-stabilized sand dunes are in close proximity to primary active dune habitat and may provide refuge for emigrants. This habitat type ranked second in its relative contribution to population

persistence and included many highly productive areas. While the contribution of natural habitat types to persistence was predictable at this coarse scale, the productivity of local habitat patches was less so. Semi-stabilized dune productivity was likely influenced by patch size, spatial effects, and population dynamics.

Approaches to assessing important habitats often assume that all suitable habitat patches contribute to population persistence, particularly if habitat models are based solely on an occurrence model. In contrast, these model results indicate that not all patches and habitat types made substantive contributions to the persistence of the study species. Despite being a pervasive element in the landscape, the removal of exposed soil habitats had a minimal influence on extinction risk, and hence these habitats do not appear to be essential for long-term kangaroo rat persistence. This approach also indicated that some habitats may actually be detrimental to persistence. While sink habitats may temporarily bolster the regional population size (Pulliam 1988, Dias 1996), the removal of all sink habitats from the kangaroo rat landscape improved overall population persistence. In the field, sinks may provide additional benefits not included in this model. However, these results suggest that the correct identification of sink habitats can be important when identifying and protecting habitat, especially if field studies happen over a short period of time when the regional population size happens to be high and sink habitats are occupied. Approaches that fail to link demographic data or dynamics with habitat models may actually undermine conservation efforts by erroneously identifying sinks as important habitats for protection.

The contribution of anthropogenic habitats to kangaroo rat viability has been contentious. In Alberta, kangaroo rats are commonly found along road-sides, particularly

during the late-summer population peak. However, road-side habitats are expected to be low quality habitats that represent population sinks as they are associated with greater soil compaction, colder burrow temperatures, greater predation risk, inadequate forage, and lower rates of survival than natural habitats (COSEWIC 2006, Teucher 2007).

Overall, road margins made a minor contribution to population persistence and patches acted as both population sources and sinks. However, it is unclear why some roads are productive and others are not. In addition, the productivity of road-side habitats can be inconsistent. In this model, the relative quality among habitat types was parameterized using survival data from a year that was observed to have higher than average survival. Thus, it is possible that the data are not representative of a typical year and may overestimate survival and the quality of secondary habitats, particularly in anthropogenic habitats. In the sensitivity analysis, reductions in secondary habitat quality by 20% resulted in many secondary habitat sources, including productive road-sides near high quality dunes, becoming sink habitats. This suggests that the productivity of road-side habitats is particularly variable and unpredictable. Further, these anthropogenic features may alter dispersal patterns because of their linear and pervasive nature in the landscape. While some roads might actually be placed to connect naturally isolated active sand dunes and increase kangaroo rat dispersal, it is unclear whether this benefit would outweigh the potential concerns associated with roads which include increased exposure to predators and parasites. Negative effects of roads might be especially acute if roads are placed between patches of natural habitat, thereby intercepting animals that might have otherwise dispersed between natural habitat patches, placing them in much lower

productivity habitat. More research may be required to elucidate these complex influences.

The use of a population viability framework provided a means to investigate whether sufficient habitat was available for the long-term persistence of the species. Other habitat-modeling approaches, such as those based on occurrence models, are typically not capable of providing this assessment. However this question is at the heart of critical habitat identification, where the aim is to determine which habitats are required for the long-term persistence or recovery of a species. Frequent regional extinctions in these simulations suggest that insufficient habitat exists for the long-term persistence of the Ord's kangaroo rat. This conclusion was robust to a range of population and habitat quality parameter scenarios explored in the sensitivity analysis. Thus, not only is current habitat in Alberta likely to be insufficient to support the population, the restoration of existing habitat is likely to be required. Another key advantage of this approach is that it can be used to identify the most valuable areas to undertake habitat restoration. Patches can be identified based on their size, location, occupancy, or productivity. The effect of restoration to larger or higher quality habitats can be compared by assessing population viability in the alternative restored landscapes. In this case study, semi-stabilized dunes made the second greatest contribution to population persistence. Thus, re-activation of stabilized dunes to actively-eroding habitats may be an effective means of improving population viability, although additional habitat alteration scenarios are needed to determine the most valuable restoration sites. Habitat removal experiments can also provide general insight into the potential efficacy of removing versus adding habitat. For example, a similar increase in kangaroo rat persistence may be attained by adding source

habitat as by removing twice as much sink habitat.

While the focus of this habitat assessment approach was to identify the productive breeding habitats that contribute to long-term population persistence, the realized contribution of a particular habitat patch through time will depend on future changes to both the habitat and non-habitat components of the landscape. Destruction or degradation of habitat patches, changes to the structure or composition of the intervening matrix, or the introduction of disturbances can reduce the performance of habitats. For example, the disruption of dispersal corridors among highly productive habitats, introduction of movement barriers, or increased hostility of the matrix may affect dispersal success, patch occupancy rates, productivity and ultimately population viability. Therefore, the assessment of critical habitats for species at risk should also consider the identification and protection of non-habitat components of the landscape (e.g., dispersal corridors, disturbance-free buffer zones etc.) upon which the success of essential habitats rely.

Conclusions

In summary, this approach to assessing critical habitat provided several advantages for identifying and prioritizing habitats for conservation. The use of spatially-explicit population viability modeling, combined with habitat removal experiments provided a direct link between habitat components and their predicted influence on regional population persistence. Local productivity also provided a fine-scale estimate of the contribution of habitat patches to persistence and another means of prioritizing habitats for conservation. Using this approach, I was able to investigate whether sufficient habitat

existed for long-term persistence, and identify sinks that may be detrimental to population persistence. Approaches to assessing critical habitats that rely on short-term occupancy patterns and do not consider long-term population dynamics may undermine conservation efforts by under- or over-estimating the value of habitat patches. Further, approaches that do not distinguish between occurrence and productivity may erroneously include sink habitats (particularly if habitat is limited or degraded) or fail to prioritize key source habitats, which may undermine the conservation efforts. Where possible, assessments of critical habitat components should be based upon habitat-specific demographic information and population dynamics, particularly in regions of variable habitat quality or for species that may exhibit source-sink dynamics.

Table 5.1. Broad habitat types and their relative habitat quality values

Habitat type	Quality value
Active sand dune	100
Semi-stable sand dune	60
Road margins	56
Exposed, sandy river valley slopes	30

Table 5.2. Habitat type and productivity removal scenarios: Predicted probability of extinction (PE) and (ranked) relative contribution to extinction risk.

Removal scenario	Area	PE	Hectares removed	
	removed (ha)		for 1% Δ in PE	Rank
<i>Habitat type</i>				
Active dunes	68.3	40.3	1.7	1
Semi-stabilized dunes	550.0	74.2	7.4	2
Exposed soils	1750.4	27.5	63.7	6
Roads/road sides	424.1	27.8	15.3	3
<i>Productivity</i>				
Sinks	1097.9	20.7	51.8	5
Sources	1694.9	72.0	23.5	4

Table 5.3. Local sensitivity analysis of population and habitat quality parameters and resulting risk of the population dropping to size thresholds of <50, <25 and 0 females. Sensitivity was calculated as the absolute Δ PE / percent Δ in parameter value.

Scenario	Risk of decline to population size threshold (%)			Sensitivity	Rank
	<50 Females	<25 Females	0 Females (PE)		
Baseline scenario	99.8	94.9	23.4	-	-
Summer survival					
-10%	100	99.9	92.0	6.86	2
-5%	100	99.8	58.2	6.96	1
+5%	98.3	83.9	8.6	2.96	4
+10%	93.4	67.4	2.9	2.05	6
Reproduction rates					
-10%	100	99.3	56.0	3.26	3
-5%	100	98.5	37.8	2.88	5
+5%	99.7	92.1	15.0	1.68	7
+10%	98.4	85.8	8.7	1.47	9
Max. dispersal distance					
7 km	99.8	96.3	25.8	0.13	15
10 km	99.7	95.1	23.1	0.02	16
Quality of secondary habitat					
-10%	100	99.7	35.3	1.19	10
-20%	100	100	55.3	1.6	8
Semi-stabilized dune quality					
40%	100	99.5	42.4	0.95	11
50%	99.8	98.1	31.9	0.85	12
70%	99.6	93.2	20.2	0.32	14
80%	88.5	88.9	16.3	0.36	13

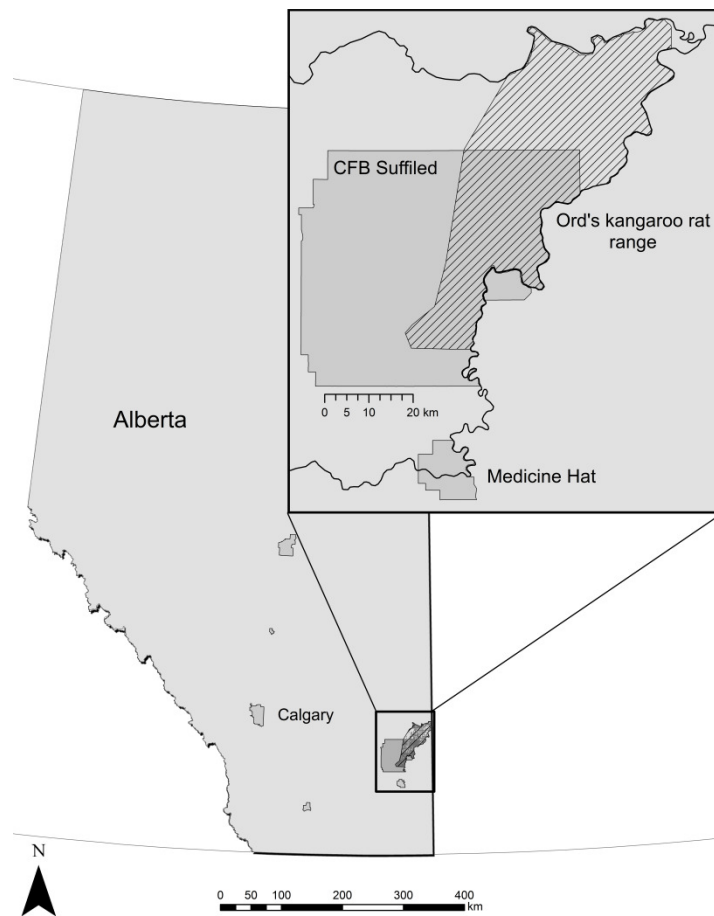


Fig. 5.1. Known range of Ord's kangaroo rats in Alberta, Canada (adapted from Alberta Ord's Kangaroo Rat Recovery Team 2005).

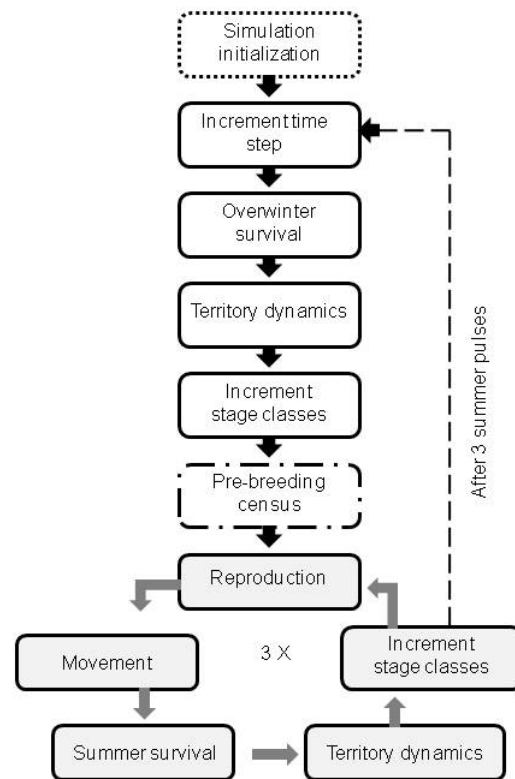


Fig. 5.2. Kangaroo rat population cycle as implemented in HexSim

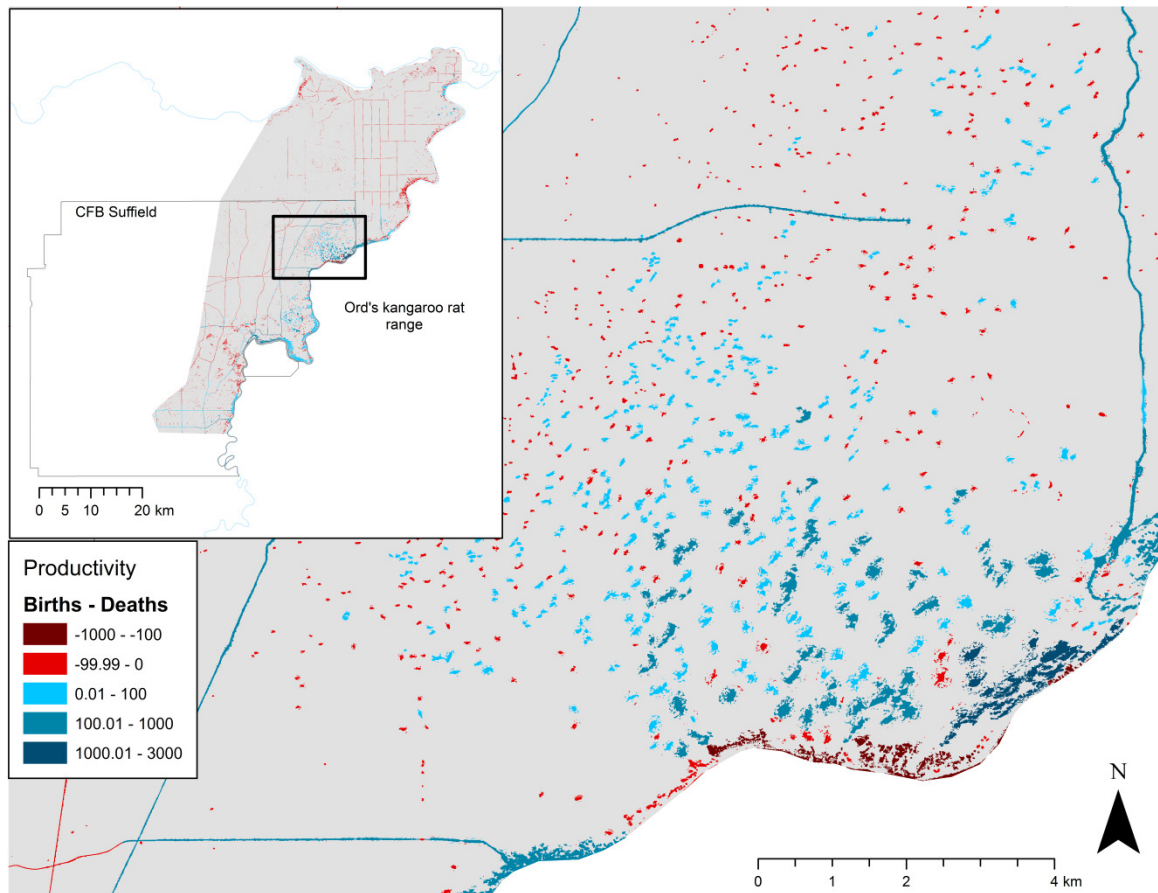


Fig. 5.3. Predicted long-term productivity of local Ord's kangaroo rat populations in a subset of their range in Alberta, Canada. Source habitats appear in blue, while sink habitats appear in red

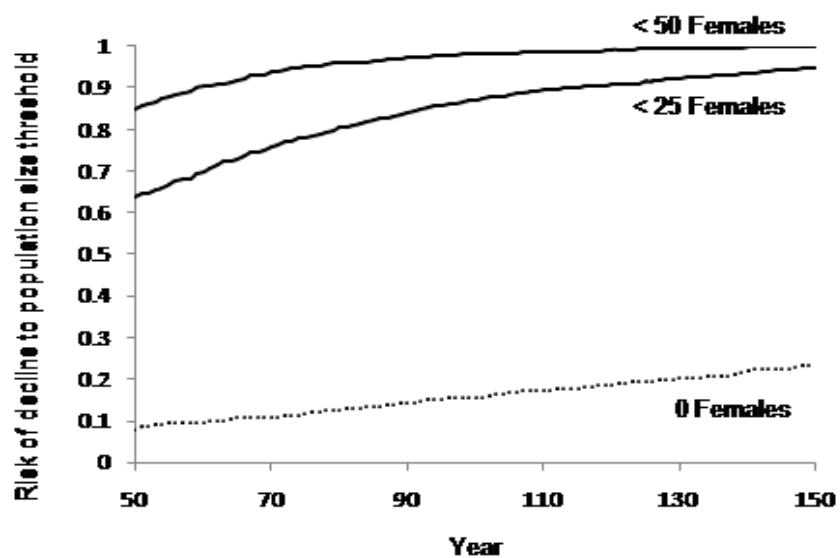


Fig. 5.4. Cumulative risk of population decline to size thresholds of 0, <25, and <50 female Ord's kangaroo rats for the baseline (pre-removal) landscape

CHAPTER 6 – CONCLUSIONS

Much of our understanding of the responses of spatially subdivided populations to habitat characteristics was initially drawn from the theories of island biogeography (MacArthur and Wilson 1967) and metapopulation dynamics (Levins 1969, Gilpin and Hanski 1991, Hanski et al. 1997, Hanski 1999, Wilson et al. 2009). These patch-based models related population dynamics and persistence to measures of habitat quantity or configuration, and habitat quality effects were often ignored or generalized. Thus, it is not surprising that the current paradigm for species conservation has focused on habitat quantity and configuration as the most important habitat variables influencing population dynamics and persistence. Yet from a conceptual perspective, the variation in density or value of resources within habitats should greatly influence population size and extinction risk. Despite emerging interest in quality-related studies on population dynamics (e.g. Dennis and Eales 1997, Thomas et al. 2001, Fleishman et al. 2002, Franken and Hik 2004, Wiegand et al. 2005, Ozgul et al. 2006), the relative influence of habitat quality on regional population extinction remains largely unexamined.

Habitat Quality

Habitat quality considerations are typically not at the forefront of investigations about population responses to habitat or landscape conditions, in part due to the difficulties in conceptualizing and measuring habitat quality. In concept, habitat quantity and configuration are relatively unambiguous. For example, habitat area is a familiar notion that is easily transferred and measured among landscapes. In contrast, habitat quality is a more abstract concept, plagued by vague interpretations that differ depending on the

landscape and species. In a plea for standard terminology, Hall et al. (1997) defined habitat quality as the ability of the environment to provide conditions appropriate for persistence, and as representing a continuum of resources available for survival, reproduction, and population persistence. However, “resources” can describe a number of potentially interactive habitat variables including vegetation types, densities of forage or prey, and microclimate conditions. Thus, habitat quality effects are complex and the operational definition of habitat quality will necessarily vary among species and landscapes. Another challenge arises when conceptually identifying the mechanism(s) by which habitat quality affects individual and population performance. For example, the mechanism linking the spatial isolation of patches to population dynamics (e.g., immigration or re-colonization rates) is explained relatively well by the costs of dispersal. However, habitat quality can be represented by a number of variables, and affect a number of different factors influencing population performance including territory or range sizes, and survival and/or reproductive rates. As such, the effects of habitat quality on population dynamics are likely to be multi-causal and not limited to a single easily describable mechanism. Thus, habitat quality tends to be less conceptually attractive than the more straightforward notions of habitat quantity and configuration.

Unlike habitat quantity and configuration which are methodologically attractive to measure, habitat quality is often difficult to measure in field studies, further compounding the issue. To be meaningful, the resources representing habitat quality should be explicitly linked with vital rates (Hall et al. 1997, Armstrong 2005). However, explicitly linking resources at individual sites with local persistence can be challenging because it requires the effort-intensive collection of biologically relevant habitat data and

association with vital rates. Even for well-established expressions of habitat quality, gathering the required data may be challenging if quality is represented by several habitat characteristics. The relationship between habitat variables and vital rates may also be confounded by animal movements, density dependence, and variation in genotypes and fitness (Armstrong 2005), complicating habitat quality assessments. Given the effort required to accurately characterize habitat quality, we need to know how important it is to consider habitat quality in persistence predictions. The aim of this research was to provide general insight into the basis for explicitly considering habitat quality in population persistence predictions by assessing the relative influence of habitat quality on regional population persistence.

Relative Importance of Quality

The habitat quantity-configuration paradigm pervades much of the conservation and landscape ecology research, from theoretical research questions and hypotheses, to applied habitat conservation and restoration. However, the results of my research provide novel and additional support for the increasing realization that the emphasis on habitat quantity and configuration may be misplaced. In the theoretical study, habitat quality out-ranked the landscape measures of habitat quantity and configuration, and was the single-most important variable influencing regional extinction risk (Chapter 2). Habitat quality also had a greater influence than patch and landscape measures of habitat quantity or configuration on the simulated dynamics of Alberta's population of Ord's kangaroo rat (Chapter 4). Modeling exercises examined a number of different species occupying a wide range of landscapes, and the primacy of habitat quality was robust to all scenarios. In particular, the generalizations generated from the theoretical study corresponded well

with the case study, despite increased complexity in the population cycle and dynamics, and the landscape (with a greater number of habitat types/qualities). The general hierarchy of the influence of habitat variables (1 – quality, 2 – quantity) was consistently observed among hypothetical and real species, which differed in their resource requirements, dispersal distance, and vital rates. The relative importance of habitat quality was also robust to varying assumptions of the potential for individuals to expand their territories to acquire additional resources in low quality habitats. This suggests that this broad hierarchy of habitat influences is likely to be consistent among a wide range of territorial species with specific habitat requirements, as well as in complex, heterogeneous landscapes.

Roles of Quantity and Configuration

The effects of habitat quantity and quality can influence persistence through a broad range of landscape conditions and result in substantial extinction risk sensitivities. In contrast, the effects of habitat fragmentation were only observed in a narrow range of conditions (Chapter 2). In the kangaroo rat landscape, patch isolation and the overall configuration of habitats did not rank as highly influential for persistence (Chapter 4), indicating that the arrangement of habitat patches is secondary to habitat quality and quantity considerations. As habitat quality can be much more important than configuration (also see Wiegand et al. 2005), this research supports the argument that the influence of habitat configuration may be over-emphasized. Other studies have similarly concluded that habitat configuration effects are of less importance than the quantity or quality of habitat. For example, local population dynamics and persistence were better explained by patch size and/or patch quality than patch isolation (e.g., Thomas et al.

2001, Fleishman et al. 2002, Franken and Hik 2004), and landscape-level studies that include dispersal mortality have concluded that habitat fragmentation influences extinction to a lesser extent than habitat amount (Fahrig 1998, Fahrig 2001, Flather and Bevers 2002). This research suggests that the details of how habitats are arranged in space are generally unlikely to compensate for the regional population persistence consequences of landscape change, including habitat loss (Fahrig 1997). Together, these studies indicate that the general importance of the spatial configuration of habitats may be over-emphasized. While not universally important, the configuration of habitats is likely to be of particular interest in identifying specific habitats for conservation (Chapter 5), and an important consideration in low resource landscapes (Chapter 2). The degree of landscape fragmentation may also determine the relative efficacy of adding habitat or improving the quality of habitat to restore habitat and recover populations (Chapter 3). However, the broad emphasis in habitat influences on extinction risk may more appropriately reside in habitat quality and quantity considerations.

Implications of Excluding Habitat Quality

Habitat quality can greatly influence extinction risk, possibly even more so than habitat quantity and configuration. This calls into question the adequacy of the habitat quantity-configuration paradigm to accurately predict the dynamics and persistence of populations inhabiting landscapes of variable quality. In general, results and predictions generated in the absence of habitat quality considerations may risk conclusions devoid of the principal explanatory variable, and management practices that are ineffective or even perilous for population persistence.

Landscape Change Predictions

In landscape studies of habitat loss and fragmentation, extinction risk predictions based on habitat quantity and configuration alone may be inaccurate and overly optimistic. For example, habitat amount-fragmentation models predict that appreciable risks of extinction generally only emerge in landscapes of low habitat amounts (e.g., Fahrig 1997, Fahrig 1998, Flather and Bevers 2002). However, when habitat quality was considered, extinctions were observed in a broader range of landscape amounts, and in particular, were observed in high habitat amount landscapes when the proportion of high quality habitat was low. Further, when the proportion of high quality habitat was reduced below 30%, extinction risk dramatically increased in the majority of habitat amount and fragmentation scenarios (Chapter 2). Particularly in low resource landscapes wherein the non-linear effects of landscape degradation may severely impact persistence, models that generalize or ignore habitat quality risk generating overly optimistic extinction risk predictions and will generally be unable to detect and avoid extinction thresholds resulting from habitat degradation. Similarly, the effects of habitat fragmentation are commonly predicted to be important only in landscapes composed of little habitat (e.g., Fahrig 1997, Flather and Bevers 2002); however, substantive fragmentation effects can emerge in landscapes of moderate to high amounts of habitat when the proportion of high quality habitat is low (Chapter 2). Without explicit consideration of habitat quality, quantity, and configuration, conservation projects risk the misuse of conservation resources on ineffective restoration and recovery plans.

Assessing Important Patch Characteristics and Habitats

Patch-based models arising from metapopulation theory commonly assume that the area of a given patch corresponds with local population size. As larger populations are generally thought to be less prone to extinction as a result of chance events (Gaggiotti and Hanski 2004), large habitat patches may be preferentially preserved to include extinction-resistant local populations and increase regional population size. However, the importance of patch quality in influencing extinction risk suggests that habitat quality, which constrains population density, is likely to obscure the expected relationship between patch size and local population abundance (Chapter 4). Hence, large patches may contain small populations in low quality habitat. The over-valuation of such habitats and their conservation over smaller, more productive habitats may undermine the effectiveness of conservation efforts. Further, large, low quality habitats may act as population sinks. If it was assumed that all large patches contain large populations that contribute to regional population persistence, sinks may be preserved or enlarged to increase habitat capacity and population size, possibly compromising regional population persistence.

Road margin habitats provided a good example of how measuring patch size alone can be highly misleading of the value of habitats for the persistence of Alberta's population of Ord's kangaroo rat. In assessing the relative contribution of specific habitats to persistence, habitat quality with quantity and configuration data, as well as movement and population dynamics were integrated to predict the productivity of individual patches. Results indicated that in the Ord's kangaroo rat range, many large area road segments were behaving like population sinks, wherein there the number of deaths within

a patch exceeded the number of births (Chapter 5). Further, kangaroo rat persistence was predicted to improve if road margin habitats, particularly large segments, were removed and replaced with an equivalent capacity of natural sand dune habitat (Chapter 4). This also suggests that approaches that do not incorporate habitat quality and population dynamics may undermine conservation efforts by under- or over-estimating the value of habitats, erroneously protecting sink habitats, or failing to prioritize key source habitats.

Together, the results of patch- and landscape-scale simulations suggest that generalizations or ‘rules of thumb’ arising from models that generalize or ignore habitat quality may not be reliable in landscapes with sub-optimal or highly variable habitat quality.

A More Inclusive Paradigm

Despite the wide-spread application of the quantity-configuration paradigm, the projects undertaken in this dissertation suggest that a more inclusive conceptual framework is required to describe the influence of habitat quality on population dynamics and extinction in landscapes of heterogeneous quality. This research presented an initial step towards developing a more comprehensive paradigm for habitat and species conservation. Yet, a broader understanding of the influence of habitat quality on population distribution, abundance, and persistence is ultimately required to make accurate predictions and conservation decisions. In particular, future research would benefit by addressing the following items.

First, my results indicate that when coarse-grained differences in quality (i.e. resources) exist among habitats, habitat quality is likely to matter. In theoretical simulations, low quality habitats had 50% (or 25% in low quality sensitivity scenarios) of

the resources per unit of area in high quality. Similarly, in kangaroo rat simulations sub-optimal habitat types were widely different than those in high quality (e.g., the value of road margin habitats resources were 56% of those in high quality). Hence, while habitat quality is likely to be important when widely different, it is unclear how different habitat qualities need to be in order to warrant their explicit consideration. A greater understanding of the conditions under which variation in habitat quality matters would be helpful in framing research questions, generating hypotheses, and prioritizing data collection.

Second, my work provides general insight into the relationship between habitat quality and extinction risk. However, I did not experimentally identify the specific and interactive mechanisms by which habitat quality affected extinction risk and gave rise to extinction risk and thresholds (i.e., when high quality was reduced below 0.3). This was beyond the scope of my dissertation.

A patch-based approach was adopted in this research, emulating the models arising from the theories of island biogeography and metapopulation biology. A corollary of this approach is that individuals possess specific habitat requirements wherein they occupy discrete habitat patches, embedded in uninhabitable matrix. A patch-based approach may be a reasonable approximation for habitat specialists like Alberta's Ord's kangaroo rat population, which are restricted to sandy soil and dunes, or forest specialists limited to treed fragments amidst clear-cuts. However, many species are not as ecologically restricted and habitats may not be clearly separated into suitable versus unsuitable patches (Wiens 1996). Thus, some animals are likely to perceive the landscape to be more of a continuum of habitat types and qualities, rather than a dichotomy of habitat

versus non-habitat; therefore, landscape mosaics may be a better conceptualization of how other types of animals respond to their environment (Wiens 1996). It is unclear how generalizations made for patch-based populations would apply to those with broader habitat associations. However, my work does provide support for representing habitat more in terms of a continuum than binary (habitat versus non-habitat) characterizations. A gradient of habitat qualities (among patches or within a landscape mosaic) may be essential to adequately model habitat and accurately predict responses to habitat composition and structure.

Conclusion

In efforts to develop theories with general applicability to real species and landscapes, ecologists sometimes fail to recognize that while assumptions of landscape homogeneity aid in computational and theoretical tractability, they are not necessarily ecologically justified. Simplifications are sometimes represented or interpreted as demonstrations of reality, rather than hypotheses for homogeneous environments (Wiens 1995). As landscapes are typically heterogeneous, ecologists need to be mindful of the simplifying assumptions of theories and resulting models, predictions, and management practices in assessing the suitability of their application for specific species and landscapes. This research indicates that the influence of habitat quality can be integral to understanding and predicting population responses to landscape conditions and change, perhaps even more so than habitat quantity or configuration. While the specific conditions under which habitat quality effects are expected to be the most acute are currently unclear, my research suggests that there are at least some situations in which habitat quality is likely to be very influential. Thus, we require a more comprehensive and realistic approach to

measuring and representing landscapes of heterogeneous quality. Decisions on the appropriate level of habitat complexity, and the application of theory, models, and management practices should be based on biological rationale, rather than simply defaulting to commonly used approaches that exclude quality. In conclusion, despite the wide-spread recognition and application of the quantity-configuration paradigm, this conceptualization is likely to be insufficient in many real landscapes. A more inclusive conceptual framework is likely required to elucidate the influence of habitat quality and accurately predict and mitigate the effects of habitat and landscape change on population extinction.

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