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Population Viability Analysis
And Assessment Of Recovery Options For The Ocelot

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A habitat-based population viability analysis for ocelots (*Leopardus pardalis*) in the United States

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ABSTRACT

Strategies are needed to recover the ocelot *Leopardus pardalis* from the endangered species list. Recently, a population viability analysis (PVA) was developed which concluded that combinations of different recovery strategies were needed to effectively reduce ocelot extinction probability in the United States (US), with habitat protection and restoration identified as the most effective recovery scenario. We expanded this PVA model by incorporating landscape data to develop a more realistic habitat-based PVA for ocelots in southern Texas. We used RAMAS/GIS software to conduct a habitat-based PVA by linking landscape data with a demographic metapopulation model. The primary goal of this study was to provide a model for evaluating ocelot recovery strategies in the US. Each model scenario was simulated 1000 times over 50 years and we defined extinction as one individual remaining. Using the RAMAS/GIS program we identified 11 possible ocelot habitat patches (i.e., subpopulations) occurring in southern Texas. In addition, based on the habitat-based PVA model we found that combinations of different recovery strategies were needed to effectively reduce ocelot extinction probability in the US, with reducing road mortality the single most effective strategy. Short-term recovery strategies should include reducing ocelot road mortality, and translocation of ocelots into the US from northern Mexico. Long-term recovery strategies should include the restoration of habitat between and around existing ocelot habitat patches and the establishment of a dispersal corridor between ocelot breeding populations.

1. Introduction

In 1982, the ocelot *Leopardus pardalis* population within the United States (US) was listed as endangered by the US Fish and Wildlife Service, and in 1989 the ocelot was included in Appendix I of CITES (Convention on International Trade in Endangered Species) (Sunquist and Sunquist, 2002). Currently, there are only two known breeding populations of ocelots in the US; one in Cameron County, Texas, and the other in Willacy County, Texas (Navarro-Lopez, 1985; Tewes and Everett, 1986; Laack, 1991; Haines et al., 2006a) (Fig. 1). However, no ocelot dispersal has been documented between the Cameron and Willacy populations (Navarro-Lopez, 1985; Tewes, 1986; Laack, 1991; Walker, 1997). Major threats faced by these pop-

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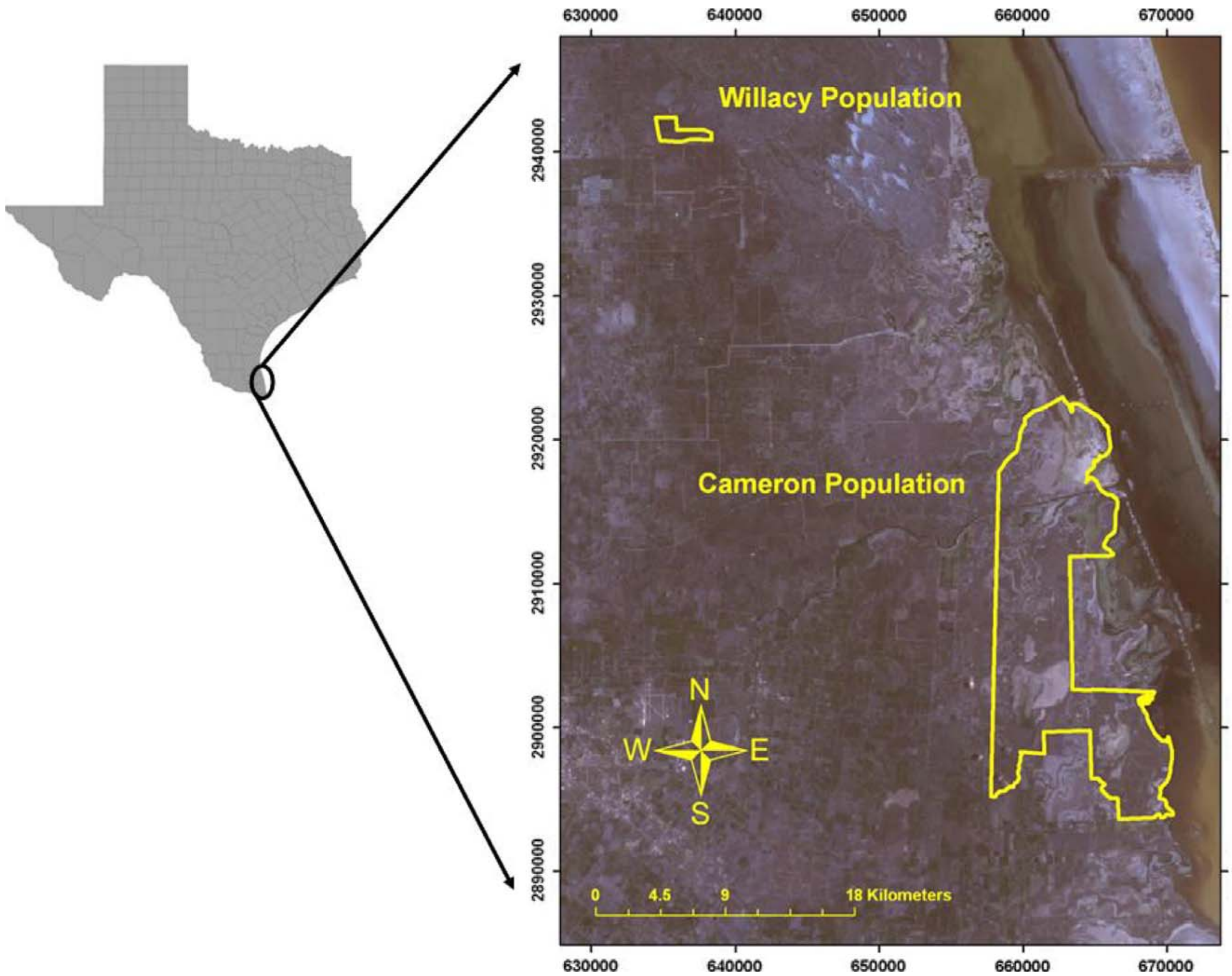

Fig. 1 – Map of Laguna Atascosa National Wildlife Refuge (LANWR) (Cameron Population) and two connected conservation easements (Willacy Population) in the Lower Rio Grande Valley (LRGV), Cameron and Willacy counties, TX, USA (UTM Coordinates in Zone 14N).

ulations include loss of habitat, road-mortalities, and genetic isolation (Tewes and Everett, 1986; Tewes and Miller, 1987; Walker, 1997; Haines et al., 2005a). Recovery strategies are needed to maintain and expand current ocelot populations in the US prior to delisting (US Congress, 1988).

Recently, Haines et al. (2005b) developed a population viability analysis (PVA) to evaluate recovery strategies for the ocelot population in Cameron County. They concluded that the most effective recovery scenario for ocelots was the protection and restoration of ocelot habitat. However, combinations of different recovery strategies were most effective at reducing ocelot probability of extinction in Cameron County over 100 years (Haines et al., 2005b).

Noon and McKelvey (1996), Beissinger and Westphal (1998), Possingham et al. (2002) and Reed et al. (2002) believed the optimal use of PVA was to compare the outcomes for different model scenarios resulting from management decisions, and that comparisons should focus on the relative effectiveness of the different management actions, particularly compared to baseline or current conditions. Boyce (1993), Maehr et al. (2002), and Ralls et al. (2002) believed the PVA process was useful as a long-term, iterative process coupled with an adaptive management approach to species recovery. In addition, Haines et al. (2005b) recommended using an adaptive management approach by monitoring ocelot populations and habitats, and continuing research to evaluate the effectiveness of recovery strategies.

The habitat-based PVA model described herein updated the first PVA by incorporating more than one population into the analysis, incorporating spatial data, and including updated input parameters. Akcakaya (2000) stated that unlike a single population model, the dynamics of a spatial metapopulation model includes spatial variation and interaction among populations, geographic configuration of habitat patches, dispersal, and spatial correlation.

We used RAMAS/GIS (Akcakaya, 2002) software to conduct the habitat-based PVA by linking landscape data from geographical information system analysis with a demographic metapopulation model based on input parameters from Haines et al. (2005a), Haines et al. (2005b), Laack et al. (2005) and Akcakaya (2000). Brook et al. (2000) found that PVA software (including RAMAS) accurately predicted rates of population change over short time-periods. In addition, the RAMAS/GIS program (Akcakaya, 2002) has been used in other studies to combine landscape data with demographic data for helmeted honeyeater *Lichenostomus melanops cassidix*, California gnatcatcher *Polioptila californica californica*, and spotted owl *Strix occidentalis caurina* (Akçakaya et al., 1995; Akcakaya and Atwood, 1997; Akçakaya and Raphael, 1998).

The objectives of this study were to (1) develop a current landscape map for Willacy and Cameron counties Texas that identifies areas important for ocelot conservation, (2) develop a habitat suitability model for ocelots in southern Texas, (3) link this model to an ocelot metapopulation model for viability analysis, (4) compare the impact of four conservation strategies (i.e., translocation of ocelots into the US from northern Mexico [translocation scenario], construction of road underpasses to mitigate ocelot-vehicle mortality [reduced road mortality scenario], restoration of ocelot habitat [habitat scenario], and establishment of a dispersal corridor between the Cameron and Willacy populations of ocelots [linkage scenario]) and their possible combinations on the viability of the ocelot metapopulation in southern Texas, (5) conduct a sensitivity analysis of model input parameters to identify parameters that significantly affect ocelot population viability, and (6) based on the results of model, conduct an *ad hoc* analysis to identify potential areas of correct culvert placement to mitigate ocelot-vehicle collisions.

2. Materials and methods

2.1. Study area

The ocelot population in Cameron County (i.e., Cameron population) resides in and around Laguna Atascosa National Wildlife Refuge (LANWR) located in eastern Cameron County, and the ocelot population in Willacy County (i.e., Willacy population) resides in and around the Yturria Ranch located in north-central Willacy County (Fig. 1). Both populations reside in extreme southern Texas within the Lower Rio Grande Valley (LRGV). The LRGV is an alluvial plain dissected by numerous natural drainages that flow into the Rio Grande or the Gulf of Mexico (Everitt and Drawe, 1993) and has a wide diversity of fertile soil types (Williams et al., 1977). The subtropical, semiarid climate is characterized by hot summers and mild winters (Thornthwaite, 1948; Lonard and Judd, 1985). Mean length of the frost-free period is 330 days with winters frequently occurring above freezing temperatures. Mean annual temperature and rainfall is 23 °C and 68 cm, respectively, although rainfall fluctuates widely through the year and among years (Norwine and Bingham, 1985; Lonard et al., 1991).

2.2. PVA software

We used the RAMAS/GIS Spatial Data program to determine the spatial structure of the ocelot metapopulation in southern Texas with a user-defined habitat suitability function based on regression coefficients used to evaluate ocelot cover importance (Akcakaya, 2000; Akcakaya, 2002). Spatial data (i.e., ocelot cover map) was linked to ocelot demographic data using the RAMAS/GIS Metapopulation program (Akcakaya, 2002) to produce a spatial metapopulation model of the Cameron and Willacy ocelot populations. Results of these model simulations were used to compare management options (Akcakaya, 2002).

To minimize error propagation and evaluate conservative probabilities of extinction, Akcakaya (2002) and Beissinger and Westphal (1998) suggested that short to medium time horizons (i.e., 10, 25, or 50 years) may be more appropriate for modeling populations. Thus, we reported population performance over 50 years to analyze the effectiveness of the various recovery scenarios and combinations of recovery strategies. In addition, each scenario was simulated 1000 times to estimate extinction risk, and we defined extinction as only one individual ocelot remaining.

2.3. Input parameters

We developed an ocelot stage-matrix based on survival and reproductive input parameters from Haines et al. (2005a,b) and Laack et al. (2005) to be incorporated into the metapopulation model and combined with spatial data (Table 1). The stage-matrix is an age-structured model in the form of a Leslie matrix (Leslie, 1945, 1948) that combines the demographic parameters of survival and fecundity to calculate population growth. Age-specific ocelot survival rates were based on estimates calculated by Haines et al. (2005a,b) with the exception of ocelot first year survival (0.68), which was calculated by Laack et al. (2005). We specified the ocelot as a polygamous specie (Tewes, 1986; Ludlow and Sunquist, 1987; Emmons, 1988; Laack, 1991; Crawshaw, 1995). We defined the age of first female ocelot reproduction as 3 years of age and the age of first male ocelot reproduction as >3 years of age (Laack, 1991), and we specified a 50/50 ocelot sex ratio at birth (Eaton, 1977; Mellen, 1989; Laack et al., 2005). We defined mean ocelot litter size as 1.2 kittens (0.44 SD) and that 75% of adult female ocelots produce a litter every year (Haines et al., 2005b; Laack et al., 2005).

We specified that all vital rates (survival and reproduction) were affected by density dependence in the model. This specification was based on ocelots being territorial with docu-

Table 1 – Stage-matrices for ocelots in southern Texas specifying reproductive and survival input parameters under the control scenario to link spatial data with demographic data in the RAMAS/GIS Metapopulation program (standard deviations in parenthesis)

	Age 0	Age 1	Age 2	Adult Age 3+
Female				
Fecundity	0.00	0.00	0.00	0.45[a] (0.17)
Survival	0.68 (0.05)	0.00	0.00	0.00
Survival	0.00	0.87 (0.02)	0.00	0.00
Survival	0.00	0.00	0.78 (0.05)	0.87 (0.02)
Male				
Fecundity	0.00	0.00	0.00	0.45[b] (0.17)
Survival	0.68 (0.05)	0.00	0.00	0.00
Survival	0.00	0.87 (0.02)	0.00	0.00
Survival	0.00	0.00	0.63 (0.10)	0.87 (0.02)

a Number of female offspring produced per adult female.
b Number of male offspring produced per adult female.

mented intraspecific mortality (Haines et al., 2005a). We specified density dependence as a ceiling model, where the population grows exponentially until reaching a ceiling population size (i.e., carrying capacity) and remains at that level (Akcakaya, 2002). This type of density dependence may occur with ocelots when all territories are occupied.

The effects of environmental variation were incorporated into the model 3 separate ways. Within the ocelot stage matrix, environmental variation was represented as the standard deviations of ocelot survival and fecundity (Table 1). In addition, environmental variation represented the standard deviation in ocelot carrying capacity, which Haines et al. (2005b) calculated as 12% for an ocelot population. The standard deviation of ocelot carrying capacity calculated by Haines et al. (2005b) was based on variations of estimates for adult male and female ocelot home range size. Furthermore, we incorporated environmental variation into the model by developing a matrix of correlation of environmental variation within the RAMAS/GIS Metapopulation program (Akcakaya, 2002). This technique is based on the approached used by LaHaye et al. (1994) which bases correlation as a function of distance. The matrix of environmental correlation was based on a correlation function that produced a curve showing the rate of correlation of mean monthly rainfall over the last 50 years between weather stations within the LRGV (National Climatic Data Center; http://www.ncdc.noaa.gov) as a function of distance between weather stations (Fig. 2a).

2.4. Ocelot cover map

The ocelot has been defined as a habitat specialist, with spatial patterns strongly linked to ⩾95% canopy cover of the shrub layer (Navarro-Lopez, 1985; Tewes, 1986; Laack, 1991; Horne, 1998; Harveson et al., 2004). In addition, Horne (1998) and Harveson et al. (2004) found that ocelots did not avoid areas with 75–95% canopy cover, but stated that ocelots avoided areas with <75% canopy cover. Thus, we developed a current ocelot cover map for Willacy and Cameron counties that identified habitat with >75% canopy cover. This analysis was conducted by delineating spatial data based on a LANDSAT ETM 7 satellite image of southern Texas (March 2003) downloaded from the Texas Synergy website (www.synergyx.tacc.utexas.edu). Based on methods used by Haines et al. (2006b) the LANDSAT imagery was used to identify, digitize,

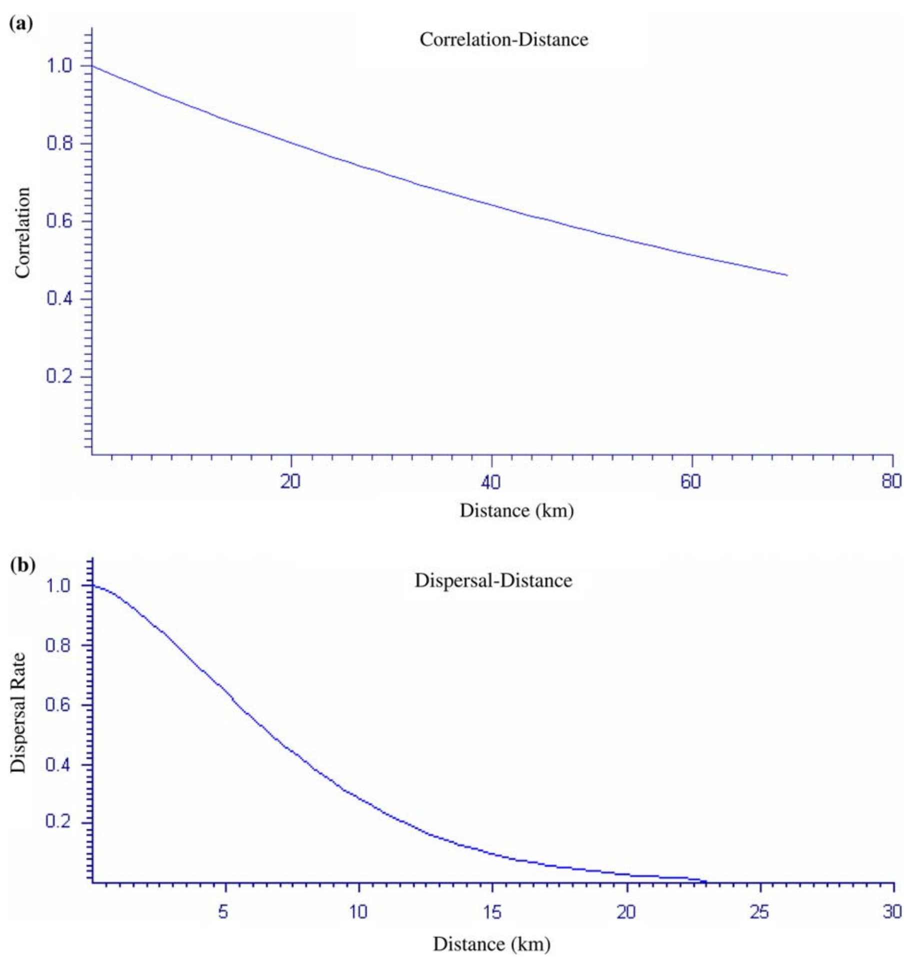

Fig. 2 – Rate of correlation and dispersal as a function of distances between habitat patches, (a) rate of environmental correlation between habitat patches as a function of the correlation of mean monthly rainfall and distances between weather stations in the Lower Rio Grande Valley (LRGV) of southern Texas, USA, and (b) dispersal rate of ocelots of age class 2–3 as a function of the proportion of 15 recorded ocelot dispersal events recorded in the LRGV.

and create shapefiles for different cover layers (i.e., >75% woody cover [closed], 26–75% woody cover [mixed], 1–25% woody cover [open], <1% cover [bare], and water) in the ArcGIS 9.0 software program (ESRI®, Inc. Redlands, Calif.).

Shapefiles of cover layers served as training sites (i.e., reference sites) to develop spectra-reflective signatures that were used in a supervised classification using the ERDAS IMAGINE 8.7 software program (ERDAS®, Inc. Atlanta, Georgia). We used the supervised classification (i.e., cover map) to identify ocelot cover in those areas where field verification of cover (i.e., accuracy assessment) could be achieved in Cameron and Willacy counties. Based on this analysis, we identified potential ocelot habitat within the Cameron and Willacy populations.

2.4.1. Accuracy assessment

An accuracy assessment of the supervised classification was conducted using the accuracy assessment tool in ERDAS IMAGINE 8.7, which created random points within a specified cover layer. We used $\geqslant$50 random reference points for each cover layer as suggested by Congalton (1991). We downloaded these random points into a GARMIN global positioning system unit (GARMIN® International Inc., Olathe, Kansas), and conducted a ground survey in Cameron and Willacy counties to find and ground truth the cover layer of each random point. However, some areas of private land were unable to be ground truthed, thus other random points were produced within an accessible area to maintain suggested sample size. An accuracy assessment was also conducted using 1996 mosaics of Cameron and Willacy counties (based on 1996 geo-referenced aerial photos) obtained from the Wildlife Research Technologies Lab located at the Caesar Kleberg Wildlife Research Institute at Texas A&M University-Kingsville. This analysis was used to verify whether the canopy cover in 1996 was similar to 2003. The minimum level of accuracy acceptable for land use and land cover classification was 85% (Anderson et al., 1976).

2.5. Ocelot telemetry

Ocelots were captured using single-door, 108 × 55 × 40 cm wire box traps (Tomahawk Trap® Co., Tomahawk, WI) from November 1996 to January 2005, and were immobilized with a 9:1 ratio of ketamine hydrochloride and acepromazine maleate (Beltran and Tewes, 1995). Immobilized ocelots were fitted with a 120 g VHF collar containing a mortality sensor and emitted a frequency of 148–149 MHz (Telonics® Inc., Mesa Ariz.). From December 1996 to March 2005, we used ground stations and radiotelemetry to locate ocelots during diurnal and nocturnal time periods. Radio signals were monitored with a directional H-antenna connected to a model TR-2 receiver (Telonics® Inc., Mesa Ariz.). Ocelot locations were determined by triangulating on the direction of the radio signal from two or three known points on the ground and using the LOAS® program to obtain location estimations (Ecological Software Solutions™). Trapping and handling of ocelots were performed in a humane manner with procedures and research methodology approved by the Texas A&M University-Kingsville Institutional Animal Care and Use Committee protocol # 1989-5-19.

2.6. Habitat suitability function

We based the habitat suitability function on results of the ocelot telemetry data in relation to the ocelot cover map. We defined the study area boundary as the minimum convex polygon of all estimated ocelot locations. In addition, we generated 1000 specified random points within the study area using the Hawth's analysis tools (Hawth's Analysis Tools 2002–2005 © Version 3.11) in ArcGIS 9.0. These specified random points were buffered 100-m from estimated ocelot locations, so no random points occurred within 100-m of an ocelot location. This was done to identify areas both used and avoided by ocelots. Distances of ocelot locations and specified random points to each cover type within the study area were calculated using the spatial analyst tool in ArcGIS 9.0.

We used logistic regression (SAS®, Inc. Cary, N.C.) to calculate a habitat suitability function for ocelots in the study area, which was used to calculate an index of habitat suitability for each pixel cell in the ocelot cover map. The response variable for the logistic regression was indicated where the response variable is binary (e.g., 0 = random locations, 1 = ocelot locations) and was based on estimated distances to cover types. We used a stepwise regression with a significance level of $p < 0.01$ for adding and removing cover type variables. After individual cover type variables were tested, we tested interaction terms to calculate significance (Akcakaya, 2002).

We validated the results of the logistic regression analysis by conducting a separate euclidean distance analysis to evaluate ocelot habitat use using ocelot telemetry locations compared to actual random points within the study area (Conner and Plowman, 2001). We used euclidean distance analysis because it is not sensitive to telemetry error, does not produce undefined values for habitat types not used, and uses individual ocelots as the sampling units (Conner and Plowman, 2001). Statistical significance was based on $p < 0.01$.

The link between the ocelot cover map and the ocelot stage-matrix was connected by two parameters: a habitat suitability threshold and a neighborhood distance. This was done using the RAMAS/GIS Spatial Data program. A habitat suitability threshold defines the minimum habitat value below which habitat is not suitable for reproduction or survival (Akcakaya and Atwood, 1997; Akcakaya, 2002). Laack et al. (2005) analyzed 10 ocelot den sites, and found they were located within close proximity to, or directly underneath, dense thornshrub cover, with the exception of 1 den site which had no vertical cover, but was found along a thornshrub corridor with dense canopy cover nearby. Thus, we defined the habitat suitability threshold as areas with >75% canopy cover which represented the minimal pixel value below which habitat would not be suitable for ocelot reproduction.

A neighborhood distance identifies nearby pixels that belong to the same habitat patch (i.e., subpopulation) (refer to Section 3.3). A neighborhood distance is usually based on the foraging distance of a species (Akcakaya and Atwood, 1997; Akcakaya, 2002). Navarro-Lopez (1985) monitored five ocelots in Willacy County and calculated their mean daily movement at approximately 800 m. Thus, we defined the neighborhood distance as a 1 km buffer around habitat patches, which was the closest available neighborhood distance to 800 m available in the RAMAS/GIS Spatial Data program. Thus, pixels consisting of >75% canopy cover that were within 1 km of each other were considered part of the same habitat patch.

2.7. Recovery scenarios

We specified the potential benefits provided by various recovery strategies. For the translocation scenario, one female ocelot of age class 2 was translocated from northern Mexico into the Cameron population every other year for 40 years. For the reduced road mortality scenario, we assumed that correct placement and construction of culverts would reduce ocelot-vehicle collisions by 50%, thus increasing ocelot survival (Haines et al., 2005b). For the habitat scenario, we assumed that an increase in habitat on preferred soil types (Harveson et al., 2004), would increase ocelot carrying capacity by 50% over 50 years. For the linkage scenario, we assumed that there was a 10% probability of dispersal between a large habitat patch in the Willacy County closest to a large habitat patch in Cameron County, and vice versa.

2.7.1. Dispersal dynamics

Results of the RAMAS/GIS Spatial Data program calculated distances between habitat patches within the two ocelot populations, which we specified to be the shortest distance from boundary to boundary. We used the RAMAS/GIS Metapopulation program to calculate a dispersal function based on a curve showing the proportions of dispersal distances for 15 recorded ocelot dispersal events recorded in the LRGV (Navarro-Lopez, 1985; Tewes, 1986; Laack, 1991) (Fig. 2b). Based on the dispersal function, a dispersal-matrix was calculated which defined dispersal rates based on distance between habitat patches. However, no dispersal event has been recorded between the Willacy and Cameron populations. Thus, we defined no dispersal between these populations. The dispersal defines the proportion of individuals in each habitat patch that move to other habitat patches. In addition, we specified that 100% of males would disperse at age class 2, whereas 50% of females of age class 2 would disperse (Haines et al., 2005a,b). Furthermore, we defined dispersal as a function of carrying capacity. When the habitat patch reached its carrying capacity, the dispersal rate was determined by the dispersal-matrix. If the habitat patch was below carrying capacity, then the dispersal rate decreased linearly as a function of the carrying capacity (Akcakaya, 2002).

2.7.2. Least cost path model

We defined a least cost path model as a path a species is most likely to use for movement based on habitat use. Least cost path models have been conducted in other studies for Florida panthers *Puma concolor coryi* (Meegan and Maehr, 2002) and Florida black bears *Ursus americanus floridanus* (Larkin et al., 2004). To develop a least cost path model for ocelots in southern Texas we developed ocelot cost weighted raster maps for ocelot habitat patches identified by the RAMAS/GIS Spatial Data program based on the ocelot cover map. Cost weighted raster maps were created for each habitat patch (refer to Section 3.3) using the spatial analyst tool in ArcGIS 9.0 under the distance option.

To develop the cost weighted raster maps we ranked closed cover (>75% woody cover) as the cover type most likely to be used by a dispersing ocelot followed by mixed cover (26–75% woody cover), open cover (1–25% woody cover), bare ground (<1% woody cover), and water as areas with decreasing likelihood for use by a dispersing ocelot. Least cost pathway models were then developed by using cost weighted raster maps to develop the path most likely to be used by a dispersing ocelot between two habitat patches using the shortest path option of the spatial analyst tool in ArcGIS 9.0.

We believed that the best potential sites for culvert placements that would reduce ocelot-vehicle collisions would occur where least cost pathways intersect with major roads (i.e., named roads). Therefore, we modeled least cost pathways between ocelot habitat patches that were separated by major roads to identify potential culvert sites.

2.8. Data analysis

After each model simulation, we recorded the probability of extinction (PE), and mean population size (*N*) for each model scenario over a 50-year period using the RAMAS/GIS Metapopulation program. We compared the effectiveness of recovery strategies using the RAMAS/GIS Comparison of Results program. The Comparison of Results program used the Kolmogorov–Smirnov test statistic *D*, which measured the maximum vertical distance between risk curves of two or more different model scenarios (Akcakaya, 2002). We compared terminal extinction risk curves between model scenarios and defined statistical significance at $p < 0.001$. We chose a conservative estimate of statistical significance because of the large number of replications we ran with the model scenarios (i.e., 1000). A large number of replications may cause small differences in extinction risk to be significant. Therefore, we validated statistical tests by visually analyzing the differences in extinction risk curves between model scenarios to confirm biological as well as statistical significance (Akcakaya, 2002).

Based on these test results we ranked the effectiveness of recovery strategies. Because of the potential inaccuracies and assumptions within PVAs, we believed the Kolmogorov–Smirnov test statistic was appropriate for analyzing the magnitude of the differences in model results instead of measuring precise estimates of extinction probability and final population size (Beissinger and Westphal, 1998; Ludwig and Walters, 2002; Haines et al., 2005b).

2.9. Sensitivity analysis

Model assumptions were tested in a sensitivity analysis. We conducted a model scenario in which all vital rates were not correlated compared to the original scenario in which vital rates were correlated, and we compared the effects of using a normal distribution compared to the original simulation of a lognormal distribution for environmental variation. Furthermore, a model scenario was conducted assuming that habitat patches 1 and 2 contained no ocelots (refer to Results Section 3.3), because ocelot occupancy was not verified within these habitat patches.

Other assumptions were tested using the RAMAS/GIS Sensitivity Analysis program. We varied rates of initial population size, density dependant dispersal, dispersal rates, and correlation rates by ±10% and analyzed the differences for the control, habitat, linkage, road, and translocation scenarios. In addition, we ran the model over 100 years, as conducted by Haines et al. (2005b), to evaluate the effectiveness of recovery strategies. However, we did not conduct a sensitivity analysis for the effects of drought on model results because Haines et al. (2005b) found it had no significant effect on model results. To identify which assumptions significantly changed model results, we used the RAMAS/GIS Comparison of Results program Kolmogorov–Smirnov test statistic (Akcakaya, 2002). We compared terminal extinction risk curves between model scenarios and based statistical significance when $p < 0.001$. In addition, we validated statistical tests by visually analyzing the differences in extinction risk curves between model scenarios to confirm biological as well as statistical significance (Akcakaya, 2002).

3. Results

3.1. *Ocelot cover map*

The cover map identified areas of closed cover, mixed cover, open cover, bare ground, and water with 88% accuracy in Willacy and Cameron counties during 2005. In addition, the cover map identified cover types with 87% accuracy in Willacy and Cameron counties during 1996. Because the results of the accuracy assessments were >85% for the cover map, we used the cover map for land use classification in Willacy and Cameron counties, Texas (Anderson et al., 1976).

3.2. *Ocelot telemetry and habitat suitability function*

We captured 30 ocelots (14 females, 16 males), from which we obtained 810 estimated locations from June 1996 to March 2005. The χ^2 goodness-of-fit for the logistic regression model was highly significant ($\chi^2_5 = 688.49$, $p < 0.01$) with closed, mixed, open, and bare cover statistically significant ($p \leqslant 0.001$). Water and interaction terms were not significant. We calculated the following habitat suitability function for ocelots in the cover map based on regression coefficients of the slope and an estimated y-intercept constant = 1.5786:

$$(0.0122 * [\text{Closed}] + 0.00168 * [\text{Mixed}] + 0.000712 * [\text{Open}] - 0.00288 * [\text{Bare}] + 1.5786).$$

Closed cover had the highest regression coefficient (0.0122) and thus was closest to ocelot locations, followed by mixed (0.00168) and open cover (0.000712), with bare ground having a negative slope value and being the farthest cover type from ocelot locations (−0.00288).

In addition, ocelot locations were found closer to closed cover ($\bar{x} = 0.13 \pm 0.16$, $t = -26.61$, $p < 0.01$) and mixed habitat ($\bar{x} = 0.66 \pm 0.49$, $t = -3.34$, $p < 0.01$) than expected based on distance ratios to actual random points using euclidean distance analysis (Conner and Plowman, 2001). There were no differences between ocelot locations and actual random points with regard to distance to bare ($\bar{x} = 1.21 \pm 0.55$, $t = 1.93$, $p = 0.07$), water ($\bar{x} = 0.93 \pm 0.63$, $t = -0.54$, $p = 0.59$), and open ($\bar{x} = 0.69 \pm 0.63$, $t = -2.72$, $p = 0.01$) cover. Furthermore, areas of closed cover were used most followed by mix, open, water, and bare cover based on a ranking of *t*-statistics associated with pairwise comparisons of corrected distances to habitat (i.e., test of the null hypothesis that [mean ocelot distance to habitat A/mean random distance to habitat A] − [mean ocelot distance to habitat B/mean random distance to habitat B).

3.3. *Spatial data*

Based on the results of the RAMAS/GIS Spatial Data program we identified 11 habitat patches (i.e., subpopulations) that had an area >3.71 km^2, which we deemed large enough to provide resources for at least one breeding male ocelot (Haines, 2006) (Table 2; Fig. 3). We concluded that habitat patches 1–3 belonged to the Willacy population and habitat patches 4–11 belonged to the Cameron population based on distances between habitat patches. We calculated carrying capacity for each patch by dividing the patch area by mean ocelot breeding range sizes defined by Haines (2006). Thus, a patch size of 4 km^2 could be used by one breeding male and two breeding females. In addition, since breeding adults constitute only half of the captured ocelot population (Laack, *personnel communication*; Navarro-Lopez, 1985; Tewes, 1986; Laack, 1991; Haines et al., 2005a) the full carrying capacity for a 4 km^2 habitat patch would be six ocelots (Table 2). We calculated a total carrying capacity of 82 ocelots based on patch sizes for the combined breeding populations of ocelots in southern Texas (Table 2). Furthermore, we assumed initial population size for each habitat patch to be one less than carrying capacity (Table 2).

We calculated distances between habitat patches which we specified to be the shortest distance from boundary to boundary using the RAMAS/GIS Spatial Data program. Based on distances between habitat patches we were able to produce an environmental correlation-matrix between habitat patches based on defined correlation rates (Fig. 2a) (refer to Section 2.3) and a dispersal-matrix between habitat patches based on defined dispersal rates (Fig. 2b) (refer to Section 2.7.1).

Table 2 – Identification of 11 habitat patches (i.e., subpopulations) within two ocelot breeding populations in southern Texas using the RAMAS/GIS Spatial Data program

Patch ID	Patch size (km^2)	K	Nt	Population (Willacy/Cameron)
1	4.00	6	5	Willacy
2	6.00	10	9	Willacy
3	4.00	6	5	Willacy
4	4.00	6	5	Cameron
5	5.00	6	5	Cameron
6	7.00	10	9	Cameron
7	4.00	6	5	Cameron
8	5.00	6	5	Cameron
9	7.00	10	9	Cameron
10	6.00	10	9	Cameron
11	4.00	6	5	Cameron
Totals	56.00	82	71	

K, carrying capacity; Nt, initial population size.

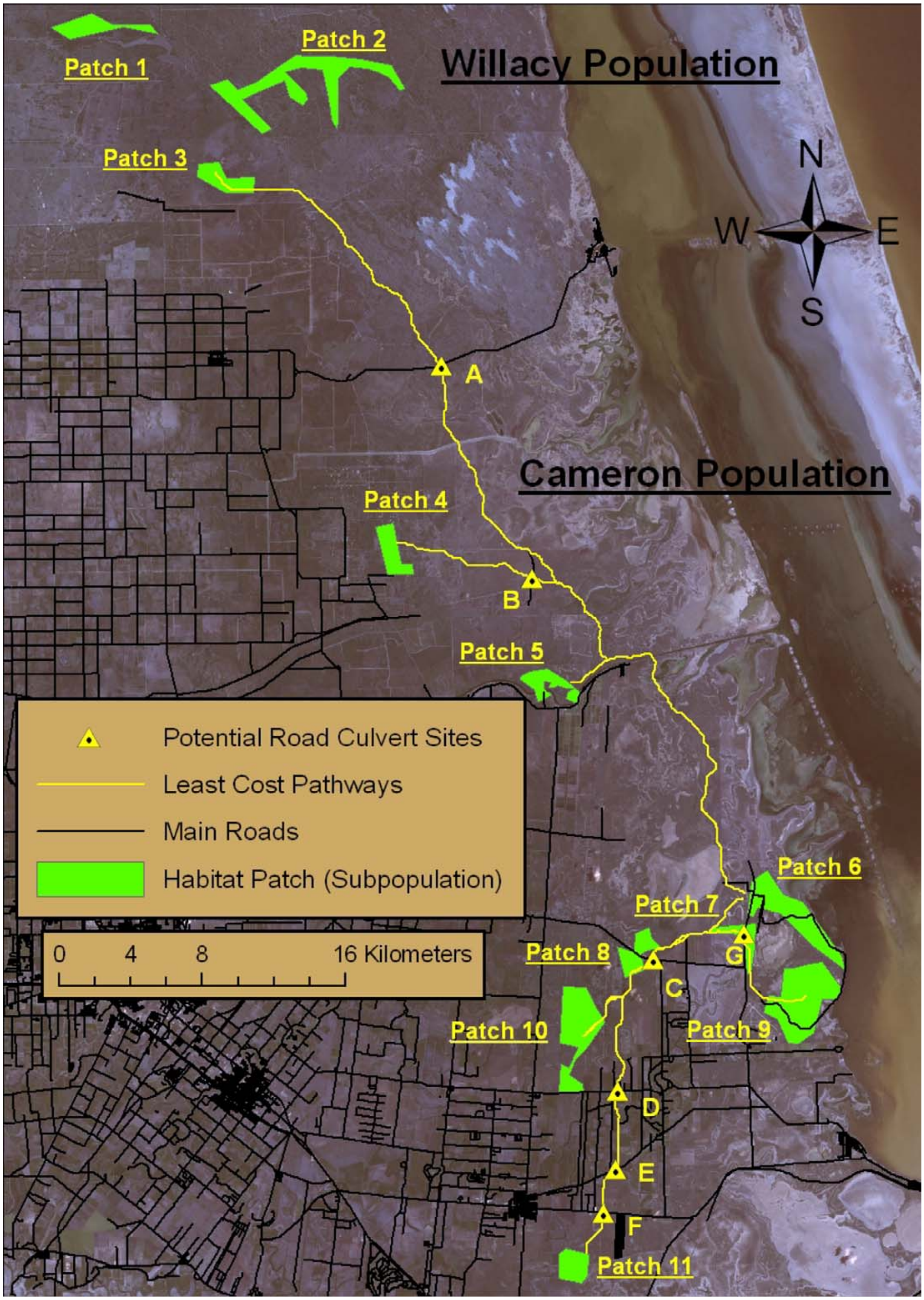

Fig. 3 – Locations of 11 habitat patches (i.e., subpopulations) identified using the RAMAS/GIS Spatial Data program within and around the Willacy and Cameron ocelot breeding populations in southern Texas. Estimated least cost pathways linking habitat patches with locations of potential culvert sites identified where least cost pathways intersect main roads (UTM coordinates for potential corridor sites: *A* = 647737.73, 2931512.64; *B* = 652812.07, 2919643.93; *C* = 659547.62, 2898355.05; *D* = 657587.58, 2891004.28; *E* = 657478.55, 2886632.86; *F* = 656755.90, 2884213.88; *G* = 664637.84, 2899493.24; all coordinates in zone 14N).

We modeled least cost paths between habitat patches in Cameron County and a least cost path between a habitat patch #3 in Willacy County and habitat patch #6 in Cameron County (Fig. 3). No least cost models were developed between habitat patches in Willacy County because of the lack of roads surrounding these patches (Fig. 3). We identified seven potential culvert sites for ocelots in southern Texas (Fig. 3).

3.4. Model output

The control scenario, which represented the scenario that no recovery strategies would be implemented in the next 50 years, estimated that probability of extinction for ocelots in southern Texas was 33% with a final population size of five individuals (Table 3). The single most effective recovery strategy estimated by the model was the reduction of ocelot road mortality (Table 3). This recovery strategy ranked the highest of all other recovery strategies for ocelots over 50 years, producing a probability of extinction of only 5%, a final population size of 18 individuals, and maintaining three habitat patches with ocelot presence (Table 3). In addition, recovery scenario combinations that incorporated the reduction of ocelot road mortality estimated lower ocelot extinction risks, larger final population sizes, and more occupied habitat patches (Table 3).

3.5. Sensitivity analysis

The only model assumption that significantly changed model results from the original simulation was running the model over 100 years, which showed that restoring habitat was more effective over the long-term than translocating ocelots into southern Texas from Mexico (Table 4). Reducing road mortality still produced the lowest probability of extinction and the lowest terminal extinction risk curves for all scenarios.

4. Discussion

The habitat-based PVA model identified reducing road mortality as the most effective strategy to reduce ocelot extinction probability in the US. This result differs from Haines et al. (2005b) which identified the protection and restoration of thornshrub habitat as most important to the viability of ocelots. However, as with Haines et al. (2005b), we found that certain combinations of recovery strategies further minimized ocelot extinction probability and maintained ocelot population size.

4.1. Habitat patches compared to continuous habitat

Differences in model results between this study and the previous PVA conducted by Haines et al. (2005b) may be due to the assumption made by Haines et al. (2005b) that both populations occurred in continuous habitat and thus had larger carrying capacities. However, based on the habitat analysis of Willacy and Cameron counties, we found that each ocelot population was partitioned into smaller habitat patches or subpopulations connected by dispersal with each habitat patch having a carrying capacity of $\leqslant$10 individuals. Therefore, we ran the model under the assumption that both the Willacy and Cameron populations reside within continuous habitats under the control scenario, as assumed by Haines et al. (2005b). We found that all recovery scenarios significantly lowered extinction risk curves, with habitat restoration having the lowest extinction risk curve followed by reduced road mortality. Translocation and population linkage both had similar extinction risk curves. Based on these simulations, the model results were similar to Haines et al. (2005b) when spatial data were excluded.

For ocelot populations residing in smaller habitat patches, it may be more beneficial to increase the rate of dispersal between habitat patches. Under the reduced road mortality scenario, ocelots of age class 2 benefited the greatest in the form of higher survival rates (Haines et al., 2005b), especially males. Therefore, the reduced road mortality scenario would also increase the rate of ocelot dispersal, because ocelots disperse during age class 2. In contrast, if the rate of dispersal is

Table 3 – Results of 16 habitat-based PVA scenarios for ocelots in southern Texas conducted over a 50-year duration

Scenario	Np	PE	N		R
			$\bar{x}$	SD	
Control	1	0.33	4.70	6.72	1
Linkage	2	0.33	4.84	6.78	1
Translocation	2	0.10	8.86	9.13	2
Translocation + linkage	2	0.10	8.87	8.93	2
Habitat	2	0.23	11.00	13.77	2
Habitat + linkage	2	0.22	11.48	13.80	2
Translocation + habitat	3	0.08	18.49	17.02	3
Translocation + habitat + linkage	3	0.07	18.95	16.94	3
Reduced road mortality	3	0.05	17.98	13.25	3
Reduced road mortality + linkage	3	0.05	17.76	13.21	3
Translocation + reduced road mortality	4	0.01	23.76	13.30	4
Translocation + reduced road mortality + linkage	5	0.01	24.77	13.74	4
Reduced road mortality + habitat	5	0.02	40.33	11.25	5
Reduced road mortality + habitat + linkage	5	0.02	39.21	24.96	5
Translocation + reduced road mortality + habitat	6	0.00	51.10	24.53	6
Translocation + reduced road mortality + habitat + linkage	7	0.01	51.41	24.34	6

Np, mean number of occupied habitat patches; PE, probability of extinction; *N*, final population size; *R*, rank of recovery strategies from least to most effective based on the Kolmogorov–Smirnov test statistic of the terminal extinction risk curve with significance $p < 0.001$.

Table 4 – Results of sensitivity analyses conducted for ocelots in southern Texas by reporting the probability of extinction after 50 years under the various recovery scenarios compared to the original simulation

Model inputs	Recovery scenarios for the RAMAS/GIS simulation				
	Control	Translocation	Road	Habitat	Linkage
Original simulation	0.33	0.10	0.05	0.23	0.33
Vital rates not correlated	0.35	0.12	0.06	0.25	0.37
Subpopulation 1 and 2 not included	0.41	0.13	0.10	0.27	0.41
Environmental variation with normal distribution	0.33	0.10	0.05	0.23	0.33
Probability of extinction over 100 years*	0.96	0.93	0.57	0.83	0.96
Initial population size					
+10%	0.35	0.12	0.05	0.23	0.34
−10%	0.35	0.12	0.05	0.20	0.33
Density dependant dispersal					
+10%	0.33	0.11	0.04	0.24	0.35
−10%	0.35	0.11	0.04	0.23	0.34
All dispersal rates					
+10%	0.34	0.12	0.05	0.23	0.36
−10%	0.33	0.10	0.05	0.22	0.32
Correlation rates (function of *b*)					
+10%	0.30	0.11	0.05	0.20	0.36
−10%	0.31	0.12	0.04	0.21	0.32

The "Road" recovery scenario refers to reduced road mortality.
* Indicates significant difference in model results based on the Kolmogorov–Smirnov test statistic of the terminal extinction risk curve with significance $p < 0.001$.

low, ocelot populations residing within fragmented habitat patches may be more susceptible to extinction then populations residing in areas of continuous habitat. Based on model simulations of 30 vertebrate species with natural populations, Reed (2004) found that dispersal between fragmented populations ameliorates, but did not eliminate, the negative effects of fragmentation.

4.2. *Other benefits of habitat restoration*

Potential benefits of increasing ocelot habitat may not have been specified in this model. Creation of habitat between habitat patches would increase ocelot population stability by making habitat more continuous for both populations. In addition, Haines et al. (2005a) stated that ocelot mortality might be indirectly related to anthropogenic habitat fragmentation, with reduced habitat availability causing ocelot populations to be more crowded, thus increasing intraspecific conflict, competition, and transient behavior. Thus, increasing ocelot habitat may help reduce these sources of mortality. Furthermore, Haines et al. (2005b) stated that an increase in ocelot habitat would not only increase ocelot carrying capacity but may also enhance dispersal potential between the Cameron and Willacy populations. Increasing the amount of habitat would increase dispersal between habitat patches, and potentially create linkage between the two breeding populations in the form of corridors.

However, in the short-term, the restoration of habitat will not have immediate benefits to the ocelot populations because of the extended time required for development of thornshrub communities. Based on data presented by Archer et al. (1988), Haines et al. (2005b) assumed that a 40-year-period was needed in southern Texas for discrete woody clusters scattered throughout a continuous grassland matrix to move toward a monophasic woodland. However, active management and reestablishment efforts can potentially accelerate the development of ocelot thornshrub cover.

4.3. *Reducing road mortality and identifying culvert locations*

As indicated by the model, benefits can be effectively achieved in a shorter period by reducing road mortality. However, this can only be done with the proper placement and construction of culverts (e.g., bridges and overpasses), based on the recommendations of Tewes and Hughes (2001) and Cain et al. (2003). Thus, identifying the locations of potentially successful culvert sites would allow researchers to analyze and validate these locations, and determine if these sites warrant the construction of culverts. Based on the least cost model analysis we identified seven potential culvert sites for ocelots in southern Texas (Fig. 3).

The proper placement of ocelot culverts may not only aid in the reduction of resident and transient ocelot mortality but also allow for potential successful dispersal by providing safer linkages with travel corridors. However, the benefit of corridors is greater when carrying capacity of habitat patches are larger (Hudgens and Haddad, 2003). In addition, Hudgens and Haddad (2003) suggested that species with slow-growing populations would only benefit from corridors in the long-term. Thus, similar to the habitat scenario, the benefits of dispersal become more apparent over a longer period when carrying capacity increases with increased habitat. Potential benefits of dispersal (i.e., primarily genetic benefits) could be maintained in the short-term by releasing ocelots from northern Mexico into the US, at least until a dispersal corridor between the Cameron and Willacy population develops.

4.4. *Future research*

As recommended by Beissinger and Westphal (1998), Ludwig and Walters (2002), and Haines et al. (2005b), an adaptive management approach needs to be applied to conservation by monitoring populations and habitats, and continuing species research to continually update and validate modeling results. In addition, validation of the potential benefits that recovery strategies provide ocelots in southern Texas are needed. However, we believe the recovery strategies, as specified in the model scenarios, represent viable benefits for the ocelot populations in southern Texas (Haines et al., 2005b).

Future research should include monitoring of ocelots along major roadways and associated potential culvert sites identified for the Cameron and Willacy populations. In addition, other techniques that could reduce ocelot-vehicle collisions (e.g., placement of wildlife crossing signs in specified areas to reduce speed) need to be evaluated for their effectiveness.

Results of this study suggest that spatial distribution of ocelot habitat patches affects the viability of the ocelot population. Additional research is needed on the distribution of habitat quality, quantity, and their changes across south Texas over time and how they affect ocelot populations. Results from this assessment could be incorporated into future habitat-based models to predict potential impacts of habitat change to ocelot carrying capacity and dispersal. Another major aspect of ocelot life history, which was not incorporated in the model, was genetic heterozygosity and possible inbreeding depressions of the ocelot populations. Thus, the model may have underestimated the importance of ocelot supplementation and ocelot population linkage as recovery strategies because the potential genetic benefits these recovery strategies may provide were not incorporated into the model. Haines et al. (2005b) recommended research on relevant ocelot genetic patterns (e.g., number of lethal equivalents, percentage of recessive alleles) and models that incorporate this genetic information.

5. Conclusion

Reduction of ocelot road mortality was the most effective recovery scenario that reduced ocelot extinction probabilities in the US. However, combinations of recovery strategies reduced ocelot extinction probabilities in the US even further. Recovery strategies that provided short-term benefits to the ocelot populations in southern Texas included reduction of ocelot road mortality, and the supplementation of ocelots into the US from northern Mexico. Successful mitigation of ocelot-vehicle collisions could be accomplished by constructing properly placed culverts with appropriate design along major roadways in southern Texas. Recovery strategies that provided long-term benefits to the ocelot populations included the restoration of habitat between ocelot habitat patches and the establishment of an ocelot dispersal corridor between the Willacy and Cameron populations. We believe these recommendations provide a model to maintain and increase ocelot population viability in the US. In addition, future research and monitoring of the ocelot populations are needed to validate model results and assumptions, and update input parameters for future modeling efforts.

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Corrigendum

Corrigendum to “A habitat-based population viability analysis for ocelots (*Leopardus pardalis*) in the United States [Biological Conservation 132 (2006) 424–436]”

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The lead author of the above article regrets that the fecundity rates for the Leslie Matrix calculated for ocelots were incorrect in Table 1 (i.e., 0.45). The correct fecundity (i.e., 0.40) has been incorporated into the correct version of

Table 1 – Stage-matrices for ocelots in southern Texas specifying reproductive and survival input parameters under the control scenario to link spatial data with demographic data in the RAMAS/GIS Metapopulation program (standard deviations in parenthesis)

	Age 0	Age 1	Age 2	Adult Age 3+
Female				
Fecundity	0.00	0.00	0.00	0.40[a] (0.17)
Survival	0.68 (0.05)	0.00	0.00	0.00
Survival	0.00	0.87 (0.02)	0.00	0.00
Survival	0.00	0.00	0.78 (0.05)	0.87 (0.02)
Male				
Fecundity	0.00	0.00	0.00	0.40[b] (0.17)
Survival	0.68 (0.05)	0.00	0.00	0.00
Survival	0.00	0.87 (0.02)	0.00	0.00
Survival	0.00	0.00	0.63 (0.10)	0.87 (0.02)

a Number of female offspring produced per adult female.
b Number of male offspring produced per adult female.

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Table 3 – Results of 16 habitat-based PVA scenarios for ocelots in southern Texas conducted over a 50-year duration

Scenario	Np	PE	N		R
			$\bar{x}$	SD	
Control	1	0.35	3.85	5.49	1
Linkage	1	0.38	3.17	5.20	1
Translocation	1	0.14	6.46	7.47	2
Translocation + linkage	1	0.14	6.57	7.37	2
Habitat	1	0.30	7.00	9.79	2
Habitat + linkage	1	0.30	6.77	9.75	2
Translocation + habitat	2	0.08	12.93	13.33	3
Translocation + habitat + linkage	2	0.11	12.67	13.21	3
Reduced road mortality	3	0.05	17.83	13.18	4
Reduced road mortality + linkage	3	0.05	18.48	13.71	4
Translocation + reduced road mortality	4	0.01	24.34	13.31	5
Translocation + reduced road mortality + linkage	4	0.01	23.72	9.98~~7~~	5
Reduced road mortality + habitat	5	0.02	41.11	25.80	6
Reduced road mortality + habitat + linkage	5	0.03	39.00	30.85	6
Translocation + reduced road mortality + habitat	6	0.00	51.89	24.21	7
Translocation + reduced road mortality + habitat + linkage	7	0.00	52.32	24.07	7

Np, mean number of occupied habitat patches; PE, probability of extinction; *N*, final population size; *R*, rank of recovery strategies from least to most effective based on the Kolmogorov–Smirnov test statistic of the terminal extinction risk curve with significance $p < 0.001$.

Table 1 found below. In addition, impacted modeling simulations for Table 3 in the above article have been corrected and are now found below under Table 3. The general conclusions of the paper outlined in the discussion remain unaffected.