



Use of monitoring data and population viability analysis to inform reintroduction decisions: Peregrine falcons in the Midwestern United States

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ABSTRACT

The peregrine falcon (*Falco peregrinus anatum*) has not yet recolonized natural cliff sites in Illinois and much of the lower Midwestern US, and remains restricted to urban areas. We constructed a landscape-linked population viability analysis using RAMAS/GIS software to compare possible reintroduction strategies for the species. Habitat-specific (i.e. cliff and urban) demographic parameters such as survival, fecundity, and dispersal rates were derived from the Midwest Peregrine Society Database for peregrines in the central Mississippi River region during 1982–2006. We simulated a base scenario of no reintroduction and 18 models of reintroduction with varying cohort sizes, supplementation schedules, and number of reintroduction sites, and used the Lake Superior population to test our model. Our analysis indicated that even without reintroductions in Illinois, the peregrine population in the lower Midwestern region is slowly increasing and is not likely to go extinct. Recolonization of cliff sites in southern Illinois likely will occur via dispersal from urban populations, however further research on dispersal rates between urban areas and cliffs is needed. Analysis indicated that the most cost-effective reintroduction strategy would be priced at approximately \$280,000 and would result in only two additional breeding pairs compared to the no-action scenario. Thus, funds would be more effectively used in other management efforts such as habitat preservation. This study provides an example of how post-release monitoring can be used to inform future reintroduction plans.

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1. Introduction

The number of reintroductions and translocations of threatened and endangered species has markedly grown over the past few decades (Seddon et al., 2007). Success rates of such programs, however, have been low and few have used an adaptive management strategy where results of post-release monitoring are used to improve future reintroduction success (Sarrazin and Barbault, 1996; Fischer and Lindenmayer, 2000). Monitoring programs following reintroductions provide years and sometimes decades of data on individuals and populations. Such data can be used to gather basic life history traits of rare species, to understand habitat selection, or to study colonization and founder effects that otherwise would have been unfeasible (Sarrazin and Barbault, 1996; Verdejo and López-López, 2008; Zuberogitia et al., 2009). Most importantly, field data from monitoring programs can provide demographic information for population viability analyses (PVA) of future reintroduction programs.

Spatially-explicit forms of population viability analyses are increasingly being used for reintroduction planning thanks to the advent of landscape analysis tools such as geographic information systems (GIS; South et al., 2000; Seddon et al., 2007). These spatially-explicit population models (SEPMs), which incorporate spatial structure, can provide better predictions of population growth for species that are divided into subpopulations and that have high dispersal rates (Southgate and Possingham, 1995; Akçakaya, 2000; South et al., 2000). Furthermore, SEPMs are often used for modeling reintroductions, translocations, or other management scenarios because of their ability to specify subpopulations (Southgate and Possingham, 1995; Akçakaya, 2000; South et al., 2000). Despite their usefulness, SEPMs are often criticized because they require detailed landscape and dispersal information along with habitat-specific demographic rates, and because they usually are not tested or validated (Dunning et al., 1995; Beissinger and Westphal, 1998).

The American peregrine falcon (*Falco peregrinus anatum*) is an ideal candidate for using monitoring data to derive habitat-specific demographic rates for spatially-explicit models. Studies conducted in California found significant differences in peregrine falcon demographic and dispersal rates among coastal, inland, and urban habitat types (Wootton and Bell, 1992; Kauffman et al., 2003, 2004). Applying these habitat-specific rates to population viability

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analyses helped improve management strategies for the California population. Unlike its western counterpart, the lower Midwestern US peregrine population is almost entirely composed of urban-nesting pairs. Initially, reintroduction programs in the Midwest used cliff releases, but these releases were terminated because of heavy predation (Redig and Tordoff, 1988). Reintroductions resumed several years later, but were concentrated in urban areas where tall buildings functioned as nest sites. Reintroduction programs for peregrine falcons have been hailed as a success throughout the nation, but the majority of the population in the Midwest still resides on man-made structures rather than natural cliffs.

In Illinois, peregrines historically nested on bluffs adjacent to the Mississippi River in the southern portion of the state (Ridgeway, 1889; Widmann, 1907; Bohlen, 1978). Currently, 11 pairs hold territories in the state, but all are nesting on buildings and bridges in Chicago (Redig et al., 2007). High site fidelity may in part explain why they have not returned to their historic cliff sites (Newton and Mearns, 1988; Tordoff et al., 1998). Therefore, reintroductions from cliff sites may be necessary to expedite the recolonization of these natural areas. Reintroductions resulting in a viable cliff-nesting population in southern Illinois could provide the additional benefit of linking regional populations of urban falcons (i.e., Chicago, IL, St. Louis, MO, Indianapolis, IN) and decreasing overall metapopulation extinction risk.

Reintroduction programs are expensive, with early Midwestern efforts costing \$80,000 to hatch 25 falcons (Redig and Tordoff, 1988). Therefore, the feasibility and cost-effectiveness of reintroductions should be evaluated by modeling and comparing different reintroduction strategies prior to management action (IUCN, 1998). In this study, we derived habitat-specific survival and fecundity rates using monitoring data from the Midwestern peregrine falcon populations, used these rates to simulate a spatially-explicit population viability analysis for a cost-benefit analysis of reintroduction scenarios, and used an independent dataset to verify model accuracy.

2. Methods

2.1. Analysis of monitoring data

The Midwest Peregrine Society web database (Midwestperegrine.org) has monitoring data for the entire Midwestern US, as well as Ontario and Quebec, Canada. In this study, only peregrines <250 km from the Mississippi River were used to estimate demographic rates, reserving birds from the upper Midwestern region for model verification.

2.1.1. Survival

The Midwest Peregrine Society dataset provided banding, resighting, and recovery data for 924 falcons during 1982–2006, from which we could interpret individual life history. Of these, 148 were born or released from cliffs and 776 from man-made structures (e.g., buildings, bridges, and smokestacks). We estimated survival rates using the Barker model in program MARK (White and Burnham, 1999). The Barker model allows the use of multiple data sources, including recaptures, live resightings between marking occasions, and dead recoveries, to produce more accurate parameter estimates (Barker and White, 2001). The parameters in this model as defined by Barker and White (2001) are:

- S_i the probability that an animal alive at time i is alive at time $i + 1$;
- p_i the probability that an animal alive and at risk of capture at time i is captured (i.e., banded or resighted);
- r_i the probability that a marked animal that dies between i and $i + 1$ is found and reported;

- R_i the probability that a marked animal alive at $i + 1$ is resighted alive between i and $i + 1$;
- R'_i the probability that a marked animal that dies between i and $i + 1$ is resighted alive in this interval before it died;
- F_i the probability that an animal at risk of capture at time i is again at risk of capture at time $i + 1$;
- F'_i the probability that an animal not at risk of capture at time i is at risk of capture at time $i + 1$.

For this study, “recaptures” were captures or resightings occurring during 1 May–1 August, as banding and observational effort were most intensive during this time period.

We used Akaike's Information Criterion adjusted for small sample sizes and lack of fit (AIC_c) in Program MARK to rank a set of candidate models that fit survival data. We expected survival to be affected by age class (i.e., juvenile, subadults, and adults) because juvenile mortality is likely to be high during dispersal from natal sites, subadult mortality is likely to be lower as they become familiar with their surroundings but need to fight for territories, and adult mortality following territory establishment is likely the lowest (Ratcliffe, 1993; Kauffman et al., 2003). We were also interested in determining if natal location (urban vs. cliff) or an interaction between age and natal location affected survival. Previous studies indicated that juveniles raised in urban areas may have a higher survival rate because of the large, easily accessible prey base (e.g., rock doves [*Columba livia*]) and lack of predators (Septon et al., 1995; Sweeney et al., 1997; Tordoff and Redig, 1997; Kauffman et al., 2003). Therefore, we tested models of survival with age effects, natal site effects, additive age and natal site effects, and interactive age and natal site effects.

Recapture (p) and recovery (r) rates are also likely influenced by age and natal sites because breeding adults in urban areas are more likely to be seen or reported. We did not expect any interaction between age and natal sites in recapture or recovery rates and therefore did not test for such effects. Resightings (R) take place during the non-breeding season and were therefore probably not influenced by age. Natal sites may have an effect on resighting because falcons are more conspicuous in urban areas. R' , or the probability of resighting a bird in the same interval it was found dead, was unconstrained because too few of these events occurred to test effects. Emigration (F) and immigration (F') were unconstrained to simulate Markov emigration (risk of capture at time i depends on whether an animal was at risk of capture at time $i - 1$; Barker and White, 2001) because peregrines show high site fidelity to breeding sites. Because these recaptures were essentially resightings at breeding sites, individuals are more likely to be at the breeding site (e.g., at risk of capture) if they were present the previous year.

We used a reduced-parameter approach to sequentially find the most parsimonious model starting with resighting probability, then recapture, then recovery, and finally survival (Barker and White, 2001; Brown et al., 2006). Rather than running all possible combinations of variables per parameter, this approach first accounted for nuisance parameters and then determined the best-fit model. We examined 15 candidate models of survival using this approach (Table 1). The median \hat{c} approach was used to test for model overdispersion (Cooch and White, 2008). Models within three AIC_c points were averaged for parameter estimation to account for model uncertainty (Burnham and Anderson, 2002).

2.1.2. Productivity

Average number of fledglings for cliff-nesting ($n = 11$) and urban-nesting birds ($n = 54$) were estimated for 2000–2006 because peregrines were not nesting on cliffs in the region prior to this time period. We used a one-way ANOVA to estimate temporal variance

Table 1

Top five Markov emigration models of survival (*s*), detection (*p*), recoveries (*r*), resighting (*R*), resighting prior to death (*R'*), emigration (*F*), and immigration (*F'*) for peregrine falcons in the lower Midwestern United States.

Model	K	AICc	ΔAICc	Weights	Description
1. $s(a3)p(a3)r(a3+n)R(\cdot)R'(\cdot)F(\cdot)F'(\cdot)$	14	2942.26	0.00	0.39	Survival with age effects; detection with age effects; recovery with age and natal site effects
2. $s(a3^*n)p(a3)r(a3+n)R(\cdot)R'(\cdot)F(\cdot)F'(\cdot)$	17	2942.66	0.40	0.32	Survival with age effects, natal site effects, and interaction; detection with age effects; recovery with age and natal site effects
3. $s(a3)p(a3)r(a3+n)R(n)R'(\cdot)F(\cdot)F'(\cdot)$	15	2944.13	1.87	0.16	Survival with age effects; detection with age effects; recovery with age and natal site effects; resighting with natal site effects
4. $s(a3^*n)p(a3)r(a3+n)R(n)R'(\cdot)F(\cdot)F'(\cdot)$	18	2944.65	2.39	0.12	Survival with age effects, natal site effects, and interaction; detection with age effects; recovery with age and natal site effects; resighting with natal site effects
5. $s(a3^*n)p(a3+n)r(a3+n)R(n)R'(\cdot)F(\cdot)F'(\cdot)$ (GLOBAL model)	15	2994.56	52.30	0.00	Global model: Survival with age effects, natal site effects, and interaction; detection with age and natal site effects; recovery with age and natal site effects; resighting with natal site effects

for urban-nesting peregrines, where within-year variance estimates sampling variance and between-year variance estimates environmental variance (White, 2000). All statistical procedures were carried out in SAS[®] version 9.1.3 with $\alpha = 0.05$ (SAS Institute, 2004). Homogeneity of variance and normality were tested by assessing residual and normal quantile plots.

2.2. Spatially-explicit population viability analysis

We used the software program RAMAS[®]/GIS software, version 5.0 (Akçakaya, 2005) to develop a stage-structured, spatially-explicit population model of peregrine falcon populations in southern Illinois and the surrounding region. The model was developed using a habitat map and 25 years of monitoring data in the Midwestern US.

2.2.1. Habitat map and patch structure

The peregrine falcon is a habitat specialist, relying primarily on cliffs for nesting (Hickey, 1942; Ratcliffe, 1993). Previous studies indicate that habitat variables such as elevation, cliff height, cliff dominance, and distance to water may help predict nesting sites in other regions (Porter et al. 1973, Gainzarain et al. 2000, Wightman and Fuller 2005). In the lower Midwest, few peregrines nest on natural habitat, thus nest locations could not be used to develop a habitat model. However, recent research (Wakamiya, 2008) showed that querying for slopes $\geq 45^\circ$ in a Geographic Information System (GIS) identified cliffs that possessed attributes consistent with literature values at peregrine nesting sites elsewhere in their range. We therefore created a map of peregrine nesting habitat for the lower Midwest by querying for slopes $\geq 45^\circ$. Digital Elevation Models of 10 m resolution were downloaded from the US Geological Survey National Map Seamless Server (<http://www.seamless.usgs.gov>) for a 950,581 km² area encompassing 35 counties in southern Illinois and a 416 km radius buffer from their edge (Fig. 1). This radius was chosen because it is the farthest distance a peregrine of the more philopatric sex (male) dispersed in the reference dataset. Thus, some females may disperse outside the study area, but the majority would be expected to remain within the study boundary. The final map was converted to a 300 m grid and imported into RAMAS/GIS. The Spatial Program in RAMAS/GIS delineated landscape patchiness based on habitat suitability and a neighborhood distance. Suitable cells separated by a distance less than the neighborhood distance were considered to be in the same patch (Akçakaya, 2005). We used a neighborhood distance of 30 km, the distance within which 80% of juveniles disperse (see *Dispersal* below). This distance also allowed cliff patches in southern Illinois to be distinct from other regions. However, some cliffs in Missouri and Kentucky were incorporated in the southern

Illinois patches thus inflating calculations of carrying capacity based on political boundaries. RAMAS/GIS does not support individual-based modeling, so patches that could only support one breeding pair were grouped with the next closest cliff patch, producing a total of nine cliff patches.

Most peregrines nest on buildings in the Midwest, so we also incorporated 24 urban centers in the study region that were occupied by ≥ 1 nesting pair in 2005 (Fig. 1). A point shapefile of these cities or towns was obtained through ESRI (2006) and converted to a 300-m resolution grid for import. Like cliff habitat, urban centers within a neighborhood distance of 30 km were grouped to form one patch. Urban centers that supported only one nesting pair in 2005 were grouped with the nearest urban patch, producing a total of four urban patches. Because Kansas City, Missouri and Chattanooga, Tennessee each contained only one pair and were >250 km from the next nearest occupied urban center, we assumed they had little influence on metapopulation dynamics and removed them from the analysis. Throughout, we differentiate “study region” and “southern Illinois patches” such that the study region incorporates all cliff and urban patches while southern Illinois patches only incorporates the cliff patches in the southern part of the state of Illinois.

2.2.2. Stage structure

The model included three stage classes: juveniles (0–1 yrs), subadults (1–2 yrs), and adults (2+ yrs). In congruence with other studies (Mearns and Newton, 1984; Tordoff and Redig, 1997; Restani and Mattox, 2000), preliminary analysis of our dataset indicated that males are the more philopatric sex and the proportion of females dispersing longer distances is higher than that of males. Therefore, only males were modeled because they are the philopatric sex and because RAMAS/Metapop allows the user to define only one dispersal-distance function. Although most species are modeled using females, many bird populations are modeled with males because they establish territories, and therefore, limit population growth (McCarthy et al., 2004; Shriver and Gibbs, 2004; Alldredge et al., 2004).

Separate transition matrices were created for cliff-nesting and urban-nesting populations using the parameter estimates derived from the monitoring data (Table 2). Peregrines typically begin breeding the second year they return to a breeding site (Mearns and Newton, 1984; Tordoff and Redig, 1997). Therefore, both subadults and adults were assumed to breed (Akçakaya, 2005). Fecundity rates were calculated as the product of age-specific survival, average number of fledglings (*f*), and sex ratio (Akçakaya, 2005). Assuming a 1:1 sex ratio (Restani and Mattox, 2000), and a post-breeding census (Mearns and Newton, 1984; Tordoff and Redig, 1997), we obtained the following stage matrix:

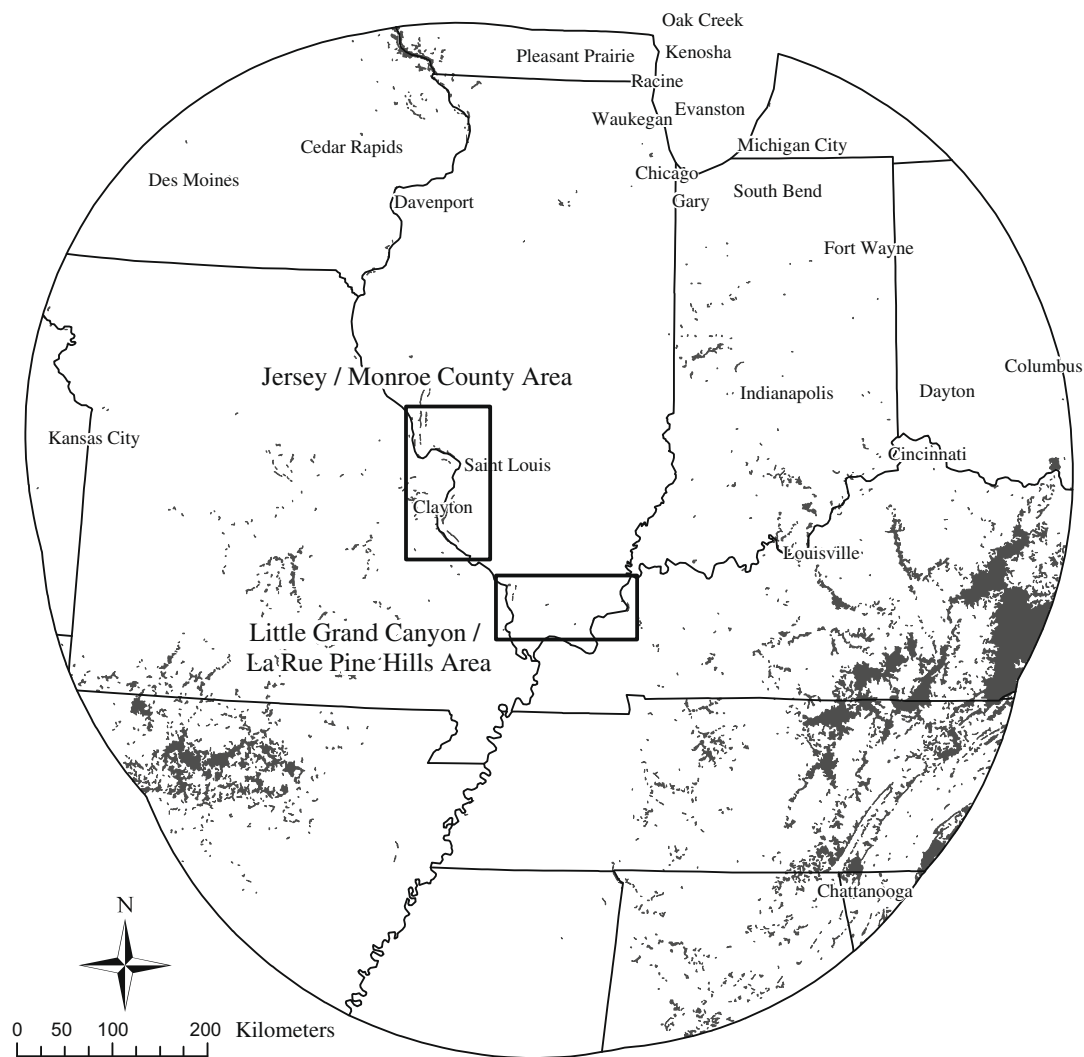


Fig. 1. Map of potential nesting habitat (black regions) for peregrine falcons in the study region identified by slope for a spatially explicit population viability analysis. Boxes represent habitat patches in southern Illinois and stars represent urban centers occupied by ≥ 1 nesting pair in 2005.

$$\begin{bmatrix} 0 & 0.5S_{sf} & 0.5S_{af} \\ S_j & 0 & 0 \\ 0 & S_s & S_a \end{bmatrix}$$

where S_j is juvenile survival, S_s is subadult survival, and S_a is adult survival.

2.2.3. Initial abundance

In the study region, peregrines are solely nesting on man-made structures. Therefore, we used an initial abundance of zero for cliff populations and estimated the number of fledglings and subadults

Table 2
Parameters used for a population viability analysis of peregrine falcons in southern Illinois and the surrounding region. Mean values and process variance are provided.

	Cliff	Urban
Initial abundance	0	31
Annual juvenile survival	0.20 ± 0.03	0.24 ± 0.02
Annual subadult survival	0.84 ± 0.13	0.85 ± 0.07
Annual adult survival	0.85 ± 0.04	0.85 ± 0.02
Sex ratio	1:1	1:1
Subadult fecundity	0.76 ± 0.15 ^a	1.11 ± 0.11
Adult fecundity	0.77 ± 0.09 ^a	1.11 ± 0.06

Source: Wootton and Bell (1992).

^a Based on a 50% increase of standard deviation of urban population fertility rates.

at a stable age distribution for each urban patch using the most recent available census (i.e., 2005) of breeding pairs in the study region.

2.2.4. Stochasticity

Environmental stochasticity was incorporated into the model using the unconditional variance estimate for each model-averaged survival derived in Program MARK. This unconditional estimate removes variance due to sampling error and model uncertainty, leaving only process variance (Cooch and White, 2008). Process variance in the average number of fledglings for urban-nesting peregrines was estimated using a one-way ANOVA (see Productivity above). Because sample sizes were too small to estimate process variance for the average fledgling number of cliff-nesting peregrines, we used a 50% increase in the standard deviation of average fledglings from urban-nesting birds. A 50% increase in standard deviation seemed reasonable because the standard deviations of survival rates differed 50% between urban and cliff-nesting populations. The variance of the product of two independent variables, i and j , is

$$\text{var}_{ij} = \text{var}_i(\text{mean}_j)^2 + \text{var}_j(\text{mean}_i)^2 + \text{var}_i\text{var}_j$$

(Goodman, 1960), which was used to estimate total process variance in fecundity. Demographic stochasticity was modeled by

drawing the number of survivors and dispersers for each class from a binomial distribution and the number of young from a Poisson distribution (Akçakaya, 2005).

2.2.5. Density dependence

Peregrine falcon populations are believed to be regulated by the number of breeding sites in the region because of their highly territorial nature (Hickey, 1942; Hunt, 1988; Ratcliffe, 1993; Kauffman et al., 2004). Therefore, we modeled density dependence using contest competition, or the Beverton–Holt function. Contest competition occurs in highly territorial populations where the number of territories does not change, but the number of individuals seeking territories does (Akçakaya, 2005). This type of density dependence has a stabilizing effect because breeding individuals that die are quickly replaced. Peregrine falcons are known for their remarkably stable populations in spite of fluctuating breeding success, indicating that contest competition is likely (Newton and Mearns, 1988). Density dependence was assumed to affect both fecundity and survival because of limitations on breeding territories and intense territorial battles leading to lower survival after carrying capacity has been reached (Herbert and Herbert, 1965; Hunt, 1988; Ratcliffe, 1993; Tordoff and Redig, 1999; Kauffman et al., 2004).

In RAMAS, contest competition is implemented by altering rates in the stage matrix so that the per capita growth rate at time t (R_t) is given by the following equation:

$$\frac{R_{\max} \times K}{(R_{\max} \times N_t) - N_t + K},$$

where R_{\max} is the maximal growth rate in the absence of density dependence, N_t is adult abundance at time t , and K is the carrying capacity of territorial adults. The maximum growth rate for cliff ($R_{\max} = 1.002$) and urban birds ($R_{\max} = 1.094$) were based on eigenanalysis of their respective stage matrices. Because the urban populations may be approaching carrying capacity, the estimates of R_{\max} for urban populations in this study are conservative.

2.2.6. Carrying capacity

Densities for peregrines are typically expressed based on length rather than area because of the linear nature of their breeding habitat. We used ArcGIS to estimate total patch length because RAMAS/GIS did not have this capability. As stated previously, RAMAS grouped several cliffs in Missouri and Kentucky with the southern Illinois patches so total carrying capacity for southern Illinois was slightly inflated. Peregrine densities vary widely depending on region. Peregrine density in New York was estimated at one pair every 11 km apart (Hickey and Anderson, 1969), whereas historical Midwestern peregrine density was estimated as one pair every 30 km (Berger and Mueller, 1969). Therefore we simulated low-, medium-, and high-density scenarios of carrying capacity using densities of one territorial male every 10, 20, and 30 km. We assumed all adult males became territorial until carrying capacity was reached.

Each cliff population was well below carrying capacity at the beginning of each simulation as initial abundance was zero. We assumed urban populations were approaching carrying capacity as Midwestern urban centers have been occupied by peregrines for >25 years and man-made structures suitable for nesting have been occupied. Therefore, we assumed each urban population could support only one additional territorial male.

2.2.7. Dispersal

Dispersal was modeled using a distance-dependent dispersal function. Only juvenile dispersal was modeled because adults typically show extreme site fidelity once territories are established

(Mearns and Newton, 1984). Natal and breeding site locations for falcons from the lower Midwestern region, as described in the Midwestern peregrine falcon database, were converted to UTM coordinates using Topozone (<http://www.topozone.com>). Using the Animal Movements tool in Hawth's Analysis tools for ArcGIS, we determined dispersal distances for 92 male peregrines that remained within habitat types (i.e., cliff–cliff or urban–urban movement). The number of dispersing juvenile males in distance class intervals of 100 km was divided by the total sample size to determine the proportion dispersing in each class (Akçakaya and Atwood, 1997). We then fitted a negative exponential curve to the proportion dispersing versus the midpoint of each distance. With a maximum dispersal distance of 416 km, the probability of a juvenile male dispersing from its natal patch (i) to another (j) was modeled using the function $p_{ij} = 1.08 * e^{-0.01d_{ij}}$, where d_{ij} is the distance between the two patches.

Sample sizes were too small to estimate the distance-dispersal function between cliff and urban sites. Because peregrines have been nesting in cities in the study region for >10 years and have not yet recolonized their cliff habitat, it is likely that dispersal rates within habitat types (e.g., urban–urban and cliff–cliff) are different from dispersal rates between habitat types (e.g., urban–cliff and cliff–urban). In California, dispersal rates from cliff to urban habitats were 3.3 times higher than dispersal rates from urban to cliff habitats (Kauffman et al., 2004). Dispersal rates between habitat types were also approximately 80–90% lower than those within habitat types. Therefore, we reduced the distance-dispersal function by 67% for cliff to urban patches and by 90% for urban to cliff patches. Density of the breeding peregrine population likely does not affect dispersal, so we did not model density-dependent dispersal (Restani and Mattox, 2000).

2.2.8. Simulations and sensitivity analysis

We simulated 19 metapopulation models (Table 4) representing different reintroduction strategies. These 19 models were run for the low, medium, and high cases of carrying capacity producing a total of 57 simulations. Models included a scenario with no reintroductions and several scenarios of reintroduction with varying cohort sizes (8–24), supplementation schedules (release every 1, 3, or 5 yrs), and number of reintroduction sites (1–2 sites). Reintroduction scenarios simulated releases of captive bred juveniles into unoccupied natural cliff areas. Reintroductions were simulated in the Monroe/Jersey county area and the Little Grand Canyon/La Rue Pine Hills area (Fig. 1). Only juveniles were reintroduced and all strategies were implemented over 10 years. These scenarios are representative of the reintroduction actions possible given the time and budget constraints of a wildlife agency. Simulations were projected for 50 years and replicated 1000 times.

2.2.9. Cost-benefit analysis

We conducted a cost-benefit analysis using the low carrying capacity scenario to determine the most cost-effective reintroduction strategy. Assuming that each falcon and hack station costs \$5000 and \$21,000, respectively (Redig and Tordoff, 1988, adjusted for inflation), we calculated the total cost of each management scenario run over a 50-year period. The best reintroduction strategy had the lowest cost-benefit ratio, where benefit was defined as the increase of the following metrics from the base scenario: minimum expected abundance, average number of adults in all cliff patches, and average number of adults in southern Illinois cliff patches. Minimum expected abundance is defined as the average over all replications of the minimum metapopulation abundance and can be used as an index of propensity to decline (Akçakaya, 2005). Scenarios that had the lowest cost-benefit ratio for all three metrics were considered most cost-effective.

Table 3
Results from a 50-year population viability analysis of peregrine falcons without reintroductions for the lower Midwest and southern Illinois under high, medium, and low scenarios of carrying capacity.

Population	Scenario	K	EMA	N_p ($\bar{x} \pm SD$)	N_{am} ($\bar{x} \pm SD$)
Lower Midwest	High	496	23.2	8.2 ± 1.8	40.1 ± 12.0
	Medium	264	23.0	8.2 ± 1.8	39.2 ± 11.7
	Low	171	23.0	8.2 ± 1.7	39.3 ± 12.1
Southern Illinois	High	47	10.9	1.0 ± 0.8	2.2 ± 2.5
	Medium	24	11.4	1.0 ± 0.8	2.1 ± 2.4
	Low	16	11.4	1.0 ± 0.8	2.1 ± 2.4

K, carrying capacity; EMA, expected minimum abundance; N_p , terminal number of occupied; N_{am} , terminal number of adult males.

Table 4
Results of a population viability analysis for peregrine falcons in the lower Midwest conducted under the low-case scenario of carrying capacity and ranked from most to least cost-effective.

Scenario	EMA	Lower Midwest cliff patches						Southern Illinois cliff patches						Cost:benefit
		t_c	N_p		N_{am}		t_c	N_p		N_{am}				
			\bar{x}	SD	\bar{x}	SD		\bar{x}	SD	\bar{x}	SD			
No reintroduction	23.0	3.4	4.5	1.5	12.8	7.4	11.4	1.0	0.8	2.1	2.4	–		
2 sites + 8 juveniles + every 3 years	26.6	2.5	5.4	1.5	17.5	9.4	2.6	1.5	0.7	4.4	3.8	0.09		
1 site + 8 juveniles + every 3 years	24.5	2.6	5.0	1.5	14.7	8.3	2.9	1.3	0.7	3.2	3.2	0.10		
1 site + 16 juveniles + every 3 years	26.6	2.5	5.3	1.5	16.4	8.7	2.6	1.4	0.7	3.9	3.5	0.10		
1 site + 24 juveniles + every 3 years	27.8	2.5	5.6	1.5	18.7	9.7	2.6	1.5	0.7	4.6	4.1	0.10		
2 sites + 16 juveniles + every 3 years	28.3	2.5	6.0	1.4	22.1	11.0	2.5	1.7	0.5	6.0	4.8	0.10		
2 sites + 24 juveniles + every 3 years	29.3	2.5	6.3	1.3	25.8	12.2	2.5	1.8	0.5	7.7	5.3	0.11		
1 site + 8 juveniles + every year	27.0	2.6	5.5	1.5	18.0	9.4	2.9	1.5	0.7	4.6	4.0	0.12		
1 site + 16 juveniles + every 5 years	25.1	2.5	4.9	1.6	14.5	8.1	2.6	1.3	0.7	3.1	3.0	0.12		
1 site + 24 juveniles + every 5 years	26.0	2.5	5.2	1.6	16.2	8.8	2.6	1.3	0.8	3.5	3.3	0.12		
2 sites + 8 juveniles + every 5 years	25.1	2.5	5.0	1.6	15.0	8.3	2.6	1.3	0.7	3.1	2.9	0.13		
2 sites + 16 juveniles + every 5 years	26.9	2.5	5.3	1.6	16.7	9.2	2.5	1.4	0.8	4.0	3.8	0.13		
1 site + 8 juveniles + every 5 years	24.0	2.6	4.8	1.5	13.7	7.8	2.9	1.2	0.8	2.6	2.8	0.14		
1 site + 16 juveniles + every year	28.8	2.5	6.1	1.4	23.0	11.3	2.6	1.7	0.6	6.1	4.6	0.14		
1 site + 24 juveniles + every year	29.6	2.5	6.5	1.2	26.7	12.5	2.6	1.8	0.5	7.7	3.6	0.16		
2 sites + 16 juveniles + every year	29.8	2.5	6.8	1.1	33.2	14.0	2.5	1.9	0.3	10.7	6.6	0.17		
2 sites + 24 juveniles + every 5 years	27.8	2.5	5.6	1.5	19.1	10.0	2.5	1.4	0.7	3.8	3.6	0.17		
2 sites + 8 juveniles + every year	28.7	2.5	6.2	1.3	23.4	10.7	2.6	1.8	0.5	6.7	4.9	0.18		
2 sites + 24 juveniles + every year	29.7	2.5	7.2	0.9	41.4	16.1	2.5	2.0	0.2	14.0	7.9	0.22		

EMA, expected minimum abundance; t_c , median time to colonization; N_p , terminal number of occupied patches in 50 years; N_{am} , terminal number of adult males in 50 year. Cost:benefit is the average cost-benefit ratio of EMA, lower Midwest cliff N_{am} , and southern Illinois cliff N_{am} , where the lowest ratio indicates the most cost-effective strategy.

2.2.10. Sensitivity analysis

We assessed model sensitivity to changes in dispersal rates, carrying capacity, and R_{max} , by varying each parameter by $\pm 10\%$ and examining the relative influence on the minimum expected abundance, the number of patches occupied in 50 years, and the median time to ≥ 1 male adult in southern Illinois. Because RAMAS limits $R_{max} \geq 1$, we set the lower limit of R_{max} at 1. Sensitivity analysis was conducted on the low-case scenario with no reintroductions.

2.3. Model verification

We produced a spatially-explicit PVA for peregrine falcons nesting along the north shore of Lake Superior to evaluate model accuracy. Parameters used in model verification matched those in the Illinois model (i.e., from the lower Mississippi River region) under the medium case scenario of carrying capacity. Reintroduction scenarios followed those actually implemented in the region. We visually compared modeled and observed population trajectories for the Lake Superior region and used the standard deviates test (McCarthy and Broome, 2000) to compare the observed number of male adults versus the predicted probability distribution of male adults. The latter method expresses observed values in terms of the number of standard deviations from the predicted mean using the formula:

$$\frac{x_{obs} - \bar{x}_{pred}}{\sigma_{pred}^2},$$

where x_{obs} is the observed number of male adults, \bar{x}_{pred} is the predicted mean number of male adults, and σ_{pred}^2 is the predicted standard deviation. The standard deviates method was used because it considers model stochasticity and accounts for increasing model variation over time (McCarthy and Broome, 2000). Predicted population sizes were based only on the abundance of the previous year to ensure independence of predicted values (McCarthy and Broome, 2000). If the standard deviates have a mean of 0 and a variance of 1 then the model predictions are accurate. A mean >0 indicates the model overestimated predicted population size, whereas a mean <0 indicates the model underestimated population size. Likewise, a variance of standard deviates >1 indicates model stochasticity is too small, whereas a variance <1 indicates model stochasticity is too large. Significant deviations from these values were determined using a one-sample t -test in SAS and a Chi-square test for standard deviations in DataPlot (McCarthy and Broome, 2000; Heckert, 2001).

3. Results

3.1. Monitoring data

3.1.1. Survival model selection

The global model fit the data well, with a median \hat{c} of 1.01, indicating little to no overdispersion. Detection probability was influenced by age class whereas recovery rates were influenced by

age class and natal sites (Table 1). Age and natal site interacted to influence survival. Natal site may have had some influence on resighting rates, however the evidence was weak. The top four models carried 99% support of the data.

3.1.2. Survival rate estimation

Model averaged annual survival based on the top four models ($\Delta AICc < 2.39$) was 0.20 ± 0.06 for cliff-fledged juveniles and 0.24 ± 0.02 for urban-fledged juveniles. Process variance was 0.03 for cliff-fledged juveniles and 0.02 for urban-fledged juveniles. Survival of subadults and adults was similar between cliff (0.84 ± 0.14 and 0.85 ± 0.05 , respectively) and urban (0.85 ± 0.07 and 0.85 ± 0.02 , respectively) habitats. Process variance was 0.13 for cliff-fledged subadults, 0.07 for urban-fledged subadults, 0.04 for cliff-fledged adults, and 0.02 for urban-fledged adults.

3.1.3. Productivity estimation

Average number of fledglings was 1.8 ± 0.5 for cliff-nesting peregrines and 2.6 ± 0.1 for urban-nesting peregrines. Process variance of average number of fledglings for urban-nesting peregrines was estimated at 0.13. Implementing a 50% increase relative to the urban estimate, process variance of average number of fledglings for cliff-nesting peregrines was estimated at 0.20.

3.2. Population viability analysis

The current peregrine population appears to be stationary without reintroduction, even under different levels of carrying capacity. The model predicted a minimum abundance of 23 adult males for the study area in all three scenarios, and an average abundance of 40 adult males in 50 years (Table 3). Changing carrying capacity did not influence population trends (Fig. 2), even when reintroductions pushed the population size past carrying capacity. Total carrying capacity for the study region was not reached in any of the models, with or without reintroductions, but the projected population slowly increased with time (Fig. 2).

Without reintroductions, the models predicted that peregrines will recolonize cliffs in the study region in approximately 3 years, but that recolonization of cliffs in southern Illinois will take approximately 11 years (Table 3). Only about half (4.5 of 8) of the cliff patches in the study region are expected to be occupied in 50 years, by a total of 13 adult males. In all three scenarios of carrying capacity, only one of the two southern Illinois patches was occupied after 50 years, for a total of two adult males.

Reintroducing juveniles to cliffs in southern Illinois increased the expected minimum abundance, number of occupied patches

after 50 years, and the average number of adults for the study region (Table 4). As expected, all metrics increased with the number of individuals released, however, the expected minimum abundance reached a plateau when more than 100 juveniles were released. Reintroductions reduced the median time to at least one adult male in southern Illinois by 74.6–78.1% (Table 4). Hacking all birds at one site versus multiple sites did not have much influence on average number of patches occupied in 50 years or the average number of adult males on cliffs. Hacking at multiple sites slightly increased the average number of adult males on cliffs in

Table 5

Results of sensitivity analysis for peregrine falcons in southern Illinois and the surrounding region using a low case scenario of carrying capacity with reintroductions to cliffs.

	EMA (%)	N_p (%)	t_c (%)
R_{max} (%)			
+10	+18.7	+34.1	−13.2
−10 ^a	−17.4	−14.6	+1.7
Dispersal matrix (%)			
+10	0.0	0.0	−19.3
−10	−1.3	−3.7	+10.5
Carrying capacity (%)			
+10	+3.9	0.0	−0.9
−10	−7.8	−3.7	+4.4

EMA, expected minimum abundance; N_p , terminal number of occupied; t_c , median time to colonization.

^a Reduced R_{max} to 1.0.

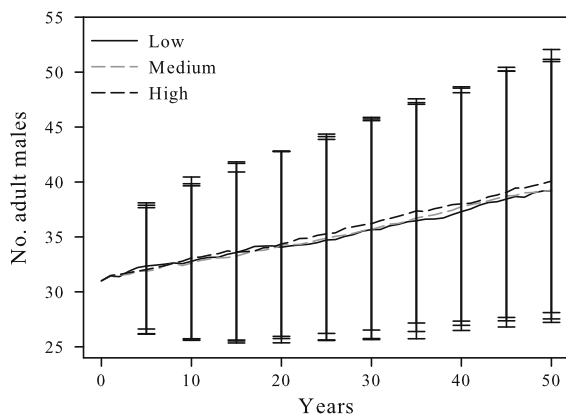


Fig. 2. Average number of adult male peregrine falcons predicted by population viability analysis under low, medium, and high levels of carrying capacity for the lower Midwestern US with no reintroductions.

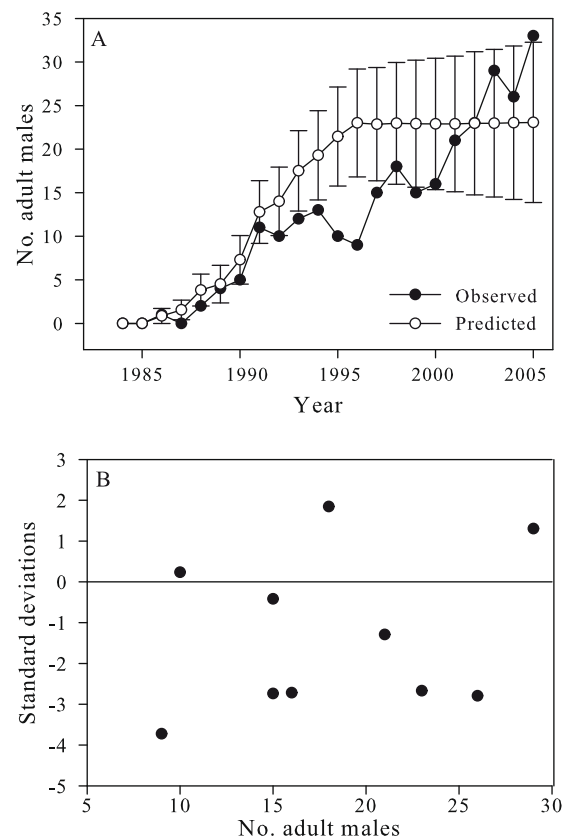


Fig. 3. Plot of (A) trajectories for observed (closed circles) and predicted (open circles) number of adult males and (B) standard deviations of the observed number of adult males for different initial abundances in the Lake Superior region during 1984–2005. Good model fit is indicated by a mean of 0 and a standard deviation of 1.

southern Illinois. Cost-benefit analysis indicated that the most cost-effective reintroduction strategy was releasing eight juveniles from two sites every 3 years (Table 4).

3.2.1. Sensitivity analysis

The model was most sensitive to changes in R_{max} . Increasing R_{max} by 10% produced an 18.7% increase in expected minimum abundance, a 34.1% increase in patch occupancy, and 13.2% decrease in median time to ≥ 1 adult in southern Illinois. Decreasing R_{max} to 1 produced a 17.4% decrease in expected minimum abundance, a 14.6% decrease in patch occupancy, and a 1.7% increase in the median time to ≥ 1 adult (Table 5). In comparison, altering carrying capacity produced a maximum change of 7.8%. Changing the dispersal matrix only affected the median time to ≥ 1 adult on cliffs in southern Illinois.

3.3. Model testing

The model population trajectory for the Lake Superior region increased steadily until reintroductions ended in 1995, after which time the number of adult males remained approximately constant (Fig. 3A). In the observed population trajectory, the number of adult males continued to increase to the present. Therefore, during the first 8 years of reintroduction, the model followed the actual population trend well. Results of the standard deviates test showed the mean of standard deviates was not significantly different from 0, but approached statistical significance ($n = 10$, $t = -2.12$, $p = 0.06$). The variance was significantly greater than one ($n = 10$, $\chi^2 = 33.8$, $df = 9$, $p < 0.001$; Fig. 3B).

4. Discussion

4.1. Population growth and demographics

The lower Midwestern population of peregrine falcons is not likely to go extinct and is in fact growing. However, metapopulation growth appears to rely primarily on peregrines nesting in cities. R_{max} was essentially one for the cliff populations, so growth of these populations can only occur via immigration from urban populations, even after the cliff patches have been colonized. Dispersal rates indicate that cliff habitats should be colonized in the next decade or two, but there is uncertainty in the estimated time to colonization, because sample sizes are currently too small to estimate dispersal rates between cliff and urban populations in the lower Midwest. We also did not incorporate environmental correlation in our population model. If population vital rates fluctuated

in synchrony, extinction risk of the metapopulation would be higher than that of an asynchronous metapopulation (Harrison and Quinn, 1989). However, we believe that the populations in this study are not strongly separated by distance, but rather by behavior. Peregrines are more likely to stay in the habitat type of their origin and show distinct differences in fecundity and juvenile survival rates depending on habitat type. Such differential dispersal may play a larger factor in synchronizing populations than spatial distance (Koenig, 1998). In our model, the spatial aspect of this behavioral correlation was reflected in the dispersal-distance function.

Results from this study are similar to those found in studies of peregrine falcons in California, where the rural population declined 1% per year, but urban populations grew an average of 29% per year during 1980–1998 (Kauffman et al., 2003). Unlike the rural population in California, which acted as a sink, however, the Midwestern rural population is slowly growing. These differences can probably be attributed to differences in prey species. Peregrines in California primarily consume migratory bird species, which may contain high levels of DDE (Kauffman et al., 2003, 2004) where as Midwestern peregrines typically prey on resident species, which have significantly lower levels of DDE residues (Banasch et al., 1992). The elevated levels of DDT in the California peregrines likely lowered their reproductive rates thus creating a sink population (Kauffman et al., 2003, 2004). Thus, model results are consistent with general expectations for the Midwest study region.

The Lake Superior population used for model verification showed concordance with expectation. However, the standard deviates test did approach significance, indicating that fit was marginal. The variance of the standard deviates test indicated model stochasticity may have been underestimated. Additionally, growth was projected only during years of supplementation and then plateaued after reintroductions stopped, while the observed population trajectory continued to increase after reintroductions ceased. Thus, further attention to the demographic rates used in estimating R_{max} was warranted.

Subadult and adult survival rates used in the model were well within the range of estimates found in North America (Table 6). Survival rates of juvenile peregrines (0.20–0.24) were on the lower end of the range of literature values (0.16–0.65; Table 6), but were similar to those estimated by Tordoff and Redig (1997) and Kauffman et al. (2003). Nesting site type may have an effect on juvenile survival, but the difference in rates between site types in this study was not as strong as that found in California (Kauffman et al., 2003). Kauffman et al. (2003) suggested their survival estimates for urban juveniles may have been biased high because young from

Table 6
Comparison of peregrine falcon demographic rates from this study compared with other studies conducted in North America.

Location	Survival						Fledglings/territorial pair		Source
	Juvenile		Subadult		Adult		\bar{x}	SE	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE			
Lower Midwest	0.24	0.02	0.85	0.07	0.85	0.02	2.49	0.13	This study
Cliff	0.20	0.06	0.84	0.14	0.85	0.05	1.81	0.52	
Urban	0.24	0.02	0.85	0.07	0.85	0.02	2.61	0.13	
California	0.38	0.08	0.86	0.05	0.85	0.02	–	–	Kauffman et al. (2003)
Cliff	0.28	0.04	–	–	–	–	–	–	
Urban	0.65	0.15	–	–	–	–	–	–	
Midwest	0.16–0.23 [†]	–	–	–	0.86	–	1.78	0.19	Tordoff and Redig (1997), Moen and Tordoff (1993)
Colorado	0.54	0.08	0.67	0.10	0.80	0.05	–	–	
Arizona	–	–	–	–	–	–	1.66	–	
New Jersey	–	–	–	–	–	–	1.38	–	Steidl et al. (1991)
Greenland Southeast	–	–	–	–	–	–	1.60	–	Mattox and Seegar (1988)
Greenland West	–	–	–	–	–	–	2.40	–	Mattox and Seegar (1988)
Quebec	–	–	–	–	–	–	2.85	–	Bird and Weaver (1988)

[†] Indicates a range rather than average.

problematic urban areas were moved and released into more favorable areas (Kauffman et al., 2003). Juvenile survival rates also may be related to reintroduction techniques. In the Western US, most peregrines were reintroduced using fostering methods, so adults protected young, whereas in the East and Midwest, peregrines were reintroduced using hackboxes and juveniles were unprotected from great horned owls (Barclay and Cade, 1983; Septon et al., 1995). However, the lower Midwest and the Lake Superior population were established using similar reintroduction techniques, so differences in survival rates due to reintroduction techniques were not expected.

Productivity of Midwestern peregrines was high compared to other regions (Table 6). The average number of fledglings per territorial pair in the Midwest was comparable to those in Alaska and Greenland, but higher than those throughout the rest of the US. Furthermore, the average number of fledglings of urban peregrines was among the highest documented in North America. The high urban rate can likely be attributed to the large and easily accessible prey base found in cities and the lack of natural predators. Cliff peregrine productivity rates in the Midwest were comparable to literature values of similar latitudes, such as New Jersey and Arizona. Thus, parameters used in the population model appear to be accurate and reasonable.

The model may have fit marginally well in the Lake Superior region because productivity is higher at more northern latitudes, and the parameter estimates were estimated from data collected south of the Lake Superior population. Estimates of peregrine productivity in Canada and Greenland (Mattox and Seegar, 1988; Bird and Weaver, 1988) were the highest among literature values for cliff-nesting individuals. Higher fecundity would have produced a larger R_{max} value, and thus increased population growth, which is consistent with the actual population trajectory. However, increasing R_{max} for the southern Illinois region seemed unreasonable because the demographic rates we derived appeared to be comparable to other populations at similar latitudes. An increase in R_{max} would have likely overestimated population growth for cliff-nesting peregrines, producing overly optimistic trends. Therefore, despite tepid agreement with the trajectory of the Lake Superior population and underestimated model stochasticity, we believe the model is a fairly good fit for the lower Midwestern area.

4.2. Management implications

Peregrine falcon reintroduction to southern Illinois is unnecessary for maintaining a viable population in the study region. The current growth rate of urban peregrines and the likely recolonization of cliffs in southern Illinois over time should be sufficient to promote a healthy, albeit slow-growing population. Reintroducing juveniles to southern Illinois would decrease the time to recolonization and increase the number of cliff-breeding pairs, but the benefits do not seem to outweigh the costs. Of the reintroduction scenarios, the most cost-effective strategies were those that released juveniles every 3 years. Of the top five reintroduction strategies, releasing eight juveniles from two sites every 3 years for a cost of approximately \$282,000 was the most cost-effective. However, if implemented, the state would only see an increase of two cliff-breeding pairs in 50 years compared to the base scenario of no reintroduction. Although travel and other costs per reintroduced bird may be reduced as the number of releases increases, spending nearly \$300,000 to increase the population by two pairs hardly seems a worthy investment, especially if the regional population is not at risk of extinction. Furthermore, the model predicts that even without reintroductions, peregrine falcons will recolonize cliffs in southern Illinois in approximately 11 years. Although there is uncertainty in dispersal rates between urban and cliff populations, and hence predictions of colonization time, the model

suggests that peregrines will recolonize their natural habitat in time. This study illustrates the value of monitoring in informing future management decisions. Limited conservation dollars can be spent in more productive ways than on reintroductions of peregrine falcons to southern Illinois.

Thus, we recommend that funds would be better used elsewhere such as purchasing land containing peregrine habitat. Many of the bluffs in Monroe County, Illinois, for example are still being used for mining. Purchasing and preserving such areas would ensure isolation from human disturbance, which peregrines typically prefer for nesting (Hickey, 1942). Additionally, many sites need to be actively managed to limit overgrowth of vegetation due to fire suppression (Septon et al., 1995). Furthermore, many cliffs suitable for peregrine nesting in Illinois are located in the unique remnant hill prairies. Protecting these areas would not only ensure the availability of habitat for peregrines, but likely would help sustain other endemic species such as the Missouri coneflower (*Rudbeckia missouriensis*), narrow-leaved green milkweed (*Asclepias fascicularis*), plains scorpion (*Centruroides vittatus*), and dark-sided salamander (*Eurycea longicauda*; IDNR, 2005).

4.3. Future research

This study has brought new insight into the growth rates and dynamics of the Midwestern peregrine population and highlighted areas that are in need of further research. Further research should be conducted to estimate annual population growth for the Midwestern population to assess density-dependent trends and to obtain more accurate estimates of R_{max} . Likewise, future data collection by the Midwest Peregrine Society can be used to produce better estimates of dispersal rates between urban and cliff populations. Such information would be useful for improving predictions of population growth and time to recolonization. Because monitoring data via the Midwest Peregrine Society are so easily accessible to the public, such parameter estimates can be obtained with relatively little cost to wildlife managers. Such data provide valuable insights into future management decisions.

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