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Quantifying the importance of patch-specific changes in habitat to metapopulation viability of an endangered songbird

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Abstract. A growing number of programs seek to facilitate species conservation using incentive-based mechanisms. Recently, a market-based incentive program for the federally endangered Golden-cheeked Warbler (*Dendroica chrysoparia*) was implemented on a trial basis at Fort Hood, an Army training post in Texas, USA. Under this program, recovery credits accumulated by Fort Hood through contracts with private landowners are used to offset unintentional loss of breeding habitat of Golden-cheeked Warblers within the installation. Critical to successful implementation of such programs is the ability to value, in terms of changes to overall species viability, both habitat loss and habitat restoration or protection. In this study, we sought to answer two fundamental questions: Given the same amount of change in breeding habitat, does the change in some patches have a greater effect on metapopulation persistence than others? And if so, can characteristics of a patch (e.g., size or spatial location) be used to predict how the metapopulation will respond to these changes? To answer these questions, we describe an approach for using sensitivity analysis of a metapopulation projection model to predict how changes to specific habitat patches would affect species viability. We used a stochastic, discrete-time projection model based on stage-specific estimates of survival and fecundity, as well as various assumptions about dispersal among populations. To assess a particular patch's leverage, we quantified how much metapopulation viability was expected to change in response to changing the size of that patch. We then related original patch size and distance from the largest patch to each patch's leverage to determine if general patch characteristics could be used to develop guidelines for valuing changes to patches within a metapopulation. We found that both the characteristic that best predicted patch leverage and the magnitude of the relationship changed under different model scenarios. Thus, we were unable to find a consistent set of relationships, and therefore we emphasize the dangers in relying on general guidelines to assess patch value. Instead, we provide an approach that can be used to quantitatively evaluate patch value and identify critical needs for future research.

Key words: conservation incentive; Dendroica chrysoparia; *dispersal; Fort Hood, Texas; Golden-cheeked Warbler; metapopulation; Recovery Credit System; sensitivity analysis.*

INTRODUCTION

Due to the challenges of managing species listed under the Endangered Species Act on private lands, much of the responsibility for conservation and recovery has traditionally been placed on state or federally owned lands. However, listed species rarely occur solely on public lands. Approximately two-thirds of listed species have populations on private lands (Groves et al. 2000), and as many as 37% depend entirely on nonfederal lands for their habitat (USGAO 1995). Moreover, populations of listed species that occur on public land often represent only a fraction of a metapopulation, regional population, or species range. Thus, for the majority of these species, effective recovery strategies must involve management of both public and private lands (Wilcove and Lee 2004).

Despite the importance of private lands for the recovery and conservation of listed species, considerable conflict has arisen due to concerns about private property rights and the distribution of conservation costs (Bean and Wilcove 1997, Doremus 2003). Therefore, a growing number of programs seek to alleviate these conflicts by replacing regulatory measures with incentive-based mechanisms (Doremus 2003, Wilcove and Lee 2004). Such conservation incentive programs are designed to promote stewardship of endangered species habitat through voluntary conservation activities by landowners who are rewarded, financially or otherwise, for their participation (Bonnie 1999, Doremus 2003, Wilcove and Lee 2004). Conservation incentives range from Safe Harbor agreements (USFWS 1999) to landowner conservation assistance programs to market-based systems. Market-

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based incentive programs such as conservation banks can provide financial gain to landowners willing to conserve habitat by selling "credits" to developers seeking mitigation (Wilcove and Lee 2004, Bean 2006). A major challenge in these programs is determining the conservation value of land parcels included in the conservation bank (Fox et al. 2006). Typically, a parcel is assigned value based on experts' assessments of habitat area or quality, although more recent approaches have proposed incorporating spatial configuration or demographic rates (Bruggeman and Jones 2008, Searcy and Shaffer 2008).

Recently, a market-based incentive program for the Golden-cheeked Warbler (*Dendroica chrysoparia*) has been implemented as a "proof of concept" in conjunction with habitat protection on Fort Hood, an 87890-ha Army training post in central Texas, USA. The Golden-cheeked Warbler is a Neotropical migrant songbird that breeds in mature, closed-canopy woodlands composed primarily of Ashe juniper (*Juniperus ashei*) and oak (*Quercus* sp.) (Pulich 1976, Ladd and Gass 1999). The species' breeding range is confined to fewer than 36 counties in central Texas (USFWS 1996). Historically (pre-European settlement), breeding habitat was probably relegated to fragmented patches along streams and rocky limestone outcrops where oak–juniper woodlands could reach maturity (Kroll 1980). However, clearing of Ashe juniper for urban expansion, agriculture, and commercial harvest has further reduced and fragmented available breeding habitat, resulting in the Golden-cheeked Warbler being listed as endangered in 1990 (USFWS 1990). Protection of existing breeding habitat has been cited as an important component of Golden-cheeked Warbler recovery (USFWS 1992). Effective habitat management on both public and private lands is particularly important for the Golden-cheeked Warbler, as most breeding habitat occurs on privately owned land (USFWS and Environmental Defense 2000).

Fort Hood contains the largest breeding population of Golden-cheeked Warblers under a single landowner (USFWS 1992). Recent population estimates on Fort Hood range from 2901 to 6040 territorial males (Cornelius et al. 2007), and Anders and Dearborn (2004) suggested a stable or slightly increasing population trend since 1992. However, despite optimistic population size and trend and the relative security of breeding habitat on the protected land of the installation, a viable population of Golden-cheeked Warblers on Fort Hood is not guaranteed. In addition to the possibility of natural catastrophes and increased demands for military training, live munitions will always pose a fire threat to breeding habitat. In fact, much of Fort Hood's active management is in response to a 1996 wildfire that destroyed or damaged ~2100 ha, approximately 15% of the available breeding habitat at that time (Cornelius et al. 2007). As such, managers at Fort Hood must consider the possibility that unintentional loss of habitat on Fort Hood will jeopardize the overall viability of Golden-cheeked Warblers and lead to more stringent training restrictions in the future. To guard against this scenario, in 2006 the Department of Defense began a three-year trial of the Recovery Credit System (RCS), which provides Fort Hood with recovery credits for funding conservation of Golden-cheeked Warbler habitat on private lands (USFWS 2007). Under the RCS, recovery credits accumulated by Fort Hood through contracts with private landowners would be used to offset unanticipated loss of Golden-cheeked Warbler habitat within the boundaries of the installation.

Critical to successful implementation of market-based incentive programs such as the RCS is the ability to value, in terms of changes to population viability, both habitat loss and potential habitat restoration or protection. Applied ecologists have debated the relative conservation value of patches differing in size and connectedness since the development of island biogeography (MacArthur and Wilson 1967, Brown 1971) and metapopulation theory (Hanski and Gilpin 1991). But despite the recognition that habitat patches vary in their contribution to viability, the specifics may be hard to generalize, suggesting that the value of habitat losses and gains should be evaluated quantitatively based on species-specific models of metapopulation dynamics (Doak and Mills 1994, Bruggeman and Jones 2008). For example, assuming a classic Levins-type metapopulation, Hanski and Ovaskainen (2000) proposed a straightforward approach for quantifying the contribution of individual patches to metapopulation capacity based on probabilities of extinction and colonization. Recognizing the importance of considering local population demographics and alternate metapopulation structures (i.e., source-sink), others have proposed approaches that explicitly account for survival and reproduction as well as immigration and emigration rates. Runge et al. (2006) introduced a metric for defining whether a particular subpopulation was acting as a metapopulation source (i.e., net contributor) or sink (i.e., net drain) to the metapopulation based on the ability to maintain itself through self-recruitment and retention of individuals combined with that subpopulation's successful emigration rate. Ozgul et al. (2009) used sensitivity analysis to determine the influence of local demography and dispersal on metapopulation viability.

Similar to Ozgul et al. (2009), we describe an approach for applying sensitivity analysis of a stochastic metapopulation projection model. But rather than focusing on changes in demographic rates, we evaluated how changes in Golden-cheeked Warbler breeding habitat, both on and off Fort Hood, might affect overall species viability. In particular, if a certain amount of habitat is lost in one area, how much habitat needs to be restored or protected in another area such that there is no change in overall viability? Specifically, we sought to answer the following questions: Given the same amount of change in breeding habitat, does the change in some

TABLE 1. Characteristics of 10 hypothetical patches used to investigate the relationship between patch importance and patch size or distance from largest patch.

Patch	Patch size (K)	Distance from largest patch
Pop1	238	1
Pop2	250	7
Pop3	300	4
Pop4	350	2
Pop5	400	8
Pop6	550	5
Pop7	700	3
Pop8	1000	6
Pop9	6000	9
Pop10 (i.e., Fort Hood)	12 371	0

Notes: Patch size is based on a classification of Golden-cheeked Warbler (*Dendroica chrysoparia*) habitat and corresponds to the number of territories a habitat patch can support at ~4.5 ha per territory (i.e., the carrying capacity). Distance units are generic and were chosen based on the current Golden-cheeked Warbler metapopulation and to have a mix of sizes and distances from the largest patch. Population 10 (Pop10) is Fort Hood, Texas, USA.

patches have a greater effect on overall persistence of the metapopulation than others? If so, can characteristics of a patch (e.g., size or its spatial location) be used to predict how the metapopulation will respond to these changes?

METHODS

Metapopulation projection model

We assessed Golden-cheeked Warbler viability using a demographically based metapopulation model where distinct patches of habitat support local breeding populations. Habitat patches, representing local breeding populations, and model structure and parameters were based on a previous study by Alldredge et al. (2004), who assessed the viability of the Golden-cheeked Warbler metapopulation in central Texas. Patch sizes, measured as the number of territories supported, ranged from 238 to 12 371, corresponding to the smallest and largest (i.e., Fort Hood) populations modeled by Alldredge et al. (2004). However, to more effectively evaluate the questions for our study, we added two additional populations and arrayed the populations spatially so as to have a mix of sizes and relative distances from Fort Hood (Table 1). This resulted in a metapopulation structure similar to that of the current distribution (Alldredge et al. 2004), but with sufficient number of populations as well as variation in sizes and relative distances from Fort Hood to provide a more robust analysis.

We used a stochastic, discrete-time projection model based on stage-specific estimates of mean survival (S) and fecundity (F), as well as various assumptions about dispersal among populations. We modeled three age classes (i.e., life stages) including hatch year (HY), second year (SY), and after-second year (ASY). The model was made stochastic by including temporal variation in survival and fecundity where the value of these parameters was randomly drawn during each time step (F_t, S_t) from a log-normal distribution (Akçakaya 2005). We also modeled demographic stochasticity by drawing the actual number of young reproduced per individual from a Poisson distribution with mean equal to F_t, drawing the actual number of survivors for each time step from a binomial distribution with probability equal to S_t, and setting the number of "trials" equal to the number of individuals (N_t). Because Golden-cheeked Warblers are territorial during the breeding season, we modeled density dependence by incorporating a "ceiling" carrying capacity (K). Thus, populations grew without any density dependence until the population exceeded K, at which time the population was either truncated to K or the excess individuals became dispersers (see *Model scenarios* section). Initial abundances for projecting future population sizes were set to 80% of K. We simulated 2000 replicate population trajectories for 20 years into the future and used the mean (across replicates) final abundance (MFA) to assess Golden-cheeked Warbler viability.

Model scenarios

Golden-cheeked Warbler dispersal is poorly understood (Ladd and Gass 1999); therefore, we included five model scenarios that reflected various assumptions of dispersal behavior. Because adults have strong site fidelity, for all scenarios including dispersal, only SY individuals (i.e., HY birds that survived and returned to breed the following year) were allowed to disperse (Ladd and Gass 1999, Alldredge et al. 2004). The first scenario, NoD, assumed no dispersal between populations. The second scenario, SymD, assumed 15% symmetric dispersal among populations (Alldredge et al. 2004). In this scenario, for each time step, 15% of the population of SY individuals would disperse from each population, with emigrants distributed equally among the remaining nine populations. Thus, a particular population would receive $N_j \times 0.0167$ immigrants from each of the j populations. Because dispersal may have inherent survival costs, our third scenario, SurvD, included a decrease in disperser survival related to distance traveled. This scenario still assumed 15% dispersal at each time step, but the proportion of individuals that survived to immigrate into other populations declined with distance from the source population. Because our distances were generic, we assumed a linear decline in survival from distance $= 0$, where survival rate was 1, to distance $= 9$ (i.e., farthest distance modeled), where survival rate was 0. Thus, a particular population would receive $N_j \times 0.0167 \times (1–0.111 \times D_j)$ immigrants from each of the j populations, where D_j is the distance from the jth population. Our fourth scenario, KD, was based on the idea that SY individuals may be strongly philopatric and only disperse if the source population exceeds K. Therefore, this scenario assumed individuals in excess of K become dispersers and subsequently

Table 2. Golden-cheeked Warbler mean survival (S) and fecundity (F) based on those reported in Alldredge et al. (2004), with minimum and maximum observed values in parentheses.

Stage	S	Temporal variance (S)	F	Temporal variance (F)
HY	0.40 (0.30, 0.50)	0.058	0	0
SY	0.57 (0.57, 0.57)	0.010	1.2 (0.8, 1.4)	0.024
ASY	0.57 (0.57, 0.57)	0.010	1.3 (1.1, 1.7)	0.006

Notes: Stages were hatch year (HY), including birds age 0 to 1 year; second year (SY), including birds age 1–2 years; and after second year (ASY), including birds >2 years old. Fecundity is the number of HY birds produced per individual SY or ASY bird.

emigrate in equal proportion to all other populations in the metapopulation. The fifth scenario, KSurvD, was similar to SurvD in that dispersers from the KD scenario experienced a declining survival rate related to the distance from the source population. There was little information available for survival and fecundity of Golden-cheeked Warbler populations other than those studied at Fort Hood. Thus, for the previous five scenarios, we assumed survival and fecundity were the same for each population (Table 2). However, metapopulation dynamics can be highly sensitive to differences in vital rates among populations (Hokit and Branch 2003), and there are several reasons why it would be reasonable to assume Golden-cheeked Warbler reproduction and survival would vary with patch area (Robinson et al. 1995, Suorsa et al. 2004). To accommodate this possibility, we included a sixth scenario, KSurvDVitals, in which fecundity and HY survival for each population increased linearly with the size of the population (Table 3). The lower and upper limits of these values correspond to the minimum and maximum observed values reported in Alldredge et al. (2004).

For each scenario, we performed a sensitivity analysis to determine which parameters had the greatest influence on metapopulation viability (i.e., MFA). We used the extended Fourier amplitude sensitivity test (FAST; Saltelli et al. 1999, 2000) to partition the variance in MFA into contributions from variation in mean survival, mean fecundity, carrying capacity, and initial abundance. To derive sensitivity indices, we varied each of these parameters by a uniform distribution of 10% centered around their nominal value and used a sample size of 300 for a total of 1200 model evaluations (i.e., number of parameters varied times sample size). We chose extended FAST because this method allows for interactions among model input parameters and nonlinear relationships with model output.

Patch leverage

Conceptually, we wanted to determine whether changing the size of particular patches by the same amount resulted in a greater effect on overall viability than others. Thus, we determined how much MFA changed in response to changes in a particular population's size (i.e., K), reflecting potential loss or gain of habitat. To quantify this relationship, we performed a sensitivity analysis of the metapopulation projection model to patch-specific changes in K. We drew 500 sets of random carrying capacities K_j for each of the $j = 1$ to 10 populations from uniform distributions that ranged ±200 of the population's original K. Thus, each population, regardless of its original size, was varied by the same amount. For each of the 500 sets of carrying capacities, the metapopulation projection model was run and MFA was recorded. Changes in MFA were related to changes in each population's carrying capacity (K_j) via linear regression. We used regression coefficients to quantify a particular patch's leverage (L_j) on metapopulation viability, measured as the expected change in

Table 3. Golden-cheeked Warbler mean survival (S) and fecundity (F) for each population under the scenario KSurvDVitals (described in *Methods: Model scenarios*).

Patch	Patch size (K)	S_{HY}	S_{AHY}	F_{HY}	F_{AHY}
Pop1	238	0.300	0.570	0.750	1.090
Pop2	250	0.300	0.570	0.751	1.091
Pop3	300	0.301	0.570	0.754	1.093
Pop4	350	0.302	0.570	0.756	1.095
Pop5	400	0.303	0.570	0.759	1.097
Pop6	550	0.305	0.570	0.768	1.104
Pop7	700	0.308	0.570	0.776	1.111
Pop8	1000	0.313	0.570	0.793	1.125
Pop9	6000	0.395	0.570	1.078	1.356
Pop10	12 371	0.500	0.570	1.440	1.650

Notes: Patch size is based on a classification of Golden-cheeked Warbler habitat and corresponds to the number of territories a habitat patch can support at ~4.5 ha per territory (i.e., the carrying capacity). Abbreviations are: HY, hatch year; AHY, after hatch year.

TABLE 4. Golden-cheeked Warbler metapopulation viability.

Scenario‡	MFA	Sensitivity§			
		S	*F*	*K*	IA
NoD	11 182	0.88 (0.88)	0.10 (0.10)	0.01 (0.02)	0.00 (0.00)
SymD	9870	0.87 (0.88)	0.11 (0.11)	0.01 (0.01)	0.00 (0.00)
SurvD	7884	0.87 (0.88)	0.11 (0.11)	0.01 (0.01)	0.00 (0.00)
KD	13 037	0.86 (0.87)	0.11 (0.12)	0.02 (0.02)	0.00 (0.00)
KSurvD	12 212	0.86 (0.87)	0.12 (0.12)	0.02 (0.02)	0.00 (0.00)
KSurvDVitals	16 879	0.86 (0.87)	0.11 (0.12)	0.02 (0.02)	0.00 (0.00)

Notes: Viability was measured by mean final abundance (MFA). Scenarios reflect various assumptions of dispersal and patch-specific vital rates as described in *Methods: Model scenarios*. Sensitivity of MFA to changes in mean survival (S), mean fecundity (F), carrying capacity (K), and initial abundance (IA) was measured as the proportion of variance in MFA explained using Fourier amplitude sensitivity analysis (FAST). Values are first-order indices with total indices in parentheses.

MFA due to changing the size of a particular patch (i.e., K_j) by one unit:

$$L_j = \frac{\Delta \mathrm{MFA}}{\Delta K_j}.$$

Relating patch characteristics to patch leverage

We related two patch characteristics, original patch size (K_j) and distance (DL_j) from the largest patch (i.e., Fort Hood), to that patch's leverage (L_j). We used these characteristics because they are commonly used to value patches for conservation credits (USFWS 2007) and if quantifiable relationships exist, they could be used to inform future applications of RCS. Specifically, we modeled L_j, as a linear function of K_j and DL_j. Preliminary analyses suggested an exponential relationship between L_j and K_j so all models were fit using the natural logarithm of K_j. The global model was

$$L_j = \beta_0 + \beta_1 \ln[K_j] + \beta_2 \mathrm{DL}_j + \beta_3 \ln[K_j] \times \mathrm{DL}_j.$$

All possible subsets where parameters β_1, β_2, or β_3 equaled 0 were fit as competing models except for the aspatial scenarios (i.e., NoD, SymD, KD) for which we only allowed for the effect of K_j. To identify important characteristics for predicting patch leverage, we used Akaike's information criteria corrected for small-sample bias ($\mathrm{AIC_c}$) to rank competing models based on their predictive ability (Burnham and Anderson 2002).

Metapopulation projections and sensitivity analyses were performed using a program written in Visual Basic with calls to R (R Development Core Team 2008) for some statistical procedures. We used the R package "sensitivity" (version 1.3-0; *available online*)[4] to implement FAST.

RESULTS

Overall metapopulation viability differed substantially among the six scenarios we modeled (Table 4). Notably, viability was lower with 15% dispersal vs. no dispersal, and higher when dispersal was density dependent (i.e., only individuals exceeding carrying capacity became dispersers). Metapopulation viability was greatest with density-dependent dispersal and vital rates related to patch size (i.e., scenario KSurvDVitals). For all scenarios, metapopulation viability was most sensitive to changes in mean survival, accounting for ~86% of the variation in MFA (Table 4).

Plots of MFA vs. changes in each population's carrying capacity (K_j) suggested a linear relationship (Fig. 1). Thus, regression coefficients (L_j) provided a reasonable measure of the expected change in MFA due to changing the size of a particular population. Among the six scenarios we modeled, there was no consistent relationship between the leverage of a particular patch and the characteristics of that patch. Instead, both the characteristic (i.e., patch size vs. distance from the largest population) that best predicted patch leverage, as well as the magnitude of the relationship, changed under different model scenarios (Tables 5 and 6). With no dispersal (i.e., NoD), there was

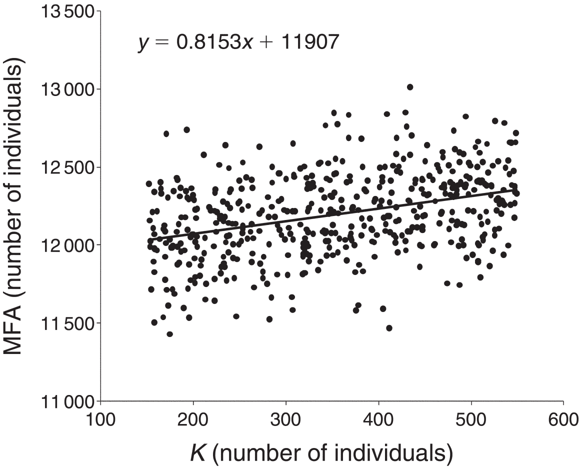

FIG. 1. Example of the leverage metric ($L_4 = 0.81$) calculated for Population 4 of the Golden-cheeked Warbler (*Dendroica chrysoparia*) in Fort Hood, Texas, under the KSurvD scenario (described in *Methods: Model scenarios*). Leverage metrics were used to measure the expected change in mean final abundance (MFA) due to changing the size of a particular population (K).

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[4] ⟨http://cran.r-project.org/web/packages/sensitivity/index.html⟩

Table 5. Model selection relating patch characteristics to patch sensitivity.

Scenario	Model	Number of parameters	r^2	AIC_c	ΔAIC_c
NoD	null	2	NA	−16.4	0
NoD	ln(K)	3	0.08	−12.9	3.4
SymD	ln(K)	3	0.87	−5.1	0
SymD	null	2	NA	11.3	16.5
SurvD	ln(K)	3	0.91	−11.0	0
SurvD	null	2	NA	9.0	20.0
KD	ln(K)	3	0.59	0.8	0
KD	null	2	NA	5.4	4.5
KSurvD	ln(K)	3	0.52	−5.6	0
KSurvD	null	2	NA	−2.6	3.0
KSurvD	ln(K) + dist	4	0.54	−0.1	5.5
KSurvD	dist	3	0.02	1.5	7.1
KSurvD	ln(K) + dist + dist × ln(K)	5	0.58	8.1	13.6
KSurvDVitals	dist	3	0.50	−2.3	0
KSurvDVitals	null	2	NA	0.3	2.7
KSurvDVitals	ln(K) + dist	4	0.51	3.5	5.8
KSurvDVitals	ln(K)	3	0.02	4.5	6.8
KSurvDVitals	ln(K) + dist + dist × ln(K)	5	0.53	12.0	14.3

Notes: Patch characteristics were the natural logarithm of patch carrying capacity (ln K) and distance from the largest patch (dist). Scenarios reflect various assumptions of dispersal and patch-specific vital rates as described in *Methods: Model scenarios*. "NA" represents not applicable.

little evidence for a relationship between patch leverage and patch size or distance from the largest patch, suggesting that changes in the size of a particular patch had the same effect on MFA regardless of the characteristics of the patch. For the four scenarios based on constant vital rates and dispersal among populations (i.e., SymD, SurvD, KD, and KSurvD), patch size was the best predictor of leverage, and distance from the largest patch was a poor predictor (Fig. 2, Table 5). For these scenarios, as original patch size increased, patch leverage decreased. This indicates that given the same amount of habitat loss or gain, changes to smaller patches have a greater effect on overall viability than larger patches. Conversely, when vital rates varied among populations (KSurvDVitals), distance from the largest patch was the best predictor of leverage and patch size was weakly related (Fig. 3, Table 5). For this scenario, as distance from the largest patch increased, patch leverage decreased.

DISCUSSION

Conservation programs designed to offset unintentional loss of habitat on Fort Hood need to objectively value the importance of changes to off-post patches relative to changes in habitat on Fort Hood. This situation is not unique to Fort Hood. Indeed, many regulatory provisions require a means by which detrimental changes in ecological resources can be mitigated at the appropriate level by off-site compensation (Bruggeman and Jones 2008). We demonstrated that sensitivity analysis of a stochastic population projection model could be used to quantify how changes in occupied habitat affect metapopulation viability. Thus, the importance of changes to individual habitat patches could be quantified in a rigorous and transparent analysis. For example, to determine how much habitat would need to be added or conserved in patch A to offset 50 lost territories in patch B, one would use the following:

$$\Delta_{\text{A}} = \Delta_{\text{B}} \times \frac{\hat{L}_{\text{B}}}{\hat{L}_{\text{A}}}.$$

If we assume dispersal scenario KD, that patch B initially held 250 territories and patch A held 6000, then $\hat{L}_{\text{B}} = \hat{\beta}_0 + \hat{\beta}_1 \ln[K_{\text{B}}]$, $\hat{L}_{\text{B}} = \hat{\beta}_0 + \hat{\beta}_1 \ln[K_{\text{B}}]$, and

Table 6. Parameter estimates with standard errors in parentheses of information-theoretic (IT) best model(s) relating patch leverage to patch characteristics.

Scenario	IT best model	Intercept	ln(K)	Distance
NoD	null	0.463 (0.027)	NA	NA
SymD	ln(K)	2.292 (0.210)	−0.232 (0.031)	NA
KD	ln(K)	1.745 (0.283)	−0.141 (0.042)	NA
SurvD	ln(K)	2.039 (0.157)	−0.211 (0.023)	NA
KSurvD	ln(K)	1.235 (0.206)	−0.089 (0.030)	NA
KSurvDVitals	dist	0.815 (0.086)	NA	−0.046 (0.016)

Notes: Models presented are those with the lowest AIC_c scores. Patch characteristics were the natural logarithm of carrying capacity (ln K) and distance from the largest patch (dist). Scenarios reflect various assumptions of dispersal and patch-specific vital rates as described in *Methods: Model scenarios*. "NA" represents not applicable.

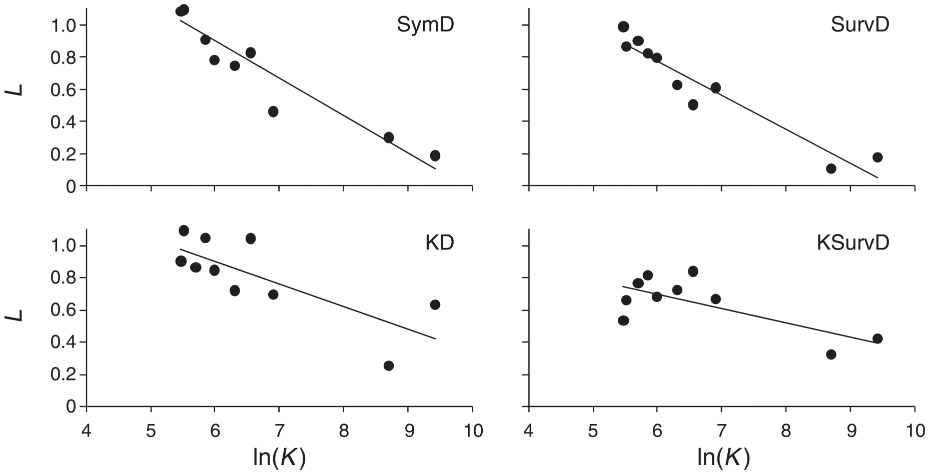

FIG. 2. Relationships between patch leverage (L) and original patch size (K) for four dispersal scenarios: SymD (15% symmetric dispersal among populations), SurvD (15% dispersal at each time step with decrease in disperser survival related to distance traveled), KD (dispersers in excess of K emigrate in equal proportion to all other populations), and KSurvD (dispersers from the KD scenario decline in survival relative to distance from the source population). For further details, see *Methods: Model scenarios*.

$$\Delta_A = 50 \times \frac{1.74 - 0.14 \times \ln(250)}{1.74 - 0.14 \times \ln(6000)} = 93.$$

So, enough habitat to accommodate approximately 93 territories would need to be added or conserved in patch A to offset the loss of 50 territories in patch B. This example emphasizes our counterintuitive result that under many of the most realistic scenarios (i.e., SymD, SurvD, KD, and KSurvD), *smaller* patches were expected to have higher leverage than larger patches where a unit change in K of these smaller patches leads to a larger change in mean final population size in the future. This is important because, in opposition to the dogma that "bigger is better," it suggests that given the *same* amount of habitat protection or restoration, it is better for future viability that these changes occur to smaller instead of larger patches.

By relating the characteristics of patches within the Golden-cheeked Warbler metapopulation to their importance, we investigated whether patch size or distance from the largest patch could be used to predict how influential changes to a particular patch would be to overall viability. However, we found it impossible to produce general guidelines for valuing habitat patches even within the limited set of scenarios we investigated. Without dispersal, changes to populations had an equivalent effect on overall viability. With dispersal, size of the patch was helpful in predicting patch leverage only when mean vital rates were the same among populations; otherwise distance from the largest patch was the best predictor. We did not set out to investigate the specific role of dispersal in metapopulation viability, but our results are consistent with other simulations of spatially structured populations that have shown how assumptions about movements among patches strongly influence inferences about population dynamics (Armsworth and Roughgarden 2005, Revilla and Wiegand 2008). Based on our results, we suggest it would be dangerous to rely on general guidelines for valuing changes to habitat patches within a metapopulation (also see Bruggeman and Jones 2008). Instead, we recommend patches be valued based on changes to overall viability that are estimated via an explicit model of metapopulation dynamics. For the RCS and other market-based incentive programs, our results point out the risk of assigning conservation value by relying on professional judgment or incomplete knowledge to estimate metapopulation parameters or habitat quality.

Although our analysis did not produce consistent recommendations, it was useful in identifying critical model assumptions and parameters that should be targeted for future research. In particular, opposing conclusions of whether patch size or distance from the largest patch were important characteristics points to the need for better information on how habitat patches

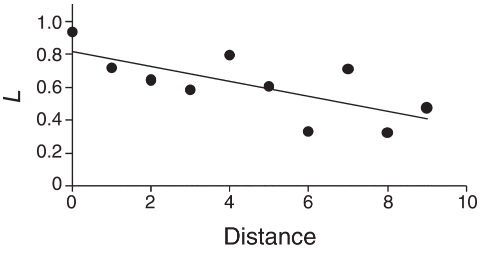

FIG. 3. Relationships between patch leverage (L) and distance from the largest patch for the KSurvDVitals scenario (fecundity and hatch year survival for each population increase linearly with the size of the population). Distance units are generic and were chosen based on the current Golden-cheeked Warbler metapopulation and to have a mix of sizes and distances from the largest patch. For further details, see *Methods: Model scenarios*.

within the Golden-cheeked Warbler metapopulation are connected via dispersal and how mean survival and reproductive rates vary among patches. Additionally, we attempted to include several realistic assumptions about the Golden-cheeked Warbler metapopulation, but, due to insufficient empirical data, recognize that our analyses did not cover all possibilities related to the spatial arrangement of habitat patches, patch-specific vital rates, spatial correlations in dynamics among populations, or effects of habitat fragmentation (i.e., edge effects; Murcia 1995). Indeed, our results indicate that overall metapopulation viability is much more sensitive to proportional changes in mean vital rates than carrying capacity (i.e., habitat). Thus, we emphasize the fact that details matter and stress the need to continue to refine and improve model parameters and assumptions to match the actual Golden-cheeked Warbler metapopulation. Specifically, we suggest future research target three important areas: (1) obtaining a range-wide habitat map for delineating unique subpopulations, (2) relating patch characteristics to changes in mean survival and reproduction, and (3) gaining a better understanding of dispersal mechanisms. This can be accomplished by placing uncertainties in model structure, assumptions, and parameter values within an adaptive management/research context (Bakker and Doak 2009). By doing so, model predictions can be evaluated with ongoing monitoring data and key components of the model (e.g., dispersal, patch-specific vital rates, and so on) can be targeted for future research (MacKenzie 2009).

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