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AN APPROACH FOR QUANTIFYING THE IMPORTANCE OF HABITAT PATCHES TO GOLDEN-CHEEKED WARBLER VIABILITY

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Abstract:

Key words:

Due to the challenges of managing Threatened and Endangered (i.e., listed) species on private lands, much of the responsibility for conservation and recovery has traditionally been placed on public lands owned by the U. S. federal government and the various states. 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 non-federal lands for their habitat (GAO 1995). Moreover, populations of listed species that occur on individual tracts of public land usually 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-based incentive programs such as conservation banks can provide financial gain to landowners willing to conserve habitat and then sell “credits” to developers seeking mitigation (Wilcove and Lee 2004, Bean 2006). Recently, a market-based incentive program (i.e., Recovery Credit System; USFWS 2007) has been suggested for the golden-cheeked warbler (*Dendroica chrysoparia*) to be implemented in conjunction with Fort Hood, an 87,890 ha Army training post in central Texas.

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). Breeding range is confined to fewer than 36 counties in central Texas (USFWS 1996). Historically (pre-Caucasian 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 2,901 to 6,040 territorial males (Cornelius et al. 2007) and Anders and Dearborne (2004) suggested a stable or slightly increasing population trend since 1992. However, despite optimistic population sizes and the relative security of breeding habitat, 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 threat to breeding habitat due to wildfires. In fact, much of Fort Hood's active management is in response to a 1996 wildfire that destroyed or damaged ~2,100 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 3-year "proof of concept" trial of a 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 any 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. 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? Current metapopulation theory suggests that certain habitat patches will influence viability more than others (Morris and Doak 2002) thus calling into question the equivalence of a 1:1 ratio in losses to gains. For example, small isolated patches are generally viewed as more vulnerable to extinction (Shaffer 1981) and therefore have traditionally been considered less important than larger more connected patches. However, this traditional view is largely untested and has been shown to fail for some metapopulation structures and dynamics suggesting that the value of habitat losses and gains should be quantitatively evaluated based on species-specific models of population dynamics (Bruggeman and Jones 2008). We describe an approach for combining sensitivity analysis with a metapopulation projection model to evaluate how changes in golden-cheeked warbler breeding habitat, both on and off Fort Hood, might affect species viability. Specifically we sought to answer the following questions: Given the same amount of change in breeding habitat, does the change in some 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 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. The model structure and parameters were based on a similar analysis conducted by Alldredge et al. (2004). However, to more effectively evaluate the questions for our study, we generalized the number and size of populations as well as their spatial arrangement. Therefore, we modeled 10 hypothetical populations with sizes, measured as the number of territories supported, ranging from 238 to 12371. These values correspond to the smallest and largest (i.e., Fort Hood) populations modeled by Alldredge et al. (2004). To investigate the relationship between the spatial location of a population and its importance, we arrayed the populations spatially so as to have a mix of sizes and relative distances from Fort Hood (Table 1).

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. The model was made stochastic by including temporal variation in S and F where the value of these parameters was randomly drawn during each time step (F_t, S_t) from a log-normal distribution (Akcakaya 2005). We modeled 3 age classes (i.e., stages) including hatch year (HY), second year (SY), and after-second year (ASY). 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 and the actual number of survivors for each time step from a binomial distribution with probability equal to S_t and 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 dependent effects 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 5 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, **SymD**, assumed 15% symmetric dispersal among populations (Alldredge et al. 2004). For each time step, 15% of the population of SY individuals would disperse from each population with emigrants distributed equally among the remaining populations. Thus, a particular population would receive N_j*0.0167 immigrants from each of the *j* populations. Because dispersal may have inherent survival costs, our 3rd scenario included a decrease in disperser survival related to distance traveled, **SurvD**. 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 simply assumed a linear decline in survival from distance = 0 where survival rate was 1 to distance = 9 where survival rate was 0. Thus, a particular population would receive $N_j*0.0167*(1 - 0.111*D_j)$ immigrants from each of the *j* populations where D_j is the distance from the j^{th} population. Our 4th scenario **KD** was based on the idea that SY individuals may be strongly philopatric and only disperse if the source population exceeds *K*. Therefore, the **KD** scenario assumed individuals in excess of *K* become dispersers and subsequently emigrate in equal proportion to all other populations in the metapopulation. The 5th 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 on survival and fecundity for populations other than Fort Hood. Thus, for the previous 5 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 6th 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).

Patch Leverage

Conceptually, we wanted to determine whether changing the size of particular patches 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 (Saltelli et al. 2000) of the metapopulation projection model. 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. Because regression coefficients provide the expected change in MFA of the metapopulation due to changing a particular population's *K* by one unit, we used regression coefficients to measure a patch's leverage (L_j) on overall metapopulation viability.

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

where L_j measures the expected change in viability caused by changing the size of a patch *j*.

Relating Patch Characteristics to Patch Leverage

We related 2 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

$$L_j = \beta_0 + \beta_1 \ln\left[K_j\right] + \beta_2 DL_j + \beta_3 \ln\left[K_j\right] \times DL_j$$

All possible subsets where parameters β_1, β_2, or β_3 equaled 0 were fit as competing models. To identify important characteristics for predicting patch leverage, we used Akaike's Information Criteria corrected for small sample bias (AICc) to rank competing models based on their predictive ability (Burnhham and Anderson 2002).

Metapopulation projections and sensitivity analyses were performed using the program MetaPVA which was programmed in Visual Basic with calls to R (http://www.r-project.org/) for some statistical procedures.

RESULTS

Overall metapopulation viability differed substantially among the 6 scenarios we modeled (Table 4). Notably, metapopulation viability was lower with 15% dispersal versus no dispersal whereas viability was 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 KDSurvVitals).

Plots of MFA versus changes in each population's carrying capacity (K_j) suggested a linear relationship (Figure 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 6 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 versus 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 no relationship between patch leverage and patch size or distance from Fort Hood 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 4 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 Fort Hood was a poor predictor (Figure 2, Table 5). For these scenarios, as original patch size increased, patch leverage decreased. 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 (Figure 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 be able to objectively value changes in off-post patches relative to changes in habitat occurring 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 showed how a stochastic population projection model could be combined with sensitivity analysis to quantify how changes in habitat translate to changes in metapopulation viability. Thus, the importance of changes in 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 could use the following

$$\Delta_A = \Delta_B \times \frac{\hat{L}_B}{\hat{L}_A}$$

If we assume dispersal scenario **KD**, that patch B initially held 250 territories and patch A held 6000 then,

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

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. 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 more important for smaller patches than for 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 Fort Hood could be used to predict how influential changes to a particular patch would be to overall viability. However, we found a lack of 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 importance only when mean vital rates were the same among populations; otherwise distance from the largest patch was the best predictor of patch importance. Based on our results, we suggest it would be dangerous to rely on general guidelines for valuing changes to habitat patches within a metapopulation. Instead, we recommend patches be valued based on changes to viability that are estimated via an explicit model of metapopulation dynamics.

Although our analysis did not produce consistent relationships, 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 Fort Hood were important patch characteristics points to the need for better information on how habitat patches 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 recognize that our analyses did not cover all possible scenarios related to the spatial arrangement of habitat patches, patch-specific vital rates,or spatial correlations in dynamics among populations. Thus, we caution against strict interpretation of our conclusions for the current golden-cheeked warbler population. Instead, our analyses emphasize the fact that details matter and we stress the need to continue to refine and improve model parameters and assumptions to match the actual golden-cheeked warbler metapopulation. 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, etc.) can be targeted for future research (MacKenzie 2009).

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

Patch Id	Patch Size (K)[a]	Distance from largest patch[b]
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 (e.g, Fort Hood)	12371	0

[a] Patch size is based on a classification 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).

[b] Distance units are generic and were chosen to have a mix of sizes and distances from the largest patch.

Table 2. Golden-cheeked warbler mean survival (*S*) and fecundity (*F*). Minimum and maximum observed values are in parentheses. Values were based on those reported in Alldredge et al. (2004).

Stage[a]	*S*	Temporal Variance (*S*)	*F*[b]	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

[a] Stages were hatch-year (HY) including birds age 0 to 1 year, second year (SY) including birds age 1 to 2 years and after second year (ASY) including birds >2 years old.

[b] Fecundity is the number of HY birds produced per individual SY or ASY bird.

Table 3. Golden-cheeked warbler mean survival (*S*) and fecundity (*F*) for each population under scenario KSurvDVitals as described in text.

Patch Id	Patch Size (K)[a]	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	12371	0.500	0.570	1.440	1.650

Table 4. Golden-cheeked warbler metapopulation viability[a].

Scenario[b]	**MFA**	**MMA**
NoD	11182	8453
SymD	9870	7926
SurvD	7884	6495
KD	13037	9724
KSurvD	12212	9179
KSurvDVitals	16879	12906

[a] Viability was measured by mean final abundance (MFA) and mean minimum abundance (MMA).

[b] Scenarios reflect various assumptions of dispersal and patch-specific vital rates as described in text.

Table 5. Model selection relating patch characteristics[a] to patch sensitivity.

Scenario[b]	**Model**	**# Parameters**	**r^2**	**AICc**	**Delta AICc**
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

[a] Patch characteristics were the natural logarithm of patch carrying capacity (ln(k)) and distance from the largest patch (dist).

[b] Scenarios reflect various assumptions of dispersal and patch-specific vital rates as described in text.

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

Scenario[c]	**IT Best Model**	**Intercept**	**ln(k)**	**dist**
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)

[a] Models presented are those with the lowest AICc score.

[b] Patch characteristics were the natural logarithm of carrying capacity (ln(k)) and distance from the largest patch (dist).

[c] Scenarios reflect various assumptions of dispersal and patch-specific vital rates as described in text.

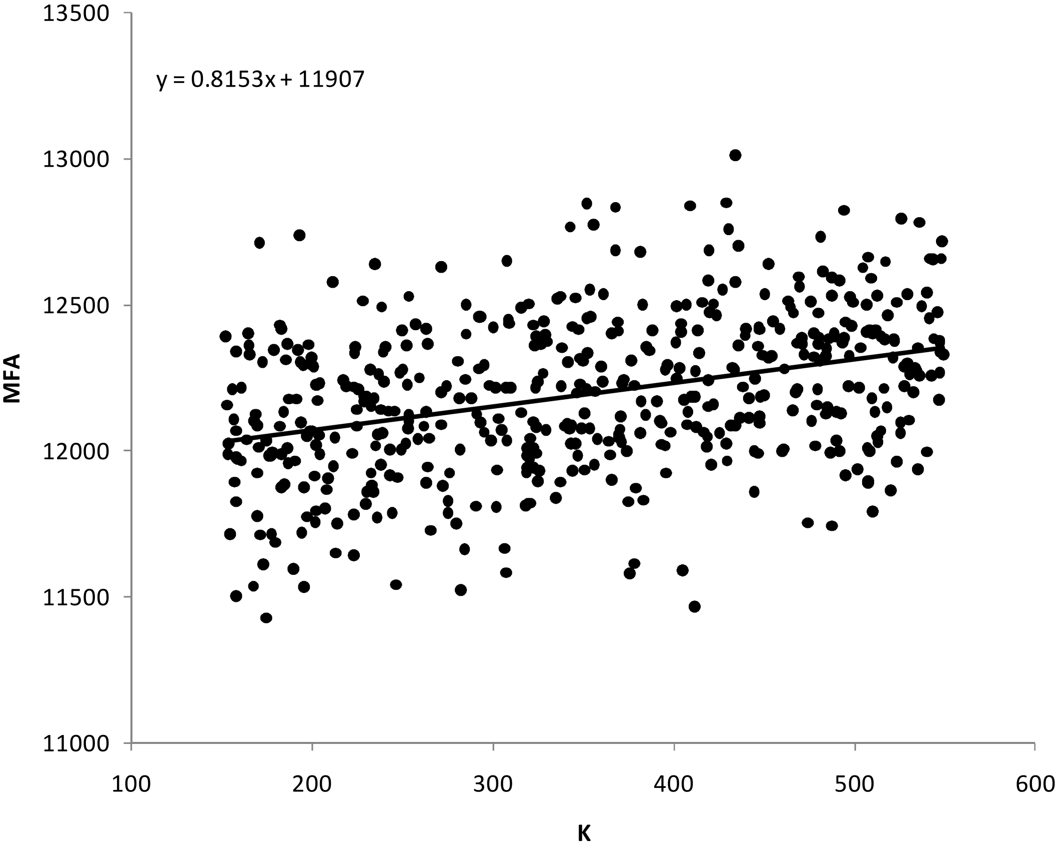

Figure 1. Example of the leverage metric (L_4 = 0.81) calculated for Population 4 under the KSurvD scenario. Leverage metrics were used to measure the expected change in mean final abundance (MFA) due to changing the size of a particular population (K).

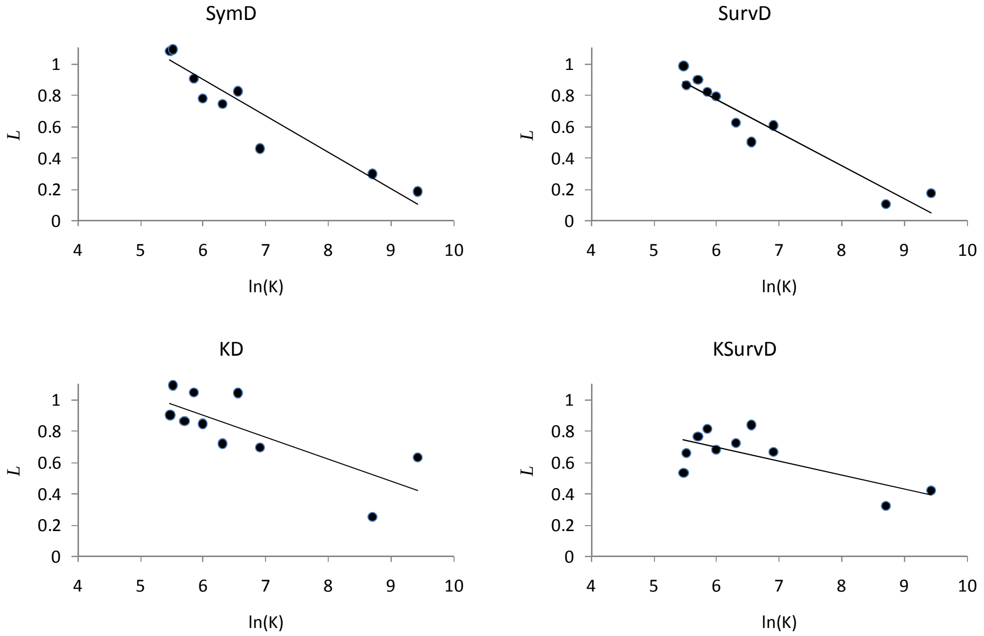

Figure 2. Relationships between patch leverage (*L*) and initial patch size (K) for 4 dispersal scenarios (SymD, SurvD, KD, KSurvD) described in the text.

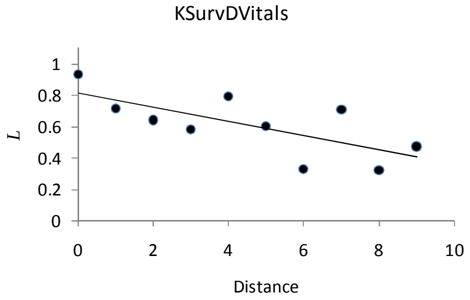

Figure 3. Relationships between patch leverage (*L*) and distance from the largest patch (D) for the KSurvDVitals scenario described in the text.