



*Management and Conservation Article*

# State-and-Transition Models for Assessing Grasshopper Sparrow Habitat Use

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**ABSTRACT** The combination of ecological site descriptions and state-and-transition models (STMs) describes potential vegetation, plant composition, and plant community dynamics and thus can be used to classify and understand dynamics of wildlife habitats across landscapes or home ranges. Numerous studies have evaluated effects of plant community dynamics on diversity and abundance of wildlife populations, but we could find no studies that examined changes in wildlife populations with respect to STMs. We compared abundance of grasshopper sparrows (*Ammodramus saviannarum*) across 5 community phases representing 2 different ecological states in the Columbia Basin, Oregon, USA, to evaluate utility of STMs for understanding and predicting potential changes in habitat use by wildlife species. We measured grasshopper sparrow abundance in 165 100-m fixed-radius point counts distributed across 17 study plots within 5 plant community phases: native perennial grassland, sagebrush-steppe, depleted sagebrush-steppe, sagebrush-steppe with an annual grass understory, and annual grassland. We used a general estimating equation with a Poisson distribution to model relative abundance and estimate differences in this abundance index between linked pairs of community phases. Grasshopper sparrows showed clear differences in abundance among community phases and were most numerous in perennial grasslands and least abundant in depleted sagebrush and sagebrush annual grass community phases. As a management tool, STM provides information that predicts the direct and indirect cumulative impacts of various management actions on vegetation composition and structure (and thus habitat). Ecological site descriptions and STMs enable land managers and scientists to assess potential and current wildlife habitat suitability and to predict potential response of wildlife populations to vegetation dynamics based on the ecological potential of the site.

**KEY WORDS** *Ammodramus saviannarum*, *Artemisia tridentata*, *Bromus tectorum*, ecological site, grasshopper sparrow, grassland, sagebrush-steppe, state-and-transition models, succession.

Application of state-and-transition models (STMs) to describe and predict plant succession on arid and semiarid lands was proposed 20 years ago (Westoby 1989, Laycock 1991). Development of these models continued to evolve and they were recently linked to ecological site descriptions (ESDs) currently being developed and compiled by several federal land management agencies (United States Department of Agriculture, Natural Resources Conservation Service 2003). State-and-transition models and their associated ESDs are tools that provide information on potential vegetation, plant community succession, and resilience (Bestelmeyer et al. 2003, 2009; Briske et al. 2008). These tools describe the variety of plant communities in space and time as well as the processes that drive changes among plant communities. State-and-transition models can be used to help predict potential vegetation changes and identify factors that drive these changes, and thus provide useful information describing potential changes in wildlife habitat across landscapes or home ranges (Hemstrom et al. 2002, Shaver 2010).

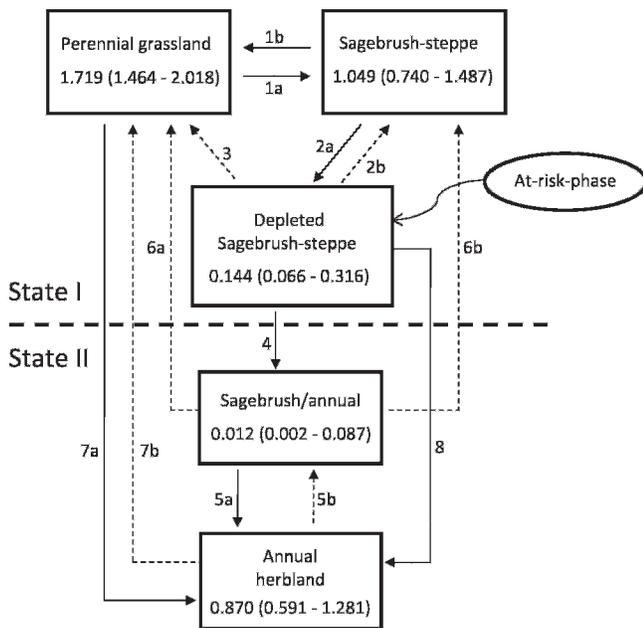
State-and-transition models are simple box-and-arrow diagrams of observed or theoretical successional phases and stable plant community states that can occur on the same spatial areas over time and are linked by their dynamic relationships. Boxes represent successional phases, grouped into different states, and arrows represent transition and disturbance agents between phases and states (Fig. 1).

Ecological site descriptions are reports that collectively classify land to ecological sites based on soil map unit components of the National Cooperative Soil Survey. An ESD is based on a set of specific soil, geologic, landform, and climatic characteristics that cause a site to differ from other kinds of land in its ability to support distinctive kinds and amounts of vegetation (Bestelmeyer et al. 2009).

Resilience, response of plant communities to disturbance or management, and resistance to invasion by introduced species varies across ecological sites. An ecological site can support  $\geq 1$  state, which are composed of a stable suite of plant community phases that interact with the environment. Community phases, analogous to successional or seral stages, are distinct plant communities that occur over time within a state and can include  $\geq 1$  at-risk phases, which are unstable as a result of a decline in resilience. At-risk phases are vulnerable to threshold crossing and subsequent transition to an alternative state (Bestelmeyer et al. 2003, 2009).

A threshold represents the limits of a state's resilience (Briske et al. 2008); once a threshold has been crossed and one state is transformed to another, return to the former state is difficult (Westoby et al. 1989, Laycock 1991, Bestelmeyer 2006). The new state results in a different suite of community phases that differ in plant composition, structure, and function and thus provide different kinds of habitat for wildlife communities. The most extensively documented example of 2 potential stable states that can occupy the same area in the North American West are a

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**Figure 1.** Box-and-arrow diagram representing a state-and-transition model for both the Loamy 8-10 PZ and Sandy 8-10 PZ ecological sites on the Naval Weapons Systems Training Facility located in Morrow County, Oregon, USA, 1995–1997. Boxes represent different phases of vegetation (successional phases) and arrows the transition and disturbance agents between phases and states. Restoration pathways are represented by dashed arrow lines. The dashed line separates 2 steady states. Relative abundance of grasshopper sparrows with 95% confidence intervals for each phase is provided within the boxes. The model includes 5 community phases in 2 states. Transition arrows between phases and states represent the following: (1a) lack of fire, (1b) fire event, (2a) inappropriate grazing, (2b) grazing disturbance removed or altered to a proper level of use, (3) combination of fire and grazing disturbance removed or altered to a proper level of use, (4) continued inappropriate grazing, (5a) fire event, (5b) lack of fire, (6a) combination reseeding with fire or herbicide, (6b) thinning of the sagebrush canopy and annual understory followed by reseeding, (7a) inappropriate grazing and frequent fire, (7b) chemical treatment of annual herbs and reseeding, and (8) fire event and continued inappropriate grazing.

native Wyoming big sagebrush-steppe (*Artemisia tridentata* ssp. *wyomingensis*; state I) and annual grassland (state II) composed of introduced species typically dominated by cheatgrass (*Bromus tectorum*; Pellant and Hall 1994, Miller et al. 2010). Once the introduced species dominates the understory it becomes a new state that is difficult to restore with passive management (e.g., simply removing the disturbance agents that may have caused the transition from one state to another, such as grazing or fire).

It is well documented that changes in plant community structure and composition can have a large influence on wildlife diversity and abundance (Coppedge et al. 2001, Rosenstock and van Riper 2001, Reinkensmeyer et al. 2007). Numerous studies have evaluated effects of plant succession on diversity and abundance of wildlife populations in forests, shrublands, and grasslands (Wiens and Rotenberry 1985, Bock and Bock 1992, Oliver et al. 1998, Knick et al. 2005). Wales et al. (2006) examined how large herbivores facilitate transitions among states containing large trees in northeast Oregon, and Reinkensmeyer et al. (2007, 2008) evaluated the change in avian populations along a successional gradient from grassland to old-growth

woodland. Bird populations have also been compared across 2 states that resulted from wildfire, grazing, or spraying (Wiens and Rotenberry 1985, Bock and Bock 1992). Hemstrom et al. (2002) used an STM to describe the dynamics of big sagebrush habitats across the interior Columbia Basin to evaluate potential broad-scale consequences of these changes on greater sage-grouse (*Centrocercus urophasianus*) habitats. However, we could find no studies that examined changes in wildlife populations in context with STMs.

The combination of ESDs and STMs could be useful for wildlife habitat assessments across landscapes or home ranges because it can be used to classify ecosystem potential, condition, and function; identify at-risk community phases; and anticipate changes in plant communities in both time and space. Potential and at-risk habitats could be readily identified and used to set management priorities and target habitats for restoration. Also, consequences of vegetative changes on wildlife populations could be predicted across states and community phases. The Bureau of Land Management, United States Forest Service, and Natural Resources Conservation Service are continuing to map soils and develop ESDs and STMs throughout the West. Currently, application and use of ESDs and STMs are primarily by federal land management and technical assistance agencies (Briske et al. 2008, Brown and Bestelmeyer 2008). Despite acceptance by rangeland and forestland ecologists, wildlife biologists have been unaware of ESDs and STMs or reluctant to adopt these models for understanding and predicting population dynamics of species using rangeland habitats, which may be partially due to the lack of habitat data, such as cover and canopy height in current ESDs. However, this limitation has been identified by agencies charged with mapping, collecting site data, and compiling ESDs, and a commitment has recently been made to begin including structural components in ESDs (Gilgert and Brown 2009).

To evaluate the utility of STMs for understanding and predicting potential changes in habitat use by wildlife species, we compared the abundance of grasshopper sparrows (*Ammodramus savannarum*) across 5 community phases representing 2 states in the Columbia Basin, Oregon, USA. The grasshopper sparrow has declined throughout much of its range as a result of habitat loss, fragmentation, and degradation of grassland habitats (Vickery 1996, Herkert 1998). Long-term monitoring in the Columbia Plateau physiographic region reveals a significant population decline of >4% annually between 1966 and 2007 (Sauer et al. 2008). We hypothesized that grasshopper sparrow abundance would differ among community phases primarily as a function of perennial grass cover, and suggest that this species could serve as an indicator of healthy and stable perennial grasslands in this region.

## STUDY AREA

The study area was located in the 19,400-ha Naval Weapons Systems Training Facility located in Morrow County, Oregon, USA (hereafter Bombing Range). Ecological sites

**Table 1.** Approximate percentage of the study area (14,200 ha) and percentage of canopy cover of sagebrush and 4 herbaceous groups separated by life form for the 5 community phases on the Naval Weapons Systems Training Facility located in Morrow County, Oregon, USA, 1995–1997. We sampled community phases with 3 study plots containing 9 sampling locations each with the exception of perennial grassland (6 plots with 9 sampling locations each) and depleted sagebrush-steppe (2 plots with 15 sampling points each). We calculated standard errors based on a 2-stage sampling design.

Community phase	% study area <sup>a</sup>	% canopy cover									
		Sagebrush		Annual grass		Short grass		Perennial grass		Forbs	
		$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
State I											
Perennial grassland	35	1.42	1.12	2.37	0.55	1.64	0.59	19.03	3.03	5.03	1.37
Sagebrush-steppe	3	12.88	2.51	10.57	5.02	1.72	0.92	11.29	4.09	3.84	0.79
Depleted sage	5	21.12	5.11	4.53	0.06	4.75	0.19	0.53	0.19	1.90	0.46
State II											
Sagebrush-annual	12	23.36	5.42	10.11	1.40	2.47	1.45	0.18	0.16	6.03	3.53
Annual grassland	45	0.08	0.08	21.86	5.75	4.54	1.82	0.59	0.20	15.13	3.59

<sup>a</sup> % of study area in each community phase at the time of study.

mapped across the Bombing Range located in the Columbia Plateau Major Land Resource Unit were Loamy 8-10 PZ and Sandy 8-10 PZ (United States Department of Agriculture, Natural Resources Conservation Service 2009). Soils varied from loamy fine sand to silt loams, with mesic temperature and xeric moisture regimes, 1 m to 2 m deep. Primary soil subgroups were Torripsamments, Haplodurids, and Haplocambids. Based on ESDs, potential vegetation on the silt loam soils was composed of tall perennial grasses dominated by bluebunch wheatgrass (*Pseudoroegneria spicata*). As sand content increased, needle-and-thread grass (*Hesperostipa comata*) became the dominant grass species. However, sagebrush-steppe composed of Wyoming big sagebrush and basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*) and tall perennial grasses also persisted as a community throughout the study area. Whether this was a result of subtle changes in soil texture and microtopography or time since fire was undetermined. Bitterbrush (*Purshia tridentata*) occurred on approximately 1,030 ha at the northern end of the site but was not included in our study. Inappropriate grazing on these 2 ecological sites resulted in a decline of tall perennial grasses and an increase in the shallow rooted perennial grass Sandberg bluegrass (*Poa secunda*) as well as shrubs including sagebrush, green rabbitbrush (*Ericameria teretifolia*), and yellow rabbitbrush (*Chrysothamnus viscidiflorus*; West 1983). Continued decline in native deep-rooted perennial grasses and forbs and the eventual decline in Sandberg bluegrass resulted in the increase of introduced annual grasses (cheatgrass usually dominant) and various introduced annual and biennial forbs. Fire can act as a trigger resulting in transition of a community phase at risk to a new steady state dominated by cheatgrass.

Based on West's (1983) succession model we identified 2 states and 5 community phases on the Bombing Range (Fig. 1). State I included intact native grassland and sagebrush-steppe. The herbaceous layer in alternate state II was dominated by cheatgrass. Community phases we sampled in state I were 1) perennial grassland (bluebunch wheatgrass or needle-and-thread grass–Wyoming big sagebrush), 2) sagebrush-steppe (Wyoming big sagebrush–native perennial deep-rooted grasses), and 3) depleted

sagebrush-steppe (considered a community phase at risk, composed of Wyoming big sagebrush with few native tall perennial grasses and codominance of Sandberg bluegrass and annual grasses; Table 1). Community phases we sampled in state II were 1) sagebrush-annual grassland (Wyoming big sagebrush with an understory dominated by cheatgrass) and 2) annual grassland (dominated by cheatgrass). At the time of our study, 14,200 ha (73%) of the Bombing Range were classified as falling within one of the described community phases, with the remainder dominated by bitterbrush shrublands, mixed shrub-grass communities dominated by green and yellow rabbitbrush, and several hundred acres converted to irrigated agriculture.

## METHODS

We established 3 40-ha plots randomly within each of 3 community phases: sagebrush-steppe, sagebrush-annual, and annual grassland. We established 6 40-ha plots randomly in perennial grassland and 2 80-ha plots randomly in depleted sagebrush-steppe. Initially we separated perennial grasslands into 3 grazed and 3 ungrazed 40-ha plots each. However, bird numbers and cover of the different life forms were similar, with the exception of tall perennial grasses, which were 25% and 13% in ungrazed and grazed, respectively. Thus, we combined grazed and ungrazed perennial grasslands for analysis.

We randomly selected plots from a 100-m map grid of the Bombing Range. We visited plots to assess community phase. If the area within a potential plot included  $\geq 2$  phases we discarded it and randomly selected another plot. We continued this process until the 5 target phases were represented by  $\geq 3$  plots. Only a small portion of the Bombing Range existed in the depleted sagebrush-steppe (approx. 660 ha), and we initially ignored that phase in site selection. Once we identified this phase we mapped it by walking the boundaries and examining aerial photographs. We randomly selected corners to establish the 2 80-ha plots. We sampled 2 larger plots (instead of 3 smaller plots) because the habitat was spatially configured in 2 large patches. If we had selected 3 plots, 2 would have shared common borders.

We established 9 sampling points within each of the 40-ha plots placed systematically (200 m apart, with a 116-m

buffer to the plot edge) and 15 points with similar spacing within the 2 larger plots within the depleted sagebrush-steppe community phase. For each of these 165 points we estimated cover of tall perennial grasses, short perennial grasses, introduced annual grasses, and forbs in 3 systematically placed 78.5-m<sup>2</sup> (5-m radius) plots. In addition, at each point, we measured shrub cover using line-intercept transects (Canfield 1941). We stretched a 50-m tape in the 4 cardinal directions from the sampling point and measured cover for each shrub by species along the 4 transects (Reinkensmeyer et al. 2007). To generate estimates for each community phase, we averaged cover values from each point and calculated standard errors based on a 2-stage design to account for lack of independence of sampling points within plots ( $n = 17$  plots and 165 sampling locations).

We estimated grasshopper sparrow abundance using 100-m fixed-radius point counts at the 165 points within the 17 plots (Ralph et al. 1993). We surveyed points 3 times during May and June in both 1996 and 1997. We began counts shortly after sunrise and completed them within 1.25 hours. We summed all detections, visual and auditory, within 100 m across the 6 surveys at each point to generate an index of abundance (Nur et al. 1999). We assumed detection probabilities among the different phases and ecological states were similar within the 100-m count radius. Assumption of equal detection probabilities is supported by an assessment of grasshopper sparrow detection probability using a separate dataset gathered using distance sampling methods in similar habitats (sagebrush with annual grass, sagebrush with tall perennial grass, annual grassland, and perennial grassland), which found there was no support for different detection functions among community phases (A. L. Holmes, PRBO Conservation Science, unpublished data). Finally, raw counts have the added benefit of allowing the use of a Poisson distribution, because zeros were commonplace and our count data did not conform to a Gaussian distribution.

To compare abundance of grasshopper sparrows among community phases, we used a general estimating equation (GEE) model with a Poisson distribution (using proc GENMOD, SAS Release 9; SAS Institute Inc., Cary, NC) and the summed count data. A random effect (plot) was described by the same variance component as a fixed effect model, but the covariance structure of the correlated measurements within a plot was estimated in an iterative fitting process using the current value of the parameter vector to compute appropriate functions of the Pearson residual. The model thus accounts for the lack of independence of individual point count stations within plots. We used the GEE of Liang and Zeger (1986) for estimating the vector of regression parameters. Following estimation of the model we calculated ratios of abundance for pairs of phases connected by transitional pathways. We present all results as estimates of abundance (or proportional differences) along with 95% confidence intervals.

We assumed a 20% difference in grasshopper sparrow abundance between community phases and states was biologically significant. This value is admittedly arbitrary,

but due to the species conservation status and the lack of information on both the regional population size and spatial extents of the different ecological states, a conservative approach was warranted. Relative abundance of grasshopper sparrows among community phases and states as we measured may be representative of similar community phases throughout the Columbia Basin (i.e., the Hanford Reach National Monument and the Umatilla Army Depot).

## RESULTS

We estimated correlation among points as 0.137, which was the value we used in the working correlation matrix for GEE parameter estimates. There was evidence of overdispersion in the data (Pearson  $\chi^2/df = 1.24$ ), which resulted in inclusion of a scaling parameter of 1.11 (square root of 1.24). The GEE analysis suggested that abundance indices differed among community phases ( $\chi_4^2 = 10.92$ ,  $P = 0.027$ ). We estimated mean abundance (mean no. of detections at a point count/survey) to be 0.87 (95% CI,  $0.591 \leq \bar{x} \leq 1.281$ ) in annual grasslands, 1.719 (95% CI,  $1.464 \leq \bar{x} \leq 2.018$ ) in perennial grasslands, 1.049 (95% CI,  $0.740 \leq \bar{x} \leq 1.487$ ) in sagebrush-steppe, 0.144 (95% CI,  $0.066 \leq \bar{x} \leq 0.316$ ) in depleted sagebrush, and 0.012 (95% CI,  $0.002 \leq \bar{x} \leq 0.087$ ) in sagebrush with annual grass understory (Fig. 1).

Estimated ratios in abundance between pair-wise comparisons of ecological phases (Table 2) suggested that a transition from native perennial grassland to annual grassland would result in a 49% reduction in grasshopper sparrow numbers (95% CI,  $18\% \leq \bar{x} \leq 68\%$ ). A transition from sagebrush with a perennial grass understory to sagebrush with an annual grass understory would result in an estimated reduction in grasshopper sparrow numbers of 99% (95% CI,  $90\% \leq \bar{x} \leq 100\%$ ). In contrast to predicted declines related to losses of native perennial grasses, transitions of the already degraded sagebrush, which currently supported low abundances of grasshopper sparrow, to annual grassland would result in an increase in habitat use. Specifically, a shift from sagebrush with annual understory to annual grassland would result in an estimated increase of 7,050% (95% CI,  $826\% \leq \bar{x} \leq 60,154\%$ ). Transitions from the depleted sagebrush community phase to annual grassland would result in an estimated increase in grasshopper sparrow of 602% (95% CI,  $236\% \leq \bar{x} \leq 1,539\%$ ).

## DISCUSSION

Grasshopper sparrow abundance differed significantly among community phases, being most abundant in the perennial grasslands and least abundant in depleted sagebrush and sagebrush annual community phases. Transition from native perennial grassland or sagebrush with a perennial grass understory to another community phase or alternate state resulted in projected decreases in grasshopper sparrow abundances. We projected increased abundances during transitions from sagebrush with annual understory or depleted sagebrush toward annual grassland; however, these

**Table 2.** Transitions among community phases, associated shift in plant community resilience, and estimated ratio between linked phases for grasshopper sparrow abundance on the Naval Weapons Systems Training Facility, Morrow County, Oregon, USA, in 1995–1997. *P*-values are for differences of least squares mean estimates of abundance between linked phases.

Transition <sup>a</sup>	Community resilience <sup>b</sup>	Abundance ratio <sup>c</sup>	95% CI		<i>P</i> > $\chi^2$
			Low	High	
1a	0	0.61	0.42	0.90	0.0021
1b	0	1.64	1.12	2.41	0.0021
2a	–	0.14	0.06	0.32	<0.001
2b	+	7.27	3.09	17.10	<0.001
3	+	11.90	5.36	26.44	<0.001
4	–	0.09	0.01	0.70	0.0052
5a	–	70.50	9.60	517.65	<0.001
5b	+	0.01	0.00	0.10	<0.001
6a	+	139.25	19.57	990.99	<0.001
6b	+	85.00	11.66	619.80	<0.001
7a	–	0.51	0.33	0.77	<0.001
7b	+	1.98	1.30	3.00	<0.001
8	–	6.03	2.52	14.41	<0.001

<sup>a</sup> Transition numbers represent the following: 1a) lack of fire, 1b) fire event, 2a) inappropriate grazing, 2b) grazing disturbance removed or altered to a proper level of use, 3) combination of fire and grazing disturbance removed or altered to a proper level of use, 4) continued inappropriate grazing, 5a) fire event, 5b) lack of fire, 6a) combination reseeding with fire or herbicide, 6b) thinning of the sagebrush canopy and annual understory followed by reseeding, 7a) inappropriate grazing and frequent fire, 7b) chemical treatment of annual herbs and reseeding, and 8) fire event and continued inappropriate grazing.

<sup>b</sup> Departure from native state: 0 = neutral, – = resilience decreased, + = resilience increased.

<sup>c</sup> Ratio of grasshopper sparrow abundances between the 2 community phases linked by the specified transition (see Fig. 1).

increases did not result in abundances as high as those found in native perennial grassland.

Our evaluation of the response of grasshopper sparrow populations with STMs illustrates that changes in abundance occur from one community phase to another within and across states. Our comparisons suggested that changes in abundance exceeded our a priori threshold of biological significance, which we defined as a 20% gain or loss in abundance with a transition between phases or states. Generally speaking, we predicted that a shift in plant composition from tall perennial grasses to a codominance of short perennial and annual grasses (depleted sagebrush-steppe) or annual grasses would result in a reduction in grasshopper sparrow abundance. This prediction is consistent with previous studies that demonstrated a strong association between grasshopper sparrows and tall perennial bunchgrass communities in this portion of their range (Janes 1983, Vander Haegen et al. 2000, Earnst et al. 2009). Of the grasshopper sparrow nests we found during our study, 36 of 37 were located at the base of a tall perennial bunchgrass, including nests located below isolated bunchgrasses within stands dominated by annual grass (A. L. Holmes, unpublished data). Additional research is needed to identify the degree to which persistence of grasshopper sparrow in the annual grass phase may be dependent upon remnant tall bunchgrasses or cover of resilient bunchgrass species such as squirreltail (*Elymus elymoides*).

State-and-transition models can provide a robust framework to evaluate potential changes in vegetation or habitats by comparing probable pathways and stable states for individual ecological sites (Stringham et al. 2001, Bestelmeyer et al. 2003, Cingolani et al. 2005, Briske et al. 2006). The combination of ESDs and STMs provides managers with the tools to catalog current vegetation into community phases and describe potential vegetation and vegetation dynamics for a particular area of interest or home range.

State-and-transition models also catalog possible prescriptions of pathways for restoration as well as kinds of disturbances leading to deterioration of ecosystem properties. Thus these models can help managers evaluate potential changes in wildlife population abundance, diversity, and sustainability across different community phases and evaluate the consequences of transitions to alternate states.

The combination of ESDs and knowledge of the current state and community phase provides information on the mechanisms that shift sites to less desirable states or community phases as well as potential for successful restoration (Shaver 2010). These dynamics are based on the properties of the ecological site in addition to the residual properties from reference states that remain within a current community phase (Briske et al. 2008). For instance, transitions from perennial grass to annual grass dominance are brought about by extended periods of livestock grazing at unsustainable levels, which depletes native tall perennial grasses and lowers the resilience of the current state resulting in a phase at risk (West 1999). Fire may then act as a trigger that initiates a transition from one state to another (West 1999, Bestelmeyer et al. 2009). The loss of tall perennial grasses may take decades (Miller et al. 1994), but the loss of sagebrush occurs abruptly. Loss of resilience in ecosystems may also take decades or occur abruptly (Beisner et al. 2003, Scheffer and Carpenter 2003). In our case, a shift from a phase at risk (sagebrush with a depleted herbaceous understory of tall native perennial grasses) or sagebrush–annual to annual grassland will result in a predicted increase in abundance of grasshopper sparrows, but not to the abundance supported in native perennial grasslands. In addition, nesting may be dependent on scattered remnant tall perennial grasses within the annual grassland. The transition from a reference state (state I) to a degraded state (state II) will likely shorten the fire return

interval and limit the ability of sagebrush to reestablish on the site (Young and Evans 1973, West 2000). This alternate steady state of introduced annual grasses, maintained by recurring fires, is not desirable because of the value of sagebrush shrubs to numerous species of wildlife, including a large portion of the regional avifauna that relies on shrubs for nesting habitat (reviewed in Knick et al. 2005). This wider dependence on sagebrush underscores the need to use multiple species to formulate and evaluate management actions. For example, whereas grasshopper sparrows may benefit from a fire that removes shrub cover and promotes grassland structure, loggerhead shrikes (*Lanius ludovicianus*), another species of conservation concern, were reduced by approximately 50% following a fire on the Bombing Range that occurred in 1998 (Humple and Holmes 2006). The fire resulted in areas of fragmented shrub cover embedded in a complex of mostly annual grasslands. Reductions in the number of nesting territories corresponded to changes in community phases from sagebrush-steppe to grasslands.

## MANAGEMENT IMPLICATIONS

Our STM was a powerful predictor of relative grasshopper sparrow abundance and provided insight into how abundance will change as a result of different disturbance agents or restoration efforts. In practice, multiple wildlife species should be evaluated, and where possible, demographic parameters such as annual survival or reproductive success should be measured in addition to abundance. For well-studied species, conceptual models may be populated with information derived from the literature. As a management tool, an STM provides information that predicts the direct and indirect cumulative impacts of various management actions on vegetation composition and structure (and thus habitat) and soil stability (e.g., Papanastasis and Chouvardas 2005, Forbis et al. 2006, Shaver 2010). Ecological site descriptions and STMs enable land managers and scientists to assess potential and current wildlife habitat suitability and to predict potential response of wildlife populations to vegetation dynamics based on the ecological potential of the site. These tools provide a framework for managers to apply ecological information evaluating management options and to set priorities for treating community phases that are at risk or are undesirable alternate states (Briske et al. 2006).

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## LITERATURE CITED

Beisner, B. E., D. T. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. *Frontiers in Ecology and the Environment* 1:376–382.

- Bestelmeyer, B. T. 2006. Threshold concepts and their use in rangeland management and restoration: the good, the bad, and the insidious. *Restoration Ecology* 14:325–329.
- Bestelmeyer, B. T., J. R. Brown, K. M. Havstad, R. Alexander, G. Chavez, and J. E. Herrick. 2003. Development and use of state-and-transition models for rangelands. *Journal of Range Management* 56:114–126.
- Bestelmeyer, B. T., A. J. Tugel, G. L. Peacock, Jr., D. G. Robinett, P. L. Shaver, J. R. Brown, J. E. Herrick, H. Sanchez, and K. M. Havstad. 2009. State-and-transition models for heterogeneous landscapes: a strategy for development and application. *Rangeland Ecology and Management* 62:1–15.
- Bock, C. E., and J. H. Bock. 1992. Response of birds to wildfire in native versus exotic Arizona grassland. *Southwestern Naturalist* 37:73–81.
- Briske, D. D., B. T. Bestelmeyer, T. K. Stringham, and P. L. Shaver. 2008. Recommendations for development of resilience-based state-and-transition models. *Rangeland Ecology and Management* 61:369–367.
- Briske, D. D., S. D. Fuhlendorf, and F. E. Smeins. 2006. A unified framework for assessment and application of ecological thresholds. *Rangeland Ecology and Management* 59:225–236.
- Brown, J. R., and B. T. Bestelmeyer. 2008. Resolving critical issues for the development of ecological site descriptions: summary of a symposium. *Rangelands* 30(4):16–18.
- Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. *Journal of Forestry* 39:388–394.
- Cingolani, A. M., I. Noy-Meir, and S. Diaz. 2005. Grazing effects on rangeland diversity: a synthesis of contemporary models. *Ecological Applications* 15:757–773.
- Coppedge, B. R., D. M. Engle, R. E. Masters, and M. S. Gregory. 2001. Avian response to landscape change in fragmented southern Great Plains grasslands. *Ecological Applications* 11:47–59.
- Earnt, S. L., H. L. Newsome, W. L. LaFramboise, and N. LaFramboise. 2009. Avian response to wildfire in interior Columbia Basin shrubsteppe. *Condor* 111:370–376.
- Forbis, T. A., L. Provencher, L. Frid, and G. Medlyn. 2006. Great Basin land management planning using ecological modeling. *Environmental Management* 38:62–83.
- Gilgert, W., and J. R. Brown. 2009. Setting the stage for enhanced ecological site description application for wildlife management in sagebrush ecosystems: a 2007 Society for Range Management workshop (abstract). Society for Range Management, Annual Meeting, 8–12 February 2009, Albuquerque, New Mexico, USA.
- Hemstrom, M. A., M. J. Wisdom, W. J. Hann, M. M. Rowland, B. C. Wales, and R. A. Gravenmier. 2002. Sagebrush-steppe vegetation dynamics and restoration potential in the interior Columbia Basin, USA. *Conservation Biology* 16:1243–1255.
- Herkert, J. R. 1998. The influence of the CRP on grasshopper sparrow population trends in the mid-continental United States. *Wildlife Society Bulletin* 26:227–231.
- Humple, D., and A. L. Holmes. 2006. Effects of a fire on a breeding population of loggerhead shrike in sagebrush steppe habitat. *Journal of Field Ornithology* 77:21–28.
- Janes, S. W. 1983. Status, distribution, and habitat selection of the grasshopper sparrow in Morrow County, Oregon. *Murrelet* 64:51–54.
- Knick, S. T., A. L. Holmes, and R. Miller. 2005. The role of fire in structuring sagebrush habitats and bird communities. *Studies in Avian Biology* 30:63–75.
- Laycock, W. A. 1991. Stable states and thresholds of range condition on North American rangelands: a viewpoint. *Journal of Range Management* 44:427–433.
- Liang, K. Y., and S. L. Zeger. 1986. Longitudinal data analysis using generalized linear models. *Biometrika* 73:13–22.
- Miller, R. F., S. T. Knick, D. A. Pyke, C. W. Meinke, S. E. Hanser, M. J. Wisdom, and A. L. Hild. 2010. Characteristics of sagebrush habitats and limitations to long-term conservation. *Studies in Avian Biology*: in press.
- Miller, R. F., T. J. Svejcar, and N. E. West. 1994. Implications of livestock grazing in the Intermountain sagebrush region: plant composition. Pages 101–147 in M. Vavra, B. Laycock and R. Pieper, editors. *Ecological implications of livestock herbivory in the West*. Society for Range Management, Denver, Colorado, USA.
- Nur, N., S. L. Jones, and G. R. Geupel. 1999. A statistical guide to data analysis of avian monitoring programs. U.S. Department of the Interior, Fish and Wildlife Service, BTP-R6001-1999, Washington, D.C., USA.

- Oliver, C. D., A. Osawa, and A. Camp. 1998. Forest dynamics and resulting animal and plant population changes at the stand and landscape levels. *Journal of Sustainable Forestry* 6:281–312.
- Papanastasis, V. P., and D. Chouvardas. 2005. Applications of the state-and-transition approach to conservation management of a grazed Mediterranean landscape in Greece. *Israel Journal of Plant Sciences* 53:191–202.
- Pellant, M., and C. Hall. 1994. Distribution of two exotic grasses on public lands in the Great Basin: status in 1992. Pages 109–112 in S. B. Monsen and S. G. Kitchen, compilers. Proceedings: ecology and management of annual rangelands. United States Department of Agriculture General Technical Report INT-GTR-313, United States Department of Agriculture Forest Service, Intermountain Research Station, Ogden, Utah, USA.
- Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. Field methods for monitoring landbirds. United States Department of Agriculture Forest Service Publication, PSW-GTR 144, Albany, California, USA.
- Reinkensmeyer, D. P., R. F. Miller, R. G. Anthony. 2007. Avian community structure along a mountain big sagebrush successional gradient. *Journal of Wildlife Management* 71:1057–1066.
- Reinkensmeyer, D. P., R. F. Miller, R. G. Anthony, and V. E. Marr. 2008. Winter bird communities in shrub-steppe and juniper woodland. *Western North American Naturalist* 68:25–35.
- Rosenstock, S. S., and C. van Riper, III. 2001. Breeding bird responses to juniper woodland expansion. *Journal of Range Management* 54:226–232.
- Sauer, J. R., J. E. Hines, and J. Fallon. 2008. The North American Breeding Bird Survey, results and analysis 1966–2007. Version 5.15. USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA. <<http://www.mbr-pwrc.usgs.gov/bbs/bbs.html>>. Accessed 3 Sep 2010.
- Scheffer, M., and S. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology and Evolution* 18:648–656.
- Shaver, P. L. 2010. Quantification of state-and-transition model components utilizing long-term ecological response data following one-seed juniper treatment on a deep sand savannah ecological site. Dissertation, Oregon State University, Corvallis, USA.
- Stringham, T. K., W. C. Krueger, and P. L. Shaver. 2003. State and transition modeling: an ecological process approach. *Journal of Range Management* 65:106–113.
- United States Department of Agriculture, Natural Resources Conservation Service. 2003. National range and pasture handbook (revision 1). Grazing Lands Team, Central National Technology Support Center, Fort Worth, Texas, USA.
- United States Department of Agriculture, Natural Resources Conservation Service. 2009. Ecological Site Description (ESD) system for rangeland and forest data. <<http://esis.sc.egov.usda.gov/Welcome/pgReportLocation.aspx?type=ESD>>. Accessed 3 Sep 2010.
- Vander Haegen, W. M., F. C. Dobler, and D. J. Pierce. 2000. Shrubsteppe bird responses to habitat and landscape variables in eastern Washington, USA. *Conservation Biology* 14:1145–1160.
- Vickery, P. D. 1996. Grasshopper sparrow (*Ammodramus saviannarum*). Account 239 in A. Poole and F. Gill, editors. *The Birds of North America*. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D.C., USA.
- Wales, B. C., L. H. Suring, and M. A. Henstrom. 2006. Modeling potential outcomes of fire and fuel management scenarios on the structure of forested habitats in northeast Oregon, USA. *Landscape and Urban Planning* 80:223–236.
- West, N. E. 1983. Western intermountain sagebrush steppe. Pages 351–397 in N. E. West, editor. *Ecosystems of the world 5: temperate deserts and semi-deserts*. Elsevier Scientific, New York, New York, USA.
- West, N. E. 1999. Management for biodiversity of rangelands. Pages 101–126 in W. W. Collins and C. O. Qualset, editors. *Biodiversity in agroecosystems*. CRC, Boca Raton, Florida, USA.
- West, N. E. 2000. Synecology and disturbance regimes of sagebrush steppe ecosystems. Pages 15–26 in P. G. Entwistle, A. M. DeBolt, J. H. Kaltenecker, and K. Steenhof, compilers. Proceedings: Sagebrush Steppe Ecosystems Symposium. Bureau of Land Management Publication No. BLM/ID/PT-001001+1150, Boise, Idaho, USA.
- Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* 42:266–274.
- Wiens, J. A., and J. T. Rotenberry. 1985. Response of breeding passerine birds to rangeland alteration in a North American shrubsteppe locality. *Journal of Applied Ecology* 22:665–668.
- Young, J. A., and R. A. Evans. 1973. Downy brome—intruder in the plant succession of big sagebrush communities in the Great Basin. *Journal of Range Management* 26:410–415.

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