Fitness landscapes and life-table response experiments predict the importance of local areas to population dynamics

KRISTIN KANE,1 JAMES S. SEDINGER,1† DANIEL GIBSON,2 ERIK BLOMBERG,3 AND MICHAEL ATAMIAN4

1Department of Natural Resources and Environmental Science, University of Nevada Reno, Reno, Nevada 89557 USA
2Department of Fish and Wildlife Conservation, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061 USA
3Department of Wildlife, Fisheries, and Conservation Biology, University of Maine, Orono, Maine 04469 USA
4Washington Department of Fish & Wildlife, Spokane Valley, Washington 99216 USA

Citation: Kane, K., J. S. Sedinger, D. Gibson, E. Blomberg, and M. Atamian. 2017. Fitness landscapes and life-table response experiments predict the importance of local areas to population dynamics. Ecosphere 8(7):e01869. 10.1002/ecs2.1869

Abstract. Animal resource requirements differ among life-history stages, and thus, habitat is most appropriately thought of as specific to a particular life stage. Accordingly, different habitats may vary in their significance as functions of (1) the sensitivity of population growth to the life stage for which the habitat is most important, (2) spatial association of each habitat to other habitats, and (3) the abundance of the habitat in question. We used an analogy to a life-table response experiment to develop spatial models linking key habitats to rates of population increase in Greater Sage-grouse. We parameterized models linking demographic rates to vegetation and physical attributes of habitats, including spatial association of some habitats to others, using a decade-long study of Greater Sage-grouse in central Nevada. We modeled the contribution of each pixel in the landscape to regional \( \lambda \) (finite rate of population increase) using functional relationships between demographic rates and the attributes of that pixel, and the sensitivity of \( \lambda \) to each demographic rate. We incorporated the following demographic rates into our model: female nesting success, survival of chicks from hatching to 45 d, and adult female annual survival. We also incorporated the probability a site was used for nesting. Chick survival (62%) and nest site selection (21%) explained most of the variance in \( \lambda \). Habitat supporting population growth occurred in mid-high elevation areas with moderate slopes, and a high percent cover of sagebrush, and in nesting areas close to late-brood habitat. Our models indicate that a relatively small proportion of habitat available to Greater Sage-grouse in central Nevada is responsible for maintenance of the population in our study system. We suggest that the general approach we describe here can be used to improve understanding of habitats most likely to regulate populations in other systems, providing an important tool in ecology and conservation.

Key words: demographic rates; fitness landscapes; Greater Sage-grouse (Centrocercus urophasianus); habitat; lambda; life-table response experiment (LTRE); regional population dynamics.

Received 30 December 2016; revised 12 April 2017; accepted 22 May 2017. Corresponding Editor: W. Alice Boyle.

Copyright: © 2017 Kane et al. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
† E-mail: jsedinger@cabnr.unr.edu

INTRODUCTION

Animals in heterogeneous environments survive and reproduce at different rates associated, in part, with variation in the structure and composition of the habitats they occupy (Fretwell and Lucas 1970, Rosenzweig 1981, Pulliam and Danielson 1991). Variation in survival and recruitment among individuals that results from habitat variability is important because the collective demographics of individuals ultimately drive population-level dynamics (Lomnicki 1980,
Bernstein et al. 1991, Sherry and Holmes 1995). The concept of source–sink dynamics was developed to explain variation in this balance (Pulliam 1988), and numerous studies have reported source–sink dynamics in wild populations (e.g., Delibes et al. 2001, Battin 2004). Some land areas may be more important in regulating population dynamics than others as demographic surpluses arise in habitat where reproduction is sufficient to sustain population growth (source habitat) and demographic deficits occur in habitat where this is not true (Pulliam 1988). Characterization of the various combinations of areas available to local populations and their influence on individuals’ space use, survival, and reproduction has, however, been less common.

Individuals commonly rely on fundamentally different habitats to meet the varying requirements for different life-history stages (Dunning et al. 1992, Fahrig et al. 2011). For example, productive processes such as growth typically require foods higher in protein (Hudson 1986, Drut et al. 1994b, Manseau and Gauthier 1994, Sedinger 1997), and consequently, individuals tend to select habitat that provides such foods when rearing young or growing themselves. In contrast, individuals may select habitat during the winter that improves thermal balance (West 1960, Kendeigh and Blem 1974) or reduces predation risk (Evans 1976, Bicudo et al. 2010, Villén-Pérez et al. 2013), but only provides the nutrients necessary to maintain energy balance. Because life-history stages vary in resource requirements, habitat use is likely to vary among life-history stages and thus should be thought of in a life stage-specific context (Hall et al. 1997). Because different life-history stages make variable contributions to population growth (Stearns 1992, Roff 2002), certain stage-specific habitats are likely to have greater influence on population dynamics than others. Understanding these variable habitat-mediated contributions is central to effective conservation planning and habitat management.

Life-table response experiments (LTREs) combine sensitivity of per capita rate of population change (λ) to specific demographic rates (Caswell 1996, 2001) with variation in those demographic rates to calculate the proportional contribution of each demographic rate to overall variation in λ. Cooch et al. (2001) used this approach to show that variation in demographic rates affecting recruitment in Lesser Snow Geese (Chen caerulescens caerulescens) had a substantially greater influence on λ than did variation in adult survival, despite λ being more sensitive to adult survival than to recruitment. The LTRE approach (Caswell 1989, Cooch et al. 2001), thus, provides a tool that can predict the contribution of specific demographic rates to regional population dynamics. If variation in demographic rates can be functionally related to specific habitat features (e.g., Holmes et al. 1996, Marchand and Litvaitis 2004, Atamian et al. 2010), then the LTRE approach can be extended to estimate the contribution of specific habitat features to regional population dynamics via their connection with demographics.

We used Greater Sage-grouse (Centrocercus urophasianus) (hereafter sage-grouse) as an example of the application of LTREs to understand the influence of stage-specific habitats on regional population dynamics. Sage-grouse have been characterized as a landscape species (Patterson 1952, Wakkinen 1990, Connelly et al. 2004) that requires a variety of seasonal resources to meet requirements for various life-history stages throughout the annual cycle. Sage-grouse are sagebrush obligates that depend on sagebrush for both food and protective cover throughout the year (Braun et al. 1977, Connelly et al. 2004). Nesting occurs in sagebrush-dominated shrub communities that support understory plants (Wallestad and Pyrah 1974, Connelly et al. 1991, Gregg et al. 1994, Kolada et al. 2009a, b), which provide both cover and relatively high-protein food for pre-nesting females and their chicks immediately after hatching (Schoenberg 1982, Drut et al. 1994b, Crawford et al. 2004). In much of sage-grouse range, drying conditions force females with young to move to more mesic sites (e.g. higher elevation shrub communities, wet meadows, and riparian areas) that support green vegetation during the late-brood-rearing period (Fischer et al. 1996, Atamian et al. 2010, Connelly et al. 2011, Blomberg et al. 2013a, Donnelly et al. 2016). We incorporated functional relationships between characteristics of habitat and components of the recruitment process into an LTRE to understand the relationships between specific habitat characteristics and population dynamics for sage-grouse in central Nevada. We lacked information on direct functional relationships between habitat characteristics and adult...
survival. However, tradeoffs occur between reproductive success and survival in this study system (Blomberg et al. 2013), allowing us to incorporate indirect relations between habitat and adult survival via reproductive costs.

METHODS

Spatial models of vital rates

We used 350 nests (of which 133 were successful and 217 were depredated), 316 random points, and 28 lek locations collected as part of a study of sage-grouse from 2003 to 2012, in Eureka County, Nevada (Fig. 1; Gibson 2015) for model building. In this study system, sage-grouse have been classified into two distinct populations: individuals associated with the Cortez Mountains or Roberts Creek Mountain (Atamian et al. 2010, Jahner et al. 2016). See Gibson et al. (2015) and Blomberg et al. (2012) for a complete description of the study area (Fig. 1). We used covariates previously identified as important to nest site selection (NSS), nest survival, and chick survival (CS; Table 1) to construct spatial models of these three response variables. Nest site selection is not a demographic rate. However, we believed it was important to include for our purposes because where females choose to nest is an important determinant of the relationship between local habitat features and recruitment of offspring. We used general logistic regression equations (Table 1) to build spatial models for these demographic rates. We entered the logistic regression equations predicting the vital rates into the Raster Calculator in ArcMap 10.1 (Environmental Systems Research Institute, Redlands, California, USA) to produce predictive surfaces for each vital rate across the entire study area.

We developed a spatial surface of NSS probabilities based on an explanatory model (Gibson et al. 2016), which included the following explanatory variables: slope, elevation, distance to the nearest lek (D_lek), amount of sagebrush within a 1000 m circular extent (All Sage 1000) and the interactions, slope × elevation, and All Sage 1000 × distance to lek. We used the Euclidean distance function in the ArcMap 10.1 toolbox to calculate the distance between a lek and each pixel within our study area, which each represented a potential nest site (Table 1). We used the Southwest Regional Gap database (SWREGAP; USGS National Gap Analysis Program 2004) to estimate landcover classified as sagebrush at a spatial extent of 1000 m at each potential nest point (All Sage 1000). We obtained raster (grid) layers of slope and elevation from a National Elevation Dataset Digital Elevation Model (NED DEM; USGS; Gesch et al. 2002).

We calculated nest success based on a model of daily nest survival which included a time-varying covariate that represented the current amount of habitat disturbed by wildfire from 1999 to 2010 (Blomberg et al. 2012), and proportion of non-sagebrush shrub cover and forb cover. Previously burned areas were typically covered by homogeneous stands of exotic grasses, either cheatgrass (Bromus tectorum) or crested wheatgrass (Agropyron cristatum). We used the National Land Cover Database (NLCD; Xian et al. 2015) to estimate non-sagebrush shrub cover and forb cover percentages for our entire study region. To construct a non-sagebrush shrub cover layer, we used the NLCD percent shrub cover layer, which represented the proportion of shrub canopy in each 30-m pixel. Percent sagebrush and percent big sagebrush are secondary components, which are nested within the percent shrub cover layer. We subtracted the percent sagebrush cover layer (proportion of sagebrush canopy in each 30-m cell) from the shrub cover layer to generate a non-sagebrush shrub cover layer. We used the percent annual herbaceous layer (annual grass and forb proportion in each 30-m pixel) as a forb cover layer. National Land Cover Database includes masked areas to identify non-shrub lands such as forests, and urban and agriculture fields. Because NLCD identified certain masked areas as only including pinyon juniper, we re-coded these areas because they actually contained nests, using previously measured estimates of the average percentage of forb cover surrounding those nests, described in Gibson et al. (2016).

We calculated predicted daily nest survival at each point using a logistic model with the above covariates and converted daily nest survival to predicted nest success assuming a 37-d exposure period. We added a fixed adjustment (0.068) to each estimate of nest success to account for negative bias in estimates of nest success associated with accelerated failure of nests due to post-flushing abandonment (Gibson et al. 2015). We
Fig. 1. Study area, nest locations (green circles), active leks (black circles), and spatial distribution of late-brood habitat (shown in red) for Greater Sage-Grouse in Eureka County, Nevada, USA.
Table 1. Habitat variables and beta coefficients used to model nest site selection, female success, CS, and female survival.

<table>
<thead>
<tr>
<th>Habitat variable</th>
<th>Beta coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest site selection</td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>-2.345</td>
</tr>
<tr>
<td>Elevation</td>
<td>0.596</td>
</tr>
<tr>
<td>Slope</td>
<td>0.507</td>
</tr>
<tr>
<td>Distance to lek</td>
<td>-0.643</td>
</tr>
<tr>
<td>Allsage 1000</td>
<td>1.431</td>
</tr>
<tr>
<td>Slope × elevation</td>
<td>-0.331</td>
</tr>
<tr>
<td>Distance to lek × Allsage 1000</td>
<td>-0.624</td>
</tr>
<tr>
<td>Female success</td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>2.981</td>
</tr>
<tr>
<td>Forb cover</td>
<td>0.254</td>
</tr>
<tr>
<td>Non-sagebrush shrub cover</td>
<td>0.295</td>
</tr>
<tr>
<td>Non-sagebrush shrub cover × forb cover</td>
<td>0.315</td>
</tr>
<tr>
<td>Fire</td>
<td>-0.117</td>
</tr>
<tr>
<td>Renesting propensity</td>
<td>0.385</td>
</tr>
<tr>
<td>CS</td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>1.647</td>
</tr>
<tr>
<td>Distance moved</td>
<td>-1.371</td>
</tr>
<tr>
<td>Week 1</td>
<td>-1.378</td>
</tr>
<tr>
<td>Week 2</td>
<td>-0.697</td>
</tr>
<tr>
<td>Week 3</td>
<td>0.054</td>
</tr>
<tr>
<td>Week 4</td>
<td>-0.097</td>
</tr>
<tr>
<td>Week 5</td>
<td>0.181</td>
</tr>
<tr>
<td>Week 6</td>
<td>1.647</td>
</tr>
<tr>
<td>Population</td>
<td>0.206</td>
</tr>
<tr>
<td>Female survival</td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>3.009</td>
</tr>
<tr>
<td>Summer</td>
<td>0.840</td>
</tr>
<tr>
<td>Fall</td>
<td>-0.516</td>
</tr>
<tr>
<td>Nest success</td>
<td>-0.3368</td>
</tr>
<tr>
<td>Brood success</td>
<td>-0.2693</td>
</tr>
</tbody>
</table>

Notes: CS, chick survival. See Gibson et al. (2016, 2017) for a full description of estimation and model selection for nest site selection and CS, respectively. See Gibson et al. (2015) for description of parameters used to model female success. Variables were estimated using the Southwest Regional GAP (SWREGAP, USGS National Gap Analysis Program 2004), National Land Cover Database (NLCD; Xian et al., 2015), and the National Elevation Dataset Digital Elevation Model (NED DEM; USGS) for vegetation and elevation, respectively. † Parameter estimates for nest site selection follow Gibson et al. (2016). Elevation and slope were extracted for the study area using the NED DEM (USGS); Distance to lek = Euclidean distance from each lek to a nest; Allsage1000 = Sagebrush coverage from Southwest ReGAP with a 1000 m radius from each nest point. Parameter estimates for female success follow Gibson et al. (2015). Forb cover and non-sagebrush shrub cover = the percentage of forb and non-sagebrush cover at each nest point, respectively; Fire = time-varying covariate representing amount of habitat burned and converted to exotic grasslands during 1999–2010; Renesting propensity = the mean probability of initiating a second nesting attempt following failure of a first nest. The habitat variables forb cover, non-sagebrush shrub cover, and fire were used in the calculation of nest success. Female success was modeled using nest success and renesting propensity (see calculated female success (FS), the probability that a female successfully hatched at least one clutch of eggs, using the following equation:

\[
FS = NS \times (\text{breeding probability}) + (1 - NS) \times (\text{renesting probability}) \times NS, \tag{1}
\]

where NS represented nest success previously calculated using the habitat variables described above, breeding probability (0.85) was the probability a female initiated a clutch, and renesting probability (0.385) represented the mean probability of a second nesting attempt by females after a first unsuccessful attempt (Blomberg et al., in press).

Survival of chicks to fledging was strongly influenced by distance moved per day and age (Gibson et al. 2016). The only broods that had chicks survive to fledging in Eureka County reached relatively small and well-defined “late-brood habitats,” primarily at higher elevations (Atamian et al. 2010), so we defined late-brood habitat for Eureka County from a habitat suitability analysis based on locations of successful sage-grouse broods near fledging (Atamian et al. 2010). For the purposes of modeling survival of chicks originating from potential nest sites, we assumed that the Euclidian distance from each potential nest point to the nearest late-brood habitat was divided into six equal intervals, representing weekly movements. We calculated daily movements from these weekly movements assuming constant daily movement. We calculated daily CS using the logit transformation of a linear model that included chick age in weeks (daily survival increased with chick age in weeks), daily distance moved, and a term for population of origin (Roberts vs. Cortez). We calculated weekly survival probabilities as the seventh power of daily survival probabilities for

(Continued)
each potential nest site–week combination and the probability chicks survived to 42 d as the product of the six weekly survival probabilities. We assigned these probabilities of chicks surviving to six weeks to all potential nest points.

Blomberg et al. (2013b) found that female sage-grouse incur costs to survival associated with reproduction, as females that hatched clutches or successfully fledged chicks had lower annual survival compared to unsuccessful females. Therefore, we constrained female survival to vary spatially as a function of the predicted female reproductive success at each point. We incorporated these tradeoffs between reproductive success and survival to account for reproductive costs using the following equation:

\[
S_{\text{annual}} = S_{\text{spring}}^2 \times (\logit(\beta_0 + \beta_{\text{summer}} + \beta_{\text{nest}} \times FS))^2 \times (\logit(\beta_0 + \beta_{\text{fall}} + \beta_{\text{brood}} \times BS))^3 \times S_{\text{winter}},
\]

where \(S_{\text{spring}}\) represented monthly survival rates during the nesting months April and May (\(S_s = 0.93\)), and \(S_{\text{winter}}\) represented monthly survival during winter months November–March (\(S_w = 0.99\); Blomberg et al. 2013b). \(\beta_{\text{nest}}\) was the negative effect of successfully hatching a nest on summer survival, whereas \(\beta_{\text{brood}}\) represented the negative effect of successfully raising a brood on fall survival. \(\beta_{\text{summer}}\) and \(\beta_{\text{fall}}\) reflected season-specific fixed effects for summer and fall, respectively. BS represented the probability of raising a chick to 42 d (standardized probabilistic value of CS), given FS, and clutch size values for adult females (7.9) and egg hatchability rates (0.92) (see Eq. 3). We used estimated mean hatchability from Taylor et al. (2012).

**LTRE analysis**

We used a two-age-class Leslie matrix (Caswell 2001) as the basis for estimating sensitivity of \(\lambda\) to demographic rates, as most of the variation in fecundity and annual survival is between juveniles (10 months) and adults (22 months and older) (Taylor et al. 2012):

\[
BS = FS \times \left(1 - (1 - \text{ChickSurvival})^{(\text{MeanClutchSize} \times \text{Hatchability})}\right),
\]

We used the mean female survival value across the landscape for adult females (0.62). To estimate a juvenile survival value (0.48), we assumed that the juvenile survival (10-month-old females) equation was the same as adult survival and only the intercept value in the equation was different, which adjusted the value of juvenile survival downward. We calculated fecundities as products of the probability of NSS, female breeding propensity (juvenile = 0.7765, and adult = 0.8507), normalized fecundity (mean number of female eggs laid by a female), FS, which incorporated renesting, CS to 42 d, and survival from fledging to the next breeding season (post-fledging survival; Table 2). We used the probability of NSS at each pixel to produce a weighted mean across the entire study area for the product of demographic rates associated with each pixel; that is, the contribution of each pixel to the mean product of demographic rates was based on the probability that pixel was initially selected as a nest site. We produced a weighted mean for the product of demographic rates by first scaling NSS so that the overall mean equaled 1.0, then multiplying the resulting values times the predicted product of demographic rates associated with that pixel based on habitat models.

**Table 2. Two-age class Leslie matrix and sensitivity matrix.**

<table>
<thead>
<tr>
<th>Variable</th>
<th>Leslie matrix</th>
<th></th>
<th>Sensitivity matrix</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Juvenile females</td>
<td>Adult females</td>
<td>Juvenile females</td>
<td>Adult females</td>
</tr>
<tr>
<td>Fecundity</td>
<td>0.10</td>
<td>0.12</td>
<td>0.13</td>
<td>0.68</td>
</tr>
<tr>
<td>Survival</td>
<td>0.48</td>
<td>0.62</td>
<td>0.17</td>
<td>0.86</td>
</tr>
</tbody>
</table>

**Notes:** Vital rates used to calculate fecundity in the matrix were female breeding propensity (juvenile = 0.7765 and adult = 0.8507; Blomberg et al., *in press*), renesting probability, and age-specific clutch size (juvenile = 3.6 and adult = 3.95; Atamian and Sedinger 2010, Blomberg et al. 2014a), post-fledging survival (0.528; Blomberg et al. 2014b), mean values of nest site selection, female success, female survival, and chick survival. Mean \(\lambda\) value from the matrix = 0.71.
We calculated the sensitivity of $\lambda$ as:

$$S_{ij} = \frac{\partial \lambda}{\partial a_{ij}},$$

where $a_{ij}$ is the $i,j$th entry of the Leslie matrix (Caswell 1978). We calculated $\lambda$ as the dominant eigenvalue of the Leslie matrix, calculated from the mean values of demographic rates described above (Table 2). We obtained the sensitivity of $\lambda$ by using the above Leslie matrix and calculated the overall deviation ($\alpha^{(m)}$) for each point in space from the reference (mean) ($\lambda^{(i)}$) as:

$$\alpha^{(m)} = \lambda^{(m)} - \lambda^{(i)},$$

(4)

where in general,

$$\alpha^{(m)} = \left( \sum_{ij} (NSS_{ij}^{(m)} - NSS_{ij}^{(i)}) \frac{\partial \lambda}{\partial NSS_{ij}} + \sum_{ij} (FS_{ij}^{(m)} - FS_{ij}^{(i)}) \frac{\partial \lambda}{\partial FS_{ij}} + \sum_{ij} (CS_{ij}^{(m)} - CS_{ij}^{(i)}) \frac{\partial \lambda}{\partial CS_{ij}} + \sum_{ij} (S_{ij}^{(m)} - S_{ij}^{(i)}) \frac{\partial \lambda}{\partial S_{ij}} + \sum_{ij} (A_{ij}^{(m)} - A_{ij}^{(i)}) \frac{\partial \lambda}{\partial A_{ij}} \right),$$

(5)

and where generally,

$$\frac{\partial \lambda}{\partial x} = \sum_{ij} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x}.$$  

To determine the contributions of the vital rates to the observed variation in $\lambda$, we modified the following equation:

$$V(\lambda) \approx \sum_{ij} \sum_{kl} C(ij, kl) S_{ij} S_{kl},$$

(6)

where $C(ij, kl)$ was the covariance of matrix elements $\alpha_{ij}$ and $\alpha_{kl}$, and $S_{ij}$ and $S_{kl}$ were the sensitivities of the vital rates for the matrix elements evaluated for the reference matrix (Caswell 2001). Specifically, we converted elements of the Leslie matrix to specific demographic rates as in Eq. 5, above. We then calculated the contributions of each demographic rate (e.g., CS) to variance in lambda by summing all of the terms in Eq. 6 including that demographic rate. Because of the inclusion of covariance terms in Eq. 6, the contributions of individual demographic rates to the total variance in $\lambda$ do not necessarily sum to 1.0.

Nest site selection is not a typical demographic rate. We included scaled NSS (NSS divided by mean NSS) in LTRE calculations, however, because we calculated mean fecundities using scaled NSS. This approach also allowed us to incorporate NSS into our assessment of the contributions to variation in $\lambda$ of specific points on the landscape. We used ArcMap to calculate proportions of areas with a substantial chance of being used for nesting (availability of sites and potential to be nested in) as the total area in the Eureka County study area divided by the area of nesting habitat with probability >0.9 chance of being used for nesting. Similarly, to assess how much of the total available land area was contributing positively to $\lambda$, we divided the area with $\lambda > 1$ by the total area in the Eureka County study area.

**RESULTS**

The probability of sites being used for nesting was highly variable, ranging from 0 to 0.95 (Fig 2). Fifty percent of the study area had a probability >0.1 of being selected for nesting based on slope, elevation, and proximity to the nearest lek, and only 6% of the study area had a probability >0.9 of being used for nesting (Fig. 2). Female success ranged from 0 to 0.51 (Fig. 3), but only 9% of the study area supported FS of >0.44, an estimate approximately consistent with a stable population (Taylor et al. 2012).

The negative effect of daily distance moved on CS created a relatively steep gradient in CS as potential nest sites were located further from late-brood habitat (Fig. 4). Female survival values ranged from 0.43 to 0.68 and negatively covaried with measures of reproductive success (Fig. 5). High-quality nesting habitat produced lower female survival (blue areas), while low-quality nesting habitat was associated with higher survival (red areas).

The mean Leslie matrix had fecundities of 0.10 for juvenile and 0.12 for adult females (Table 2), $\lambda$ was most sensitive to adult survival (0.86) and least sensitive to juvenile survival (0.17). The retrospective analysis (LTRE), however, revealed that variation in CS explained most of the observed variance in $\lambda$ (62%), followed by NSS (21%); no other demographic rates contributed substantially to variation in $\lambda$. 

KANE ET AL.
Fig. 2. Probability of selection of points for nesting based on slope, elevation, distance to leks, and amount of habitat classified as sagebrush within 1000 m of a point. Probabilities range from 0 (blue) to 0.95 (red).
Fig. 3. Probability surface of female success (FS) (the probability a female hatched a clutch, including renests following failure of first nests) based on shrub height, areas burned in last decade, forb, and non-sagebrush shrub cover. Probabilities of FS range from 0 (blue) to 0.51 (red).
Fig. 4. Probability of chick survival based on the relationship between the weekly distances a chick moved and weekly survival. Probabilities range from 0 (blue) to 0.54 (red).
Fig. 5. Annual survival of females based on whether a female nesting at a given location hatched a nest and raised a brood. Survival values range from 0.43 to 0.68.
DISCUSSION

Spatial habitat influence on population dynamics

We found that only ~8% of land available in Eureka County, served as a net source for sage-grouse ($\lambda > 1$; Fig. 6). Our results indicate that the availability of nesting sites and their proximity to leks, and late-brood habitat had the greatest influence on population dynamics via their effect on recruitment. Habitat used for nesting was located in moderately high elevation sites near leks with greater amounts of sagebrush shrub cover. Sage-grouse usually choose nests sites within 3 km of leks (Coates et al. 2013); these areas include relatively dense sagebrush shrub cover, which improves nest concealment (Redmond et al. 1982, Crabtree et al. 1989, Kolada et al. 2009a, b). Our finding that lower elevation sites yield low values of $\lambda$ may explain why sage-grouse prefer to use higher elevation areas for nesting and brood rearing. Higher elevation areas are also more resilient to disturbances than lower elevation areas (Chambers et al. 2014). Areas with low probabilities of nesting contributed little to population growth, both because they were unlikely to be used for nesting in the first place, and they were relatively distant from high-elevation mesic areas used as late-brood habitat, resulting in low recruitment of young hatched in these areas (Gibson et al. 2016).

The effects of habitat on demographic rates have been investigated in other systems (e.g., Holmes et al. 1996, Murphy 2001, Jones et al. 2004, Pidgeon et al. 2006, Peterson et al. 2016). For example, Arlt et al. (2008) linked demography to land use in northern wheatears (Oenanthe oenanthe). They found habitat-specific differences in population growth rates and also identified the demographic parameters that had the greatest impact on variation in $\lambda$ among land use types. Aldridge and Boyce (2007) developed spatial models predicting occurrence of sage-grouse nests and brood-rearing sites and assessed contributions of specific habitats to recruitment. They found that some habitat that was selected by sage-grouse actually resulted in lower rates of nest success or CS, indicative of maladaptive habitat selection. Kirol et al. (2015) explored relationships between occurrence and survival at multiple spatial scales and predicted relative probability of female sage-grouse occurrence throughout the summer. Their approach to identifying habitats important to sage-grouse persistence was similar to ours as they used resource selection functions for all life stages weighted by their importance to $\lambda$. Their use of a fitness metric to identify habitats contributing to population persistence of sage-grouse represents a substantial advance in the assessment of habitat quality.

The LTRE approach we used allowed us to determine (1) the contribution of specific habitat features to regional population dynamics and (2) that population growth rate varies as a function of the proportion of different habitat types available. We also go a step further than most studies and decompose the variation in $\lambda$ into contributions from multiple vital rates. Our results reveal that certain habitats may be more important than others in regulating population growth rate. This result is driven in part by spatial association of nesting habitat to late-brood-rearing habitat. Females nesting too far from late-brood habitat failed to recruit young because of mortality associated with movement from nests to late-brood habitat.

Numerous populations experience periods when a specific resource limits a demographic rate. Limiting demographic rates will often represent some aspect of the recruitment process because productive processes, for example, egg production (Bolton 1991), growth (Sedinger and Raveling 1984, Manseau and Gauthier 1994, Sedinger et al. 2001), and lactation (Ricklefs et al. 1996), represent periods when demand is great for foods high in nutrient concentration (Williams 1966, Martin 1987). To the extent that gradients in availability of such foods exist, areas that provide these foods will limit rates of population growth if recruitment explains most of the variation in $\lambda$. In the example we present here, elimination of brood-rearing habitats representing only about 2% of the landscape (Atamian et al. 2010) would have eliminated recruitment, thereby increasing rates of population decline. The extremely limited distribution of late-brood-rearing habitat also reduced the value of substantial areas of otherwise potential nesting habitat. A link between mesic resources and sage-grouse population dynamics was also found by Donnelly et al. (2016). Despite encompassing only 2.4% of the landscape, mesic sites (wet meadows and riparian areas) influenced sage-grouse breeding distributions. We suggest that it may
Fig. 6. Surface representing the population growth rate (lambda) based on the contributions of all vital rates. Red represents habitats where $\lambda \geq 1$, and dark blue represents habitats where $\lambda \sim 0$. 
often be the case that relatively limited areas may regulate population dynamics over much larger landscapes.

**Habitat influence on dynamics of sage-grouse populations**

Probability of a site being selected for nesting was the second most important predictor of habitat influence on \( \lambda \), accounting for 21% of the variance in \( \lambda \). Females select nest sites based at least in part on vegetation characteristics that increase the probability that their clutches hatch and that their chicks will survive (Wallestad and Pyrah 1974, Gregg et al. 1994, DeLong et al. 1995, Kolada et al. 2009a, b, Gibson et al. 2015, 2016). In our study system, females selected nest sites with moderate to large amounts of sagebrush in areas with mid-high elevation and slopes, where they experienced greater breeding success (Gibson et al. 2016). This result may have been influenced by the very dry conditions reported during most of our study period (2003–2012). Mid-high elevation nesting habitat was more limited than habitat at lower elevation (Atamian et al. 2010), and in Eureka County, only 6% of the landscape offers this type of high-quality nesting habitat. The relatively small proportion of habitat that supports successful nesting results in a subset of the breeding population nesting in sub-optimal habitats where they experience lower probabilities of annual reproductive success (Connelly et al. 1991, Gibson et al. 2016).

Sage-grouse exhibit strong fidelity to specific sites in seasonal habitats (Berry and Eng 1985, Dunn and Braun 1985, Rolstad and Wegge 1988, Fischer et al. 1993). We are unsure of the mechanism that appears to restrict shifts in nesting location by female sage-grouse. Bergerud and Gratson (1988) hypothesized that successful females should exhibit fidelity to nesting sites in successive years, and unsuccessful females, if predation risk is high, should shift nesting areas. Our results suggest, however, that unsuccessful females do not change habitat preferences at sufficiently high rates to produce a shift in the mean quality of nesting habitat at the population level (Gibson et al. 2016).

Chick survival explained 62% of the variation in \( \lambda \) associated with the high spatial–temporal variation in this demographic rate (Gibson et al. 2017). Sage-grouse chicks require relatively high protein foods, primarily forbs and insects for growth (Patterson 1952, Klebenow and Gray 1968, Peterson 1970, Hagen et al. 2007, Blomberg et al. 2013a), and availability of these foods is positively associated with growth and recruitment (Johnson and Boyce 1990, Drut et al. 1994a). However, these foods are only available in sufficient quantities in mesic meadows and higher elevation shrub communities during the latter part of brood rearing in the Great Basin (Gregg and Crawford 2009, Gibson et al. 2017). Only broods that reached late-brood habitat were successfully fledged (Gibson et al. 2017), and this habitat represented only 2% of the entire study area (Atamian et al. 2010). Chicks hatching in nests further from late-brood habitat had a lower probability of being recruited, as chick mortality increased with increasing daily movements. Consequently, nests located further from late-brood habitat were of limited value for producing recruits. Increased CS when nesting close to high-fledged-survival habitat types is also present in ovenbirds (Streby and Andersen 2011) and golden-winged warblers (Streby et al. 2016). This result suggests that increasing the quantity, or improving quality, of late-brood habitat may have the most profound influence on population dynamics because doing so would enhance the value of surrounding nesting habitat.

Our result that recruitment was most limiting to population growth rate has been found in other studies (see also Dahlgren et al. 2016). Taylor et al. (2012) also found that FS and CS explained more of the variation in \( \lambda \) than did survival rates. Walker et al. (2008) found that adult female survival, FS, and CS were all equally important. Lastly, Johnson and Braun (1999) found that sage-grouse population growth in North Park, Colorado, was most sensitive to the combination of chick and juvenile survival. Studies of population dynamics of other Galliformes have also concluded that recruitment processes have greater potential to influence \( \lambda \) than female survival (Sandercock et al. 2005, Tirpak et al. 2006, Clark et al. 2008, Hagen et al. 2009). These findings are consistent with the hypothesis that variation in survival may be constrained by selection (Sæther et al. 1996, Sæther and Bakke 2000, Connelly et al. 2011).

Population growth rate estimates from our models are lower than those reported by...
Blomberg et al. (2013c). In our study area, ~8% of the landscape contributed to a population growth rate \( \geq 1 \) (Fig. 6). Our calculation of regional mean \( \lambda \) included large areas with both a low probability of use and low probability of producing recruits. The estimate of \( \lambda \) based only on areas supporting 75% of nests was 0.91, comparable to estimated \( \lambda = 0.93 \) based on lek counts (Blomberg et al. 2013c), suggesting that regional population dynamics are largely governed by a subset of females occupying a relatively small fraction of available habitat.

**Application of LTRE to conservation planning**

Application of the LTRE approach can improve understanding of the relationships between key habitat features and regional population dynamics. As importantly, this approach can assist conservation efforts by identifying specific habitats most likely to limit population growth. In sage-grouse, the species we use in our example, managers often focus on the largest vegetation communities used by the species (Connelly et al. 2000b, Crawford et al. 2004) likely because these communities are most conspicuous. It is true that over the long term such communities must be conserved for the long-term viability of the species, but in the short term, it may be more efficacious to enhance a very small proportion of the landscape used by sage-grouse, late-brood habitat in our example. We suggest the limiting nature of relatively small proportions of landscapes may be more common than is frequently thought. We provide a mechanism for assessing this hypothesis.

**Acknowledgments**

Funding was provided through a contract with the Nature Conservancy. J. Sedinger was supported by the Nevada Agricultural Experiment Station. We thank all individuals and organizations involved with sage-grouse research in Eureka County, as acknowledged in Gibson (2015). We would also like to thank Tom Dilts for all of his help with the use of ArcMap.

**Literature Cited**


Marchand, M. N., and J. A. Litvaitis. 2004. Effects of habitat features and landscape composition on the population structure of a common aquatic turtle in...


