A multispecies test of source–sink indicators to prioritize habitat for declining populations

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Abstract: For species at risk of decline or extinction in source-sink systems, sources are an obvious target for habitat protection actions. However, the way in which source habitats are identified and prioritized can reduce the effectiveness of conservation actions. Although sources and sinks are conceptually defined using both demographic and movement criteria, simplifications are often required in systems with limited data. To assess the conservation outcomes of alternative source metrics and resulting prioritizations, we simulated population dynamics and extinction risk for 3 endangered species. Using empirically based habitat population models, we linked babitat maps with measured site- or babitat-specific demographic conditions, movement abilities, and behaviors. We calculated source-sink metrics over a range of periods of data collection and prioritized consistently high-output sources for conservation. We then tested whether prioritized patches identified the babitats that most affected persistence by removing them and measuring the population response. Conservation decisions based on different source-sink metrics and durations of data collection affected species persistence. Shorter time series obscured the ability of metrics to identify influential babitats, particularly in temporally variable and slowly declining populations. Data-rich source-sink metrics that included both demography and movement information did not always identify the habitats with the greatest influence on extinction risk. In some declining populations, patch abundance better predicted influential babitats for sbort-term regional persistence. Because source-sink metrics (i.e., births minus deaths; births and immigrations minus deaths and emigration) describe net population conditions and cancel out gross population counts, they may not adequately identify influential babitats in declining populations. For many nonequilibrium populations, new metrics that maintain the counts of individual births, deaths, and movement may provide additional insight into habitats that most influence persistence.

Keywords: abundance, Black-capped Vireo, conservation, declining population, Greater Sage-Grouse, habitat prioritization, individual-based model, Ord's kangaroo rat, source-sink dynamics, source-sink metrics

Una Prueba Multiespecie de Indicadores Fuente - Sumidero para Priorizar el Hábitat para las Poblaciones Declinantes

Resumen: Para las especies en riesgo de declinación o extinción en sistemas de fuente – sumidero, las fuentes son un objetivo obvio para las acciones de protección del bábitat. Sin embargo, la manera en la que se identifican y priorizan los bábitats fuente puede reducir la efectividad de las acciones de conservación. Aunque las fuentes y sumideros se definen conceptualmente usando tanto los criterios de movimiento como los demográficos, generalmente se requieren simplificaciones en sistemas con datos limitados. Para evaluar los resultados de conservación de las medidas alternativas de fuentes y las priorizaciones resultantes, simulamos dinámicas poblacionales y el riesgo de extinción de tres especies en peligro de extinción. Con el uso de modelos de población basados en el bábitat, relacionamos los mapas de bábitat con las condiciones demográficas específicas de sitio o de bábitat, las babilidades de movimiento, y los comportamientos. Calculamos las medidas de fuente – sumidero en una gama de periodos de recolección de datos y priorizamos

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las fuentes constantes de producción alta para la conservación. Después probamos si los fragmentos priorizados identificaron a los bábitats que más afectaron la persistencia al removerlos y medir la respuesta de la población. Las decisiones de conservación basadas en diferentes medidas de fuente – sumidero y con recolecciones de datos de diferente duración afectaron la persistencia de las especies. Las series de tiempo más cortas dificultaron la babilidad de las medidas para identificar los bábitats influyentes, particularmente en poblaciones con variabilidad temporal y con declinación lenta. Las medidas de fuente – sumidero ricas en datos que incluyeron la información demográfica y de movimiento no siempre identificaron los bábitats con la mayor influencia sobre el riesgo de extinción. En algunas poblaciones declinantes, la abundancia de fragmentos predijo de mejor manera los bábitats influyentes para la persistencia regional a corto plazo. Ya que las medidas de fuente – sumidero (es decir, nacimientos menos muertes; nacimientos e inmigraciones menos muertes y emigraciones) describen las condiciones netas de la población y anulan los conteos poblacionales brutos, puede que no identifiquen adecuadamente los bábitats influyentes en poblaciones declinantes, muertes y movimientos individuales pueden proporcionar un entendimiento adicional de los bábitats que más influyen sobre la persistencia.

Palabras Clave: abundancia, canguro-ratón, conservación, dinámicas de fuente – sumidero, medidas de fuente – sumidero, población declinante, priorización de hábitat, urogallo de las artemisas, vireo gorrinegro

摘要:对于源~汇系统中面临种群下降和灭绝风险的物种,栖息地保护行动的一个显著目标是对"源"的保护。 然而,对"源"栖息地的识别和保护优先排序的方式可能会降低保护行动的有效性。"源"和"汇"理论上是根据 种群统计和迁移参数而定义,但数据有限的系统常常需要对其简化。为评估备选源的参数与其保护优先区的保 护成效,我们模拟了三个濒危物种的种群动态和灭绝风险。我们还用基于经验的栖息地种群模型,将栖息地地图 与测定的位点或栖息地特异性的种群统计参数、迁移能力和行为进行结合。我们计算了不同数据收集周期的 源~汇参数,并优先保护有持续高输出的"源"。接下来通过去除优先保护的斑块并测定物种的响应,我们检验了 这些斑块是否能代表对物种续存影响最大的栖息地。基于不同源~汇参数和数据收集周期的保护决策会影响物 种续存。短时间序列的数据阻碍了对重要栖息地度量的能力,特别是对短期内波动和缓慢下降的种群而言。包 含了种群统计和移动信息丰富的源~汇参数,并非能常常确定对物种灭绝风险影响最大的栖息地。在一些下降 种群中,斑块丰度更能预测物种在短时间内区域续存的重要栖息地。源~汇参数(如出生减去死亡;出生和迁入 减去死亡和迁出)描述种群净变化,抵消了总的种群数量计数,因此它们或许不能充分地确定下降种群的重要栖 息地。对许多非平衡的种群来说,可以对个体的出生、死亡、迁移连续计数的新参数或能帮助我们更好地了解 对物种续存影响最大的栖息地。【**翻译:初怡思;审校:魏辅文**】

关键词:源~汇动态, 栖息地保护优先性, 基于个体的模型, 丰度, 源~汇参数, 保护, 下降种群, 美洲跳鼠, 艾草松鸡, 黑顶莺雀

Introduction

Many species at risk of decline or extinction are suspected to operate in source-sink systems, wherein some areas are net exporters of individuals and others are net importers (Pulliam 1988). In source-sink systems, sources are an obvious target for habitat protection (Margules & Pressey 2000; Carroll et al. 2003); however, it is seldom possible to conserve all source habitats and habitat prioritization is often required. Identifying local populations as sources (Howe et al. 1991) or sinks can be an important first step in prioritizing habitats (Runge et al. 2006). Prioritizing consistent, high-output sources (hereafter strong sources), rather than sinks or areas that are not consistently sources, can further direct habitat conservation decisions (Heinrichs et al. 2016). However, the methods used to identify sources and sinks differ greatly among studies (Furrer & Pasinelli 2016), driven by the constraints of data collection and availability. Many methods are used to quantify source-sink dynamics, and little is known about the effectiveness of alternative

approaches to identifying key habitats that influence long-term persistence.

Defining sources and sinks is a data-intensive task that requires understanding the demographic and movement characteristics of each discrete population or habitat. Theoretical metrics generally define sources as areas where births outweigh the number of deaths and where births and immigrations outweigh deaths and emigrations (Holt 1985; Pulliam 1988). However, empirical methods of identifying sources and sinks often fall short of conceptual formulations due to challenges in collecting demographic and movement data (Peery et al. 2006; Furrer & Pasinelli 2016). Simple metrics are used in place of more data-intensive conceptualizations, including site-specific counts of terrestrial animals (i.e., abundance; Gilroy & Edwards 2017), local population growth rates, or a combination of abundance and inter-population movement rates (Furrer & Pasinelli 2016). These measures are prone to misclassifications of sources and sinks because they do not account for underlying demographic and movement mechanisms that result in differential population

conditions (Runge et al. 2006; Gilroy & Edwards 2017). Because simple source-sink metrics could result in the continued protection of sinks, some have cautioned against their use for prioritizing habitats for species conservation (e.g., Hanski 1998).

More complex source-sink metrics use mark-recapture data to estimate survival and fecundity and evaluate sources and sinks by virtue of the balance of births and deaths (e.g., Breininger & Oddy 2004; Walker et al. 2016). Others additionally evaluate patch contributions based on demographic and emigration information (Runge et al. 2006) or link multiple lines of inference (e.g., abundance, demography, movement exchanges, genetic conditions) to assess source-sink status (e.g., Caudill 2003; Andreasen et al. 2012; Contasti et al. 2013). As more types of data are used to define local population and habitat conditions, greater confidence is often awarded to source-sink assessments and their ability to identify source habitats that greatly influence population persistence (hereafter referred to as influential habitats). However, this assumption is largely untested.

Species at risk of decline and extinction are often in need of immediate action, and decisions on which population and habitats to protect are limited by available data and the resources to enact protection on the ground. Important conservation decisions are made on as little as a few years of data and considered robust if informed by 5-10 years of data. When few years of data are available, we often expect data-rich metrics (e.g., complex source-sink metrics) to better identify influential local habitats and populations than data-poor metrics (e.g., patch abundance), particularly if source-sink dynamics are temporally stable (Howe et al. 1991; Watkinson & Sutherland 1995; Gilroy & Edwards 2017). Yet stochastic or cyclic variation can obscure the long-term contributions of habitats to population persistence within short time frames (Runge et al. 2006; Contasti et al. 2013), leading to suboptimal habitat prioritizations and conservation outcomes. In particular, sources that behave like sinks when densities are high (i.e., pseudosinks) can exhibit high temporal variability (Watkinson & Sutherland 1995; Dias 1996; Johnson 2004). If sources are assessed only during times of low population density, rather than across a spectrum of population densities, their contributions to persistence could be overestimated.

To examine the degree of agreement among different prioritization approaches to identify habitats that strongly influence regional population persistence, we simulated habitat prioritizations and resulting population outcomes for 3 endangered species. Using empirical habitat-population models, we linked habitat maps with measured site-specific or habitat-type-specific demographic conditions, movement abilities, and behaviors. We calculated a range of source–sink metrics to create alternative habitat prioritizations. We resampled long-term simulated data to create short-term data series and recalculated the source-sink metrics. We then tested whether each metric prioritization (for each period) identified the most influential habitats by removing them from the system and simulating the population response. Those with the greatest response (i.e., increase in extinction risk) best characterized the most influential patches for longterm persistence.

We expected the most biologically detailed metrics and longer time series to identify habitats that contributed the most to persistence. Because the combination of demographic and movement information allows the disentanglement of gains via reproduction versus immigration (and losses via death versus emigration), we expected demography- and movement-informed metrics (BIDE) to best identify the most valuable habitats (e.g., Figueira & Crowder 2010). We expected demography-only and abundance metrics to be weaker in their ability to identify sources and influential habitats, particularly with short time series. In highly dynamic systems (i.e., those with high variation in intra- or interannual demography and population densities), we expected longer time series of data would be required to evaluate and prioritize populations (Gonzalez & Holt 2002; Loreau et al. 2013). We expected that the choice of metric and the duration of data collection would matter most for species with slow or moderate rates of decline, where subtle differences among local populations can accumulate over time to greater extent than in rapidly declining species. Finally, we expected high-abundance sinks to be important landscape elements that could outweigh the influence of some source habitats. In declining populations where a large proportion of the population occupies sink patches, the removal of patches containing a high abundance of animals could result in a large reduction in population size (Howe et al. 1991; Heinrichs et al. 2015). If extinction risk is more responsive to removals that limit population size than those targeting the most productive sources, abundance may better indicate the most influential habitats for short-term persistence.

Methods

Case Studies

We simulated movement, habitat selection, demography, and emergent source-sink dynamics for Black-capped Vireo (*Vireo atricapilla*) at Fort Hood, Texas (U.S.A.), and Ord's kangaroo rat (*Centrocercus urophasianus*) and Greater Sage-Grouse (*Dipodomys ordii*) in Alberta (Canada), all endangered species. These species represent a range of small and declining populations, landscape conditions, population variability, and ecological contexts in which source contributions to population persistence may differ. Populations differed in their rates of decline, degrees of stochastic variability, strength of source-sink dynamics, and were subject to different



Figure 1. Log change in Greater Sage-Grouse, Black-capped Vireo, and Ord's kangaroo rat abundance (left) and extinction risk (PE) (right) in scenarios without experimental removal of sources averaged over 100 simulation replicates. Ord's kangaroo rat female population size and PE were calculated for 100 time steps (beyond an initial 10-year burn-in period required for the model to approach the empirical population size; data not shown). Black-capped Vireo male abundance and PE were calculated for the same (10-110) time steps in both Brown-beaded Cowbird control (vireo low) and no cowbird control (vireo bigb) scenarios. Greater Sage-Grouse male and female abundance and PE were calculated for time steps 1-35.

drivers of source-sink dynamics (e.g., parasitism, lowquality habitat).

We used previously developed, spatially explicit, individual-based models and baseline predictions for our case study species: Ord's kangaroo rat (Heinrichs et al. 2010), Black-capped Vireo (Wilsey et al. 2014), and Greater Sage-Grouse (Heinrichs et al. 2018). All models made extensive use of empirical habitat and population data and were constructed in the HexSim simulation modeling environment (Schumaker et al. 2017). Habitat conditions (habitat availability, structure, habitat selection values, habitat quality, etc.) were linked to population outcomes through individual interactions with the landscape. Through this process, sources and sinks were emergent properties arising from individual movement and habitat selection decisions and the demographic consequences of residing in their chosen location or locations.

Slow Decline in a Small Population

In southeastern Alberta, Ord's kangaroo rat (hereafter kangaroo rat) occupies discrete sandy habitat patches, including actively eroding sand dunes or blowouts, partially stabilized sand dunes, and the margins of sandy roads (Gummer et al. 1997; Gummer 1999; COSEWIC 2006). Differential habitat quality among habitat types gives rise to source-sink dynamics (Heinrichs et al. 2010, 2015). High-quality source habitat includes actively eroding and naturally sandy areas where overwinter survival and predation risk is low. Conversely, low-quality sink areas include disturbed sandy areas and sandy road margins associated with high predation and parasitism risk, low forage quality, cold burrow temperatures, and low overwinter survival rates (Teucher 2007). The population is subject to substantial intra- and interannual population fluctuations in abundance (COSEWIC 2006), and high reproductive rates lead to the opportunistic occupancy of low-quality habitats within a year and variable overwinter survival causing interannual fluctuations (Kenny 1989; Gummer et al. 1997; Gummer & Robertson 2003). We used the baseline scenario developed by Heinrichs et al. (2010) to simulate long-term kangaroo rat population dynamics. Sources, sinks, and pseudosinks emerged as a result of differences in habitat quality among habitat types and high interannual variation in survival. This system represented the slowest rate of population decline and most gradual increase in extinction risk among the case-study systems (Fig. 1).

Rapid Decline in a Large Population

The Fort Hood military installation hosts >5000 male Black-capped Vireos (Cimprich & Heimbuch 2012; Wilsey et al. 2014). They occupy relatively discrete shrub habitat patches along with Brown-headed Cowbirds (Molothrus ater). Cowbirds often parasitize vireo nests, particularly in low-quality habitat (created by military training activities), which creates ecological traps (Remes 2000) that limit vireo persistence in the absence of cowbird control (Battin 2004; Wilsey et al. 2014). In baseline simulations, the number and strength of source habitats depended on the prevalence of nest parasitism (Heinrichs et al. 2015). In alternative scenarios, we simulated realistic scenarios of vireo population dynamics in the presence and absence of cowbird control (developed by Wilsey et al. 2014) and assessed source-sink dynamics under both alternatives (Heinrichs et al. 2015). In the absence of cowbird control, vireos were subject to high rates of nest parasitism (75% in high-quality and 85% in low-quality habitat) (Wilkins et al. 2006). Under cowbird control, vireos were subject to low rates of nest parasitism (5% in high-quality and 15% in low-quality habitat). The high parasitism scenario represented the scenario with the most rapid decline from the largest initial population size (Fig. 1). Environmental stochasticity was represented in fecundity, adult, and juvenile survival rates by annually drawing from representative distributions (Wilsey et al. 2014), resulting in a lesser degree of population variation than kangaroo rats. Sources could become pseudosinks with changes in local population densities. To assess the influence of population trends on model outcomes, we compared this rapidly declining population (high-parasitism) scenario with the stable-population (low parasitism) scenario.

Decline in a Small Population

In Alberta, the critically endangered Greater Sage-Grouse occupies a fragmented sagebrush landscape in southeastern Alberta, and they move seasonally among nesting, summer, and winter resource areas (Aldridge & Boyce 2007; Carpenter et al. 2010). As a sagebrush obligate species, habitat use is constrained by the availability of sagebrush cover, and site selection is influenced by fidelities to breeding, natal, and nesting locations and avoidance of development (Aldridge & Boyce 2007). Baseline simulations indicate that sources are embedded among sinks throughout the sage-grouse range in Alberta and evident in areas with high nest success and chick survival (Heinrichs et al. 2018). Conversely, sinks occur in high-selection habitats that have reduced chick survival or nesting success or both (Aldridge & Boyce 2007; Heinrichs et al. 2018). We used the baseline scenario developed by Heinrichs et al. (2018) to represent a very small population with an intermediate rate of decline (Fig. 1). Stochastic variation was represented in survival and reproduction by annually drawing from representative distributions (Heinrichs et al. 2018). This induced variable population densities through time but at a lesser magnitude than those observed for kangaroo rats.

Simulations

We linked empirical habitat-selection models developed for each species to empirically derived data describing population sizes, demographic rates, densities, range sizes, movements, and behavior. Within the spatially explicit individual-based models, simulated individuals dispersed among habitat areas to select a range with suitable resources or conditions. The quality of the range influenced population density, survival, and reproductive rates. For kangaroo rats, location-based outcomes were influenced by survival rates that were specific to different habitat types. For the sage-grouse model, we used demographic risk maps to specify locations with relatively higher and lower likelihoods of nest success and chick survival. In vireo scenarios, habitat suitability values were used to indicate areas of low- and high-quality habitat associated with relatively higher and lower nest parasitism (Supporting Information). All models included preemptive density-dependent habitat selection, wherein areas with the best resources relative to local competition were chosen and occupied. Models also included different magnitudes of environmental stochasticity that corresponded to the estimated variation in empirical survival or reproduction rates. The details of each model, including model starting conditions, are in Heinrichs et al. (2010), Wilsey et al. (2014), Heinrichs et al. (2018), Heinrichs et al. (2015), and outlined in the Supporting Information.

The source-sink status of a patch was determined by the collective experiences of individuals within a given habitat. Patch occupancy and abundance were influenced by patch size, shape, quality, location, landscape context, resources and other local conditions. Further, the source-sink status of a patch was influenced by species and population attributes including life-history characteristics, location-specific demographic rates, population densities, movement abilities, and site fidelities. For kangaroo rats and vireos, discrete (contiguous) patches were used as the spatial unit of sourcesink evaluation. For sage grouse, we used hexagonal pixels to summarize data on population size, births, deaths, immigrations, and emigrations (Supporting Information).

To classify sources and sinks and assess source strength, we used three different metrics, ranging in complexity and data requirements: productivity, BIDE, and abundance. Productivity quantified the total number of births minus deaths that were recorded for each patch. Patches in which the number of births exceeded deaths over the simulation period were deemed sources (and vice versa for sinks). In the BIDE metric, movement was explicitly counted in BIDE as (births + immigration) – (death + emigration) for a given patch. For abundance we calculated the mean number of individuals occupying each patch at the end of the year. For each species, we sorted and ranked patches based on their metric values. Strong sources were indicated by large positive values and prioritized for conservation. In each system, we selected a small proportion of sources to test the ability of metrics to reliably identify a subset of patches with strong influences on persistence. Prioritizations resulted in identifying 25 and 50 kangaroo rat patches, 12 and 23 vireo patches, and 10 and 20 sage-grouse patches, based on selecting the top-scoring 0.39% and 0.78% source patches, respectively (in alternative prioritization scenarios for each landscape). These arbitrary percentages were chosen to result in a reasonable number of patches for which habitat conservation actions could be implemented. To evaluate the sensitivity of results to the selected number of patches, we explored 2 alternative percentages. We expected to see greater differences in experiment outcomes when more patches were prioritized because the metrics characterize the strengths of weaker sources differently.

We used the full duration of the baseline simulations (i.e., 35 years of data for sage grouse and 100 years for kangaroo rats and vireos; 100 replicates) and associated metric results to represent the optimal amount of sourcesink data for each case study. To characterize how shorter time series of data collection could alter values derived from source-sink metrics and habitat prioritizations, we subsampled the baseline data sets and recalculated all metrics with only 2, 5, and 10 years of data (starting at time-step 1 and using 100 replicates). To quantify the importance of priority patches for long-term persistence, we simulated the regional population outcomes of removing priority patches as indicated by results of all 3 metric calculations evaluated over all 4 periods and the 2 source-proportion scenarios. Source habitats were removed from habitat maps by replacing them with nonhabitat matrix. Hence, simulated individuals could only use nontarget sources, including the remaining weaker sources, and all sinks. The probability of extinction (PE) (0 remaining individuals) was quantified through time (35 years for sage grouse, 100 years for kangaroo rats and vireos). We used 25 simulation repetitions so as to omit outliers while maintaining reasonable processing time. A quasi-extinction (QE) threshold of 1000 was used in place of PE for the low-parasitism vireo scenario because the population was stable. We plotted speciesspecific PE and QE results for each metric*period combination to compare the performance of each metric in identifying the most influential source habitats. Metrics that resulted in higher PE predictions, based on the removal of source habitats, identified habitats that had greater influence on long-term persistence. Conversely, metrics associated with lower PE predictions were less effective at identifying influential sources because their associated removals affected the population to a lesser degree.

Results

Slow Decline in a Small, Dynamic Population

With the removal of key sources, the small kangaroo rat population declined to near-certain extinction within 45–90 time steps (Fig. 2). Over 100 years of simulated data collection, PE was most sensitive to the removal of sources based on patch abundance, followed by productivity and BIDE. As the period of data collection was reduced to ≤ 20 years, metrics yielded increasingly dissimilar predictions. When data collection was reduced

to 5-10 years, the removal of key sources as predicted by the BIDE metric resulted in substantially lower risks of extinction than other metrics. At 2 years, source removals based on abundance resulted in the greatest PE (indicating the most discernment in selecting influential habitats), followed by productivity and BIDE. Abundance generally yielded the best predictions and was the most robust to temporal data limitations. The BIDE metric performed poorly in most periods, worsening with fewer years of data collection. Productivity prioritizations were particularly sensitive to short (i.e., 2- to 5-year) time series of data. When fewer sources were prioritized and tested with removal (i.e., 25 instead of 50), PEs were more alike but the metrics rankings were similar.

Rapid Decline in a Larger Population

In the very rapid decline of Vireos from the highest starting population size (under the high parasitism scenario), the removal of key habitats resulted in extinction in as little as 30 time steps; around 35 time steps there was a sharp threshold increase in PE (Fig. 3). Results were more similar among metrics through time compared to kangaroo rats, as the population rapidly trended towards extinction. Yet prioritizations still resulted in large differences in PE during time steps 30-40. For example, around time step 35, productivity and BIDE resulted in a PE of approximately 0.25 versus 0.70 for abundance. The greatest difference among metric results was observed with the longest time series. Among periods, prioritizations based on abundance were the most effective at identifying influential habitats and productivity was generally the least discerning. With reduced data-collection periods, metric predictions became more similar.

Stable, Large Population

When cowbird nest parasitism was controlled, the stable population of vireos did not result in extinction and had a low risk of falling to a quasi-extinction threshold of 1000 males (Fig. 4). Prioritization metrics consistently identified similar habitat patches that hosted a large number of birds, reducing the long-term population size. Resulting risks of quasi-extinction were similar among all prioritization metrics and periods.

Intermediate Decline in a Smaller Population

The removal of key sources from the moderate-sized sage-grouse population caused the risk of extinction to increase rapidly between 10 and 20 time steps (years 2010–2020) (Fig. 5). Differences among metric predictions were roughly similar for a given year. In the longest time series (35 years), extinction risk was most sensitive to habitats removed based on productivity. With only a few years of data collected, metrics informed by 2 years



Figure 2. Ord's kangaroo rat probability of extinction (PE) responses to key source babitat removals based on productivity, demographic- and movement-informed metrics (BIDE), and abundance-based source-sink metric prioritizations, calculated over 25 repetitions beyond the 10-year burn-in period. For a given year, the higher PE values indicate metrics with greater predictive value in identifying babitats with greater importance to regional population persistence.

of data yielded somewhat opposite results. Productivity poorly identified influential habitats, and BIDE best predicted the most influential patches. There was little spread among other metrics, particularly with 5 and 10 years of data collection.

Discussion

Our results indicate that the methods by which habitats are conserved could impact species management outcomes. Yet, the importance of the choice of metric depends on the nuances of the ecological system, including the rate of population decline and variability, duration of data collection, and the number of patches being prioritized. Simple metrics such as abundance outperformed more complex metrics in identifying key habitats that allow for persistence in some case studies, whereas complex metrics more accurately identified influential source habitats in others.

Simple Metrics and Patch Abundance

When source-sink dynamics are observed or suspected, management prioritizations often weigh protecting habitats with the largest number of animals against prioritizing putative sources. Simply prioritizing habitats based on abundance alone risks the misidentification of strong sinks, potentially compromising conservation outcomes (Hanski 1998). For example, abundance was a poor indicator of sage-grouse sources (65-100% misclassification rate). Sage-grouse abundance also ineffectively indicated influential habitats for regional persistence, particularly where grouse actively selected and flocked together in strong sink habitats with low nest success and chick survival (Aldridge & Boyce 2007).

By contrast, conserving high-abundance sinks can be crucial for short-term viability of other species (Howe et al. 1991; Heinrichs et al. 2015). For example, abundance generally identified the most influential habitats for the short-term persistence of the black-capped Vireo under high parasitism pressure. A very large



Figure 3. Black-capped Vireo probability of extinction (PE) under high Brown-beaded Cowbird parasitism and removal of important source habitat based on productivity, demographic- and movement-informed metrics (BIDE), and abundance-based source-sink metric prioritizations, calculated over 25 repetitions beyond the 10-year burn-in period (graphs truncated to years 25-55). For a given year, higher PE values indicate metrics with greater predictive value in identifying habitats with greater importance to regional population persistence.

number of Vireos (about 4000) occupied the targeted high-abundance patches, all of which were sinks (based on productivity and BIDE metrics in all periods). In comparison, minimal losses resulted from the removal of sources, indicating that small-capacity sources were less influential than large-capacity sinks in avoiding near-term extinction (also see Howe et al. 1991; Heinrichs et al. 2015).

Complex Metrics and Source-sink Equations

For sage-grouse, metrics that included demography better identified influential habitats than abundance. The importance of including demography could have been influenced by the population's size, rate of decline, lesser variation in 'patch' abundance, or the use of fine-scale demographic risk maps. Although BIDE outperformed simpler metrics when only a few years of data were collected, productivity resulted in equivalent conservation outcomes with longer data sets. This suggests that long-term evaluations (≥ 10 years of data) may not provide additional insight with the collection of movement data (Supporting Information).

Contrary to expectations (e.g., Runge et al. 2006), BIDE was not always the best predictor of influential habitats, even in more slowly declining populations. In the variable kangaroo rat system, BIDE required >20 years of data to better identify influential sources than simpler metrics. The BIDE metric also made underwhelming predictions for the rapidly declining Vireo population. This resulted in part because extinction risk can be more responsive to low population sizes than to the presence of strong, productive sources . Further, BIDE's difference equation does not explicitly characterize the local population size and thus does not fully convey the impact of a declining population.

The BIDE metric is calculated based on the difference between factors that cause the population to grow (births



Figure 4. Black-capped Vireo quasi-extinction probabilities (QE) under low Brown-beaded Cowbird parasitism and removal of important source babitat based on productivity, movement-informed metrics (BIDE), and abundance-based source-sink metric prioritizations, calculated over 25 repetitions beyond the 10-year burn-in period. For a given year, bigher QE probabilities (i.e., QE < 1000 males) indicate metrics with greater predictive value in identifying babitats with greater importance to regional population outcomes.

and immigration) and shrink (death and emigration) and calculates the balance among these factors. Because the counts of each event are effectively lost, a large but balanced local population can have a BIDE of 0 and a small unbalanced local population can have a very large (strong) BIDE value. Further, by subtracting emigrants, the BIDE equation can also undervalue small but highly productive sources that emit a large number of offspring that disperse elsewhere and support the declining regional population (e.g., small number of kangaroo rats in sand dunes). Net conditions and difference equations conveniently describe stable-state populations (Pulliam 1988); however, declining, nonequilibrium populations are not always regulated by density-dependent emigration and habitat selection (Caughley 1994), as assumed by traditional source-sink theory (Delibes et al. 2001). Hence, we suggest source-sink calculations based on difference equations may not always be appropriate for identifying influential habitats for declining populations. In prioritizing conservation of habitat for declining populations, both abundance and source-sink strength may

need to be weighed, rather than inferring influence based on the net source-sink conditions.

Habitat Prioritizations for Effective Conservation

The means by which habitats are prioritized for declining species in source-sink systems may matter most for species with gradual rates of decline and dynamic population fluctuations and species inhabiting large proportions of sink habitat (i.e., where abundance is a misleading indicator of source-sink status [Van Horne 1983]). Simulated populations of kangaroo rats persisted longer than Black-capped Vireo (high parasitism) and Greater Sage-Grouse populations, allowing this population more time to respond to habitat conditions than species with stronger declining trends. In more rapidly declining populations, the choice of metric still mattered, albeit over a shorter time frame (e.g., about 10-15 years for sage grouse and highly parasitized vireos). Large differences were observed among metrics within a given year,



Figure 5. Greater Sage-Grouse extinction probability (PE) influenced by removals of important source babitat based on productivity, demographic- and movement-informed metrics (BIDE), and abundance-based source-sink metric prioritizations, calculated over 25 repetitions (graphs truncated to years 5-35). For a given year, higher PE indicates metrics with greater predictive value in identifying babitats with greater importance to regional population persistence.

particularly for vireos under high parasitism pressure, indicating that the loss of key habitats can have dramatic short-term consequences and conservation efforts focused on improving high-abundance sinks could immediately increase persistence (Vandermeer et al. 2010). In removing key sources and testing the result on extinction risk, we evaluated how remaining habitat could compensate for the loss of influential sources. Metrics that identified irreplaceable habitats resulted in greater impacts on extinction risk, indicating the contribution of these habitats to long-term persistence. We did not test the sufficiency of key habitats to support long-term persistence. However, future research could remove all but the key habitats and evaluate resulting extinction risk. In general, empirical experiments (e.g., microcosms) that test the ability of source-sink metrics to identify influential habitats for persistence through removal experiments could increase confidence in our model-based evaluations of source-sink metrics. Population metrics that additionally calculate a patch's location relative to the regional network may help in the construction of simplified sourcesink metrics.

Our results indicate that in source-sink systems, metrics identifying the most influential patches may need to simultaneously weigh patch abundance and sourcesink contributions to persistence. Tailored metrics and new theory may be required to protect key habitats for declining species in source-sink systems and to understand the conditions under which data collection can be simplified. Our 3 different case studies represented a range of population conditions, rates of decline, life histories, and habitat selection behaviors; however, these do not represent all species and habitat conditions. To understand the ecological contexts in which new and existing source-sink metrics can indicate habitats that improve persistence, future analyses should explore a broader range of declining populations in source-sink systems.

Our results suggest that the choice and success of metrics may depend on a population's rate of decline, the degree to which temporal variability creates pseudosinks, and the proportion of the population occupying sink patches. Yet species differ broadly in how they select and compete for habitat and the degree to which they modify habitat through intensive use (Loehle 2012, 2013). Our species used contest competition to secure resources and remained at or returned to familiar habitats where resources were not permanently altered. Future analyses should explore the sensitivity of source-sink metrics to alternative competition and habitat selection mechanisms (e.g., scramble competition), seasonal group movements, resource depletion (i.e., 2way interactions among population and habitat conditions), and directional habitat modification. Together, the complexities of nonequilibrium populations with diverse life histories and nonstationary environments may require a re-envisioning of tools, metrics, and practical theory to identify the conditions under which measures of sourcesink dynamics can be reliably used to indicate habitats that benefit population persistence.

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Supporting Information

Additional model information (Appendix S1) is available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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