FINAL REPORT

Sources and Sinks: Elucidating Mechanisms, Documenting Patterns, and Forecasting Impacts

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14. ABSTRACT

A comprehensive understanding of source-sink dynamics can be critical for successfully managing at-risk species. We used field and modeling approaches to better understand the emergence and stability of sources and sinks and assess the implications of future system changes on population persistence. Modeling results identified the types of species and landscapes that are likely to exhibit strong source-sink dynamics and multi-species results indicated that management actions based on assumptions that sink habitats are generally harmful (or helpful) risk undermining conservation efforts. Black-capped vireo (*Vireo atricapilla*) field data and analyses documented source-sink patterns that were influenced by inter-annual variation and cowbird control on and near Fort Hood Military Installation in Texas. Most habitats outside of Fort Hood behaved like population sinks, and models indicated that persistence was sensitive to rates of inter-population exchange and the effects of future habitat restoration and climate change). Comparisons of black-capped and white-eyed vireos yielded insights into the unique limitations faced by black-capped vireos including a reduced breeding period and narrower use of habitat. This project highlights the importance of understanding source-sink dynamics in spatially-structured populations, as well as the need for applied source-sink theory and methods for conserving declining species in complex and changing landscapes.

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Executive Summary

Populations are often spatially structured, and understanding the effects of spatial structures such as sources and sinks, metapopulations, patchy networks, and isolated populations on population dynamics is critical for successful management. In this multi-part project, we used both field and modeling approaches to develop a better understanding of the emergence, stability, effective measurement of source-sink dynamics, as well as the management implications of source-sink dynamics for species at risk of decline or extinction. In the first phase (Phase 1) of the project, we modeled source-sink dynamics in multiple species to evaluate the factors that strengthen source-sink dynamics and to predict the implications of management decisions based on source-sink characterizations. The second phase (Phase 2) of the project identified sources and sinks for endangered black-capped vireos (*Vireo atricapilla*) on and around Fort Hood Military Installation in Texas by collecting multi-year field demographic data across spatially structured populations. In Phase 3, we developed a predictive modeling framework for the black-capped vireo using empirical data from Phase 2 to explore the contributions of sources and sinks and the effects of their differential management. A fourth phase of research (Phase 4) sought to compare the habitat and preferences of endangered black-capped vireo to more robust white-eyed vireo (*Vireo griseus*) populations near Fort Hood to aid in explaining their differential outcomes and the unique challenges faced by black-capped vireos. In examining source-sink dynamics from both theoretical and applied perspectives, this work resulted in a better understanding of the general drivers of source-sink dynamics and implications for conserving different kinds of source-sink populations in complex landscapes, as well as provided system-specific guidance on the management of black-capped vireos.

Source-sink modeling (Phase 1) yielded insights into the general species and landscape factors that influence the emergence and strength of ensuing source-sink dynamics within metapopulations. In a series of controlled experiments using a spatially explicit, individual-based model, we varied patch quality, patch size, the dispersion of high and low quality patches, population growth rates, dispersal distances, and environmental stochasticity in a factorial design. **Our results suggest that species capable of rapid growth, occupying landscapes with patches of disparate qualities, with interspersed higher and lower quality habitats, that also experience relatively stable environments (i.e. fewer negative perturbations), are more likely to exhibit strong source-sink dynamics.** Strong source-sink dynamics emerged under diverse combinations of factors, suggesting that simple inferences of process from pattern will likely be inadequate to predict and assess the strength of source-sink dynamics.
In a second analysis, we assessed the contribution of sinks to regional population persistence of declining populations by simulating source-sink dynamics for three very different endangered species: black-capped vireos at Fort Hood, Texas, Ord's kangaroo rats (*Dipodomys ordii*) in Alberta, and northern spotted owls (*Strix occidentalis caurina*) in the northwestern United States. We used empirical data from these case studies to parameterize spatially explicit individual-based models. We then used the models to quantify population abundance and persistence with and without long-term sinks. The contributions of sink habitats varied widely. Sinks were detrimental, particularly when they functioned as black-hole sinks for declining populations (e.g., Alberta's Ord's kangaroo rat) and benign in robust populations (e.g., black-capped vireos when brown-headed cowbird, *Molothrus ater*, parasitism was controlled). Sinks—including ecological traps—were also crucial in delaying declines when there were few sources (e.g., in

black-capped vireo populations with no cowbird control). Sink contributions were also nuanced; for example, sinks that supported large, variable populations were subject to greater extinction risk (e.g., northern spotted owls). In each of our case studies, new context-dependent sinks emerged, underscoring the dynamic nature of sources and sinks and the need for frequent re-assessment. **Our results imply that management actions based on assumptions that sink habitats are generally harmful or helpful risk undermining conservation efforts for declining populations.**

In a third analysis, we assessed population outcomes of habitat conservation based on different source-sink characterizations and patch abundance for black-capped vireos, kangaroo rats, and greater sage-grouse (*Centrocercus urophasianus*) in Alberta. **Our results indicate that simple metrics such as local abundance can identify important habitats for short-term persistence, but their ability to detect sources and important habitats for long-term persistence is generally poor.** In some rapidly declining populations, the preservation of high abundance sinks can yield a more positive impact on short-term persistence than smaller key sources. As source populations are generally needed for recovery and longer-term persistence, a balanced approach that considers both habitats that are important for short-term (e.g., some sinks) abundance, while preserving habitats that are required for long-term persistence, is likely to yield the greatest conservation benefit.

Documenting source-sink patterns (Phase 2) of black-capped vireos in the field near and on the Fort Hood Military Installation in central Texas involved monitoring seven vireo populations on Fort Hood and nearby private and state lands that varied in vegetation and nest parasitism rates. From data collected on our study sites and from an additional four populations monitored by the Fort Hood Natural Resources Management Branch, we calculated measures of fecundity and survival and assessed populations as sources or sinks using population matrices. Sites with cowbird control had greater overall nest success; most source populations had cowbird control in all study years. To investigate tradeoffs in habitat selection among life stages (i.e. nesting, juvenile survival) and inform the management of breeding populations, we monitored breeding territories and tracked juvenile vireos using radio-telemetry. Vireos in general selected shrubland and forest habitats; canopy cover may present a tradeoff that improves juvenile survival but reduces breeding success. We recorded vocalizations at vireo nests and found little evidence for tradeoffs in social communication and mediation of parasitism or predation risk. Vireos did benefit, however, by optimizing temporal patterns in vocalizations. Finally, we documented some flexibility in mating strategy through an observation of polygyny in a territorial male vireo. **We conclude that successful management of vireo breeding populations will consider habitat needs across the entire reproductive cycle, cowbird control will increase nest success, and breeding sites that provide nearby or adjacent forested areas may improve survival of recently independent juveniles.**

To predict future black-capped vireo source-sink patterns and impacts (Phase 3), we compiled empirical site and demographic information (including data gathered in Phase 2) within a spatially explicit, individual-based model. This data-driven vireo model integrated a previous habitat suitability model (from RC-1541, "Forecasting the Relative and Cumulative Effects of Multiple Stressors on Populations") with location-specific demography, territory sizes, and life history information to model the current and potential future abundance and dynamics of vireos

across Fort Hood and surrounding counties. We explored the impact of alternative rates of exchange among regional breeding populations as well as the potential differential contributions of sources and sinks to regional vireo viability. Furthermore, we explored the effects of increased off-base cowbird control and habitat restoration on public lands on regional source-sink dynamics and population trajectories. Lastly, we assessed how climate change, through its effects on survival and reproduction, could affect vireo abundance and source-sink dynamics using results from a climate-demography analysis (Phase 3, task 2). We found that most habitats off of Fort Hood behaved like population sinks and that rates of exchange among on- and off-base populations can measurably alter regional population outcomes and source-sink dynamics. The stability of source-sink characterizations differed with the type of system change. **Management actions may need to weigh interventions that improve regional abundance against those that alter regional source-sink dynamics as abundance and source-sink states are sensitive to different kinds of system changes. Climate change may result in general population increases, suggesting that future source-sink dynamics may be driven more by density-dependence and inter-population dispersal than contemporary populations.**

To better inform the management of black-capped vireos, we sought to understand in what ways this species differs from the closely related and more numerous white-eyed vireo occupying the same landscape (Phase 4). We monitored both species across several study sites on Fort Hood and in the surrounding counties and captured, banded, and monitored individuals. We mapped territory locations and calculated sizes, observed nesting and foraging behavior, counted eggs and fledglings, calculated survival, tracked movement with radio telemetry, and conducted presence-absence surveys in different habitat types. Our results indicate that a number of habitat, life history, and behavioral factors may be important in defining differential outcomes for vireo species on Fort Hood. **We found substantive differences in habitat use, return dates, reproductive behaviors, and vocalizations that may help explain the opposite population trajectories of black-capped and white-eyed vireos.** White-eyed vireos used a wider variety of habitat types than black-capped vireos, which may confer survival and reproductive advantages over more limited habitat selection. White-eyed vireos arrived on the breeding grounds and initiated nests earlier than black-capped vireos, possibly avoiding brown-headed cowbird parasitism and reducing the risk of nest depredation by snakes, which increase as the breeding season progresses. White-eyed vireos also continued to breed later in the season, allowing for additional nesting attempts. White-eyed vireos were also less conspicuous during nest building and visitation, which may aid in concealing nests from cowbirds.

Background

Understanding the structure and dynamics of populations is a key component of successful management (Soulé 1987). Populations that are spread across heterogeneous landscapes may take on a number of spatial structures, including metapopulation structures, source-sink structures, patchy yet highly connected populations, and isolated populations (Levins 1969, Wiens 1976, Pulliam 1988, Hanski and Gilpin 1997, Thomas and Kunin 1999). Identifying and understanding source-sink dynamics can be particularly important for management. Sources can

be defined as populations with intrinsic growth rates great enough to produce a surplus of individuals, some of which then emigrate to other populations (Runge et al. 2006). By contrast, sinks are populations that are not self-sustaining and require immigration to persist (Pulliam 1988). The concept can be extended to habitat patches, territories, or portions of the landscape. Thus, particular areas or patches of habitat can be considered to be sources or sinks (e.g., Breininger and Oddy 2004).

Although differential habitat quality is the basic factor that structures source-sink dynamics (Pulliam 1988, Dias 1996), there are several factors that can differentially affect reproduction and survival spatially and several other factors that can influence the strength of sources and sinks (Dunning et al. 1992). Competitors, predators, parasites, and disease have the potential to generate source-sink dynamics if their effects are spatially patterned. In addition, landscape structure and composition can affect the strength of sources and sinks and hence their impact on a population as a whole. For example, the distance between sources and sinks and the relative proportion of sources and sinks in a landscape can affect the strength of source-sink dynamics (Pulliam 1988). Other factors such as edge effects, matrix permeability, and dispersal abilities and modes have the potential to affect immigration and emigration rates and hence source-sink dynamics. In some species, even social structure can enforce source-sink dynamics (Marzluff and Balda 1989). Understanding the relative influence of these factors on the strength of source-sink dynamics is an important component of managing spatially structured populations.

Sources and sinks can take various forms depending on their ecological context. For example, a sink can be an "ecological trap" when individuals are attracted to low quality sinks over higher quality habitats (Dwernychuck and Boag 1972, Battin 2004). Evidence for ecological traps can be found in a number of studies (Battin 2004). Because the traps attract individuals, they have the potential to have significant negative effects on a population. Ecological traps are the result of poor habitat selection generally resulting from novel conditions to which a species has not had sufficient time to adapt. For example, due to the expansion of cattle grazing across the United States, brown-headed cowbirds have expanded their range into new areas. The cowbird is a nest parasite, laying eggs in the nests of other species and leaving other birds to raise the cowbird nestlings at the expense of the hosts' own offspring. Thus, cowbirds have the potential to generate ecological traps by converting what might still be perceived as relatively high quality habitat into a sink (Johnson and Temple 1986).

Although ecological traps can have strong negative effects on a population, not all sinks are ecological traps and not all sinks have negative effects on a population. For some sinks, there may be no back-migration from the sink to sources, but for other sinks, some individuals may move from the sink to source habitats (Dias 1996). These "leaky sinks" from which individuals do move to source habitats can serve as reservoirs of individuals that can then rescue a source if it collapses. Such sinks have the potential to reduce the temporal fluctuation within sources (Foppen et al. 2000).

Detecting sources, sinks, and ecological traps can be difficult. Relatively long-term demographic monitoring is often necessary to observe meaningful trends in birth, death, and immigration rates (Dias 1996). Similarly, observing reproductive output in a given habitat patch in a single year will likely provide little clue as to whether that habitat serves as a source or a

sink because environmental variability can result in reproductive failure or high fecundity in both source and sink habitats in a given year. Additionally, source habitats can be misclassified as sinks when high immigration rates (or a temporally abundant resource) increases a population above the local carrying capacity, resulting in a high number of deaths relative to births. When immigration rates are low, such pseudo-sinks serve as sources (Watkinson and Sutherland 1995). Thus, the temporal scale over which demographics need to be monitored to identify sources and sinks will depend, in part, on the nature of environmental variability.

In addition to birth, death, immigration, and emigration rates, other factors such as population turnover rates, temporal variability in population sizes, or autocorrelation in population size may prove to be useful indicators of source-sink dynamics in some systems (e.g., Howe et al. 1991, Beshkarev et al. 1994, Winker et al. 1995). Whereas environmental variability on a relatively fine time scale can make detecting sources and sinks difficult, variability on a broader time scale can help define the nature of source-sink dynamics. For example, for many organisms, habitat quality depends on a dynamic interaction between disturbances such as wind and fire and the succession of vegetation communities. For these organisms, habitats are ephemeral, changing in quality over time and space in a shifting mosaic. Over long enough time scales, all landscapes are dynamic and the nature of sources and sinks can change. For example, if the proportion of habitat that serves as a sink grows large enough, it is possible to destabilize the source-sink dynamic (Dias, 1996).

Human activities that alter landscapes and/or patterns of environmental variability have the potential to change source-sink dynamics. For example, fire suppression, introduced species, and land-use change all have the potential to alter landscape pattern, environmental variability, habitat quality, and dispersal. In addition, climate change not only has the potential to alter source-sink dynamics by altering vegetation structure, food resources, and predator and competitor communities (Schneider and Root 2002, Parmesan 2006), but also by altering patterns of environmental variability (e.g., weather, fire regimes, hydrology). Managing for populations that are prone to source-sink dynamics requires an understanding of which patches, habitats, or subpopulations are sources and which are sinks; how those sources and sinks affect the population; and the implications of differentially managing those sources and sinks. Here, we use a combination of population modeling and field studies to improve our understanding of these factors for spatially structured species in general, as well as specifically for the black-capped vireo near the Fort Hood Military Installation in Texas.

The Black-capped Vireo

The black-capped vireo is a small shrub-nesting bird. Once stretching across much of Texas, Oklahoma, and reaching into southern Kansas, its range is now restricted to a relatively small number of somewhat isolated populations in Texas, Oklahoma, and northern central Mexico. The black-capped vireo requires early successional vegetation consisting of broad-leaved deciduous shrubs with leafy cover that extends to the ground. In some parts of their range, where water is more limiting, shrubs form the climax vegetation community and thus habitat is more stable. However, over much of their range, fire has historically created dynamic habitat patterns. In western Texas, flooding has similarly created temporally patchy riparian habitats. To date, much of the habitat of the black-capped vireo has been converted to agriculture,

developed, or has grown into taller woodlands as a result of widespread fire suppression. The species was listed as endangered by the U.S. Fish and Wildlife Service in 1987.

In addition to habitat loss, nest parasitism by brown-headed cowbirds has posed a significant threat to black-capped vireo populations in the past (Garber 1961, Grzybowski 1995) and potentially continues to do so for some populations today. Parasitism rates were estimated to be at least 90% in some populations (Tazik and Cornelius 1993, Kostecke et al. 2005). A cowbird trapping and removal program initiated in 1988 at Fort Hood has resulted in decreased parasitism rates. Nest success rates of less than 5% in 1988 and 1989 rose to over 40% by 1996 (Weinberg et al. 1998). Cowbird control is likely responsible for the rebound of the Fort Hood vireo population from 87 breeding males in 1987 (Tazik et al. 1993) to an estimated 7184 (95% CI 5787-8919) breeding males in 2006 (Cimprich 2009). Given the degree of recovery, and the cost of cowbird control, Fort Hood has been experimenting with relaxing cowbird control on the western half of the base. The implementation of cowbird control on Fort Hood may have converted this large population from a sink to a source. However, there are several other populations within the species' range that may act as sinks. Both differential habitat quality (Noa et al. 2009) and differential rates of cowbird parasitism may be largely responsible for source-sink dynamics in this species.

Two genetics studies have indicated that individual populations of black-capped vireos are relatively isolated (Fazio et al. 2004, Barr et al. 2008). However, the two studies come to different conclusions about the potential for directional gene flow and source-sink dynamics. In addition, recent recaptures of banded individuals indicate some natal dispersal between populations (Cimprich et al. 2009). In addition to differences in habitat quality and cowbird parasitism, there are several other factors that likely influence source-sink dynamics in the vireo. Given that habitat quality depends, in part, on the seral stage of the vegetation community, the amount and distribution of higher quality and lower quality habitat patches will largely be dictated by rates of succession, fire return intervals, and fire behavior. Both fire and rates of succession are driven, in part, by climate. Thus, climate change will likely influence vegetation quantity and quality through its effects on fire regimes, temperature, precipitation, and drought. Climate change will also likely affect demography through physiological challenges as well as indirectly through impacts on vegetation and interspecific interactions.

Beyond climate change, source-sink patterns in vireo habitat can also be altered by differential cowbird control and habitat restoration. In addition to the effects of these individual factors on source-sink dynamics, there may be interactions between factors that accentuate or diminish their impacts and result in spatial and temporal changes in source-sink dynamics and regional population outcomes. For example, if restoration efforts on public lands are not accompanied by cowbird control, these new habitats may become sinks or ecological traps, yielding net population losses rather than gains. Successfully managing the black-capped vireo across its range will require an understanding of the relative contribution of different sources and sinks to the population as well as an understanding of how climate change, cowbird parasitism, cowbird control, and habitat restoration can affect the population as a whole. Such an understanding will allow managers to make critical decisions about how to manage specific populations, where to focus habitat restoration and cowbird-control efforts, and potentially, how to develop adaptation strategies for addressing climate change.

The White-eyed Vireo

Congeneric black-capped and white-eyed vireos occupy similar habitat, are both sensitive to cowbird parasitism, and yet exhibit opposite population trajectories. Hence, important behavioral and demographic differences must exist between these species to account for their relative abundances. Existing literature indicates that the white-eyed vireo occupies a greater range of habitat types (including those with greater tree cover) than the comparatively rare black-capped vireo. If so, the white-eyed vireo may maintain larger, better connected regional populations, enabling larger populations to exist on the landscape. Yet other important ecological differences may also contribute to the success of the white-eyed vireo. By contrasting habitat, behavioral, and demographic aspects of the two species' population ecologies, we will better identify the specific aspects of the black-capped vireo's source-sink dynamics that relate to its endangered status. In doing so, our results will address the aspects of the black-capped vireo's source-sink dynamics that uniquely limit its population on DOD lands.

Population-modeling framework (HexSim)

Much of the modeling in this project makes use of HexSim. HexSim, originally PATCH (Schumaker 1998), is a computational environment for assembling spatially-explicit, individual-based simulation models. It was designed to evaluate the consequences for terrestrial wildlife populations of multiple interacting stressors, including—but not limited to—landscape and climate change, natural and anthroprogenic disturbance, species interactions, disease, and environmental toxins. HexSim does not have fixed data requirements. Rather, it allows users to develop more or less complex simulations based on the quality of data available. The development of HexSim was funded by SERDP (Sustainable Infrastructure Project #SI-1541) and previous versions of the model have been used to simulate populations of Red-cockaded Woodpeckers, desert tortoises, Black-capped Vireos, kangaroo rats (Heinrichs et al 2010), grizzly bears and gray wolves (Carroll et al. 2004), fisher and lynx (Carroll, 2007), amphibians (Rustigian et al. 2003), and several other vertebrate species (Lawler and Schumaker 2004, Schumaker et al. 2004). Here, we describe the utility and flexibility of the HexSim modeling framework, and provide examples of models constructed with HexSim that demonstrate its applicability across a range of life histories, landscapes, and disturbance regimes.

HexSim is unique in being the only spatially explicit individual-based modeling environment capable of creating a wide range of species and system-specific population forecasts. HexSim provides its users with a large variety of mechanisms that can link simulated individuals with maps of habitat and environmental conditions, and other drivers of population dynamics (Figure 1). These features enable HexSim to simulate realistic population responses to static and dynamic future landscape conditions, thus supporting data-driven management assessments. The ability to capture a wide range of life histories and habitats, individual traits, movement strategies, genetics, and spatially distributed stressors add to the novelty and utility of this framework.

HexSim offers advantages over other software tools in that it is:

- User-friendly, with a complete graphical user interface (GUI), avoiding the use of large data entry tables.
- Mechanistic. Unlike statistical or probabilistic models, mechanistic models can be more robustly used for forecasting trends into the future. HexSim provides scientists with a way to develop defensible forecasts that inform management strategies addressing future changes in environmental conditions and disturbance regimes.
- Spatially-explicit. Much of ecological theory was developed using non-spatial mathematical models. The real-world application of aspatial theory to inform actual conservation and management decisions has repeatedly illustrated the shortcomings inherent in non-spatial models of complex ecological systems. Today, spatially-explicit models have become essential tools for both research and management.
- Individual-based. Only individual-based models can mechanistically simulate species-interactions like predation and competition, tally the consequences of sub-lethal exposure to toxic substances, track disease spread, or forecast changes in genetic diversity over time, etc.
- Multi-population and Multi-stressor. Most populations of conservation concern are impacted by multiple interacting natural and anthropogenic stresses that vary in space and time. HexSim models can address this level of complexity, and help researchers forecast the consequences of human activities on populations *in the real world*, not a laboratory.
- Eco-evolutionary. Plant and animal populations must be both demographically and genetically healthy to persist. HexSim is the only sophisticated demographic modeling framework that incorporates an advanced genetics toolkit. Other demographic models ignore genetics entirely, incorporate it in a cursory fashion, or are non-spatial. The few tools that carefully examine population genetics contain minimal demography.
- Defensible. Although the HexSim user-base is still growing, this modeling platform has been applied in a wide array of different peer-reviewed modeling studies. HexSim is now a mature tool that has been extensively tested over a period exceeding ten years. HexSim has also been subjected to extensive internal and external QA and peer review, and has been broadly accepted by the international scientific community. HexSim has already been used in several studies with direct policy implications, which has greatly increased the evaluation of its reliability and usability. Further, it has been used as a teaching tool in graduate and undergraduate ecology classes, has formed the basis of numerous graduate dissertations, and been used as an integral research tool in grant-funded research.

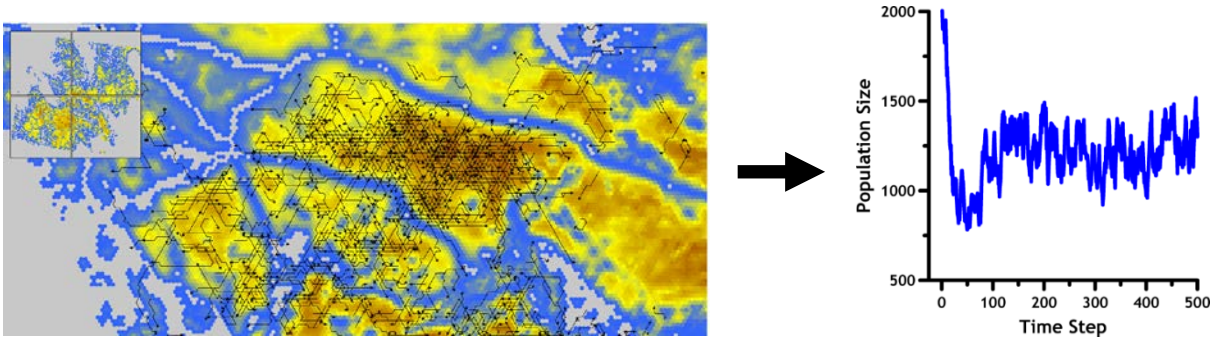

Figure 1. An illustration of HexSim movement (left) and population dynamics (right).

HexSim offers a flexible platform that is frequently used to construct simulation models for populations of concern. HexSim is also used to advance ecological and genetic theory (Heinrichs et al. 2016a, 2016b, Day and Schumaker *in prep*.), to study disease spread, and in a variety of other research areas. As there are no specific data requirements, parameter values, data sources, acceptance criteria, or other constraints, models can be constructed for a wide range of species (there are existing models for mammals, birds, reptiles, amphibians) and systems (terrestrial, aquatic, riverine, and benthic environments. Every process in a HexSim model is selected by users, and every parameter value is supplied when the simulation is developed. Thus HexSim models can be designed to respect data limitations, being complex and biologically nuanced when more data is available, and parsimonious or even hypothetical when data is limited. HexSim models are built around a user-defined life cycle. The life cycle consists of a sequence of life-history events including survival, reproduction, movement, resource acquisition, species interactions, and many other actions that can be customized to the species and context. HexSim uses spatial data (i.e., user-supplied maps) to capture landscape structure, habitat quality, stressor distribution, and other types of information. Population structure is represented in initial spatial population distributions and changes through time and with movement, habitat selection and interaction with spatial stressors. Hence, HexSim can accommodate a range of landscapes and population structures – from discrete patches, to continuously varying terrestrial habitat quality (Figure 2), and aquatic (intertidal, benthic) and stream networks.

HexSim applications begin with the definition of one or more wildlife populations. Each population has a set of parameters that define resource needs, space use, traits, memory, genetics, and habitat maps. Each population is also assigned a life cycle composed of multiple events (e.g., movement, habitat selection, survival, reproduction). Outputs from HexSim include records of population size and tabular and pixel-based summaries of births, deaths, movement, and other processes. The model also produces map-based outputs depicting spatial results including observed demographic sources and sinks.

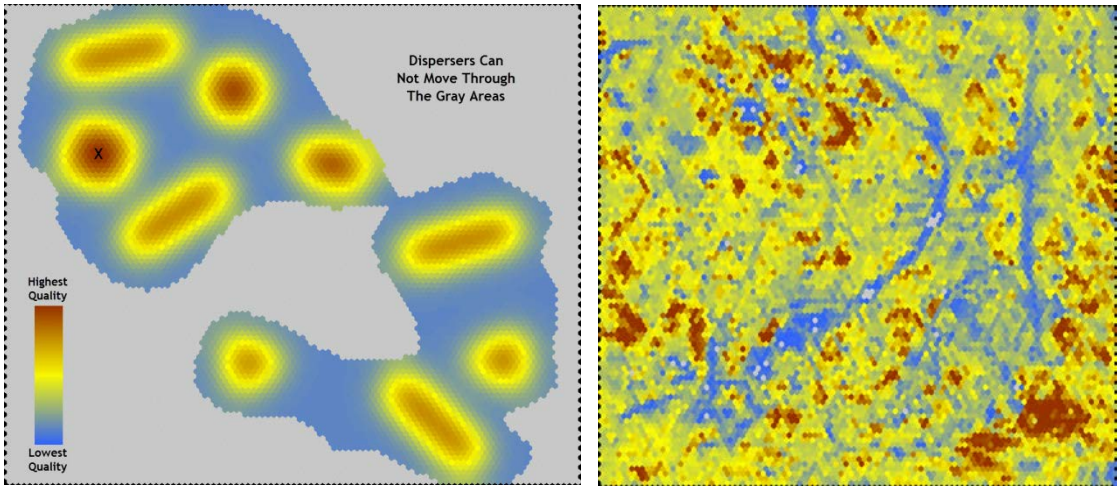

Figure 2. Example landscapes that can be used in HexSim. The left frame depicts patchy and discrete habitat surrounded by low quality (blue) and inhospitable matrix (gray). The right frame represents habitat with continuously varying habitat quality.

HexSim applications that have been developed to explore source-sink theory further highlight the model's utility. Source-sink models have traditionally represented landscapes as arrays of habitat patches, and then prescribed both patch source-sink attributes, and the rate at which individuals move between patches. Such models often do little more than illustrate the system-wide dynamics of a model whose behavior was dictated by its author. In contrast to other population models such as RAMAS and modeling approaches such as graph theory, HexSim does not assume a source-sink or metapopulation structure. One does not design a network of sources and sinks, but rather provides landscapes and individuals and then tracks the spatial patterns in survival, reproduction, immigration, and emigration that emerge from the interactions among landscape patterns and ecological processes. In addition to using this framework for Phase 1 of the study, we also used HexSim to develop a careful mechanistic simulation of the Black-capped Vireo system in Phase 3 of the study. In general, the development of HexSim and derived source-sink models, has highlighted where ecological theory is too simplistic and is helping to develop useful theory for unstable and complicated ecological systems (Heinrichs et al. 2010, Heinrichs et al. 2015b, 2016b, Schumaker et al. 2014). It has also led to specific management recommendations for the management of source-sink populations in a range of systems (Heinrichs et al. 2010, 2015a, Schumaker et al. 2014), and uniquely provides the means to spatially forecast emergent source-sink dynamics.

Basic models constructed in the HexSim modeling framework are often easily expanded to incorporate the elements needed to spatially evaluate population sources and sinks. Source-sink dynamics emerge from the collective demographic and/or movement experiences of individuals in user-defined locations in the landscape. As such, HexSim's source-sink analysis tools are particularly well suited to populations with measured site-specific demographic and movement rates, although source-sink dynamics can be evaluated with lesser amounts of data. Expansion of models to evaluate source-sink dynamics consists of developing a "patch" map (or similar unit to summarize population outputs), recording individual locations during simulations and using

productivity and projection matrix tools (reports) to summarize source-sink population conditions in each patch (Figure 3). The use of productivity and projection matrix tools are described in the online tutorial (http://www.hexsim.net/resources/tutorials/source-sink-tutorial), which provides a step by step guide for building the model components necessary to simulate and evaluate source-sink dynamics in a generic system. The tutorial is followed by a real example using the Northern spotted owl with includes creating user-defined units of source-sink summary and the use of (supplied) accessory programs to combine different data reports. These instructions can be used to modify any HexSim-created model to evaluate and map emergent source-sink dynamics

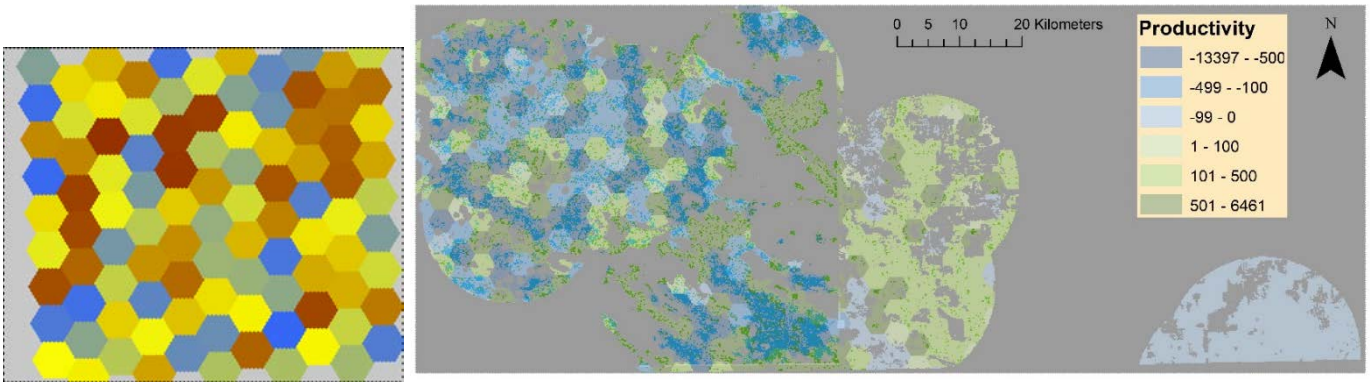

Figure 3. Source-sink map (right) created for Greater sage-grouse using HexSim's projection matrix and productivity reports and hexagonal source-sink sampling patches (left) using the HexSim utility 'build hexmap hexagons', as described in the online tutorial.

References

Barr, K. R., D. L. Lindsay, G. Athrey, R. F. Lance, T. J. Hayden, S. A. Tweddale, and P. L. Leberg. 2008. Population structure in an endangered songbird: maintenance of genetic differentiation despite high vagility and significant population recovery. Molecular Ecology 17:3628-3639.

Battin, J. 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. Conservation Biology 18:1482-1491.

Beshkarev, A. B., E. S. Jon, P. Angelstam, H. Andrén, and A. B. Blagovidov. 1994. Long-term dynamics of hazel grouse populations in source- and sink-dominated pristine taiga landscapes. Oikos 71:375-380.

Breininger, D. R., and D. M. Oddy. 2004. Do habitat potential, population density, and fires influence scrub-jay source-sink dynamics? Ecological Applications 14:1079-1089.

Carroll, C., R. F. Noss, P. C. Paquet, and N. H. Schumaker. 2004. Extinction debt of protected areas in developing landscapes. Conservation Biology 18:1110-1120.

Carroll, C. 2007. Interacting effects of climate change, landscape conversion, and harvest on carnivore populations at the range margin: marten and lynx in the northern Appalachians. Conservation Biology 21:1092-1104.

Cimprich, D. A. 2009. Monitoring of the black-capped vireo during 2008 on Fort Hood, Texas. Endangered species monitoring and management at Fort Hood, Texas: 2008 annual report. The Nature Conservancy, Fort Hood Project, Fort Hood, Texas.

Cimprich, D. A., C. W. Sexton, P. K. McDowell, G. Lasley, and W. S. Simper. 2009. Long-distance dispersals records for the black-capped vireo. Bulletin on the Texas Ornithological Society 42:44-47.

Dias, P. C. 1996. Sources and sinks in population biology. Trends in Ecology & Evolution 11:326-330.

Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex habitats. Oikos 65:169-175.

Dwernychuck, L. W. and D. A. Boag. 1972. Ducks nesting in association with gulls: an ecological trap? Canadian Journal of Zoology 50:559-563.

Fazio, V. W., D. B. Miles, and M. M. White. 2004. Genetic differentiation in the endangered black-capped vireo. Condor 106:377-385.

Foppen, R. P. D., J. P. Chardon, and W. Liefveld. 2000. Understanding the role of sink patches in source-sink metapopulations: reed warbler in an agricultural landscape. Conservation Biology 14:1881-1892.

Garber, J. W. 1961. Distribution, habitat requirements, and life history of the black-capped vireo (*Vireo atricapillus*). Ecological Monographs 31:313-336.

Grzybowski, J. A. 1995. Black-capped Vireo (*Vireo atricapillus*) *in* A. Poole and F. Gill, editors. The Birds of North America, No. 181. The Academy of Natural Sciences; Washington D.C.: The American Ornithologists Union, Philadelphia, PA.

Hanski, I. A., and M. E. Gilpin. 1997. Metapopulation biology: ecology genetics, and evolution. Academic Press, San Diego, California.

Heinrichs, J. A., D. J. Bender, D. L. Gummer, and N. H. Schumaker. 2010. Assessing critical habitat: Evaluating the relative contribution of habitats to population persistence. Biological Conservation 143:2229–2237.

Heinrichs, J. A., D. J. Bender, D. L. Gummer, and N. H. Schumaker. 2015a. Effects of landscape and patch-level attributes on regional population persistence. Journal for Nature Conservation 26:56–64.

Heinrichs, J. A., D. J. Bender, and N. H. Schumaker. 2016a. Habitat degradation and loss as key drivers of regional population extinction. Ecological Modelling 335:64–73.

Heinrichs, J. A., J. J. Lawler, and N. H. Schumaker. 2016b. Intrinsic and extrinsic drivers of source-sink dynamics. Ecology and Evolution 6:892–904.

Heinrichs, J. A., J. J. Lawler, N. H. Schumaker, C. B. Wilsey, and D. J. Bender. 2015b. Divergence in sink contributions to population persistence. Conservation Biology 29:1674–1683.

Howe, R. W., G. J. Davis, and V. Mosca. 1991. The demographic significance of "sink" populations. Biological Conservation 57:239-255.

Johnson, R. G. and S. A. Temple. 1986. Assessing habitat quality for birds nesting in fragmented tallgrass prairies. Pages 245-249 *in* J. Verner, M. L. Morrison, and C. J. Ralph, editors. Wildlife 2000: modeling habitat relationships in terrestrial vertebrates. University of Wisconsin Press, Madison, Wisconsin.

Kostecke, R. M., S. G. Summers, G. H. Eckrich, and D. A. Cimprich. 2005. Effects of brown-headed cowbird (*Molothrus ater*) removal on black-capped vireo (*Vireo atricapilla*) nest success and population growth at Fort Hood, Texas. Ornithological Monographs:28-37.

Kostecke, R. M., and D. A. Cimprich. 2008. Adult and juvenile survival of black-capped vireos within a large breeding population in Texas. Condor 110:251-259.

Lawler, J. J., and N. Schumaker, H. 2004. Evaluating habitat as a surrogate for population viability using a spatially explicit population model. Environmental Monitoring and Assessment 94:85-100.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237-240.

Marzluff, J. M., and R. P. Balda. 1989. Social, demographic, and evolutionary consequences of dispersal in a group-living bird, the pinyon jay. Ecology 70:316-328.

Noa, L. A., D. H. Hirth, T. M. Donovan, and D. Cimprich. 2009. Demographic differences of black-capped vireos in 2 habitat types in central Texas. Journal of Wildlife Management 71:1042-1049.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology and Systematics 37:637-669.

Pulliam, H. R. 1988. Sources, sinks and population regulation. American Naturalist 132:652-661.

Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. Desante. 1993. Handbook of Field Methods for Monitoring Landbirds. General Technical Report PSW-GTR-144, U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany.

Runge, J. P., M. C. Runge, and J. D. Nichols. 2006. The role of local populations within a landscape context: defining and classifying sources and sinks. American Naturalist 167:925-938.

Rustigian, H. L., M. V. Santelmann, and N. H. Schumaker. 2003. Assessing the potential impacts of alternative landscape design on amphibian population dynamics. Landscape Ecology 18:65-81.

Schneider, S. H. and T. L. Root. 2002. Wildlife Responses to Climate Change, North American Case Studies. Island Press, Washington, D.C.

Schumaker, N. H. 1998. A user's guide to the PATCH model. EPA/600/R-98/135, U.S. Environmental Protection Agency, Corvallis, OR.

Schumaker, N. H., T. Ernst, D. White, and P. Haggerty. 2004. Projecting wildlife responses to alternative future landscapes in Oregon's Willamette Basin. Ecological Applications 14:381-400.

Schumaker, N. H., A. Brookes, J. R. Dunk, B. Woodbridge, J. A. Heinrichs, J. J. Lawler, C. Carroll, and D. LaPlante. 2014. Mapping sources, sinks, and connectivity using a simulation model of northern spotted owls. Landscape Ecology:579–592.

Soulé, M. E. 1987. Viable populations for conservation. Cambridge University Press, New York.

Tazik, D. J., and J. D. Cornelius. 1993. Status of the black-capped vireo at Fort Hood, Texas, Volume III: population and nesting ecology. Technical Report EN-94/01/ADA 277544, US Army Corps of Engineers, CERL, Champaign, IL.

Tazik, D. J., J. D. Cornelius, and C. Abrahamson. 1993. The Black-capped Vireo on the lands of Fort Hood, Texas, Volume I: distribution and abundance. Technical Report EN-94/01, US Army Corps of Engineers, CERL, Champaign, IL.

Thomas, C. D., and W. E. Kunin. 1999. The spatial structure of populations. Journal of Animal Ecology 68:647-657.

Watkinson, A. R., and W. J. Sutherland. 1995. Sources, sinks and pseudo-sinks. Journal of Animal Ecology 64:126-130.

Weinberg, H. J., T. J. Hayden, and J. D. Cornelius. 1998. Local and installation-wide Black-capped Vireo dynamics on the Fort Hood, Texas military reservation. USACERL Technical Report 98/54, US Army Corps of Engineers Construction Engineering Research Laboratories.

Wiens, J. A. 1976. Population responses to patchy environments. Annual Review of Ecology and Systematics 7:81-120.

Wilsey, C. B., J. J. Lawler, D. Cimprich, and N. H. Schumaker. 2014. Dependence of the Endangered Black-Capped Vireo on Sustained Cowbird Management. Conservation Biology 28:561–571.

Winker, K., J. H. Rappole, and M. A. Ramos. 1995. The use of movement data as an assay of habitat quality. Oecologia 101:211-216.

Objectives

The objectives of this multi-phase study were to 1) elucidate the mechanisms that drive source-sink dynamics and key factors influencing the outcomes of species at risk in source-sink systems, 2) document source-sink patterns for the endangered lack-capped vireo on and around Fort Hood, 3) forecast the impacts of system changes and management actions on black-capped source-sink dynamics, 4) compare black-capped and white-eyed vireo habitat use, demography, and behavior to identify the factors and conditions that are uniquely limiting black-capped vireo populations. In doing so, we developed models, simulations, tools, and analyses that inform species conservation in source-sink systems, and place-based management actions for the black-capped vireo near Fort Hood. Below, we outline the specific objectives for each phase of research along with an overview of the methodological approach, and follow section with detailed task-specific descriptions of relevant background material, methods, results, and discussions, and references.

Phase and Task-specific Objectives and Methods Overview

Phase 1

The objective of Phase 1 of this study was to elucidate the mechanisms driving source-sink dynamics and the key factors influencing the outcomes of species at risk in source-sink systems. More specifically, we investigated the following three questions: (Task 1.1) What are the relative roles of habitat quality, species traits, landscape patterns, and temporal environmental variability on source-sink dynamics? (Task 1.2) How do sinks and ecological traps influence population outcomes in different ecological contexts? (Task 1.3) To what degree are source-sink characterizations likely to be generally effective in identifying important habitats for protection in conserving species at risk? We conducted three separate studies to address each of these questions. In our discussion of the results of each of these studies, we highlight the implications of management decisions based on the correct or incorrect identification of sources and sinks as well as the implications of assumptions of source and sink contributions to regional population outcomes.

Task 1.1 – Quantify the relative influence of species' life-history attributes and landscape patterns and conditions on the emergence and strength of source sink dynamics in generalized systems

In Task 1.1, we explored the relative effects of both spatial (e.g., habitat amount, quality, fragmentation) and temporal patterns (e.g., demographic stochasticity through time and temporally available habitats) and species life history characteristics (e.g., movement abilities, habitat selection strategies, survival and reproductive strategies) on the emergence and strength of source-sink dynamics in generalized terrestrial systems. To test several hypotheses and predictions about species and landscape characteristics, we designed a number of factorial experimental scenarios that were run in the spatially-explicit, individual-based modeling framework, HexSim. We tallied the emergent patch-specific births, deaths, immigrations, and emigrations and assessed the relative influence of factors using generalized linear models.

Task 1.2 – Assess the roles of sink habitats and determine the consistency with which they affect the persistence of species of conservation concern

In Task 1.2, we used HexSim models for three species at risk in different source-sink systems to compare the contributions of fluctuating sinks, pseudo-sinks, and ecological traps to regional population persistence. To test multiple competing hypotheses, we simulated population dynamics for three very different species at risk and assessed their population sizes, source-sink strength, and persistence before and after the removal of sinks. To facilitate inferences among systems, we summarized the results within the contexts of species abundance, rates of decline, degree of fluctuation, strength of sinks, and degree to which sinks facilitate connectivity. The results of our sink removal analyses were displayed as maps and used to develop hypotheses about the positive or negative impacts of different sink management approaches.

Task 1.3 – Examine the degree to which different population prioritization approaches are able to identify the most important habitats for long-term regional population persistence

In Task 1.3, we used species-specific HexSim models, including some of those developed for Task 1.2, to simulate population dynamics and identify sources and sinks using alternative metrics and durations of data collection. The strongest percentage of sources or highest abundance patches were prioritized for simulated habitat protection. Their contributions to long-term persistence were quantified by digitally removing these patches, and the metrics with the strongest impact on persistence were identified. We discuss the management implications of making conservation decisions for declining species based on short-term data, source-sink assessments that lack movement data, and the conditions under which abundance may better indicate the importance of habitats to population persistence.

Phase 2

The objective of the second phase of this study was to document current demographic and space-use patterns, including source-sink dynamics, for the endangered black-capped vireo on and around Fort Hood. We conducted field studies to quantify population abundance and demography across Fort Hood and discrete populations in nearby counties. Specifically, we examined the following questions: (Task 2.1) How different are abundance and demography among spatially-structured habitats, and how do they contribute to source-sink dynamics? What demographic parameters most influence vireo population growth? (Task 2.2) How does habitat use by breeding and juvenile black-capped vireos differ? Do patterns of habitat use differ between subpopulations across central Texas? (Task 2.3) Do black-capped vireo vocalizations near their nests affect the likelihood of parasitism or nest predation? Do vireos respond to different parasitism risk regimes by changing their vocalization patterns? (Task 2.4) Are black-capped vireos strictly socially monogamous, or is their breeding strategy more flexible?

We selected several study areas on and within roughly 100 km of Fort Hood where there were known vireo populations, and we monitored birds to assess location-specific variation in

survival, fecundity, movement, and growth rates. On the base, we targeted vireos nesting in relatively poor habitat within close proximity to long-term study sites (Kostecke and Cimprich 2008). Off base, we targeted several small habitat patches that were roughly 10 ha in size, containing about 20 vireo territories per site, so that demographic estimates were possible. Sites spanned a range of shrub heights and levels of cowbird control. In each of the years of the multi-year field study, we searched for nests, observed behavior, captured and color-banded birds, re-captured, and mapped territories using standard protocols (International Bird Census Committee 1970, Ralph et al. 1993). These basic attributes provided estimates of population size, connectivity, and sustainability that were used to assess source-sink dynamics. The field component of our project was designed to inform our modeling efforts (Phase 3) and characterize the population structure in a realistic landscape setting. Five years is sufficient to estimate fecundity, survival, and movement, but we did not expect to obtain precise estimates that are representative of long-term fluctuations during this time. Yet, our estimates provided a starting point for parameterizing our models (see Phase 3), which we used to better understand the implications of our estimates (and their uncertainty) for management recommendations.

Task 2.1 – Describe and quantify the source-sink dynamics among central Texas black-capped vireo populations and the relative importance of demographic parameters

In Task 2.1 we monitored breeding vireos at eleven sites across central Texas, both on and off the Fort Hood Military Installation, which varied in cowbird control level from 2011 through 2015. From observations of fecundity and survival, we calculated stochastic and deterministic population growth rates and assessed populations as sources or sinks using population matrices. We also calculated quasi-extinction probabilities and the sensitivity and elasticity of population growth to specific demographic parameters. Based on our results, we discuss the spatial and temporal variability in population dynamics and the role of evolving cowbird control regimes on long-term vireo population viability.

Task 2.2 – Compare habitat use by territorial adult black-capped vireos during the breeding season and juvenile vireos in the post-breeding season

In Task 2.2, we monitored and delineated breeding vireo territories from late March through early July using spot-mapping techniques and used radio telemetry to track juvenile vireos in July and August, 2012-2014. We compared vegetative characteristics of nest sites, breeding territories, and juvenile home ranges using direct field measurements of structure as well as remotely-sensed aspects of the landscape. We also compared patterns of habitat use with nest and territory success as well as juvenile survival. Finally, we discuss the implications of age-specific habitat requirements on effective vireo management.

Task 2.3 – Investigate the correlation between the rate of vocalizations by black-capped vireos near their nests and the risk of nest predation and parasitism by cowbirds, considering different nesting stages and time of day

In Task 2.3, we made audio-recordings at black-capped vireo nests at five sites across central Texas in 2013 and 2014 that varied in cowbird abundance. We calculated vocalization rates (songs/minute) considering three nesting stages (building, laying, and early incubation) and three

times of day (morning, midday, and evening). We then compared vocalization rates with nest fate to evaluate two hypotheses describing vireo response to predation and parasitism risk: the predator-attraction hypothesis and the parasite-assessment hypothesis. We discuss how flexibility in vireo defense strategies may allow individuals to minimize risk of nest parasitism/predation while maximizing social bonding.

Task 2.4 – Evidence of flexibility in black-capped vireo breeding strategy

In Task 2.4, we visited study sites throughout the vireo breeding season, monitored pairs, and attempted to locate all nests. We visited known nest locations every three to four days until failure or fledging and recorded the number of host eggs and cowbird eggs (if present), the number and approximate age of nestlings, and parental presence at the nest. We present evidence for the first documented case of black-capped vireo polygyny and discuss flexibility in vireo breeding strategy.

Phase 3

The objective of the third phase of this study was to integrate the results of the field-based analysis into a spatially-explicit vireo population model to forecast vireo source-sink dynamics and assess the impacts of system changes and management actions on regional population outcomes and source-sink stability. In doing so, we aimed to answer the following: How important are the current on-base source populations to regional vireo viability? How are off-base populations likely to contribute to regional viability? How might habitat restoration programs on public lands affect the overall population if these habitats are sinks or ecological traps? How would the initiation or increase of cowbird control in off-base populations affect regional source-sink dynamics? How could climate change impact vireo demography and ensuing source-sink dynamics?

We used the HexSim modeling framework to integrate field data (Phase 2) with information from previous population and habitat studies, including habitat maps, abundance, demographic and movement estimates, territory sizes, and behavioral information. Fort Hood habitat was characterized using the habitat suitability map from the previous SERDP-funded project (SI-1541, "Forecasting the Relative and Cumulative Effects of Multiple Stressors on At-risk Populations"). Adjacent areas were mapped using a cumulative time series of territory maps. To assess patch-specific contributions to regional population dynamics, we iteratively removed key habitats and measured the impact of removals on both population outcomes and network-wide source-sink states. Similarly, we augmented cowbird control in off-base sites or added restored habitats to the network and evaluated their impact on system dynamics. Lastly, we examined the future impacts of climate-induced shifts in vireo demography using past responses to climatic conditions and future climate projections.

Phase 4

The objective of the fourth phase of this study was to identify the factors and conditions that are uniquely limiting black-capped vireo populations by comparing black-capped and white-eyed vireo habitat use, demography, and behavior. To do so, we conducted a 2-year field study of

populations within Fort Hood and surrounding counties. In each of the study locations in Phase 2 of the study (black-capped vireo field data collection), we captured, banded, surveyed, monitored, and radio-tracked white-eyed vireos. We estimated nesting success, juvenile survival, and movement using the same analytical techniques that were applied to the black-capped vireo. To address questions of habitat use and species overlap, we measured several basic habitat attributes including species composition, canopy cover, height diversity, and nesting substrate within territories. We performed observations and recordings at nests and compared differences in species behavior related to parasitism and nest success. We also compared spot-mapping results for each site to quantify overlap in territories, relative territory sizes, and habitat attributes between the species.

Phase 1: Source-Sink Modeling

Phase 1 Overview

Task 1.1: Many factors affect the presence and exchange of individuals among subpopulations and influence not only the emergence, but also the strength of ensuing source-sink dynamics within metapopulations. Yet their relative contributions remain largely unexplored. To help identify the characteristics of empirical systems that are likely to exhibit strong versus weak source-sink dynamics and inform their differential management, we compared the relative roles of influential factors in strengthening source-sink dynamics. In a series of controlled experiments using a spatially explicit individual-based model, we varied patch quality, patch size, the dispersion of high and low quality patches, population growth rates, dispersal distances, and environmental stochasticity in a factorial design. We then recorded the spatial source-sink dynamics that emerged from simulated habitat and population factors. Long-term differences in births and deaths were quantified for sources and sinks in each system and used in a statistical model to rank the influences of key factors. Our results suggest that systems with species capable of rapid growth, occupying habitat patches with more disparate qualities, with interspersed higher and lower quality habitats, that also experience relatively stable environments (i.e., fewer negative perturbations), are more likely to exhibit strong source-sink dynamics. Strong source-sink dynamics emerged under diverse combinations of factors, suggesting that simple inferences of process from pattern will likely be inadequate to predict and assess the strength of source-sink dynamics. Our results also suggest that it may be more difficult to detect and accurately measure source-sink dynamics in slow-growing populations, highly variable environments, and where a subtle gradient of habitat quality exists.

Task 1.2: Population sinks present unique conservation challenges. The loss of individuals in sinks can compromise persistence; but conversely, sinks can improve viability by improving connectivity and facilitating the recolonization of vacant sources. To assess the contribution of sinks to regional population persistence of declining populations, we simulated source-sink dynamics for three very different endangered species: Black-capped Vireos (*Vireo atricapilla*) at Fort Hood, Texas, Ord's kangaroo rats (*Dipodomys ordii*) in Alberta, and Northern Spotted Owls (*Strix occidentalis caurina*) in the northwestern United States. We used empirical data from these case studies to parameterize spatially explicit individual-based models. We then used the models to quantify population abundance and persistence with and without long-term sinks. The contributions of sink habitats varied widely. Sinks were detrimental, particularly when they functioned as black-hole sinks for declining populations (e.g., Alberta's Ord's kangaroo rat) and benign in robust populations (e.g., black-capped vireos when cowbird *Molothrus ater* parasitism was controlled). Sinks—including ecological traps—were also crucial in delaying declines when there were few sources (e.g., in black-capped vireo populations with no cowbird control). Sink contributions were also nuanced; for example, sinks that supported large, variable populations were subject to greater extinction risk (e.g., northern spotted owls). In each of our case studies, new context-dependent sinks emerged, underscoring the dynamic nature of sources and sinks and the need for frequent re-assessment. Our results imply that management actions based on assumptions that sink habitats are generally harmful or helpful risk undermining conservation efforts for declining populations.

Task 1.3: The effective targeting of conservation resources is the intention of habitat prioritization approaches for species at risk of decline or extinction. In source-sink systems, sources are an obvious target for habitat protection actions; however, the means by which important habitats are identified can introduce error into the prioritization process and reduce the effectiveness of conservation actions. Although sources and sinks are conceptually defined using both demographic and movement criteria, simplifications are necessarily made in systems with limited data. To assess the conservation outcomes of alternative habitat prioritizations, we simulated population dynamics and extinction risk outcomes for three endangered species. Using empirically-based habitat-population models, we linked habitat maps with measured site or habitat-specific demographic conditions and movement abilities, or propensities. We simulated data collection over a range of time periods and used a series of source-sink metrics to identify target habitats. We then tested the ability of prioritizations in each time period to identify the most important habitats by removing them from the system and measuring the population response. Our results indicate that the way in which key source habitats are prioritized for conservation can yield different persistence outcomes, depending on the system dynamics, timing, location, and duration of data collection, and the number of patches that are being prioritized. Accurate characterizations of sources, sinks, and their strengths may matter most for gradually declining species, and in landscapes with a large proportion of the population occupying sink habitats. Although simplified source-sink metrics (e.g., only survival and reproduction) can be used in place of ones that include more data collection (i.e., including movement data), their success in reliably identifying sources and sinks and their contributions to persistence can be variable. Simple metrics such as local abundance can identify important habitats for short-term persistence, but their ability to detect sources and important habitats for long-term persistence is generally poor. In some rapidly declining populations, the preservation of high abundance sinks can yield a more positive impact on short-term persistence than smaller key sources. As source populations are generally needed for recovery and longer-term persistence, a balanced approach that considers both habitats that are important for short-term (e.g., some sinks), as well preserves habitats that are required for long-term persistence (key source habitat) is likely to yield the greatest conservation benefit for declining species.

1.1 Intrinsic and extrinsic drivers of source-sink dynamics[1]

1.1.1 Introduction

Spatial variation in habitat quality is the basic factor that structures source-sink dynamics in heterogeneous landscapes (Pulliam 1988, Dias 1996). Demographic surpluses in higher quality habitats (e.g., sources) and deficits in lower quality habitats (e.g., sinks) commonly arise, and movement among local populations can stabilize dynamics at regional scales (Dias 1996). At steady state, some local populations become net exporters of individuals (i.e., sources) where births outweigh deaths (b > d) and emigrants outnumber immigrants (e > i), and other populations become net importers (i.e., sinks) where the opposite demographic and movement conditions hold (Pulliam 1988). Although differences in habitat quality (see Hall et al. 1997) provide a basis for source-sink dynamics to emerge, other habitat and population characteristics can affect reproduction and survival through space and time, and play a role in strengthening or weakening source-sink dynamics (Dunning et al. 1992). Habitat characteristics including differences in patch sizes and qualities, as well as the proximity of high quality to low quality habitats have the potential to influence the strength of sources and sinks. Similarly, species and population factors such as growth rates, dispersal abilities, and demographic responses to environmental variability can affect the severity of source-sink dynamics, driving sources and sinks to become more or less extreme. Although these habitat and population factors have been individually found to affect source-sink dynamics, their relative importance is not well understood.

Populations are increasingly conceptualized and managed based on their source-sink status or the suspected presence of source-sink dynamics within the system. Hence, there is a clear practical need to be able to distinguish among source and sink populations. Differential management of sources and sinks can be particularly important in avoiding counter-productive actions associated with falsely assuming that an animal's realized niche in a sink habitat represents their fundamental niche (Pulliam and Danielson 1991, Boughton 2000). Further, the large continuum of source-sink strengths ranging from minor asymmetries to overwhelming directional flows of individuals, suggests that an understanding of the strength of the system and the factors that augment or diminish its strength has the potential to guide effective decisions and actions. Yet to date, studies have primarily evaluated the conditions under which source-sink dynamics are incited, with limited evaluations of the factors that strengthen dynamics once incited.

Source-sink literature points to dispersal and habitat selection behavior as providing the basis for emergent source-sink dynamics in heterogeneous landscapes, directing the flow of individuals among habitats and resulting birth, death rates, and local densities. Source-sink dynamics can arise as a result of random dispersal (e.g., diffusion), as well as with passive dispersal mechanisms (e.g., exchange of a fixed or stable proportion of dispersers among asymmetrically

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sized populations; Boughton 2000). Ideal pre-emptive habitat selection behavior can also lead to source-sink dynamics, with animals that arrive first pre-empting the use of the best sites, maximizing their reproductive output and fitness. As population density increases, late arrivals are forced to settle in lower quality habitats, potentially leading to lower reproductive success and higher mortality, possibly creating population sinks (Pulliam and Danielson 1991). In empirical populations, realistic animal dispersal and habitat selection can incorporate all these elements into more complex decision processes that influence chosen locations and ensuing source-sink outcomes. We combine these forces to incite source-sink dynamics in a range of landscapes and life history characteristics, using a novel approach that incorporates mechanistic density-dependent habitat selection, the concepts of passive diffusion in emigrating from disparate sized habitat patches, diffusion in the form of quasi-random walks through matrix to find habitat, and ideal pre-emption in excluding late-comers from the best sites.

To compare the relative influences of habitat and population factors on the strength of emergent source-sink systems in animal metapopulations, we simulated dynamics in a range of controlled landscapes, using realistic movement and territorial behavior for differing life history characteristics, using a spatially explicit individual-based population model. We used a set of hypothetical landscapes and species and six potential drivers (population growth rates, differential patch qualities and sizes, patch quality patterns, dispersal distances, and levels of environmental variation), in a factorial design to rank the influence of the different factors. To assess the consistency of landscape and population drivers of source-sink strength, we also examined their relative influence among alternative density-dependent habitat selection scenarios with varying degrees of awareness of the landscape, habitat quality, and abilities to optimize fitness. Many animals occupy sink habitats, resulting from an inability to discern adverse fitness consequences (i.e., an ecological trap; Howe et al. 1991, Battin 2004a), an unwillingness to emigrate elsewhere (e.g., strong site fidelities), or an improbability of surviving to the next opportunity to relocate (e.g., high overwinter mortality for kangaroo rats; (Holt and Gaines 1992, Heinrichs et al. 2010). With limited knowledge of the landscape, we expected that animals that are better able to detect habitat quality will select fitness-optimizing territories to a greater extent than less discerning animals, and should produce weaker source-sink systems (and the converse to have stronger dynamics).

We expected the strength of source-sink systems to depend on habitat and populations factors influencing local population densities and density-dependent emigration, and to be driven by differences in habitat quality. As patch occupancy is a necessary pre-condition for local habitat quality to be important, factors increasing the population size and consistency of potential colonizing populations were expected to strengthen source-sink dynamics. The ability for populations to grow, reach carrying capacities, and induce density-dependent fitness consequences and emigration was expected to be a key driver of source-sink strength. We also expected that systems that were not challenged by periodic population depressions would produce stronger sources and sinks than those affected by perturbations. We also expected that greater accessibility and propensity of individuals in sources to diffuse to sinks would strengthen source-sink dynamics. At stable state, we expected asymmetric patch sizes to strengthen system dynamics through passive dispersal mechanisms that incite source-sink dynamics. Species with longer dispersal distances relative to their territory size were expected to select better territories and maximize their fitness to a greater degree than shorter dispersers, weakening source-sink

dynamics. Although we do not directly derive hypotheses for empirical populations, these general expectations lend themselves to thorough testing with empirical data. If supported, these hypotheses could be used to indicate systems with a high the degree of correlation and dependency among populations, systems where source-sink dynamics may require additional effort to detect and quantify, and the degree to which density-dependent regulation may be influencing population outcomes.

1.1.2 Methods

1.1.2.1 Approach

To explore the influences of alternative landscapes and species and population traits, we designed a series of simple neutral landscapes (Gardner and O'Neill 1991) and ecological profiles (e.g., Vos et al. 2001, Wiegand et al. 2005). The neutral habitat models produced an array of landscapes that varied in patch size disparity, patch quality disparity, and proximity of high quality to low quality patches, while holding landscape conditions (habitat amount, overall quality, and fragmentation) constant. The ecological profiles were designed to represent a wide range of population growth rates (fecundity), dispersal distances, and responses to environmental variation. A spatially explicit individual-based model was then used to quantify emergent source-sink dynamics in all combinations of neutral landscapes and ecological profiles. Animal births, movements, and deaths were recorded throughout the landscape and used to assess the long-term difference in births and deaths for each local population, hereafter referred to as productivity. For each scenario, the difference in productivity among sources and sinks was used to measure source-sink strength. The influence of each landscape and population trait was assessed and ranked using linear regression.

1.1.2.2 Landscapes

We developed eight equivalent landscapes, each consisting of eight discrete circular patches embedded in an uninhabitable matrix which was permeable to movement (Figure 1.1.1). Landscapes varied in the disparity of patch sizes and qualities, as well as the proximity of high to low quality patches, according to a factorial design. Although the distribution of patch sizes and qualities varied among landscapes, the total amount of habitat (10%), average quality of habitat, and locations of patch centroids remained constant in all landscapes.

Patch size disparity scenarios (low and high) were created by drawing individual patch sizes from 2 sets of bimodal distributions (with means of 125 size units) and modes of 100 and 150 in the low disparity scenario (hereafter, size disparity 50), and 50 and 200 for the high disparity scenario (hereafter, size disparity 150) and adjusted to meet total habitat amount criteria. In addition, we explored two scenarios in which the distribution of patch qualities varied to lesser and greater extents among patches. We assigned patches a habitat quality score (1-100 resource units), drawn from bimodal distributions (means = 50); to create a low disparity scenario (using modes of 40 and 60, hereafter referred to as quality disparity 20), and a high disparity scenario (using modes of 20 and 80, hereafter referred to as quality disparity 40) and adjusted to meet landscape quality criteria. We varied the proximity of high to low quality patches using two

patterns. Patches were either arranged along a habitat quality gradient, such that lowest and highest quality patches were clustered on opposite sides of the landscape (Figure 1.1.1a), or high and low quality patches were interspersed and proximate (Figure 1.1.1b).

1.1.2.3 Population Model and Ecological Profiles

We used the spatially explicit individual-based modeling platform HexSim (version 2.3; Schumaker 1998, 2008), to construct a 3-stage, females-only population model (Figure 1.1.2). Simulated animals interacted with habitat by moving through the landscape (200 x 231 hexagonal pixels) and searching for available territories. Each animal aimed to obtain an exclusive territory with the maximum possible resources within their maximum range size of 3 pixels (i.e., 3 pixels x quality score of 100 = 300 resources units). Individuals with smaller ranges were able to expand if adjacent areas were available for use in a later time step. Those able to meet the median resource requirement of 150 units by acquiring half of the maximum possible resources were given average survival rates of 0.74 for adults, and 0.52 for juveniles, based on mean survival rates and life-history data for 155 avian populations (Stahl and Oli 2006), and 50 mammal populations (Heppell et al. 2000). Territory holders that acquired more or less than the median target level of habitat received linearly scaled survival rates that increased or decreased with their level of resources.

In initial simulations, we created a breadth of ecological profiles to explore a range of responses to growth rates, environmental variation, and dispersal abilities. We were interested in examining the rate at which populations were able to recover from population declines and return to carrying capacities, rather than exploring r vs K life history strategies that often trade-off survivorship and fecundity. Hence, we modeled populations with a range of growth rates. Population growth rates were emergent properties of simulations but were influenced by the ability of species to reproduce. We explored a range of growth rates by varying fecundity rates (0.75, 1.25, 1.75) among species. Territory-holding adult females could reproduce, but floaters (without territories), juveniles, and subadults could not. Resulting growth (λ) values varied between ~ 0.5 and 2.0. We simulated 3 different levels of environmental variation that influenced the severity of periodic adverse conditions: no variation, minor variation, and major variation. Random selections from the lower half of a truncated normal distribution, i.e., with a mean of 1.0 and standard deviations of 0.0 (no variation), 0.1 (minor variation), or 0.5 (major variation), determined the degree to which periodic environmental events reduced survival rates for all individuals. The affected year was selected from a stratified random sample with 10 events /100 years. The affected year and associated severity were replicated across all simulations run for a given scenario.

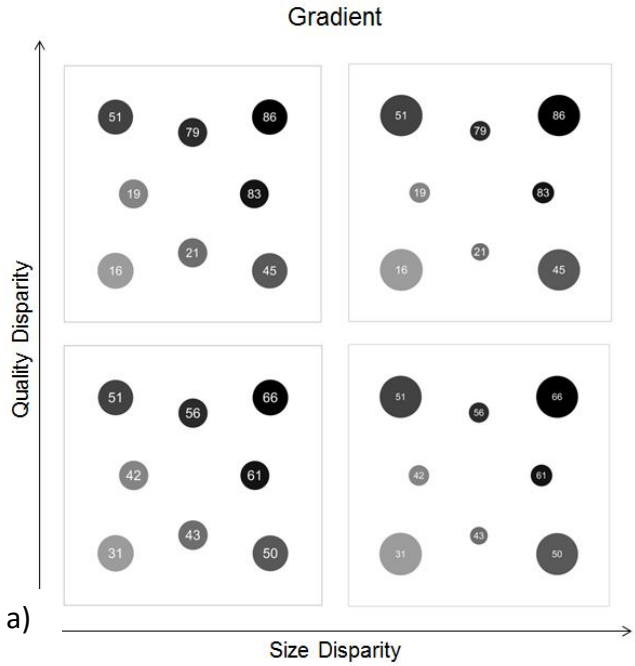
We created two movement scenarios for comparison by assigning juveniles (and new floaters) dispersal distances that were sufficient to 1) reach the nearest few neighbor patches (200 pixels) or 2) move anywhere in the landscape (2000 pixels). In both these scenarios (nearest neighbors and unlimited neighbors), individuals moved in a quasi-random walk with forward momentum (75% autocorrelation in path direction). Exploration for a suitable territory was triggered if an individual encountered 3 adjacent hexagons of habitat after moving over 50 hexagons away from their natal territory, allowing individuals at the center of a patch to leave even the largest patches and generating a greater degree of passive dispersal away from smaller (rather than larger)

patches. Dispersing individuals had a preference to move towards high quality habitat in their vicinity, with a strength that increased linearly with the pixel score. Hence, individuals were more likely to passively disperse away from low-quality than high-quality patches. Natal dispersal was mechanistically influenced by local density conditions. When density was high, natal dispersers travelled farther searching for a vacant location than if density was low.

1.1.2.3.1 Naive Selection

To assess the influences of habitat and population factors on the strength of source-sink dynamics, we first evaluated population outcomes using a naive habitat selection strategy. In this scenario, animals had limited knowledge of the landscape and were unaware of patch locations and habitat qualities and densities beyond their individual experiences. Animals moved through the landscape in search of habitat, and those unable to obtain a suitable territory did not survive to the year. Individuals sought to occupy the highest quality, empty habitat within their search area, but had a limited spatial extent in which to make this determination after dispersing. Hence, individuals often occupied the first available, suitable territory that was encountered and remained there until death, with no subsequent movement to optimize fitness. The first animal to claim a territory pre-empted subsequent individuals from using associated resources. In high density conditions, mechanistic emigration re-located juvenile dispersers to other patches.

For the naive habitat selection scenario, we simulated population dynamics using the above described modeling construct for 144 scenarios in a factorial design, combining 18 ecological profiles with 8 neutral landscapes; however, rapid extinctions occurred in 8 scenarios, reducing the sample size to 136. Simulations began with 100 females placed randomly within habitat patches, and population dynamics were assessed for the last 100 years of a 300-year simulation, wherein population abundance generally fluctuated about a consistent mean. For each scenario, we ran 10 replicate simulations. Response surfaces were constructed to expand the parameter space and visualize combinations of influential variables that yielded particularly strong or weak source-sink dynamics (i.e., top three factors). Additional levels of population growth potential (fecundity = 0.5, 1.25, 1.75) in combination with patch quality disparity (disparity alternative 40 with modes of 30 and 70), or environmental variation (0.25, 0.75, 1) were examined for visualization. Pattern, patch size disparity, and dispersal distance factors were held constant at levels that increased the strength of source-sink dynamics.



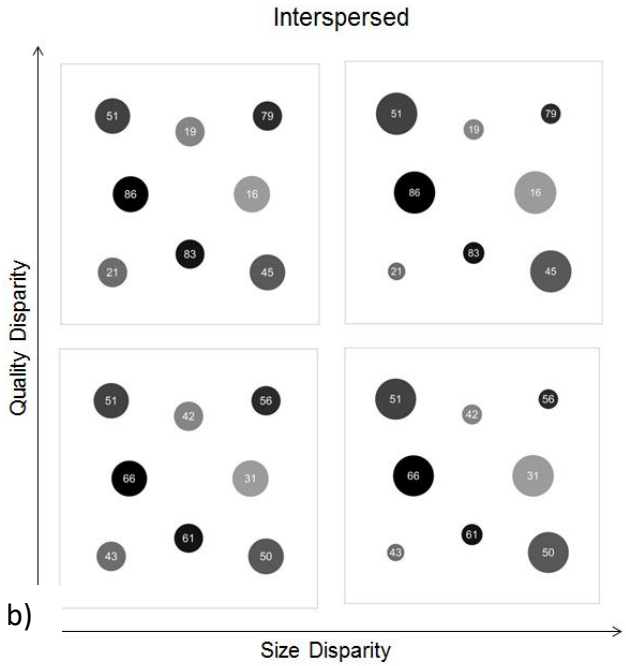


Figure 1.1.1. Neutral landscapes varying in patch size disparity (x axes), patch quality disparity (y axes; with higher numbers representing greater resource scores), and spatial gradient (a) or interspersion (b) of high and low quality patches.

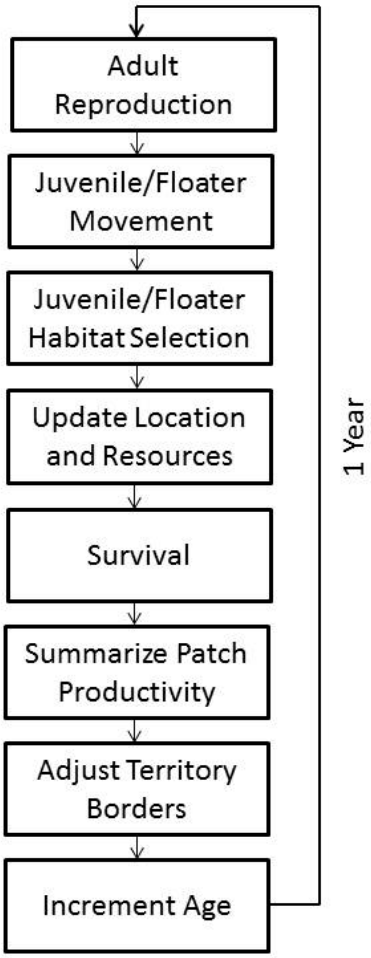


Figure 1.1.2. Annual cycle of simulation events as implemented in the naive population model. Initialization events, intermediary updating and census functions are not shown.

1.1.2.3.2 Informed Selection

To evaluate the sensitivity of the drivers of source-sink strength to habitat awareness and selection, we evaluated an alternative scenario in which animals were cognizant of habitat quality and able to adjust their location through time to better optimize their fitness. Individuals did not have complete knowledge of their surroundings but could discern low quality from high quality and could emigrate from lower quality patches in search of higher quality patches each year. Animals were also more discerning of habitat quality during movement and initial habitat selection (requiring high-quality pixel values to trigger early stopping during movement), and their dispersal movements among patches were highly successful (individuals whose movement ended in the non-habitat matrix were allowed to proceed to the nearest patch), emulating increased knowledge of the landscape. In lower quality patches, all individuals would emigrate

each year in search of higher quality habitat. This quality-induced emigration was required for all individuals in the lowest quality patch in each landscape, and any other patches with mean pixel scores < 31/100, implicating another two low-quality patches in higher quality disparity scenarios (quality disparity 20, 60, and additionally 40; see below). Pre-emptive habitat selection was strengthened by allowing older individuals to pre-empt younger individuals arriving at the same location.

The informed habitat selection simulations focused on a subset of parameter space, chosen to maximize the breadth of parameter space for variables found to be important in the initial, naive scenario. Specifically, we evaluated the relative influences of the following drivers on the emergent strengths of sources and sinks using the following 36 factorial combinations: Population growth potential (fecundity = 0.50, 1.00, 1.75), habitat quality disparity (alternatives 20 and 60; along with 40 which uses quality modes of 30 and 70), the pattern of high and low quality patches (interspersed vs. gradient), and the degree of environmental variation (stochasticity SD = 0, 1.0). Based on the results of the naive selection strategy, we held patch size disparity and dispersal distance variables constant at their strongest levels.

1.1.2.4 Source-Sink Metrics and Analysis

We recorded the locations of individual births, immigrations, deaths, and emigrations, summarized the data for each patch, and assigned a productivity metric equal to births – deaths to each patch. Patches were deemed sources if local births exceeded deaths, and sinks if deaths exceeded births over a 100-year period. Movement among patches was accounted for in this metric by the individuals' subsequent contribution to the local birth or death tally and using this construct, births - deaths approximates emigration – immigration at steady state (Schumaker et al. 2014). To assess the system-wide strength of source-sink dynamics, we also developed a second metric called productivity disparity, calculated as the difference between the average productivity (b-d) values of all sources and the average productivity values of all sinks in each landscape. At steady state, we expected little variability in the source-sink status and strength of patches in each scenario, therefore, demographic and movement information were averaged across the 10 replicate simulations. We assessed the influences of habitat and population factors on productivity disparity using analysis of variance (ANOVA) and ranked each factor using standardized effect sizes.

Alternative response metrics were also explored in the naive selection analysis to assess the sensitivity of the order of importance of the habitat and population traits to the choice of metrics. We examined metrics that used emigration and immigration data to weight patch productivity values and functionally describe patch contribution to the regional network. We also calculated the long-term difference in productivity between the single most productive source and the single most consumptive sink in each landscape. Importance rankings were generally robust to the chosen metric, with the same top two factors being consistently identified across all models, and only minor variation in rankings observed among the less influential variables. We used the metric (productivity disparity) associated with the highest R^2 model value to select the response variable in the naive selection models, and retained the same metric for the informed selection models. For the naive selection scenario, we subsequently examined the relative influence of supporting factors while holding the most influential variable constant.

1.1.2.5 Response Surfaces

Response surfaces (Figure 1.1.3) were constructed to expand the parameter space and visualize combinations of influential variables that yielded particularly strong or weak source-sink dynamics (i.e., top three factors). Lesser-ranked factors held constant at levels that produced the maximum influence (i.e., levels that generally increased the strength of source-sink dynamics). Pattern was held constant with high quality patches interspersed with low quality patches, as was patch size disparity (using highly disparate patch sizes with disparity level 150), and dispersal was limited to the nearest few neighboring patches (200 pixels). In scenarios examining the relationship between fecundity and quality disparity, there was no environmental variation (i.e., static). In fecundity-variation scenarios, quality disparity was held constant with disparity level 60 (modes of 20 and 80).

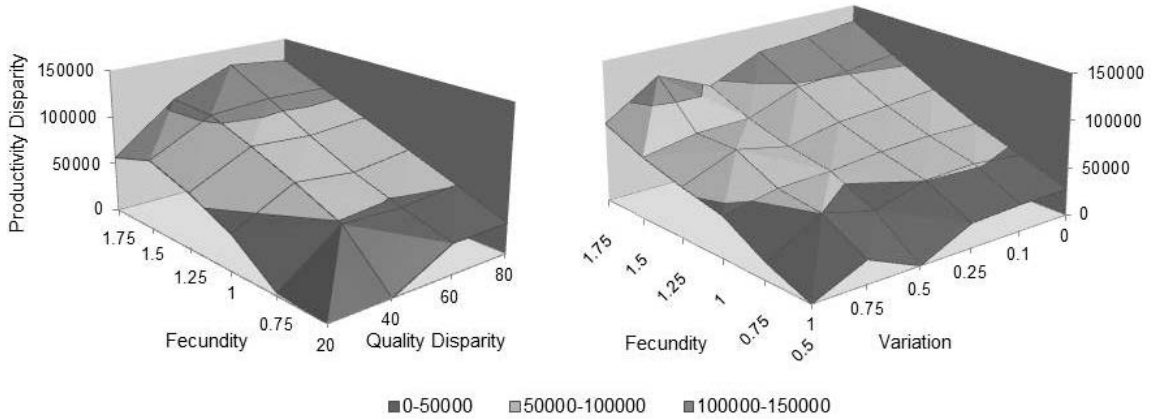


Figure 1.1.3. Productivity disparity response surfaces for the top ranked factor, growth, with a) quality disparity (rank = 2), and b) environmental variation (rank = 3) in the naive scenario.

1.1.3 Results

1.1.3.1 Naive Selection Scenarios - General Observations

Despite each landscape containing an equal number of high and low quality patches, the observed number of sources and sinks ranged from 7 sources and 1 sink to 2 sources and 6 sinks at stable state. We did not observe any systems with only sources or only sinks at steady-state. The system with the highest productivity disparity had the following characteristics: highest growth (fecundity) rate and highest patch quality disparity levels, no environmental variation, high quality interspersed with low quality patches, and limited dispersal ability (and low patch size disparity). These variables and associated levels also predicted the system with the single strongest source, with the substitution of higher patch size disparity over low size disparity (Figure 1.1.4a). The system producing the single strongest sink was almost identical to that producing the strongest source, differing only in that the strongest sink scenario did not limit dispersal to the nearby neighbor patches.

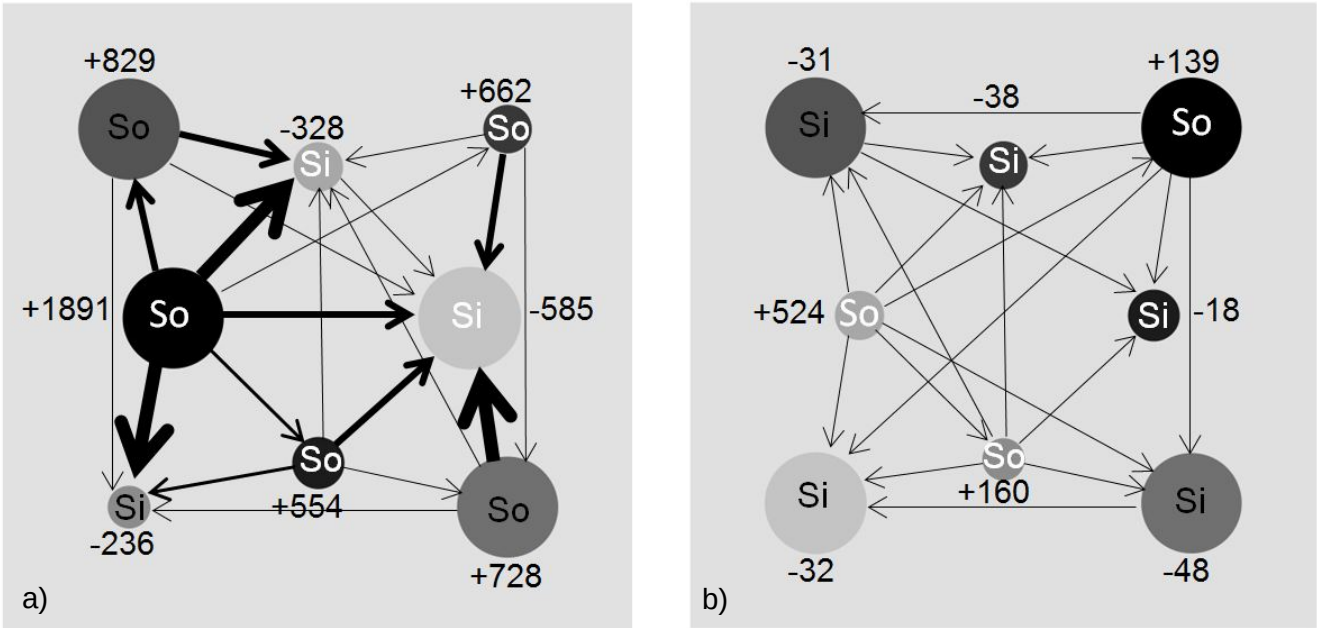


Figure 1.1.4. Study system yielding the strongest single source a), and a contrasting system with weaker dynamics and sources and sinks b). Strength of sources (So), sinks (Si), and net movement (arrows) among habitat patches in strong a) and weak source-sink dynamics b) examples. Local productivity (births-deaths) is expressed as an annual average. Thicker lines represent greater net annual movement, averaged among replicates. Exchanges of ≤ 1 net individuals were excluded. Darker circles represent higher quality habitat patches.

We expected the weakest source-sink systems to be produced by the species-landscape combinations with the opposite characteristics of the strongest source-sink systems. Rapid extinction precluded analysis of this specific scenario, but of those that reached steady-state, the weakest source-sink dynamics were produced by systems with the lowest fecundity and patch quality disparity. The weakest source-sink systems were also characterized by an intermediate level of stochastic variation, interspersed pattern of high and low quality patches, and limited dispersal. We expected that longer dispersal distances would weaken the effect of source-sink pattern on the severity of dynamics, and we observed this effect in gradient but not in interspersed landscapes.

The source-sink status of individual patches was not always easily inferred from local habitat quality. Although source status tended to be more predictable in stronger source-sink systems (e.g., Figure 1.1.4a), source-sink status was less related to quality in weaker systems (e.g., Figure 1.1.4b with opposing growth rates, levels of variation, and landscape patterns, and equivalent quality, size, and dispersal characteristics to those in Figure 1.1.4a). Under weaker source-sink dynamics, some of the higher quality patches behaved as weak population sinks, whereas some of the moderate quality patches were the most productive sources in the landscape.

In response surfaces, the influence of population growth was modulated by habitat quality disparity (e.g., Table 1.1.1). The strength of source-sink dynamics under low quality disparity was nearly a third of that observed under high disparity conditions, with a threshold increase in productivity disparity under a moderate disparity scenario. Higher levels of quality disparity yielded more incremental increases in productivity disparity with increasing levels of fecundity (Table 1.1.1). Greater environmental stability (i.e., lower levels of variation) along with higher fecundity rates generally produced stronger source-sink systems. Some degree of compensation was observed among growth and secondary factors. Productivity disparity was particularly responsive to reductions in environmental variation or increases in quality disparity when fecundity rates were low.

Table 1.1.1. Influence of habitat and population variables on productivity disparity holding the population growth level constant at 1.75 in the naive scenario (N =48), as described by standardized effect sizes (R^2 = 0.86; F Ratio = 51.35; Prob >F = < 0.0001).

Variable	Rank	Estimate	SE	t Ratio	Prob>|t|	Std Beta
Intercept		60249.54	6111.37	9.86	<.0001*	0
Quality	1	1076.46	90.70	11.87	<.0001*	0.6867
Pattern [gr]	2	-14456.28	1813..92	-7.97	<.0001*	-0.4611
Variation	3	-52345.10	8396.84	-6.23	<.0001*	-0.3607
Dispersal	4	-7.32	2.02	-3.63	0.0008*	-0.2102
Size		-19.91	36.28	-0.55	0.5861	-0.0318

Variation = stochastic environmental variation; Pattern = proximity of high to low quality patches; Quality = patch quality disparity; Size = patch size disparity; Dispersal = dispersal ability.

1.1.3.2 Naive Selection Scenarios - Factorial Analysis

When animals were limited in their ability to discern and respond to habitat quality in the naive habitat selection scenarios, population growth potential (as approximated with fecundity) had the greatest effect on productivity disparity (Table 1.1.2), with higher growth potential associated with greater productivity differences among sources and sinks. The disparity in quality among habitat patches exerted the second greatest influence on productivity disparity, with greater quality disparity yielding stronger source-sink dynamics. Species responses to environmental variation as well as the proximity of sources to sinks (pattern) also ranked highly, accounting for ~ 39% and 38% of the influence of growth on productivity disparity (respectively, Figure 1.1.5). All else being equal, lesser degrees of environmental variation and scenarios with high quality interspersed with low quality patches, rather than along a quality gradient, resulted in greater productivity disparity. Disparity in patch size, and dispersal distances had weaker influences on the strength of source-sink dynamics, with 8 % of the influence of the top ranked variable (Figure 1.1.5). Shorter-distance dispersal was associated with stronger source-sink dynamics, as was greater disparity in patch sizes. These variables were significant at $p < 0.1$, and were modestly more influential when alternative metrics were tested.

When population growth rate was held constant at each level, habitat quality consistently became the most important driver of source-sink strength (Figure 1.1.6). The slowest growing populations displayed the greatest response to habitat quality disparity among patches, with lesser contributions from other variables. In contrast, the fastest growing populations displayed a diminished response to habitat quality although it was still the most influential factor.

Table 1.1.2. Influence of habitat and population variables on productivity disparity in the naive habitat selection scenario (N =136), as described by standardized effect sizes (R^2 = 0.86; F Ratio = 134.64; Prob >F = < 0.0001)

Variable	Rank	Estimate	SE	t Ratio	Prob>|t|	Std Beta
Intercept		67275.23	14598.50	4.61	<.0001*	0
Growth	1	60088.11	2772.75	21.67	<.0001*	0.7154
Quality	2	971.13	55.58	17.47	<.0001*	0.5754
Variation	3	-44426.36	5319.20	-8.35	<.0001*	-0.2759
Pattern [gr]	4	-2202.95	265.29	-8.30	<.0001*	-0.2713
Dispersal		-2.15	1.22	-1.76	0.0809	-0.0575
Size		-36.65	22.02	-1.66	0.0984	-0.0544

Growth = Reproductive potential; Variation = stochastic environmental variation; Pattern = proximity of high to low quality patches; Quality = patch quality disparity; Size = patch size disparity; Dispersal = dispersal ability. The following non-significant variables were not ranked: Dispersal and Size.

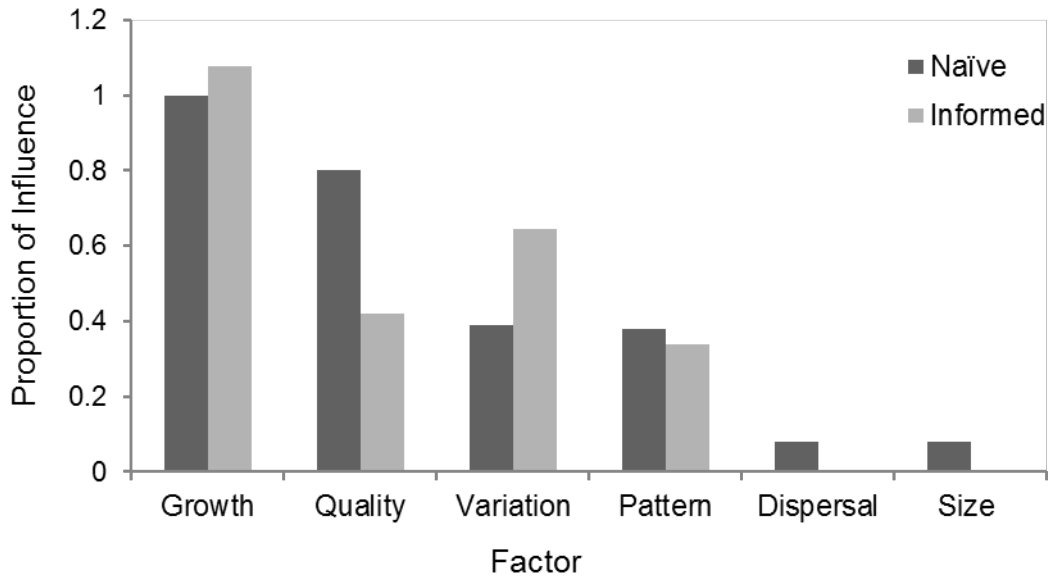


Figure 1.1.5. Proportional influences (Std β_i / Std $\beta_{i\ Max}$) of key habitat and population factors in both naive and informed habitat selection scenarios.

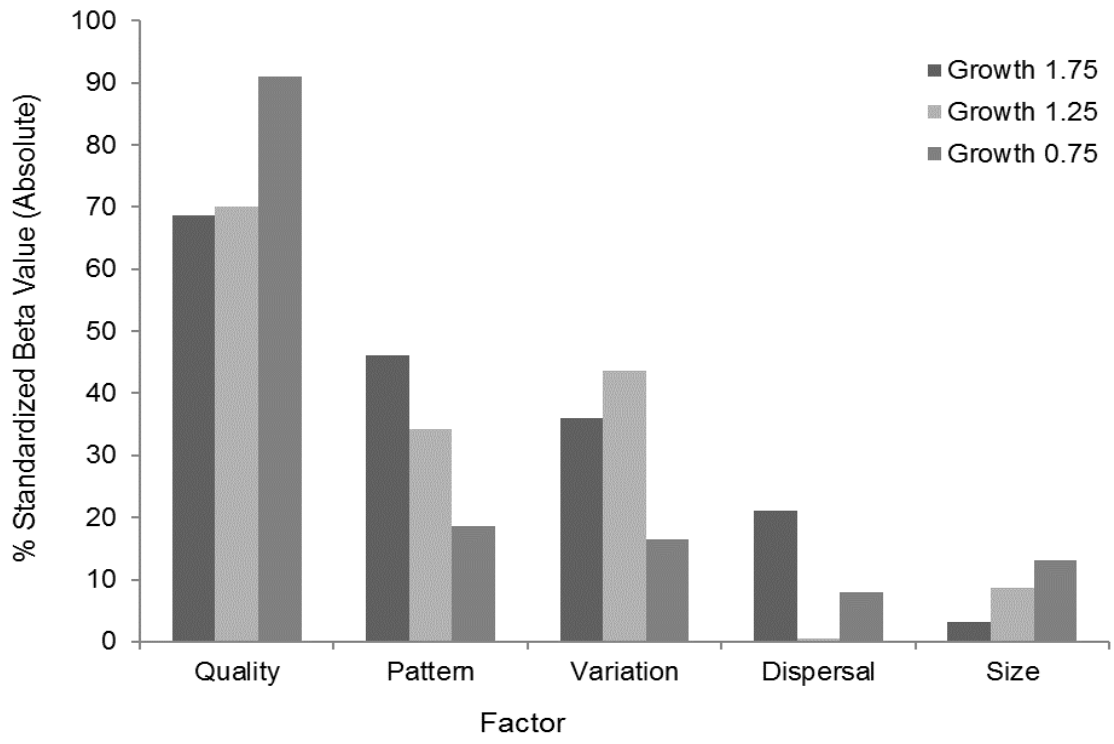


Figure 1.1.6. Relative influences (Absolute Std β_i values * 100) of key habitat and population factors, holding population growth levels constant at 1.75, 1.25, and 0.75 in the naive habitat selection scenario.

1.1.3.3 Informed Selection Scenarios – Factorial Analysis

When animals had increased knowledge of the landscape and were more successful at moving to and selecting better habitat, population growth potential still emerged as the most influential variable (Table 1.1.3) driving the strength of source-sink dynamics, with slightly greater influence than in the naive selection scenario. The rank order of the second-most influential variable was inverted compared to the naive scenario, with the influence of environmental variation becoming more important than patch quality disparity (Figure 1.1.5).

Table 1.1.3. Influence of habitat and population variables on productivity disparity in the informed habitat selection scenario (N =28), as described by standardized effect sizes (R^2 = 0.78; F Ratio = 20.03; Prob >F = < 0.0001).

Variable	Rank	Estimate	SE	t Ratio	Prob>|t|	Std Beta
Intercept		-21680.37	12406.52	-1.75	0.0939	0
Growth	1	43781.14	5878.86	7.45	<.0001*	0.7707
Variation	2	-26373.48	5757.39	-4.58	0.0001*	-0.4607
Quality	3	562.19	190.92	2.94	0.0073*	0.3010
Pattern [gr]	4	-6873.41	2825.47	-2.43	0.0232*	-0.2420

Growth = Reproductive potential; Variation = stochastic environmental variation; Pattern = proximity of high to low quality patches; Quality = patch quality disparity. Dispersal distance (short) and patch size disparity (level 150) were held constant among simulation scenarios.

The strongest mean difference among source and sink strength was observed in a scenario with the highest examined growth potential level (fecundity = 1.75), no environmental catastrophes (variation = 0.0), the greatest level of quality disparity among patches (80), and an interspersed pattern of high- and low-quality patches. The habitat-population scenario with the opposing characteristics, that was expected to have the weakest source-sink dynamics, went extinct before data were collected. The weakest observed dynamics were generated from the combined influences of the lowest growth level (fecundity = 0.5), higher environmental variability (1.0), a moderate level of patch quality disparity (40), and patches arranged along a gradient of qualities. In general, the emergent source-sink systems that were influenced by informed habitat selection were weaker than those produced by naive habitat selection. On average, the informed habitat selection scenario produced source-sink dynamics that were 73% of the strength of those of the naive scenarios (using only comparable scenarios with short dispersal distances and high patch size disparity), with less variation in source-sink strength among populations and landscapes.

Table 1.1.4. Influence of habitat and population variables on productivity disparity holding the population growth level constant at 1.25 in the naive scenario (N =48), as described by standardized effect sizes (R^2 = 0.81; F Ratio = 34.78; Prob >F = < 0.0001).

Variable	Rank	Estimate	SE	t Ratio	Prob>|t|	Std Beta
Intercept		32854.59	5780.95	5.68	<.0001*	0
Quality	1	882.74	85.79	10.29	<.0001*	0.7003
Variation	2	-50958.56	7942.90	-6.42	<.0001*	-0.4367
Pattern [gr]	3	-8611.50	1715.86	-5.02	<.0001*	-0.3416
Size		-44.17	34.32	-1.29	0.2051	-0.0876
Dispersal		-0.13	1.91	-0.07	0.9473	-0.0045

Variation = stochastic environmental variation; Pattern = proximity of high to low quality patches; Quality = patch quality disparity; Size = patch size disparity; Dispersal = dispersal ability.

Table 1.1.5. Influence of habitat and population variables on productivity disparity holding the population growth level constant at 0.75 in the naive scenario (N =40), as described by standardized effect sizes (R^2 = 0.79; F Ratio = 26.14; Prob >F = < 0.0001)

Variable	Rank	Estimate	SE	t Ratio	Prob>|t|	Std Beta
Intercept		-2797.26	4834.00	-058	0.5666	0
Quality	1	846.76	79.03	10.71	<.0001*	0.9092
Pattern [gr]	2	-3402.34	1421.95	-2.39	0.0224*	-0.1864
Variation		-16160.19	8349.95	-1.94	0.0613	-0.1642
Size		-47.73	28.44	-1.68	0.1024	-0.1308
Dispersal		-3402.34	1.58	1.03	0.3114	0.0801

Variation = stochastic environmental variation; Pattern = proximity of high to low quality patches; Quality = patch quality disparity; Size = patch size disparity; Dispersal = dispersal ability.

1.1.4 Discussion

1.1.4.1 Relative Influence

Many factors have been found to incite source-sink dynamics, yet their relative contributions in strengthening dynamics remained relatively unexplored. In an effort to help identify the characteristics of systems that are likely to exhibit strong source-sink dynamics, we compared the roles of influential factors in strengthening source-sink dynamics in a series of controlled simulation experiments to generate hypotheses for future exploration with empirical data. Our

results suggest that systems with species capable of rapid growth, occupying habitat patches with more disparate qualities among patches, and in relatively stable environments (i.e., fewer negative perturbations), are more likely to exhibit strong source-sink dynamics. The pattern of high and low-quality habitats was also influential in inciting and strengthening dynamics. Dispersal ability and differences in patch sizes had weaker impacts. Although some factors were much stronger drivers than others, strong source-sink dynamics emerged under a range of factors in multiple different scenarios, suggesting that multiple lines of data and inference are likely to be needed to predict the strength of source-sink dynamics.

In both the naive and informed habitat selection scenarios, the strongest driver of source-sink dynamics was population growth (i.e., fecundity). Although the intuitive expectation is that differential habitat quality drives source-sink dynamics, our simulations suggest that heterogeneous habitat quality provides an influential stage upon which density-regulated populations can act to further strengthen source-sink dynamics. Smaller, slow-growing populations operate more frequently below carrying capacity, where there is less impetus for density-dependent emigration from natal patches, and less exposure to survival and reproductive limitations. This weakened sources and sinks over populations capable of faster slower growth in our simulations. Although stronger source-sink dynamics were associated with higher population sizes, this relationship was increasingly variable in regional populations with stronger dynamics, indicating that that population size alone is unlikely to generally predict source-sink severity. The combination of population growth potential and population size relative to carrying capacities may be a better predict the strength of source-sink dynamics. As demographic rates are themselves a function of inherent species characteristics, as well as current and past environmental drivers (Treurnicht et al. 2016), future research could further decompose population growth in specific systems to gain a more complete indication of the key demographic drivers influencing source-sink dynamics.

Our results indicate that systems with greater disparity in habitat quality among patches are likely to incite and produce stronger source-sink dynamics, with the strongest dynamics emerging in systems with both high quality disparity and population growth. Species with inherently lower capacities for population growth (e.g., lower fecundity rates) with a naive habitat selection strategy may be particularly sensitive to the disparity of habitat quality among patches (Figure 1.1.6) and the ensuing source-sink dynamics may be largely driven by habitat quality differences. Species subject to greater intensities and durations of density-dependent population regulation were still primarily influenced by habitat quality disparity, but other factors weighted in more heavily than in low growth scenarios. This may indicate that in robust, intensely density-regulated populations, other supporting factors increase in importance. Across different kinds of systems, habitat quality information is likely to be helpful in inferring the presence of source-sink dynamics; however, this information alone is unlikely to accurately predict the strength of dynamics. Habitat quality disparity may better indicate the strength of source-sink dynamics among populations of the same species or groups of species with a similar low potential for population growth. Response surfaces indicate that threshold effects may exist (e.g., low quality = ~ 40% of value of high quality), above which quality disparity among patches may produce much stronger source-sink dynamics. Such thresholds may complicate source-sink strength inferences based on quality disparity data. Habitat quality disparity may also be more important than described here for species who are unable to expand their territories

to compensate for a low quality or quantity of resources, or philopatric social organisms that share resources (e.g., scramble competition) with an unwillingness to relocate or break up the group.

Environmental stability and the spatial pattern of sources and sinks were also important in predicting the strength of sources-sink dynamics. When used in combination with population growth and quality disparity information, environmental stability may indicate the presence and strength of source-sink dynamics, particularly for species with informed habitat selection. Temporal fluctuations in demographic rates can influence the magnitude and duration of density-dependent effects (e.g., alteration of dispersal patterns; Holt 1996, Virgl and Messier 2000) and influence the strength of source-sink dynamics. In our model, populations subject to weak environmental variation experienced only minor reductions in abundance and maintained higher average population sizes than populations more strongly affected by variation. Through time, higher quality patches were likely strengthened as a result of more consistent occupancy and higher local population densities. Emigration from highly occupied patches to lesser quality patches strengthened sinks, and created greater disparity in productivity among sources and sinks. For species with informed habitat selection, population stability leading to density-dependent movement consequences was more important than habitat quality disparity. With the recognition of lower quality habitat, the ability to leave in search of better habitat, and high dispersal success, these species could seek out locations that better optimize their fitness, predictably weakening source-sink dynamics. Future studies could invoke different kinds of environmental stochasticity affecting population dynamics including positive autocorrelation (e.g., Crone 2016).

The likelihood that individuals leaving sources can successfully reach a sink is generally expected to affect the strength of sources and sinks (Pulliam 1988, Walters 2001, Holland et al. 2009). Sinks that are proximate to sources (e.g., interspersed) are more likely to be encountered and occupied by emigrants from sources, strengthening nearby sinks and their contribution to overall dynamics. Conversely clustered sinks (e.g., low quality patches along a habitat quality gradient) can result in lower population persistence (Matthews and Gonzalez 2007), indicating that lower population sizes and high local extinction rates may reduce the long-term severity of sinks and diminish overall strength of source-sink dynamics. The pattern of high and low quality patches modified the strength of source-sink dynamics in all scenarios, with interspersed quality patches strengthening, and gradients weakening source-sink dynamics similarly among both naive and informed selection scenarios. We found limited support for dispersal ability mediating the effect of spatial patterning of habitat quality on the strength of source-sink dynamics. In gradient landscapes, naive species with unlimited dispersal had weaker source sink dynamics compared to dispersal-limited species. However, in interspersed landscapes, source-sink severity was similar among short and long dispersers, likely owing to their tendency to immigrate into nearby and easily encountered patches, with identical habitat selection criteria to short dispersers. Similarly, Walters (2007) found that the effects of breeding-patch configuration outweighed dispersal characteristics (including distance) on dispersal success, suggesting that the influence of source-sink patterning may generally outweigh that of dispersal in strengthening sources and sinks.

The exchange of individuals among populations is a necessary condition for source-sink dynamics to arise, as the existence of sink populations often rely on immigration from sources (Gunderson et al. 2001, Schooley and Branch 2007). Hence, the increased ability of animals to travel across the landscape in search of optimal habitat (relative to inter-patch distances) was expected and observed to weaken source-sink dynamics. In the naive habitat selection scenario, animals with short dispersal distances (relative to inter-patch distances) were limited to settling in nearby patches regardless of their quality, strengthening proximate sinks and source-sink dynamics. Animals capable of longer distance dispersal (but similarly limited perceptual ranges) were able to migrate to distant, more isolated patches, increasing their immigration and occupancy rates, and weakening the effect of source-sink pattern on the severity of dynamics. In our limited exploration of dispersal, an animal's ability to search the landscape for new habitat was not a key factor driving the strength of source-sink dynamics. However, dispersal ability might be more important in species that rely more on random explorative searches for habitat, with greater dispersal abilities coupled with higher habitat selection criteria (than those examined here), and in landscapes with a complex, heterogeneous matrix.

All else being equal, we expected that landscapes with disparate patch sizes would have stronger sources than those with similar patch sizes. Larger patches have greater capacities, receive more immigrants via diffusion movements in the matrix (i.e., higher encounter rates; Bowman et al. 2002), and emit fewer emigrants resulting from passive dispersal, which can strengthen source patches (Walters 2001). In turn, stronger sources would be expected to create stronger sinks and overall source-sink dynamics by elevating sink immigration and occupancy rates. Although more disparate patch sizes often strengthened source-sink dynamics, patch size disparity was not a prominent driver of source-sink strength, likely owing in part to the effects of other factors on emigration routes and rates. Patch size disparities may be more important in species that rely more on passive dispersal and more random diffusion than explored here, and in systems with strong responses to patch edges.

1.1.4.2 Implications for Source-Sink Populations

Hypothetical source-sink systems provide a controlled means of gauging the relative influences of a number of general ecological conditions and can serve as a tool for generating testable hypotheses, but these models lack the case and context-specific details of complex natural systems. Yet in an informal evaluation of modeled source-sink dynamics for black-capped vireos and Ord's kangaroo rats based on Heinrichs et al. (2015), we found support for population growth rates indicating the strength of source-sink dynamics across systems. Heinrichs et al. incorporated species life history details (demography, movement, density-dependent habitat selection) and landscape information into realistic spatially explicit individual-based models, and then computed habitat patch productivity as has been done here. Their population growth rates successfully predicted the rank order of the overall strength of source-sink dynamics across these case study systems and scenarios. Despite this, the degree to which the strength of source-sink dynamics can be predicted in individual systems may still depend on the importance of case-specific details and dependencies (e.g., Loehle 2012), hence, empirical data is required to further test and develop these hypotheses.

Results from theoretical source-sink research are often criticized for being difficult to operationalize in empirical systems, and management based on demographic and source-sink concepts may often be constrained by many practical constraints (e.g., Kerr et al. 2016) including the costs of intensive data collection. Yet, uncertainty in the demographic conditions, source-sink characterization, and strength of source-sink systems can undermine management efforts (Barthold et al. 2016, Griffith et al. 2016). A conceptual understanding of the nature of dynamics among subpopulations could be helpful in guiding and targeting the intensive resources required to collect data to assess and evaluate cross-system patterns of source-sink intensities. Well-developed and tested theory predicting the expected strength of source-sink systems can provide a low effort screening tool to identify situations in which source-sink analyses should be undertaken and used to inform management strategies. Conservation and management actions may need to be different for systems with weak versus strong source-sink dynamics, and approaches and decisions made for systems with weak dynamics may not hold for those with strong dynamics. Knowledge of the strength of source-sink dynamics present within a system should be also helpful in indicating the degree of interdependency and the importance of connectivity among populations, and in identifying actions that could be used to alter the severity of source-sink dynamics, particularly for declining species. For instance, systems with particularly strong sources and/or sinks may have patches that disproportionately contribute to and drive regional population dynamics (Schlaepfer et al. 2002, Kawecki 2004, Runge et al. 2006). In such metapopulations, it may be particularly important to accurately identify and assess the strengths and contributions of sources and sinks prior to the selection of local habitats for protection, restoration, or monitoring population trajectories. For example, the strongest and most central source (b-d=1891) in Figure 1.1.4a drives the performance of all of its neighbors and would likely be a primary target for preservation. Weaker sources or sinks may be targets for habitat restoration, and strong sinks (e.g., b-d=-585 in Figure 1.1.4a) may also be particularly suitable sites for monitoring changes in source reproductive output (Jonzen et al. 2005), or targeted for habitat removal.

Lastly, generalizations about the factors influencing source-sink severity could be helpful in identifying systems wherein source-sink dynamics may be difficult to detect and where local source-sink identifications might prove difficult or require increased accuracy. Lesser differences in productivity among sources and sinks are expected in systems with weaker source-sink dynamics, making the status of local populations more difficult to identify with confidence, particularly given the difficulty in collecting demographic information and the uncertainty inherent in such data (Runge et al. 2006, Johnson 2007, Robinson and Hoover 2011). Our results suggest that demographic differences among subpopulations may be easier to detect and measure in populations that are not continually challenged by stochastic events, capable of rapid growth, and that inhabit heterogeneous quality landscapes with interspersed high and low quality patches. Conversely, it should be more difficult to detect and measure source-sink dynamics in slow-growing populations, highly variable environments, and where a subtle gradient of habitat quality exists. This suggests that if all else is equal, populations wherein reproduction is consistently (intrinsically or extrinsically) suppressed, and populations subject to significant periodic survival stressors (e.g., weather events, exposure to toxins, disease, interspecific interactions), are less likely to exhibit large differences in demographic measurements. Similarly, populations inhabiting landscapes with gradations in habitat quality (e.g., mirroring the transition of underlying vegetation or geologic conditions) are expected to have weaker

sources and sinks. In weak source-sink systems, data collection may need to be more comprehensive to detect meaningful differences in productivity among local populations.

1.2 Divergence in sink contributions to population persistence[2]

1.2.1 Introduction

A growing body of modeling and empirical studies suggest that population sources and sinks may be common in nature (Wiens and Van Horne 2011) and increasingly prevalent in rapidly changing landscapes. A large number of individuals may occupy sink habitats (where births <deaths and emigration < immigration), particularly in human-modified landscapes, making the appropriate management of sinks (sensu Pulliam 1988) a key element in long-term conservation planning for species at risk of decline and extinction (Howe et al. 1991). Yet much of the source-sink theory and literature pertains to stable equilibrium populations in static environments. Hence, the degree to which predictions based on classical source-sink biology apply to declining and imperiled species remains unclear.

Source-sink theory has also largely developed from mathematical approaches, creating hypotheses that are often difficult to test with empirical data. Thus, managing declining populations and populations in variable environments based on conclusions drawn from equilibrium population theories may prove ineffective. Using an innovative spatially explicit agent-based modeling approach, we explored the emergence and severity of source-sink dynamics in a range of populations at risk of decline and extinction. We used a series of case studies to explore the nuances of how source-sink dynamics operate in non-equilibrium empirical systems. Drawing from the source-sink literature, we assessed the factors and circumstances under which sinks are expected to improve or reduce population size and persistence. We simulated the removal of sinks to assess their contributions to population size and persistence in each case study and devised hypotheses for further evaluation.

The impact of sink habitats on regional population persistence is likely to depend on a number of factors, including the nature of the species, the spatial patterns of sources and sinks, and population size and trajectory. In declining populations with low growth rates, persistence may depend more on the impacts of sinks than sources (habitats in which births > deaths and emigration > immigration) (Pulliam 1988, Howe et al. 1991). With few individuals and small margins for loss in sink habitats, small declining populations may be more sensitive to the presence of sink habitats than large stable populations. Conversely, small populations may also benefit more from the short-term benefits of sinks than larger populations. For example, sinks can bolster regional abundance, which helps avert stochastic extinction of small populations.

1.2.1.1 Highly Dynamic Populations

In changing environments, sinks (in addition to sources) can function in the short term as refuges from spatially asynchronous perturbations, harboring individuals that can emigrate or produce

[2]This work was published as: Heinrichs, J. A., J. J. Lawler, N. H. Schumaker, C. Wilsey, and D. Bender. 2015. Divergence in sink contributions to population persistence. Conservation Biology 29: 1674–1683.

offspring that later disperse to sites of local extinctions (e.g., Foppen et al. 2000, Frouz and Kindlmann 2001, Falcy and Danielson 2011). In highly variable environments, weaker sinks can also temporarily behave like sources during periods of favorable conditions and contribute to population growth. Pseudosinks (i.e., sources that behave like sinks when densities are high) can revert to source conditions under low densities (Watkinson and Sutherland 1995, Dias 1996, Johnson 2004). Even relatively consistent sinks may prove beneficial in the long term if the ecological context or landscape undergoes substantial directional change.

1.2.1.2 Strong Sinks and Ecological Traps

Suboptimal sites such as sinks generally do not provide long-term habitat (Van Horne 1983, Howe et al. 1991) and the presence of sink habitats within a regional network may be ultimately detrimental to population persistence. The degree to which sinks compromise persistence may depend on their strength and context. The presence of strong sinks, with a large ratio of deaths to births, may reduce regional population size and persistence. Gunderson et al. (2001) found that high mortality rates in sinks could lead to reduced population growth in sources. Similarly, Delibes et al. (2001b) concluded that sufficiently high mortality in sinks could lead to extinction of subpopulations in sources. The impact of strong sinks may be magnified in areas where few individuals are able to survive and emigrate elsewhere (Holt and Gaines 1992). Similarly, ecological traps (low-quality habitats that are preferred over high quality habitats) may be particularly detrimental if they attract and divert a substantial number of immigrants away from source habitats (Howe et al. 1991, Battin 2004).

1.2.1.3 Sinks that Facilitate Connectivity

The presence of sinks in a fragmented or disconnected system may aid in connecting source populations, which strengthens abundance and persistence. Sinks may provide corridors (e.g., linear features such as roads, cutlines) or stepping stones (e.g., discrete patches) that facilitate dispersal and allow individuals to avoid saturated habitats and more widely distribute individuals among source populations (Vögeli et al. 2010).

To assess the roles of sink habitats and determine the consistency with which they affect the persistence of species of conservation concern, we used empirical data to simulate source-sink dynamics for three very different endangered species. We quantified population abundance and persistence, with and without long-term sinks, and assessed the degree to which sinks affect long-term population outcomes. We considered the implications of our findings for prioritizing source and sink habitats for management and the potential consequences of misdiagnosing sink contributions in each case study. Using our case-study results, we develop sink contribution hypotheses relating to strong sinks and ecological traps, sinks in highly dynamic populations, and sinks that facilitate connectivity.

1.2.2 Methods

1.2.2.1 Case Studies

We simulated source-sink dynamics for three endangered species: black-capped vireos (*Vireo atricapilla*) at Fort Hood, Texas (U.S.A.), Ord's kangaroo rats (*Dipodomys ordii*), in Alberta, Canada, and northern spotted owls (*Strix occidentalis caurina*) in the northwestern United States. We chose these species in part because they represent small and declining populations in a range of ecological contexts in which sink contributions to population persistence may differ. They occupy very different landscapes with different sink strengths and magnitudes of population fluctuations; have a range of population sizes, trends, and rates of decline; and are subject to different drivers of source-sink dynamics (habitat quality, nest parasitism, interspecific competition, etc.). More specifically, the black-capped vireo and northern spotted owl systems are thought to contain ecological traps or strong sinks, and Canada's Ord's kangaroo rats are an example of a highly dynamic population with sinks that facilitate connectivity. We used empirical data to construct spatially explicit, individual-based models in the HexSim simulation modeling environment (Schumaker 2013). This approach allows sources and sinks to be emergent properties of the simulations.

1.2.2.1.1 Ecological Traps and Potentially Rapid Decline (Vireos)

On the Fort Hood Military Installation, the black-capped vireo occupies relatively discrete shrubby habitat patches in a landscape shared with brown-headed cowbirds (*Molothrus ater*). Brown-headed cowbirds have expanded their range and parasitize vireo nests in areas that were previously high-quality vireo habitat; thus, cowbirds have functionally converted these areas into ecological traps that may limit population persistence (Gates and Germaine 1978, Johnson and Temple 1986, Remes 2000, Battin 2004) . Hence, the source-trap status of vireo habitat is largely driven by parasitism pressure and the presence or absence of cowbird control. The population has been deemed conservation reliant and requires the ongoing removal of cowbirds to maintain population stability (Wilsey et al. 2014) and avoid potentially rapid decline. Using the population model developed by Wilsey et al. (2014), we simulated realistic scenarios of vireo source-sink dynamics in the presence and absence of cowbird control and assessed the role of sinks in both cases. In the absence of cowbird control, vireos were affected by high parasitism rates (75% in high- and 85% in low-quality habitat; Wilkins et al. 2006). Under cowbird control, vireos were subject to low parasitism rates (5% in high- and 15% in low-quality habitat).

1.2.2.1.2 Very Small, Highly Dynamic Populations with Connective Sinks (Kangaroo Rats)

Canada's Ord's kangaroo rat occupies discrete sandy habitat patches in southern Alberta, including actively eroding sand dunes or blowouts, semi-stabilized sand dunes, and the margins of sandy roads (Gummer et al. 1997, Gummer 1999, COSEWIC 2006). Sinks arise from differences in habitat quality among habitat types. Sandy roads and associated disturbed ground are known to facilitate movement but are associated with higher rates of disturbance, predation, parasitism, low forage quality, cold burrows, and low overwinter survival rates (Teucher 2007). This highly dynamic population experiences substantial seasonal and inter-annual fluctuations in

abundance (COSEWIC 2006). High seasonal reproductive rates can lead to opportunistic occupancy of low quality habitats, where overwinter survival can be < 10%, and extirpation in patches is common (Kenny 1989, Gummer et al. 1997, Gummer and Robertson 2003). Heinrichs et al. (2010) found that sinks tended to have negative impacts on the kangaroo rat population. We expanded this simulation to quantify the effects of sink removal on population size, variability, patch occupancy, and source-sink dynamics.

1.2.2.1.3 Strong Sinks (Northern Spotted Owl)

The range of the northern spotted owl spans several states along the pacific coast, where there is continuous variation in habitat quality rather than discrete, local habitat patches. Principal threats to the spotted owl include habitat loss and degradation, loss of habitat connectivity, and increasing competition with an invasive species (i.e., barred owls, *Strix varia*; USFWS 1992). Interspecific competition with barred owls presents an important range-wide threat. In a shrinking landscape, owl species compete for breeding and foraging habitat, and the increasing number of barred owls has reduced spotted owl site occupancy, reproduction, and survival rates (USFWS 2011). Sources and sinks primarily result from differential habitat quality and interspecific interactions with barred owls. Our spotted owl model (adapted from Schumaker et al. 2014) simulates region-specific encounter rates with barred owls. Habitat quality-dependent spotted owl survival rates are reduced in the presence of barred owls, resulting invariable sink strengths (including some strong sinks). The model was parameterized with data from several smaller spatial demographic modeling regions in the northwestern United States.

1.2.2.2 Simulations

Habitat maps for each species were derived from empirical habitat suitability models and linked with empirically derived demography or density, range size, and movement data within the spatially explicit individual-based models. Modeled individuals dispersed among patches or areas of the landscape to select a suitable range. The amount and quality of resources within each range influenced simulated density, and individual survival and reproduction rates. Habitat-specific survival rates were used to describe differences in habitat quality for kangaroo rats, and habitat suitability values were assumed to represent habitat quality for vireos and spotted owls. All models included environmental stochasticity (see additional case study information below).

All models were initiated with population sizes in excess of the carrying capacity to ensure that populations were initially well-distributed among habitats. In kangaroo rat and black-capped vireo simulations, the first 10 years of simulation data were omitted to exclude model startup effects and the following 100 years of patch-specific births (B), deaths (D), immigration (I), and emigration (E) data were collected. For the spotted owl, 100 years of patch-specific data were collected starting at year 50, when the model approximated present day conditions (USFWS 2011). Post-hoc analyses indicated that the B-D metric used in our analyses was generally correlated with E-I and net flux (net exchanges of individuals among pairs of patches), suggesting that source-sink classifications based on metrics that specifically include movement are unlikely to alter sink contribution outcomes in these models.

Behaviors of animals in sources and sinks were emergent properties of our simulations and resulted from collective experiences of individuals in each patch. The source-sink status of a patch was influenced by the constraints and opportunities provided by the habitat (e.g., patch quality, location, size, shape) and the species and population attributes (life history characteristics including demographic structure and rates, population size etc.,), interspecific interactions (e.g., parasitism by cowbirds, competition with barred owls), and movement. For each patch or sampling block, the total number of births minus deaths was recorded (hereafter referred to as productivity) and provided the basis for classifying sources and sinks. Patches in which the number of deaths exceeded births over 100 years (i.e., negative productivity values) were deemed long-term sink habitats (and vice versa for sources; positive productivity values). The strength of sinks was characterized by the degree to which productivity values differed from zero. Sinks were deemed weak if productivity values were close to zero (i.e., -200 to 0) and strong if values were far from neutral (i.e., -201 to -35000). Immigration and emigration movements were implicitly represented in source-sink calculations; dispersal events influenced source-sink status by altering the number of subsequent births and deaths in the new location. For each species and scenario, we conducted 100 stochastic model runs. The details of each model are in Wilsey et al. (2014), Heinrichs et al. (2010), and Schumaker et al. (2014).

For each species, initial (baseline) model runs were conducted to identify long-term (100 years) sink habitats. Sink habitat patches were then digitally removed from the habitat map and replaced with non-habitat matrix. Because owl habitat was difficult to discretize, we used 34 sampling blocks (8417 km ^{2}) rather than patches or larger management zones to identify source and sink regions. Simulations were re-run with landscapes composed only of areas identified as long-term sources in the baseline runs. For all simulations, population size, variability, and trajectory were recorded, along with patch occupancy and regional population extinction-risk measures. To assess the impact of sinks on the populations of the three species, we directly compared metrics derived from the baseline (including sinks) and sink-removal scenarios.

1.2.2.3 Additional Case Study Information

The following summarizes the habitat and population models implemented for each case study. Additional details can be found in the referenced publications.

1.2.2.3.1 Black-capped Vireos in Texas

Wilsey et al 2012 created a habitat suitability model using presence data for territorial vireo males (2002-2003), along with vegetation type, soil data, and LiDAR-derived metrics of vegetation structure. Models were fit using a machine-learning algorithm (random forests), and a permutation analyses was used to assess variable importance. Vireo habitat selection was best predicted (in order of importance) by vegetation composition (type), soil depth, woody vegetation edge density, height, and percent cover. ROC curves were used to assess model fit and select a threshold for identifying and excluding non-habitat from the continuous model output (Wilsey et al. 2012). Patches were characterized by contiguous habitat areas in the mapped (thresholded) statistical model. The probabilities of vireo presence were assumed to represent habitat quality for the purposes of movement and territory establishment. Individuals were labelled as having constructed a low- or high-quality territory (using the midpoint habitat

value) and were assigned higher or lower rates of parasitism that reduced their fecundity (Wilsey et al. 2014). Population outcomes under scenarios of active cowbird control and no cowbird control were contrasted. Cowbird parasitism rates were 5% (with cowbird control) and 75% (without cowbird control) in high-quality habitats, and 10% higher in low-quality habitat. A moderate potential growth rate ($\lambda = 1.14$) was used in our vireo models; however, realized growth rates were a product of density, individual locations, and their exposure to nest parasitism. Environmental stochasticity was represented in fecundity, adult, and juvenile survival rates by annually drawing from representative distributions (see Wilsey et al. 2014).

1.2.2.3.2 Ord's Kangaroo Rat in Alberta

Dipodomys ordii is a small nocturnal rodent adapted to live in arid, sandy environments. It is the only species of kangaroo rat to occur in Canada and its distribution in Alberta is constrained to the Middle Sand Hill region of Southeastern region of the province (Bender et al. 2010). The species requires open, sparsely vegetated and sandy habitats to allow burrowing and hopping (Bartholomew and Caswell 1951, Armstrong 1979, Hallett 1982, Kenny 1989, Gummer 1999). Habitat was identified using a resource selection function approach. A regression model incorporated kangaroo rat occurrence records (701; 2006-2007) along with a range of landscape variables in a use-available design (Boyce et al. 2002). AIC model selection resulted in the full model being accepted, and indicated that habitat selection was influenced by elevation, slope, proximity to eolian sand, exposed soil, sparsely vegetated soil, and river valleys. The statistical model was validated and mapped to create a relative probability of occurrence map (see Bender et al. 2010). The habitat model identified active sand dunes, semi-stabilized sand dunes, road margins, and exposed sand along river valleys as areas that are likely to be selected by kangaroo rats. Habitat patches tended to be discrete but if they were comprised of more than one habitat type, a majority rule was used to assign an overall habitat type. Ratios of overwinter survival rates (Teucher 2007) were used to assign relative habitat quality values to active sand dunes and roads margin habitats. Population monitoring data (15 years) were used to infer quality values for lesser used semi-stabilized sand dunes and exposed sand along river valleys. Environmental stochasticity was included by annually drawing a mean overwinter survival rates from a normal distribution (mean 0.48; SD 0.13). Habitat quality values were used within the population model to modify the mean survival rates of individuals occupying those regions (Heinrichs et al. 2010).

1.2.2.3.3 Northern Spotted Owls in the U.S. Pacific Northwest

Strix occidentalis caurina occupy structurally complex, mature and old-growth forests in the Cascade Mountains and coastal ranges of Washington, Oregon and northern California (USFWS 2011). A range-wide spotted owl habitat suitability map was developed using MaxEnt. Habitat suitability was assessed using spotted owl location data, and habitat variables relating to nesting-roosting and foraging habitat (i.e., vegetation type/species, cover, tree size, elevation, precipitation, temperature, edge etc.). Models were cross-validated, and ROC curves were generated to measure each model's discrimination ability (USFWS 2011). A continuous, space-filling habitat model was implemented in HexSim and rectangular "sampling blocks" (8417 km^2) were used as the basis for classifying sources and sinks. Habitat suitability values were used to indicate the quality of resources that owls could acquire from their home range. Individual owl survival was modified by the level of resources contained within their home range (relative to a

target level). Spotted owl encounters with barred owls were tracked probabilistically (rather than explicitly) and used to reduce spotted owl survival (USFWS 2011). Environmental stochasticity was included in simulations, and acted both survival and reproduction rates. Base survival and fecundity rates were randomly altered by annually selecting modifying coefficients (survival 0.975-1.025; reproductive 0.5, 1, 1.5). See Schumaker et al. (2014) for additional details. Our northern spotted owl model used a finer spatial resolution (34 sampling blocks) than a previous model effort with larger modeling regions (11) and physiographic provinces (12; Schumaker et al. 2014). Although the results were largely congruent, with the majority of the landscape behaving as population sinks that generally reduced persistence, the number, strengths, areas, and locations of sinks differed among spatial scales, suggesting that sink status and contributions can depend on the spatial scales at which sources and sinks are defined.

1.2.3 Results

1.2.3.1 Black-capped Vireo

Under the active cowbird control scenario, there was little risk of regional population extinction (Figure 1.2.1a). Low rates of nest parasitism produced a stable vireo population of 4500-5000 breeding pairs occupying 97% of habitat patches. Sources generally coincided with areas of high quality habitat. Approximately half the patches were classified as long-term sinks, 64% of all habitats (Table 1.2.1). Sinks were generally small and peripheral to source patches. The removal of all sinks had no observable effect on population size or variability, trajectory, or extinction risk (Figure 1.2.1a). The number and strength of sources differed little among baseline and sink-removal scenarios. A few new, weaker sinks (36) emerged from previously unoccupied patches, all of which were relatively small and peripherally located (Figure 1.2.2).

In the absence of cowbird control measures, vireos rapidly declined toward extinction (Figure 1.2.1b). Under high parasitism pressure, the removal of all sinks (and 98% of habitat) accelerated population decline. Time to extinction was reduced from approximately 40 years to 20 years. The remaining sources (20) were weak, with a nearly equal number of births and deaths. New sinks (55) emerged from previously unoccupied, neutral, or source patches. All were relatively small, and most were located on the periphery of larger patch complexes.

In the absence of cowbird control, patch occupancy was low (59%) and the remaining sources (81) were weaker than those in the cowbird control scenario. The strongest of these weak sources had <0.3% of the productivity of that in the cowbird control scenarios, and average source productivity was half that of sources in the cowbird control scenario (Table 1.2.1). Most (93%) of the occupied patches were population sinks. On average, sinks in the absence of cowbird control were 28 times stronger than those with cowbird control. In the absence of cowbird control, the least productive sink was >500 times the strength of the strongest sink under cowbird control.

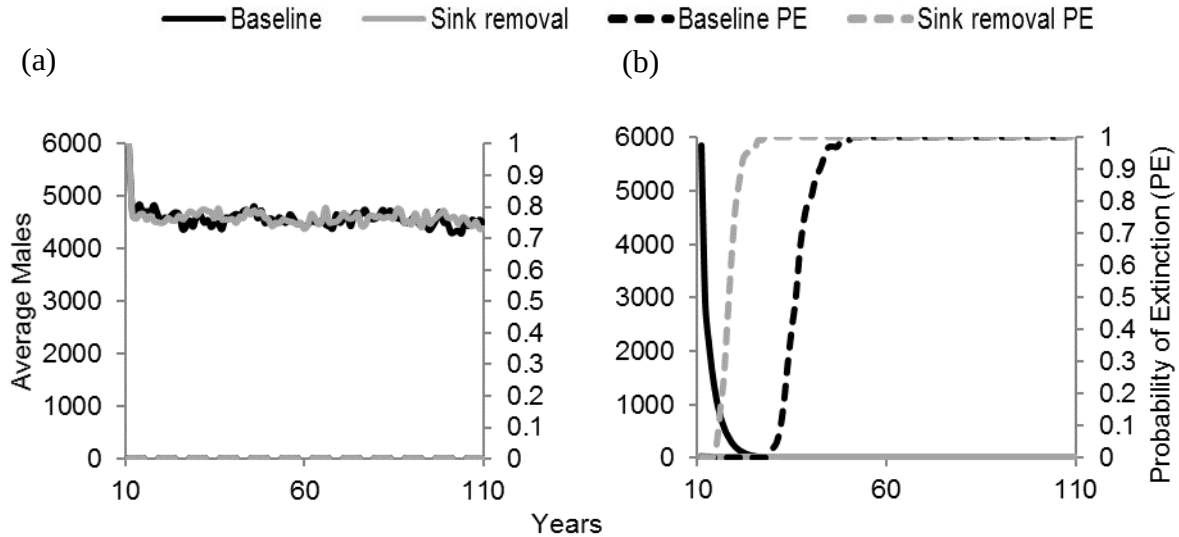


Figure 1.2.1. Black-capped vireo population size and extinction risk under (a) cowbird control and (b) no cowbird control in baseline (i.e., including all habitat and sink habitat removal scenarios over time. The population size in the sink removal scenario is very small (appearing as nearly 0) and declines to 0 at approximately year 30.

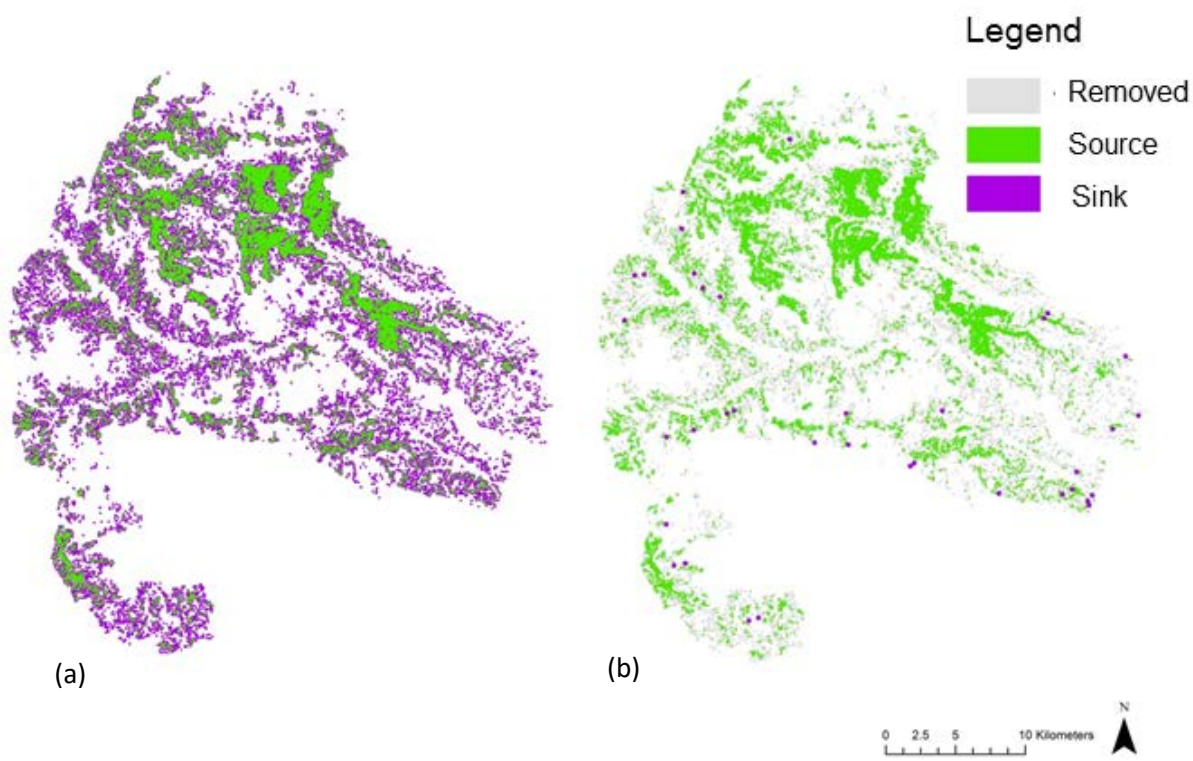


Figure 1.2.2. Black-capped vireo baseline (a) and sink-removal (b) landscapes under low parasitism rates.

Table 1.2.1. Summary of species-specific productivity data for baseline (base) and removal of habitat sinks (rem) scenarios.

	Black-capped vireo				Ord's kangaroo rat		Northern spotted owl	
	cowbird control		no cowbird control					
Habitat characteristics	base	rem	base	rem	base	rem	base	rem
Habitat patches								
total	2975	1478	2975	1347	6414	5178	34	8
percent occupied (*n*)	97 (2896)	97 (1435)	59 (1742)	7 (93)	26 (1655)	7 (365)	100 (34)	100 (8)
habitat removed* (%)		64		98		17		78
Sink habitats								
number	1497	**36**	1628	**55**	1236	**159**	26	**6**
mean productivity	-7	-2	-196	-2	-19	-6	-4974	-6886
max productivity	-59	-5	-33350	-3	-1376	-42	-12454	-12956
productivity SD	4	1	1509	1	61	7	3687	5526
Source habitats								
number	1399	1399	81	20	342	185	8	2
mean productivity	3987	3992	1862	1	363	644	6215	2285
max productivity	735706	738694	2934	2	45527	43828	22848	4509
productivity SD	34799	34882	943	1	2728	3586	7214	3146

* Sink habitat patches were digitally removed from the habitat map and replaced with non-habitat matrix.

1.2.3.2 Ord's Kangaroo Rat

In the presence of sinks in the baseline simulation, the kangaroo rat population declined to a small size and exhibited a corresponding increase in extinction risk (Figure 1.2.3). A small percentage of patches were occupied (approximately 26%; Table 1.2.1), which left vacant many of the small, isolated (but otherwise suitable) patches in the landscape. Active sand dunes functioned as long-term population sources, as did a smaller proportion of other patch types. The remainder of occupied patches functioned as long-term population sinks, including many road segments, semi-stabilized sand dunes, and exposed soil areas.

When all sinks identified in the baseline scenario (1236) were removed, the probability of extinction was reduced by about 0.1 (Figure 1.2.3). Despite a 17% reduction in the amount of

habitat, there was little change in mean population size. The average strength of remaining sources increased, but almost half the original source patches (46%) transitioned to another state (i.e., became unoccupied, neutral, or sinks). Newly emerging sinks (159) were (on average) three times weaker than those in the baseline scenario. The new sinks were often adjacent to areas of high productivity (i.e., sources; Figure 1.2.4), which suggests that some may be pseudosinks.

1.2.3.3 Northern Spotted Owl

When projected 100 years into the future, the spotted owl population declined, and extinction risk increased correspondingly through time. All habitat was occupied in the baseline scenario, and the majority of areas (26 of 34 total sampling blocks) acted as population sinks (Figure 1.2.5). Removal of observed demographic sinks (which were caused in part by barred owls) eliminated roughly 78% of available habitat, thus causing a dramatic reduction in population size (Figure 1.2.6) and variability (results not shown). The smaller, more stable regional population exhibited a lower risk of extinction. When sinks were removed, two of the eight original sources remained as connected sources but had reduced productivity (and reduced variability in productivity). Six areas that were sources in the baseline simulation became sinks. These new sinks were stronger and more variable than the original sinks that were removed and (owl density increased except in one area), indicating that these may be pseudosinks. In general, the amount of sink habitat removed did not predict sink contributions.

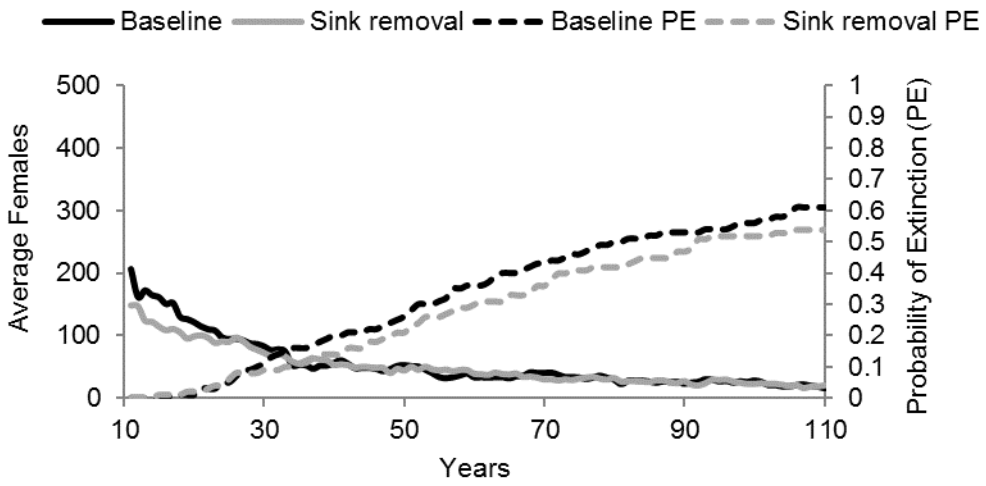


Figure 1.2.3. Change in kangaroo rat population size and extinction risk in baseline (i.e., with all habitat) and sink-removal scenarios over time.

Figure 1.2.4. Ord's kangaroo rat baseline (a) and sink-removal (b) landscapes.

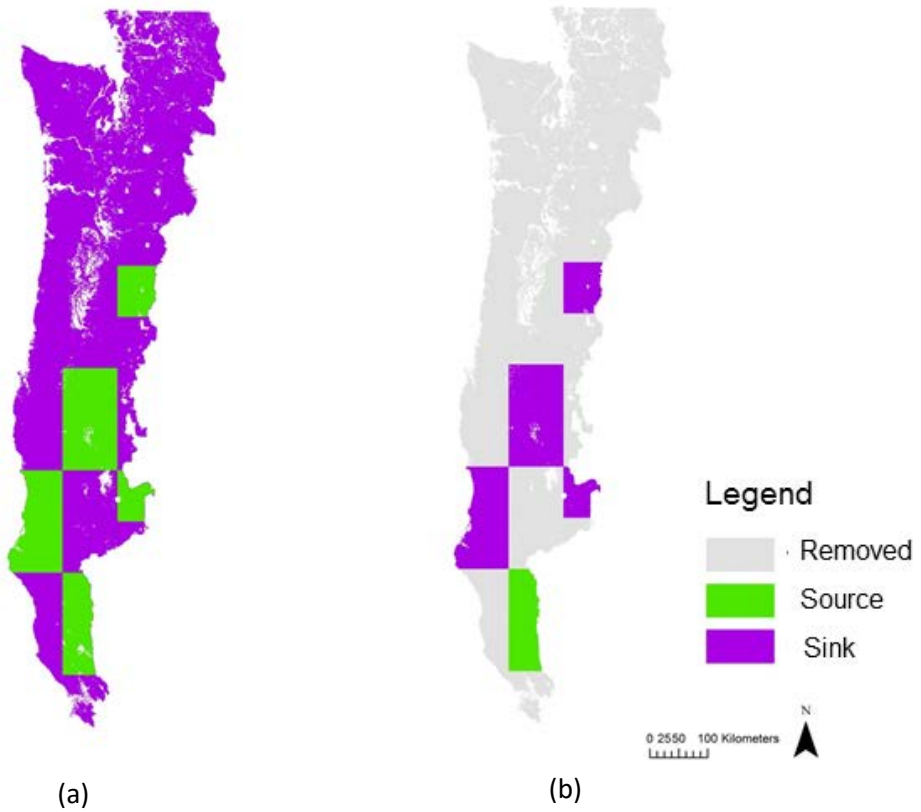


Figure 1.2.5. Northern spotted owl baseline (a) and sink-removal (b) landscapes.

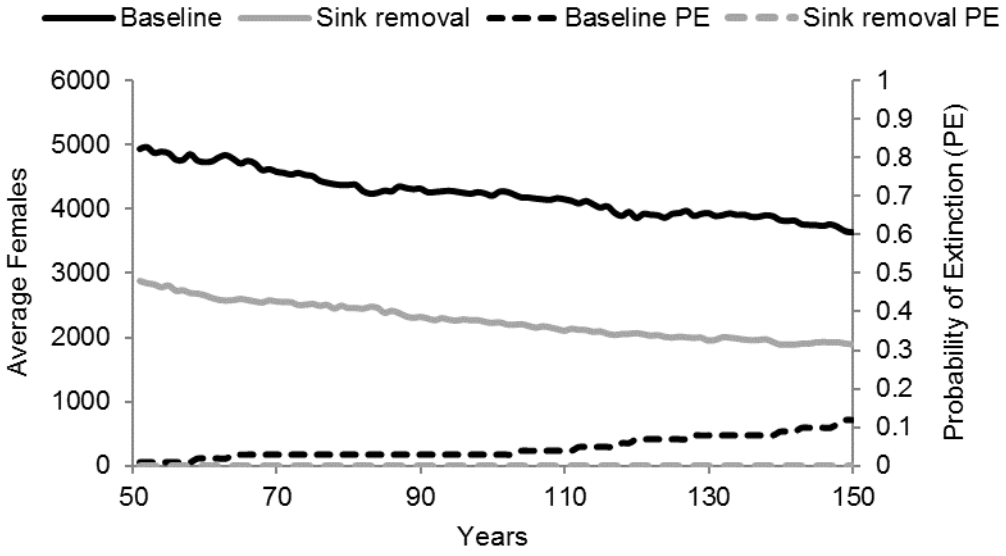


Figure 1.2.6. Change in northern spotted owl population size and extinction risk baseline (i.e., with all habitat) and sink-removal scenarios over time.

1.2.4 Discussion

The loss of many organisms in sink habitats may lead to the conclusion that sinks are often harmful for long-term persistence (Hansen 2011, Wiens and Van Horne 2011). However, surviving sink occupants can bolster regional population sizes, increase a population's distribution, and occasionally rescue source populations (Holt 1985, Pulliam 1988, Falcy and Danielson 2011), possibly encouraging the opposite generalization (i.e., that sinks are helpful for long-term population persistence). Despite theoretical progress, little is known about how sinks function in complex empirical systems and contribute to the persistence of small, declining populations. We simulated the removal of sinks to assess the degree to which sinks actually support or compromise abundance and persistence in each case study. Our results demonstrate that sinks can be both harmful and helpful depending on the ecological context (Table 1.2.2) and suggest that the impact of sinks can be difficult to infer from the strength of sinks, the amount of variability in the system and the degree to which sinks facilitate movement. Management actions based on untested generalizations of sink contributions could result in adverse consequences for many species of conservation concern.

Table 1.2.2. Expected and observed contributions of sinks to population size and persistence, with positive, negative, and neutral (N) effects when sinks are removed.

Sink type	Possible sink contribution	Observed sink contribution	Case study
Strong sinks and ecological traps	Occupancy of or attraction to sinks diverts individuals away from sources, reducing population sizes in sources (negative)	stable population with high source occupancy (neutral)	Vireo - cowbird control
		rapidly declining population with few sources (negative)	Vireo - no cowbird control
		sink de-stabilize dynamics (negative)	Northern spotted owl
		sinks bolster population size (positive)	
Sinks in highly dynamic populations	sinks bolster population sizes (positive)	sinks emit few individuals back to sources in unfavorable years (negative)	Ord's Kangaroo rat
	sinks rescue sources during population fluctuations (positive)		
Sinks facilitating connectivity	increase distribution, occupancy, and recolonization of sources (positive)	intervening sinks direct movement away from sources and lower occupancy of sources (negative)	Ord's kangaroo rat

1.2.4.1 Strong Sinks and Ecological Traps

Strong sinks are often thought to absorb individuals that could have otherwise occupied source habitat, which reduces source occupancy and abundance. Similarly, ecological traps are generally characterized as detrimental to populations (e.g., Delibes et al. 2001a, Kristan 2003, Battin 2004a). However, strong sinks and ecological traps are not universally detrimental to regional populations. Our results suggest that the impact of traps on long-term population persistence can depend on whether the population is stable or declining and on the availability of source habitat (e.g., black-capped vireos). The impact of strong sinks also depends on the degree to which sinks bolster abundance and stabilize population dynamics (e.g., northern spotted owls).

Under our cowbird control scenario (low parasitism pressure), vireos increased to a stable regional population size with well occupied, highly productive sources. Population size, extinction risk, and occupancy rates differed little among baseline and removal scenarios, and ecological traps, which constituted the majority of habitat by area, contributed little to overall vireo population dynamics and persistence. A single change in ecological context in the vireo system (removing cowbird control) yielded very different results. Under high parasitism pressure, the population rapidly declined toward extinction. Although the same amount of habitat was available in both baseline scenarios, traps were stronger and fewer birds were able to persist without cowbird control, resulting in lower occupancy and source productivity values, and nearly all vireo patches and populations were classified as traps. With few sources, the regional population became dependent on traps to delay extinction. This yielded a positive, albeit short-term, contribution to persistence. Although trap habitats do not always support long-term persistence, their continued presence in landscapes with little and sub-optimal habitat may provide a window of opportunity during which management actions could address and reverse the causes of decline for populations at risk of near-term extinction.

The influence of strong population sinks on population outcomes can also depend on the degree to which sinks increase abundance and stabilize population dynamics. In the spotted owl system, sinks had different and sometimes contradictory influences on population size, stability, and extinction risk. The removal of sinks, along with a large proportion of habitat (78%), caused a reduction in population size of approximately 40% (about 2000 females), but it also lowered the risk of extinction. Smaller populations are generally thought to be more vulnerable to extinction as a result of stochastic events; however, in this case, the smaller post-removal population sizes were less variable than those in the pre-removal landscape under similar stochastic conditions.

1.2.4.2 Highly Dynamic Populations

Sinks in spatially and temporally fluctuating systems have the potential to make a positive contribution to persistence. Although sinks can be beneficial, they are unlikely to be crucial for all declining populations in variable environments. Among other factors, the contributions of sinks to regional persistence are likely to depend on the characteristics of the sinks and the nature of the population variation. In kangaroo rats, high seasonal reproduction and emigration from sources can result in pulsed occupancy of sink habitats. In favorable years, sinks can bolster regional population sizes and provide emigrants to rescue sources after local stochastic

extinctions. However, in unfavorable years, few kangaroo rats survive the winter in strong sinks, which limits contributions to overall population size and yields a net negative influence on long-term persistence. Sink contributions may be positive in systems where the favorable years outnumber the unfavorable, where environmental perturbations are spatially asynchronous, and in systems with a high degree of sink emigration to sources. Future changes in habitat (e.g., affecting sources but not sinks) and interspecific conditions (e.g., spatially varying parasitism, competition) may prompt current vireo and spotted owl dynamics to become much more variable. This may cause some detrimental sinks to become beneficial under changing conditions.

1.2.4.3 Sinks that Facilitate Connectivity

In favorable conditions, sinks are thought to serve as stepping stones (i.e., connecting sources) that increase distribution, re-colonization success, and source occupancy. However, our results suggest that a net positive contribution of connective sinks is likely to depend on the configuration of sources and sinks, the species' ability to discriminate among low- and high-quality habitats, and their success in emigrating to sources. In the kangaroo rat system, the margins of sandy roads facilitate movement throughout the landscape, but the observed inability of kangaroo rats to discriminate among low and high-quality sites led to the opportunistic occupancy of easily found road margins over sand dunes, which left high quality areas under-saturated. Harsh overwinter conditions often restricted the life span of kangaroo rats to <1 year in poor quality areas, limiting emigration from low-quality habitats and weakening the ability of individuals in sinks to emigrate to sources in future years. In the spotted owl landscape, sinks that connected source populations facilitated movement among high quality areas to a greater extent than when replaced with matrix, but did not improve persistence. Sinks that facilitate connectivity may be more important for vireos during migration (i.e., at a broader spatial extent) than in breeding habitat. Connecting sinks might be more beneficial in systems where source areas are easily found and preferred over sinks and where sink conditions permit successful emigration to sources.

1.2.4.4 Dynamic Nature of Sources and Sinks

Sources and sinks are emergent properties of the interaction of a host of population and habitat variables (Dunning et al. 1992, Loreau et al. 2013). Sink contributions are likely to be further influenced by the key factors driving source-sink dynamics, including species characteristics, population size, rate of growth or decline, landscape attributes, ratio of sources to sinks, and the amount and connectivity of habitat. Hence, it is not surprising that even with our simplistic approach of simulating the removal of all sink habitat, new context-dependent sinks emerged with changes in occupancy, density, and distributions. Despite the wide range of sink contributions, the emergence of novel (context-dependent) sinks was consistent among cases in post-removal landscapes. This result underscores the fact that sources-sink status is a largely context-dependent label, requiring re-evaluation with concurrent environmental and ecological shifts.

Populations at risk of decline and extinction are often affected by multiple factors that influence and modify sink contributions to persistence and accurately assessing the contributions of sinks to population dynamics and persistence can be challenging, particularly in systems with complex source-sink dynamics. Repeated and multi-scale assessments of the factors influencing local and regional source-sink dynamics are likely required to estimate the short- and long-term influences of sink habitats on population persistence and to effectively inform the conservation and management of sink habitats and populations. Because our aim was to assess the consistency of sink contributions to population persistence from a very general perspective, our results describe long-term, average contributions. However, for management aims, future research should examine the sensitivity of source-sink classifications and associated sink contributions to the metrics and the periods used to define them. In particular, the success of spotted owl management actions is likely to depend on robust characterizations of sinks and their impacts on persistence. In largely contiguous or space-filling landscapes, multiple spatial scales should be assessed to identify the most appropriate scale of analysis (Loreau et al. 2013, Schumaker et al. 2014)

1.2.4.5 Conservation and Management of Sinks

Source populations are, appropriately, the focus of conservation and management efforts because they often provide the stable populations required for long-term regional persistence (Dias 1996). Yet sinks can make important contributions to conservation goals. Under some circumstances, conservation actions aimed at sinks can be more effective than those aimed at sources. For example, in landscapes with recurring disturbance in sources (but not sinks), improvements in growth rates in sinks can be more effective than increasing the rate of post-disturbance habitat recovery (Falcy and Danielson 2011, Wiens and Van Horne 2011). In conservation-reliant species, the strength and impact of sinks and traps can be directly linked to management actions (e.g., cowbird control for black-capped vireos). Increasing cowbird control in traps can increase reproductive success, weaken traps, and local and regional persistence, and is likely to be more effective than source improvements. In general, an understanding of how the intensity of cowbird control influences the strength of traps and their resulting contributions to persistence may inform selection of target areas (e.g., to maintain existing core source areas) and intensity of control in non-source areas. Active management of sink populations may also be a viable addition or alternative when conservation actions aimed at sources are limited by the practical constraints of land ownership and cost.

Our results support the idea that sinks can be helpful in improving long-term persistence, but we caution against conservation and management actions based on generalizations of sink contributions. Although sinks can facilitate connectivity and bolster population sizes in dynamic systems, sinks are not always beneficial in the long-term. Sink contributions may be detrimental in rapidly declining populations, landscapes with few sources, and problematic if sinks keep or divert emigrants away from sources. For example, despite the potential for sinks to make positive contributions to kangaroo rat persistence (by increasing population size and distribution), the continued proliferation of low-quality areas (including roads) is likely to be detrimental if kangaroo rats continue to occupy poor areas over high-quality sand dunes. Accurately identifying sinks and removing them (e.g., restoring sink roads and their margins) could improve persistence.

Source-sink status and strength should be expected to vary through time, with environmental variability and directional system changes. In systems with greater dependence on sink populations, management actions based on frequent and accurate assessments of sink habitats could mean the difference between the preservation and loss of species. For species at risk of decline and extinction, frequent monitoring of sink habitats (in addition to source habitats) might also identify opportunities for long-term or temporary improvements (e.g., partial habitat restoration, temporary competitor or parasite control, or supplemental feeding during times of scarcity) that enhance the contribution of sinks to persistence. In systems with greater dependence on source populations, frequent assessments of sink contributions can also aid in prioritizing sink habitats for conservation, recovery, or removal as population dynamics respond to variable and shifting conditions.

1.3 A multi-species test of source-sink indicators and their use in prioritizing habitat for species of conservation concern

1.3.1 Introduction

In source-sink systems, sources are an obvious target for identifying important habitats; however, it is seldom possible or palatable to conserve or target all source habitats for intensive management and habitats are prioritized using a number of different means. Accurate identifications and classifications of populations as discrete sources and sinks are important to empirical biologists and those making conservation and management decisions (Runge et al. 2006). Further, identifying areas that consistently operate as strong sources (rather than sinks, or weak sources that fluctuate among source and sink) can add another filtering strata by which habitats can be assessed. However, the means by which sources are identified and characterized differs among theoretical and applied approaches, and empirical systems, is largely driven by data collection and availability constraints. Despite the use of many methods to quantify source-sink dynamics in empirical populations, we know little about how effective these approaches are at identifying populations and habitats that are measurably important for long-term persistence. Defining sources and sinks is a data-intensive task, requiring an understanding of 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), the factors contributing to source-sink states become more apparent and more conceptually rich, realistic depictions of source-sink dynamics result.

Due to the challenges of collecting demographic and movement data, empirical methods of differentiating sources and sinks for terrestrial animals often fall short of conceptual formulations. Simple metrics are used in place of more data-intensive conceptualizations, and include site-specific counts of animals (i.e., abundance), local population growth rates, or a combination of abundance and inter-population movement rates. However, these measures are prone to misclassifications of sources and sinks as they do not account for underlying demographic and movement mechanisms that result in differential population conditions (Runge et al. 2006). Empirical studies of source-sink dynamics are increasingly bridging the gap between the empirical and conceptual by using labor-intensive methods such as mark-recapture to estimate apparent survival and fecundity, evaluating sources and sinks by virtue of the balance of births and deaths (e.g., Breininger and Oddy 2004). Some demographic studies explicitly account for emigration in source-sink classifications (Runge et al. 2006), and others link together 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). The choice of source-sink metric is still necessarily based on a study's capacity for data-collection and evaluation, and the implications of using alternative metrics to make conservation decisions are poorly understood.

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. Hence, important conservation decisions can be made on as little as a few years of data, and considered fairly robust if made on 5-10 years of data. Even in the absence of directional change, stochastic or cyclic variation can obscure the long-term contribution of habitats to population persistence within these time-frames (Runge et al. 2006, Contasti et al. 2013). Although we generally agree that more data is better, there could be a point of diminishing returns wherein additional data does not yield better source prioritizations. Conversely, there could be conditions in which attempting to prioritize habitats based on source-sink characterizations does not yield improvement in conservation outcomes. Some metrics may also be more robust to shorter time series of data, lending themselves to more accurate predictions than others when data is limited.

To examine the degree to which different prioritization approaches are able to identify the most important habitats for long-term regional population persistence, we simulated population dynamics and habitat prioritization outcomes for 3 endangered species. Using empirically-based habitat-population models, we linked habitat maps with measured site-specific or habitat type-specific demographic conditions and movement abilities, or propensities. We simulated data collection over a range time periods and used a series of source-sink metrics to create habitat prioritizations. We then tested the ability of prioritizations in each time period to identify the most important habitats by removing them from the system and measuring the population response. Those with the greatest response (i.e., increase in extinction risk) best characterized the most important patches for long-term persistence.

Using this approach, we expected that the metrics that included the most biological detail by explicitly considering both local demographic and movement characteristics would identify the habitats with the greatest contributions to persistence, particularly with longer time series of data. As the combination of demographic and movement information allows the disentanglement of gains via reproduction versus immigration (and losses via death versus emigration), movement-informed metrics, by definition, better discriminated sources from sinks than approaches using only demographic or abundance data. Hence, we expected measures that include both demography and movement to best identify the most valuable habitats. Specifically, we expected our network influence metric, that additionally considered the contribution of the focal source to other patches in the network (via successful emigration), to outperform other metrics in identifying key sources. We expected simple metrics such as abundance and demographic-only to be weaker in their ability to accurately identify sources, thereby weakening their ability to identify important source habitats. With fewer years of data collection, we expected the simple metrics that do not explicitly include movement to perform more poorly than complex metrics, with less information to correctly identify important habitats. Further, when more habitat patches were prioritized for conservation, we expected metrics to produce more dissimilar results arising from diffing abilities to characterize the strength of moderate and weak sources. Lastly, 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.

1.3.2 Methods

1.3.2.1 Case Studies

We simulated movement, habitat selection, demography, and emergent source-sink dynamics for three endangered species: black-capped vireos at Fort Hood, Texas (as described in Task 1.2), Ord's kangaroo rats (as described in Task 1.2), and greater sage-grouse (*Centrocercus urophasianus*) in Alberta, Canada. These species represent a range of small and declining populations, landscape and population conditions, and ecological contexts in which source contributions to population persistence may differ. Populations differed in their rates of decline and strength of source-sink dynamics, and were subject to different drivers of source-sink dynamics (e.g., parasitism, low-quality habitat).

We used previously developed spatially explicit individual-based models of 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. *in preparation*). All models made extensive use of empirical habitat and population data and were constructed in the HexSim simulation modeling environment (Schumaker 2015). Habitat conditions (habitat availability, structure, habitat selection values, habitat quality etc.) were linked to population outcomes by individual interactions with the landscape. Specifically, sources and sinks were emergent properties of individual movement and habitat selection decisions (guided by habitat maps), and the demographic consequences of residing in their chosen location.

1.3.2.1.1 Slower Decline in a Small Population

In Alberta, the Ord's kangaroo rat (hereafter kangaroo rat), occupies discrete sandy habitat patches, with (Gummer et al. 1997, Gummer 1999, COSEWIC 2006) differential habitat quality among habitat types giving rise to source-sink dynamics (Heinrichs et al. 2010, 2015). Source, high quality habitat includes actively eroding and natural sandy areas where overwinter survival and predation risk is lower. Conversely, low quality sink areas include disturbed sandy areas and sandy road margins that are associated with higher predation and parasitism risk, lower forage quality, colder burrow temperatures, and lower over-winter survival rates (Teucher 2007). The population experiences substantial inter-annual population fluctuations in abundance (COSEWIC 2006), with high reproductive rates leading to the opportunistic occupancy of low quality habitats (Kenny 1989, Gummer et al. 1997, Gummer and Robertson 2003). Among the case studies, this system represented the slowest rate of population decline and most gradual increase in extinction risk (Figure 1.3.1).

1.3.2.1.2 Rapid Decline in a Larger Population

The Fort Hood Military Installation hosts more than 5000 male black-capped vireos (Cimprich and Heimbuch 2012, Wilsey et al. 2014), occupying relatively discrete shrub habitat patches along with brown-headed cowbirds. In baseline simulations, the number and strength of source habitats depended on the prevalence of cowbird nest-parasitism (Heinrichs et al. 2015). In alternative scenarios, we simulated realistic scenarios of vireo population dynamics both in the

presence and absence of cowbird control (developed by Wilsey et al. 2014) and assessed source-sink dynamics under both alternatives (as in Task 1.2). In the absence of cowbird control, vireos were subject to high nest parasitism rates (75% in high- and 85% in low-quality habitat; Wilkins et al. 2006). Under cowbird control, vireos were subject to low nest parasitism rates (5% in high- and 15% in low-quality habitat). The high parasitism scenario represented the scenario with the most rapid decline from the largest initial population size (Figure 1.3.2). To assess the influence of population trend on modeling outcomes, we compared this rapidly declining high parasitism scenario with the stable low parasitism scenario.

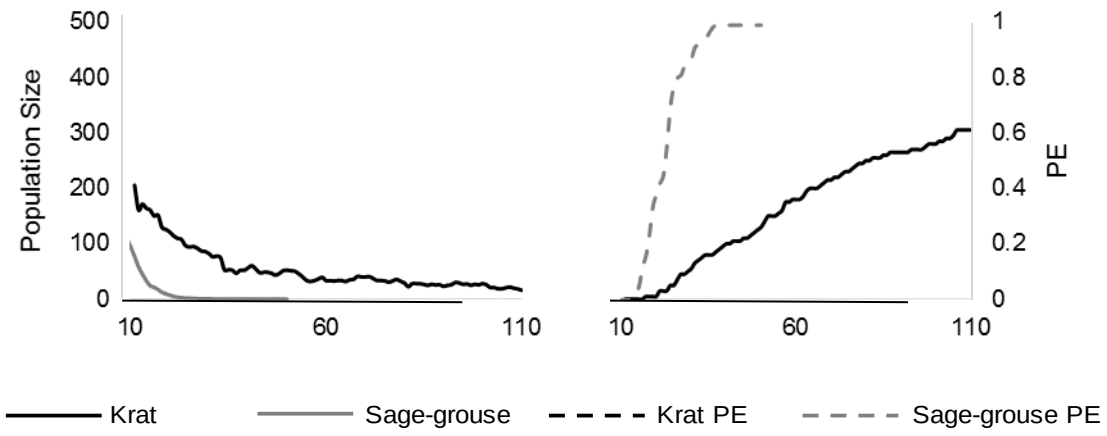


Figure 1.3.1. Change in Ord's kangaroo rat and greater sage-grouse population sizes and extinction risks in baseline (i.e., with all habitat) scenarios over time. Sage-grouse simulations were only run for 50 years.

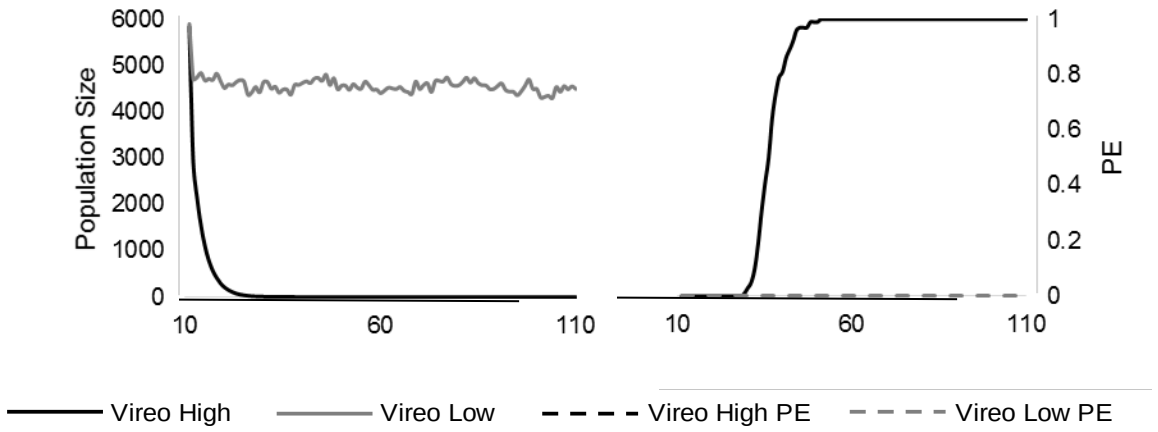


Figure 1.3.2. Black-capped vireo population size and extinction risk under cowbird control (vireo low) and no cowbird control (vireo high) in baseline scenarios (i.e., including all habitat) over time.

1.3.2.1.3 Intermediate Decline in a Smaller Population

In Alberta, the critically endangered greater sage-grouse occupies a fragmented sagebrush landscape, moving seasonally among nesting, summer, and winter resource areas (Aldridge and Boyce 2007). As a sagebrush obligate species, habitat use is constrained by sagebrush cover, and site selection is further guided by fidelities to breeding, natal, nesting locations, the availability of resources in each season, and avoidance of development (Aldridge and Boyce 2007). Baseline simulations indicated that sources are embedded among sinks throughout the sage-grouse range in Alberta, and were evident where resource selection also indicated areas of high nest success and chick survival (Heinrichs et al. *in preparation*). Sinks emerged in highly occupied habitats associated with reduced chick survival and/or nesting success (Aldridge and Boyce 2007, Heinrichs et al. *in preparation*). Using a habitat-population model, we used a population scenario that best matched empirical population trends (i.e., that assumed annual survival rates of 0.64, 0.4, and 0.64, respectively for juveniles beyond 56 days, yearlings, and adults). This scenario represented an intermediate rate of decline and the smallest population size (Figure 1.3.1).

1.3.2.2 Simulations

We linked empirical habitat selection models that were developed for each species to empirically-derived population data, including population sizes, demographic rates, densities, range sizes, movement, and behavior data. 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/or reproductive rates. For kangaroo rats, habitat type-specific survival rates described variation in habitat quality. The sage-grouse model used demographic risk maps to specify locations with 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 higher and lower levels of nest parasitism). All models included density-dependent and pre-emptive habitat selection. Models also included varying magnitudes of environmental stochasticity, corresponding to estimated measures of variation in survival and/or reproduction rates. The details of each model are in Heinrichs et al. (2010), Wilsey et al. (2014), and Heinrichs et al. (*in prep*.), the first two of which are additionally summarized in the Heinrichs et al. (2015) 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 was influenced by patch size, quality, location, landscape context, shape, resources and conditions. Further, the source-sink status of a patch was impacted by species and population attributes including life history characteristics, location-specific demographic rates, population densities, and movement abilities and propensities. For kangaroo rats and vireos, discrete (contiguous) patches were used as the spatial unit of source-sink evaluation. However, because sage-grouse habitat varies among seasons (as represented by nesting and brood-rearing habitat maps), and is generally more continuous and difficult to discretize, we used a series of nested (hexagon) pixel maps to spatially evaluate sources and sinks, hereafter referred to as habitats or patches. Baseline simulations (using 100

repetitions) were run over a number of time periods to collect patch-specific data on population size, births, deaths, immigrations, and emigrations.

To classify sources and sinks and assess source strength, we used four different metrics, ranging in complexity and data requirements. 1) Productivity: The total number of births minus deaths was recorded for each patch. Patches in which the number of births exceeded deaths over the simulation time period were deemed sources (and vice versa for sinks). 2) BIDE: In contrast to productivity, which implicitly accounts for immigration and emigration, movement is explicitly counted in BIDE as births + immigration – death + emigration for a given patch. 3) Source network influence: This measure quantifies the degree to which a source (based on births > deaths) is successful in creating and emitting emigrants who are then successful at immigrating to another patch. We calculated this as (births – deaths) * number of successful emigrants, where births>deaths for a given patch. 4) Abundance: Lastly, we calculated the mean number of individuals occupying each patch, from the start of data collection, to the end of the time period of interest. We calculated each of the four metrics using 2, 5, 10, 20, and 50 (sage-grouse) or 100 (kangaroo rat and vireo) years of simulated population data (excluding burn-in times during which data were not collected).

Strong sources were indicated by large positive metric values, and were ranked by their strengths to identify priority sources for conservation. In each system, we identified the same proportion of sources creating highly selective (0.39%) and moderately selective (0.78%) scenarios. This resulted in the prioritization of 25 and 50 kangaroo rat patches, 12 and 23 vireo patches, and 3 and 7 sage-grouse patches. We removed priority sources under (160) alternative species*metric*time*selectivity scenarios to test which combination of metric, period of data collection, and source selectivity scenario best identified sources that are important for long-term persistence of each species. Target source habitats were digitally removed from the habitat map(s) and replaced with non-habitat matrix. Simulations were re-run with landscapes comprised of non-target sources, including weaker sources and all sinks, and the probability of extinction (0 remaining individuals; PE) was quantified through time (over 50 or 100 years depending on the species) using 25 repetitions. A quasi-extinction threshold of 1000 was used in place of PE for the low parasitism vireo scenario. To compare the performance of each metric in identifying the most important source habitats, we compared PE predictions through time. Metrics that resulted in higher PE predictions identified sources that were more important for long-term persistence. Conversely, metrics associated with lower PE predictions were less effective at identifying important sources, and their removal impacted the population to a lesser degree. We repeated these comparisons for each time period of source-sink data collection and evaluated relative metric performance among time periods as well.

1.3.3 Results

1.3.3.1 Slower Decline in a Small Population

With the removal of key sources, the small kangaroo rat population declined to near-certain extinction within 45-90 time steps (Figure 1.3.3). Over 100 years of simulated data collection, extinction risk (PE) was most sensitive to the removal of sources based on patch abundance,

followed by productivity, and BIDE. Removing patches based on network influence had the smallest effect on extinction risk, indicating that it was the least effective method of identifying sources that were important to long-term population persistence. As the period of data collection was reduced to 20 years or less, metrics made 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 extinction risk (indicating the most discernment in selecting important habitats), followed distantly by network influence, then productivity and BIDE. Abundance generally yielded the best predictions and was the most robust to temporal data limitations. BIDE performed poorly in most time periods, worsening with fewer years of data collection. Network influence and productivity prioritizations were particularly sensitive to short (i.e., 2-5 year) time series of data. When fewer sources were prioritized and tested with removal (i.e., 25 instead of 50), extinction risks were impacted to a lesser extent among metrics, although the rankings of metrics were similar. Of note, network influence performed slightly better using the larger than the smaller number of prioritized sources (results not shown).

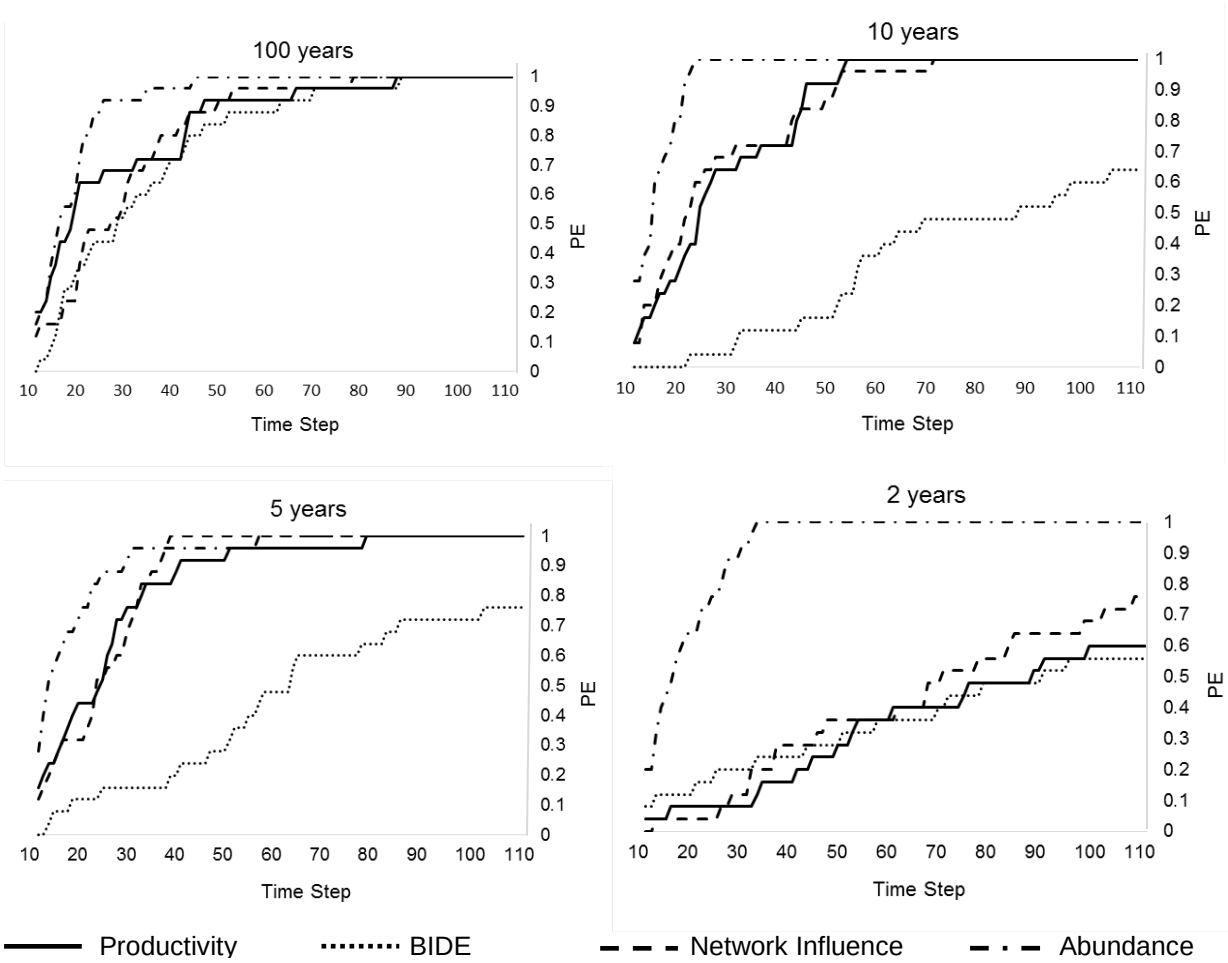


Figure 1.3.3. Ord's kangaroo rat extinction responses to key source removals based on different metric prioritizations

1.3.3.2 Rapid Decline in a Larger Population

In this very rapid decline from the highest starting vireo population size, the removal of key sources resulted in extinction within as little as 30 time steps, with a sharp threshold increase in extinction risk around 35 time steps (Figure 1.3.4). A lesser degree of difference was observed among metrics through time compared to kangaroo rats as the population rapidly trended towards extinction. Yet prioritizations still resulted in large differences in extinction risk within time steps 30-40. For example, at approximately time step 35 in the 100 year simulations, productivity and BIDE resulted in a PE of ~ 0.15 versus ~0.70 for abundance. The greatest differences among metrics was observed with the longest time series. Among time periods, prioritizations based on abundance were the most effective at identifying important habitats and productivity was generally the least discerning. As the data collection period was reduced, metric predicts became more similar. When fewer target sources were removed (12 rather than 23), the network influence metric was less successful in predicting the importance of sources for persistence (results not shown).

1.3.3.3 Black-capped Vireo – Low Parasitism

When cowbird nest parasitism was controlled, the stable population did not result in extinction and had a low risk of falling to a quasi-extinction threshold of 1000 males (Figure 1.3.5). Prioritization metrics consistently identified similar habitat patches that hosted a large number of birds, deflating the long-term population size. Resulting risks of quasi-extinction were similar among all prioritization metrics and time periods.

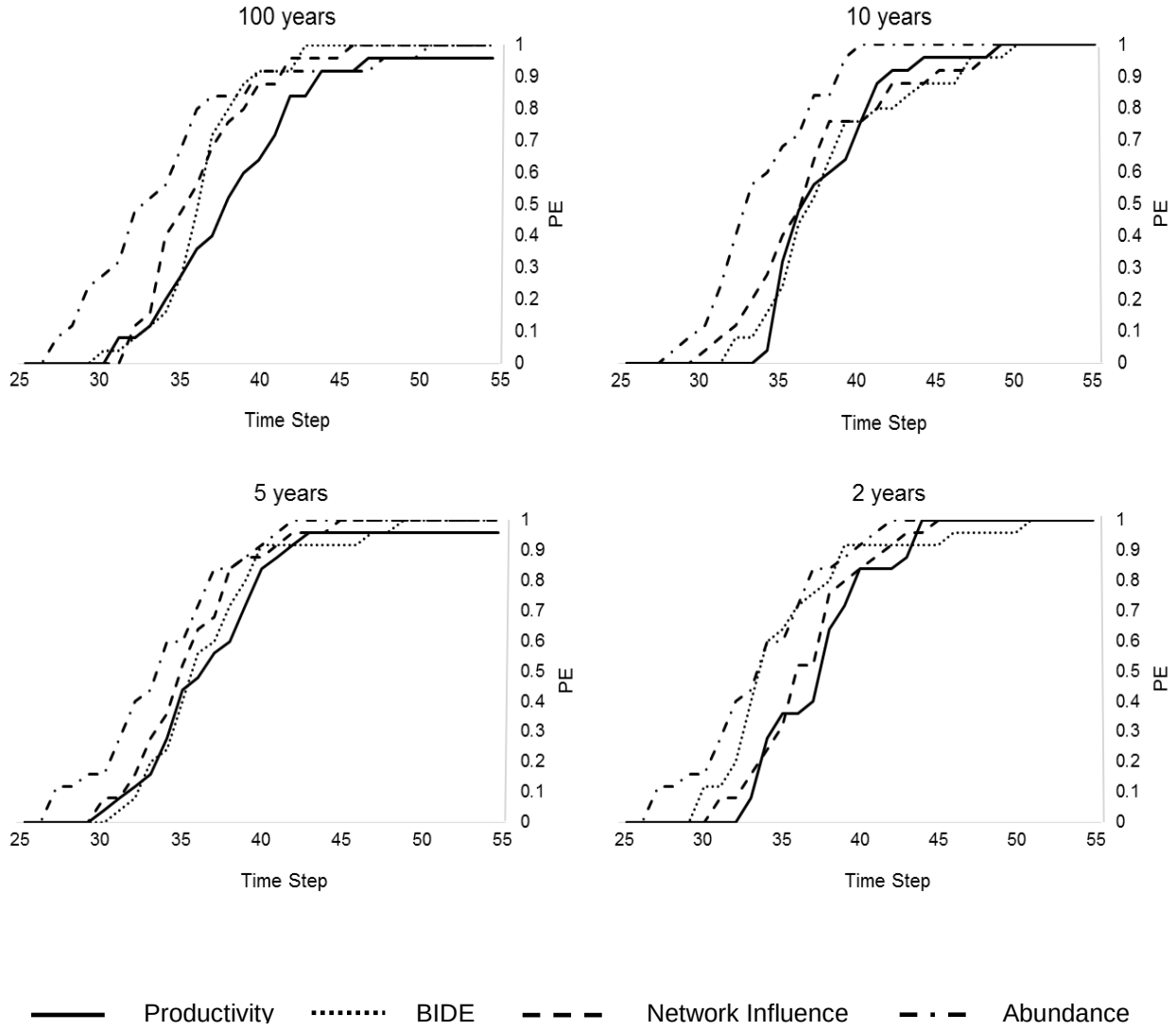


Figure 1.3.4. Black-capped vireo - high parasitism scenario extinction responses to key source removals based on different metric prioritizations

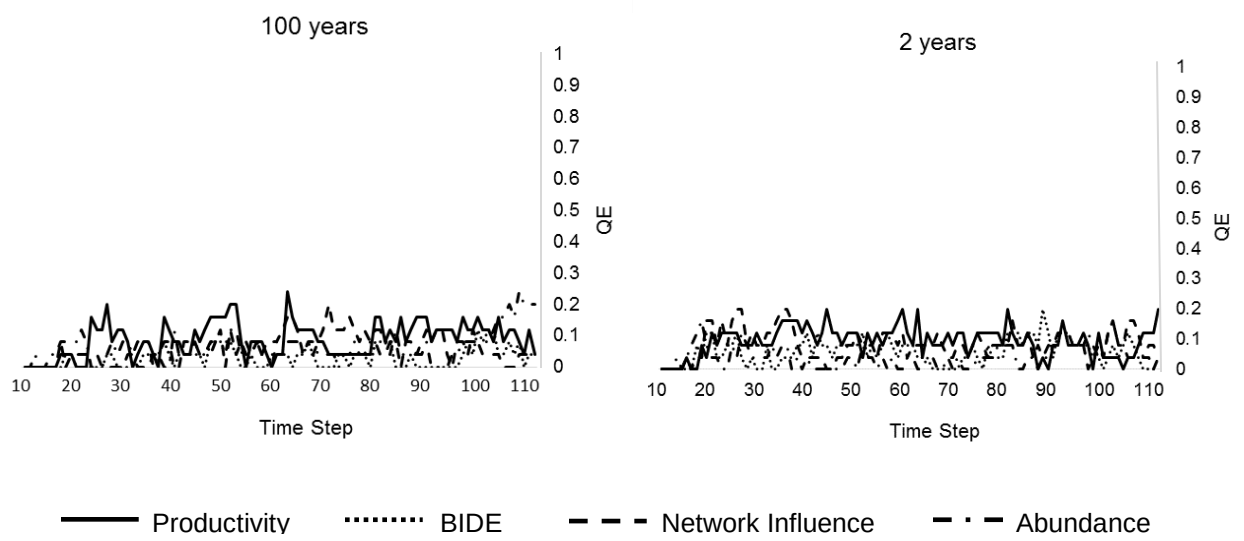


Figure 1.3.5. Black-capped vireo - low parasitism scenario extinction responses to key source removals based on different metric prioritizations

1.3.3.4 Intermediate Decline in a Smaller Population

The removal of key sources from this moderately sized sage-grouse population caused the risk of extinction to rapidly increase between 10 and 20 time steps (representing the years 2010-2020; Figure 1.3.6). Although extinction risk rapidly increased, there was less of a threshold response than for vireos. Differences among metric predictions were more similar for a given year. Using the longest time series (50 years), extinction risk was most sensitive to sources removed based on the source's network influence and the least responsive to BIDE. As the duration of data collection was reduced, metric predictions produced more dissimilar results that peaked at 5-10 years, and subsided at 2 years. With only a few years of data collected, metrics produced relatively similar results, with BIDE slightly outperforming other metrics and abundance performing among the worst. When fewer sources were prioritized and tested, network influence was generally less impactful.

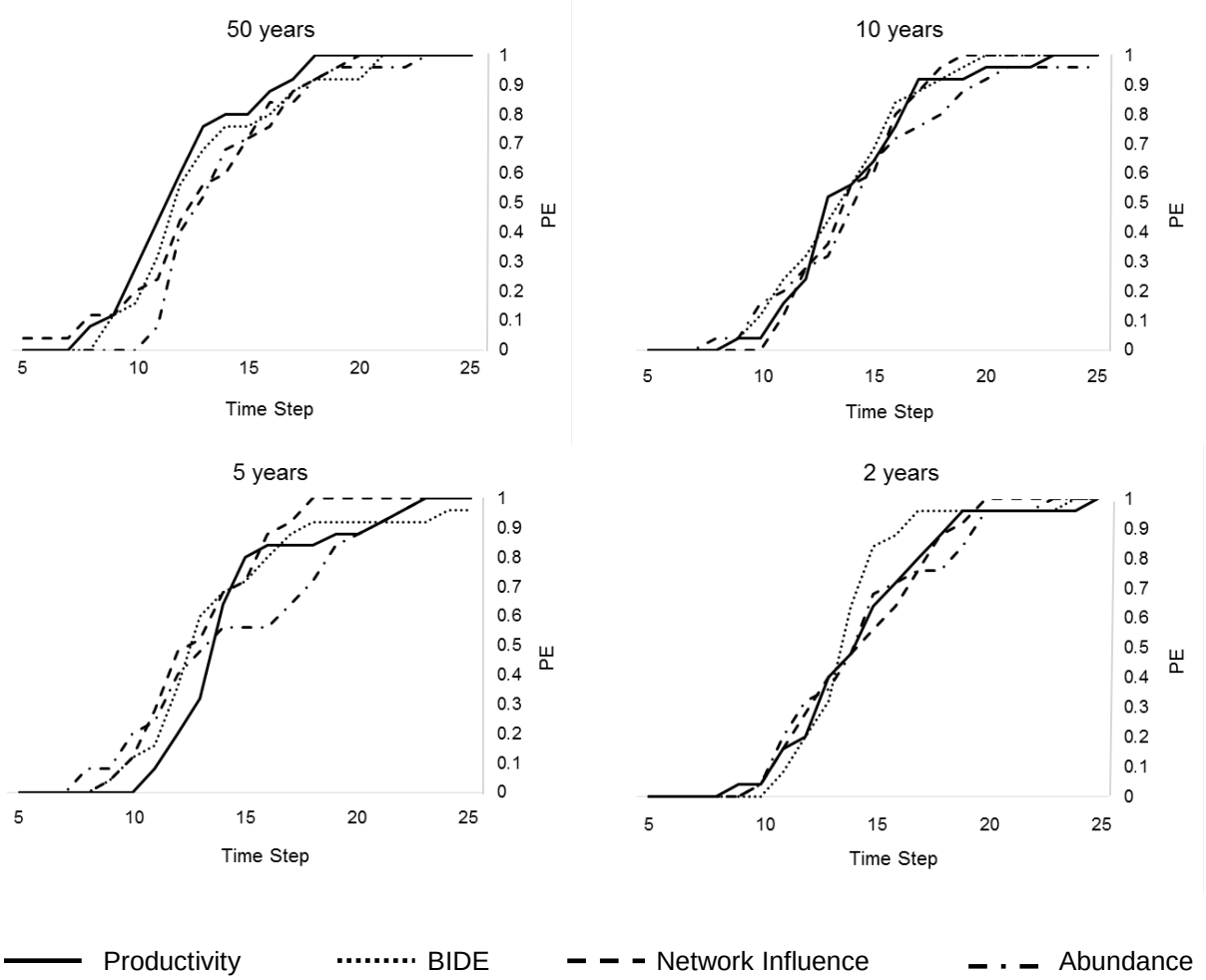


Figure 1.3.6. Greater sage-grouse extinction responses to key source removals based on different metric prioritizations.

1.3.4 Discussion

Our results indicate that the metrics used to assess the degree to which a given habitat serves as a source or a sink have the potential to impact management outcomes. In turn, these impacts depend on system nuances, the rate of population decline, the timing, location, and duration of data collection, and the number of patches that are being prioritized. Simple metrics such as abundance outperformed more complex metrics in some case studies, whereas complex metrics more accurately identified important habitats in others.

1.3.4.1 Simple Metrics

When source-sink dynamics are observed or suspected, habitat prioritizations often weigh protecting habitats with the largest number of animals against prioritizing putative sources that may contain fewer animals. Prioritizing based on abundance alone risks the misidentification of strong sinks and their continued influence on the population, particularly using short-term data. Where sinks are expected to be detrimental, their selection could compromise conservation outcomes. For example, in Alberta, greater sage-grouse actively select and occupy habitats with low nest success and chick survival, a behavior that results in part from maladaptive cues and preferences for familiar sites (Aldridge and Boyce 2007). When birds consistently flocked together in preferred but high consequence areas (e.g., poor survival), abundance poorly predicted the value or importance of habitats for persistence. For example, nesting abundance was a poor predictor of source-sink status, with 71- 86% of selected patches resulting in the targeting of sinks rather than sources (using the BIDE metric). If sage-grouse are able to successfully re-locate (as in our simulations), preserving high abundance but poor survival areas instead of productive sources could perpetuate the use of sinks, and have a net negative effect on persistence.

By contrast, when sink contributions are less detrimental or more benign, the conservation of high abundance sinks may be crucial for supporting short-term population viability. For the black-capped vireo under high parasitism, habitat prioritization based on abundance generally identified the most important habitats for short-term persistence, outperforming more complex metrics. When target patches were removed based on abundance, the population was dramatically reduced by nearly 4000 birds. All high abundance patches were classified as sinks (using productivity and BIDE metrics, at all time periods). Much more minimal losses were associated with removals for other metrics, indicating that sources were less impactful in preserving this population than sinks. In this rapidly declining population, sinks provided an important benefit by delaying extinction and providing a window in which conservation actions could have been be initiated to avert extinction (Heinrichs et al. 2015). However, as the abundance metric failed to prioritize sources over sinks, habitat protection based on this metric alone could be a temporary fix. As the population recovers, the long-term need to include productive sources may take priority over conserving sinks.

Abundance also predicted the most important patches for kangaroo rats over all times periods, and performed better than more complex metrics with short-term data. Although dispersal to alternative habitats was possible, the removal of high abundance patches resulted in higher risks of extinction, indicating that alternative habitats could not compensate for the loss of target patches. Although sinks are generally detrimental in this kangaroo rat system (Heinrichs et al. 2010, 2015), high abundance patches were comprised of a mix of sources and sinks, ranging from 38 % (100 years) – 72% (2 years) sinks as defined by BIDE. This indicates that the contributions of sinks are not equal across all sinks and that at least some are likely to be required to avoid population losses. In this system, abundance was better correlated with source status because the timing of the abundance census (e.g., not immediately following reproduction). The indiscriminate occupancy of low quality habitat leads to low over-winter survival in poor years, with few kangaroo rats surviving to emigrate to higher quality habitat (Teucher 2007, Heinrichs et al. 2010). However, in our simulations, abundance data were

recorded following winter (and before reproduction), when the highest consistent population sizes were associated with high quality, source habitat. In contrast, field data is primarily collected throughout the spring and winter and data often reflects the opportunistic occupancy of low-quality habitats by dispersing juveniles. Hence, we expect abundance based on field data to be a poorer indicator of habitat quality, source-sink status and importance of habitat.

1.3.4.2 Complex Metrics

Metrics that included demography better identified important habitats in the sage-grouse system, where abundance measurements were less able to discern among sources and sinks, and where large asymmetries in patch sizes were absent. At all periods of data collection, BIDE, productivity, or network influence out-performed abundance, with BIDE and network influence performing best with the least amount of data (2 - 10 years). For sage-grouse, productivity and BIDE classified sources and sinks similarly, suggesting that although short-term decisions may be best based on both demography and movement, equivalent conservation results might be achieved using demography alone. In addition, when more patches were selected for prioritization using long-term data, the results slightly favored more complex source-sink metrics. This may result from the greater discriminatory power of complex metrics to evaluate the combined influences of demography, movement, and network position of patches with weaker signals (e.g., weak sources) in long-term data sets.

In the more slowly declining kangaroo rat population, our results indicate that more than 20 years of data may be required to reliably identify important sources using complex metrics such as BIDE. Even though the productivity metric better identified important habitats with 5 or more years of data in this system, the ability of this metric to discern sources from sinks was limited, making simpler metrics helpful in targeting habitats for short-term persistence, but less successful in identifying source habitats for long-term recovery and persistence. For example, where the BIDE metric predicted 50% of the high abundance target patches to be sinks, productivity only identified 15% (averaged over all time periods) as sinks. By contrast, for rapidly declining vireos, BIDE metrics yielded better predictions than productivity for all time periods of data collection. This differential indicates that movement data added meaningful explanatory power and the collection of even two years of demographic and movement data could be used to meaningfully begin to identify priority source areas.

Contrary to our expectations, the performance of metrics across time periods was not always intuitive or consistent. As the duration of data collection changed, the population dwindled for all case studies except for vireos under low parasitism pressure. Populations varied in their starting sizes and how quickly they declined to near extinction. Hence, for some populations there were diminishing returns on the quality and availability of data when measured over longer time periods. The most slowly declining population, that of the kangaroo rat, displayed relatively consistent patterns in metrics among time frames of data collection even when predictive abilities of individual metrics shifted with the consideration or more or less data. By contrast, the shortest lived population, sage-grouse, had the least consistent predictions among periods of data collection. This difference suggests that the sample or population size is an important consideration, in addition to the dataset length, in estimating the power of metrics to detect reliable signals in declining populations.

Also contrary to our expectations, BIDE was not the best predictor among complex metrics in part because strong sources were not always the most important elements supporting near-term persistence. The strength of the source was related to the number of occupants when births, deaths and movements were tallied; however, the difference in these conditions signaled source importance as per the conceptual formulation. Hence, highly productive sources could also be relatively small (compared to high abundance sinks for kangaroo rats and vireos). As the conceptual formulation of BIDE and much of source-sink theory was developed for stable populations (i.e., at equilibrium) (Pulliam 1988), the difference between births + immigration and deaths + emigration may not be entirely appropriate for declining populations if they are not regulated by similar mechanisms. For example, if patches are under-occupied as a result of demographic challenges (e.g., harsh winter conditions, disease, strong natal dispersal cues), immigration and emigration rates may not be providing the expected meaning that they would in populations regulated by density-dependent habitat selection, operating at their carrying capacity.

The predictive ability of source-sink metrics also varied among case studies, with some life histories less suited to habitat prioritizations based on source-sink characterizations. For example, once a breeding territory was established for simulated vireos, they remained nearby until death, seamlessly attributing births and deaths to the same habitat. The more complicated sage-grouse life history includes the post-hatch movement of broods to summer locations, where deaths occur. In many locations where nesting habitat doubles as summer/brood-rearing habitat (as observed in Alberta sage-grouse habitat), source-sink metrics provided a spatially balanced characterization of births and deaths. In these locations, demographics and movement information provided the means to differentiate maladaptive habitat selection from contributions to population persistence. However, in locations with non-overlapping seasonal uses (e.g., exclusive summer brood-rearing; ~ 20% of habitat), source-sink metrics were more likely to indicate a nesting site to be a source if the primary use of that area was reproduction. Conversely, sinks were implicated in brood-rearing habitat chick and adult mortality were likely to occur. Hence, in areas with a single seasonal use, source-sink characterizations likely misrepresented the annual value of habitats for persistence by over-valuing nesting areas with non-overlapping seasonal uses. Although this issue could be overcome to some extent by increasing the grain of the source-sink evaluation, doing so would preclude the evaluation of differences among local habitats and the scale of management interest.

1.3.4.3 Habitat Prioritizations for Effective Conservation

Our results indicate that the way in which habitats are prioritized for declining species in source-sink systems is likely to matter most for species with gradual rates of decline, and those inhabiting large proportions of sink habitat (i.e., where abundance is a misleading indicator of source-sink status). In our kangaroo rat simulations, populations persisted longer (up to 100 years) than in the vireo high parasitism and sage-grouse case studies, allowing populations more time to respond to habitat conditions than possible with stronger extinction trends. In rapidly declining populations, the choice of metric still mattered, albeit over a shorter time frame (e.g., ~ 10 -15 years for sage-grouse and highly parasitized vireos). Large differences were observed among metrics within a given year, particularly for vireos under high parasitism pressure, indicating that the loss of key habitats can have dramatic short-term consequences.

Prioritization approaches also yielded very different results for systems with large populations occupying sink habitats. Although we conceptually idealize sources as being the most important elements of a landscape, this may not always hold true for the short-term conservation of declining populations. Our results indicate that in some rapidly declining populations, the preservation of high abundance sinks can have a more positive impact on persistence than key sources. Although small sources can have a dramatic effect on the population by consistently producing offspring that can then emigrate to other patches, supporting geographically much larger sink habitats (Kanda et al. 2009), the regional population size can temporarily outweigh source-contributions to persistence. As all of our simulated populations went extinct in our simulations (in all scenarios), the benefits of prioritizing high abundance sinks over sources are likely to be short-term. At stable equilibrium, productive sources are generally required for long-term population persistence to balance eventual losses in sinks. Hence, as populations transition from declining to stable or recovering, the important elements of the landscape are likely to change with population abundance and density regulation, landscape changes, and recovery goals.

Our results highlight that simple metrics such as local abundance can identify important habitats, but their ability to detect sources is generally poor and depends on the case-specific details including the timing of data collection. Although important in the short-term, the exclusive protection of high abundance areas without consideration of strong consistent sources, is likely to yield delayed but inevitable extinction (Dias 1996). By contrast, strategies that conserve only the strongest sources without regard to local abundance could result in near-term extinction. For example, if population sizes were reduced as a result of a lack of protection for animals in sinks and subsequent habitat loss or degradation, the smaller population would be more vulnerable to extinction due to stochastic events. A balanced approach that leverages the advantages of important habitat for short-term and long-term persistence is likely to yield the greatest conservation benefit. Effective long-term conservation plans must balance the shorter-term needs of declining populations with the longer-term recovery goals of creating an environment that indefinitely sustains the population.

The use of simplified rather than complex source-sink metrics (e.g., only survival and reproduction) to prioritize habitats for long-term population persistence can produce meaningful and valuable results. However, their success in reliably identifying sources and sinks and their contributions to persistence can be variable. Our results underscore the need to understand the system-specific drivers of source-sink dynamics to infer the circumstances under which data collection might be simplified, and to explore alternative characterizations of important habitats in designing habitat conservation and species recovery strategies.

Phase 1 References

Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered Greater Sage-Grouse. Ecological Applications 17:508–526.

Andreasen, A. M., K. M. Stewart, W. S. Longland, J. P. Beckmann, and M. L. Forister. 2012. Identification of source-sink dynamics in mountain lions of the Great Basin. Molecular Ecology 21:5689–5701.

Armstrong, D. M. 1979. Ecological distribution of rodents in Canyonlands National Park, Utah. Great Basin Naturalist 39:199–205.

Barthold, J., A. Loveridge, D. Macdonald, C. Packer, and F. Colchero. 2016. Bayesian estimates of male and female African lion mortality for future use in populaiton management. Journal of Applied Ecology 53:295–304.

Bartholomew, G. A., and H. H. Caswell. 1951. Locomotion in kangaroo rats and its adaptive significance. Journal of Mammalogy 32:155–169.

Battin, J. 2004a. When good animals love bad habitats: ecological traps and the conservation of animal populations. Conservation Biology 18:1482–1491.

Battin, J. 2004b. When good animals love bad habitats: ecological traps and the conservation of animal populations. Conservation Biology 18:1482–1491.

Bender, D. J., D. L. Gummer, R. Dzenkiw, and J. A. Heinrichs. 2010. An occurrence-based habitat model for the Ord's kangaroo rat (Dipodomys ordii) in Alberta. Alberta Species at Risk Report Series. Alberta Sustainable Resource Development, Fish and Wildlife Division, Edmonton, Alberta.

Boughton, D. A. 2000. The Dispersal System of a Butterfly : A Test of Source-Sink Theory Suggests the Intermediate-Scale Hypothesis. American Naturalist 156:131–144.

Bowman, J., N. Cappuccino, and L. Fahrig. 2002. Patch size and population density: The effect of immigration behavior. Conservation Ecology 6:9.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Breininger, D. R., and D. M. Oddy. 2004. Do habitat potential, population density, and fires influence Scrub-Jay source-sink dynamics? Ecological Applications 14:1079–1089.

Caudill, C. C. 2003. Empirical evidence for nonselective recriutment and a source-sink dynamics in a mayfly metapopulation. Ecology 84:2119–2132.

Cimprich, D. A., and M. Heimbuch. 2012. Monitoring of the black-capped vireo during 2012 on Fort Hood, Texas. Endangered Species monitoring and management at Fort Hood, Texas: 2012 annual report.

Contasti, A. L., F. M. Van Beest, E. Vander Wal, and P. D. McLoughlin. 2013. Identifying hidden sinks in growing populations from individual fates and movements: The feral horses of Sable Island. Journal of Wildlife Management 77:1545–1552.

Cosentino, B. J., R. L. Schooley, and C. A. Phillips. 2011. Spatial connectivity moderates the effect of predatory fish on salamander metapopulation dynamics. Ecosphere 2.

COSEWIC. 2006. COSEWIC assessment and update status report on the Ord's kangaroo rat Dipodomys ordii in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa. vii + 34 pp.

Crone, E. 2016. Contrasting effects of spatial heterogeneity and environmental stochasticity on population dynamics of a perennial wildflower. Journal of Ecology 104:281–291.

Delibes, M., P. Ferreras, and P. Gaona. 2001a. Attractive sinks, or how individual behavioural decisions determine source–sink dynamics. Ecology Letters 4:401–403.
Delibes, M., P. Gaona, and P. Ferreras. 2001b. Effects of an attractive sink leading into maladaptive habitat selection. The American Naturalist 158:277–285.
Dias, P. C. 1996. Sources and sinks in population biology. Trends in Ecology and Evolution 11:326–330.
Dunning, J. B., B. J. Danielson, and R. H. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65:169–175.
Falcy, M. R., and B. J. Danielson. 2011. When sinks rescue sources in dynamic environments. Pages 139–154 *in* J. Liu, V. Hull, A. T. Morzillo, and J. A. Wiens, editors. Sources, sinks and sustainability. Cambridge University Press, Cambridge.
Foppen, R. P. B., P. J. Chardon, and W. Liefveld. 2000. Understanding the role of sink patches in source-sink metapopulations: reed warbler in an agricultural landscape. Conservation Biology 14:1881–1892.
Frouz, J., and P. Kindlmann. 2001. The role of sink to source re-colonisation in the population dynamics of insects living in unstable habitats : an example of terrestrial chironomids. Oikos 1:50–58.
Gardner, R., and R. O'Neill. 1991. Pattern, process, and predictability: the use of neutral models for landscape analysis. Ecological Studies 82:289–307.
Gates, J. E., and S. S. Germaine. 1978. Avian nest dispersion and feldging success in field-forest ecotones. Ecology 59:871–883.
Griffith, A., R. Salguero-Gomez, C. Merow, and S. McMahon. 2016. Demography beyond the population. Journal of Ecology 104:271–280.
Gummer, D. L. 1999. Distribution and abundance of Ord's kangaroo rats in Canadian Forces Base Suffield National Wildlife Area. Report for Canadian Wildlife Service, Edmonton, Alberta.
Gummer, D. L., M. R. Forbes, D. J. Bender, and R. M. R. Barclay. 1997. Botfly (Diptera: Oestridae) Parasitism of Ord's Kangaroo Rats (Dipodomys ordii) at Suffield National Wildlife Area, Alberta, Canada. The Journal of parasitology 83:601–604.
Gummer, D. L., and S. E. Robertson. 2003. Evaluation of survival and activities of Ord'skangaroo rats: one year after construction of the North Suffield gas pipeline. Report for Alberta Conservation Association, Edmonton.
Gunderson, G., E. Johannesen, H. P. Andreassen, and R. A. Ims. 2001. Source-sink dynamics: how sinks affect demography of sources. Ecology letters 4:14–21.
Hall, L. S., P. R. Krausman, and M. L. Morrison. 1997. The habitat concept and a plea for standard terminology. Wildlife Society Bulletin 25:173–182.
Hallett, J. G. 1982. Habitat selection and the community matrix of a desert small-mammal fauna. Ecology 63:1400–1410.
Hansen, A. 2011. Contribution of source-sink theory to protected area science. Pages 339–360 *in* J. Liu, V. Hull, A. T. Morzillo, and J. A. Wiens, editors. Sources, sinks and sustainability. Cambridge University Press, Cambridge.
Heinrichs, J. A., D. J. Bender, D. L. Gummer, and N. H. Schumaker. 2010. Assessing critical habitat: Evaluating the relative contribution of habitats to population persistence. Biological Conservation 143:2229–2237.
Heinrichs, J. A., J. J. Lawler, N. H. Schumaker, C. B. Wilsey, and D. J. Bender. 2015. Divergence in sink contributions to population persistence. Conservation Biology 29:1674–

1683.
Heppell, S. S., H. Caswell, and L. B. Crowder. 2000. Life Histories and Elasticity Patterns: Perturbation Analysis for Species with Minimal Demographic Data. Ecology 81:654–665.
Holland, E. P., J. N. Aegerter, and C. Dytham. 2009. Comparing resource representations and choosing scale in heterogeneous landscapes. Landscape Ecology 24:213–227.
Holt, R. D. 1996. Adaptive Evolution in Source-Sink Environments: Direct and Indirect Effects of Density-Dependence on Niche Evolution. Oikos 75:182–192.
Holt, R. D., and M. S. Gaines. 1992. Analysis of adaptation in heterogeneous landscapes: implications for the evolution of fundamental niches. Evolutionary Ecology 6:433–447.
Holt, R. D. 1985. Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. Theoretical Population Biology 28:181–208.
Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.
Howe, R. W., G. J. Davis, and V. Mosca. 1991. The demographic significance of "sink" populations. Biological Conservation 57:239–255.
Johnson, D. M. 2004. Source-sink dynamics in a temporally heterogeneous environment. Ecology 85:2037–2045.
Johnson, R. G., and S. A. Temple. 1986. Assessing habitat quality for birds nesting in fragmented tallgrass prairies. Pages 245–249 *in* J. Verner, M. L. Morrison, and C. J. Ralph, editors. Wildlife 2000: modeling habitat relationships in terrestrial vertebrates. University of Wisconsin Press, Madison.
Jonzen, N., J. R. Rhodes, and H. P. Possingham. 2005. Trend detection in source-sink systems: When should sink habitats be monitored? Ecological Applications 15:326–334.
Kanda, L. L., T. K. Fuller, P. R. Sievert, and R. L. Kellogg. 2009. Seasonal source-sink dynamics at the edge of a species' range. Ecology 90:1574–1585.
Kawecki, T. J. 2004. Ecological and evolutionary consequences of source-sink population dynamics. Pages 387–414 *in* I. Hanski and O. E. Gaggiotti, editors. Ecology, Genetics, and Evolution of Metapopulations. Elsevier Academic Press, Oxford.
Kenny, R. J. L. 1989. Population, distribution, habitat use, and natural history of Ord's kangaroo rat (Dipodomys ordii) in the sand hill areas of south-western Saskatchewan and south-eastern Alberta. University of Manitoba, Winnipeg, Manitoba.
Kerr, N., P. Baxter, R. Salguero-Gomez, G. Wardle, and Y. Buckley. 2016. Prioritizing management actions for invasive populations using cost, efficacy, demography, and expert opinion for 14 plant species worldwide. Journal of Applied Ecology 53:305–316.
Kristan, W. B. 2003. The role of habitat selection behavior in population dynamics: source-sink systems and ecological traps. Oikos 103:457–468.
Loehle, C. 2012. A conditional choice model of habitat selection explains the source-sink paradox. Ecological Modelling 235–236:59–66.
Loreau, M., T. Daufresne, A. Gonzalez, D. Gravel, F. Guichard, S. J. Leroux, N. Loeuille, F. Massol, and N. Mouquet. 2013. Unifying sources and sinks in ecology and Earth sciences. Biological reviews of the Cambridge Philosophical Society 88:365–79.
Matthews, D. P., and A. Gonzalez. 2007. The inflationary effects of environmental fluctuations ensure the persistence of sink metapopulations. Ecology 88:2848–2856.
Pulliam, R. H. 1988. Sources, sinks, and population regulation. The American Naturalist 132:652–661.

Pulliam, R. H., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. The American Naturalist 137:S50–S66.
Remes, V. 2000. How can maladaptive habitat choice generate source-sink population dynamics? Oikos 91:570–582.
Runge, J. P., M. C. Runge, and J. D. Nichols. 2006. The role of local populations within a landscape context: defining and classifying sources and sinks. The American Naturalist 167:925–938.
Schlaepfer, M. A., M. C. Runge, and P. W. Sherman. 2002. Ecological and evolutionary traps. Trends in Ecology and Evolution 17:474–480.
Schooley, R. L., and L. C. Branch. 2007. Spatial heterogeneity in habitat quality and cross-scale interactions in metapopulations. Ecosystems 10:846–853.
Schumaker, N. H. 1998. A users guide to the PATCH model. EPA/600/R-98/135. Environmental Protection Agency, Envrionmental Research Laboratory, Corvallis, Oregon.
Schumaker, N. H. 2013. HexSim. U.S. Environmental Protection Agency, Environmental Research Laboratory, Corvallis, Oregon, USA.
Schumaker, N. H. 2015. HexSim (Version 3.2.8). U.S. Environmental Protection Agency, Environmental Research Laboratory, Corvallis, Oregon. Available from http://www.epa.gov/hexsim.
Schumaker, N. H., A. Brookes, J. R. Dunk, B. Woodbridge, J. A. Heinrichs, J. J. Lawler, C. Carroll, and D. LaPlante. 2014. Mapping sources, sinks, and connectivity using a simulation model of northern spotted owls. Landscape Ecology:579–592.
Stahl, J. T., and M. K. Oli. 2006. Relative importance of avian life-history variables to population growth rate. Ecological Modelling 198:23–39.
Teucher, A. C. 2007. Factors affecting Ord's kangaroo rats (Dipodomys ordii) in natural and anthropogenic habitats. University of Calgary, Calgary, Alberta.
Treurnicht, M., J. Pagel, K. Esler, A. Schutte-Vlok, H. Nottebrock, T. Kraaij, A. Rebelo, and F. Schurr. 2016. Environmental drivers of demographic variation across the global geographic range of 26 plant species. Journal of Ecology 104:331–342.
USFWS. 1992. Draft final recovery plan for the northern spotted owl. Portland, Oregon.
USFWS. 2011. Revised Recovery Plan for the Northern Spotted Owl (Strix occidentalis caurina). Portland, Oregon.
Virgl, J. A., and F. Messier. 2000. Assessment of source-sink theory for predicting demographic rates among habitats that exhibit temporal changes in quality. Canadian Journal of Zoology 78:1483–1493.
Vögeli, M., D. Serrano, F. Pacios, and J. L. Tella. 2010. The relative importance of patch habitat quality and landscape attributes on a declining steppe-bird metapopulation. Biological Conservation 143:1057–1067.
Vos, C. C., J. Verboom, P. F. M. Opdam, and C. J. F. Ter Braak. 2001. Towards ecologically scale landscape indices. The American Naturalist 183:24–41.
Walters, S. 2001. Landscape pattern and productivity effects on source–sink dynamics of deer populations. Ecological Modelling 143:17–32.
Walters, S. 2007. Modeling scale-dependent landscape pattern, dispersal, and connectivity from the perspective of the organism. Landscape Ecology 22:867–881.
Watkinson, A. R., and W. J. Sutherland. 1995. Sources, sinks and psuedo-sinks. Journal of Animal Ecology 64:126–130.
Wiegand, T., E. Revilla, and K. A. Moloney. 2005. Effects of habitat loss and fragmentation on

population dynamics. Conservation Biology 19:108–121.
Wiens, J. A., and B. Van Horne. 2011. Sources and sinks: what is the reality? Pages 507–519 *in* J. Liu, V. Hull, A. T. Morzillo, and J. A. Wiens, editors. Sources, sinks and sustainability. Cambridge University Press, Cambridge.
Wilkins, N., R. A. Powell, A. A. T. Conkey, and A. G. Snelgrove. 2006. Population status and threat analysis for the black-capped vireo. Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX.
Wilsey, C. B., J. J. Lawler, and D. a. Cimprich. 2012. Performance of habitat suitability models for the endangered black-capped vireo built with remotely-sensed data. Remote Sensing of Environment 119:35–42.
Wilsey, C. B., J. J. Lawler, D. Cimprich, and N. H. Schumaker. 2014. Dependence of the Endangered Black-Capped Vireo on Sustained Cowbird Management. Conservation Biology 28:561–571.

Phase 2: Black-capped Vireo Demography

Phase 2 Overview

Varying habitat, connectivity, and demography across the landscape can result in a source-sink population structure, with implications for the management of endangered species. In particular, the identification and characterization of source-sink dynamics in the black-capped vireo near Fort Hood, Texas, has the potential to alter current and future conservation and management actions. The largest well-studied population of this songbird is located on the Fort Hood Military Installation, but its role in landscape-level vireo population dynamics is largely unknown. From 2011 through 2014, we monitored seven vireo populations on Fort Hood and nearby private and state lands that varied in vegetation and nest-parasitism rates. From data collected on our study sites and from an additional four populations monitored by the Fort Hood Natural Resources Management Branch, we calculated measures of fecundity and survival and assessed populations as sources or sinks using population matrices. Sites with cowbird control had greater overall nest success and most source populations had cowbird control in all study years. Differences in demographics between reserves and islands highlight the need to consider broad-scale population dynamics in management decisions. Furthermore, annual variability in the role of individual populations in overall metapopulation dynamics must be considered in designing effective management plans. For black-capped vireos, management informed by monitoring efforts on the Fort Hood NRMB sites alone may be inefficient or inappropriate for smaller or more isolated populations operating under inconsistent cowbird control regimes.

Spatially structured populations often experience different predator communities and availability of habitat, encouraging tradeoff strategies that weigh reproductive success and survival. To investigate black-capped vireo tradeoffs in habitat selection, we monitored breeding territories and tracked juvenile vireos using radio-telemetry. Vireos in general selected shrubland and forest habitats; canopy cover may present a tradeoff that improves juvenile survival but reduces breeding success. We recorded vocalizations at vireo nests and found little evidence for tradeoffs in social communication and mediation of parasitism or predation risk. Vireos did benefit, however, by optimizing temporal patterns in vocalizations. Finally, we documented some flexibility in mating strategy through an observation of polygyny in a territorial male vireo. We conclude that successful management of vireo breeding populations will consider habitat needs across the entire reproductive cycle—cowbird control will increase nest success and breeding sites that provide nearby or adjacent forested areas may improve survival of recently independent juveniles.

2.1 Source-sink population dynamics driven by a brood parasite: a case study of an endangered songbird[3]

2.1.1 Introduction

Since its introduction by Pulliam (1988), the source-sink model of metapopulation structure has broadened our theoretical understanding of ecology, while also informing conservation and management of rare species. Source populations are reproductively successful and produce young that, due to density regulation, disperse from natal locations (Pulliam 1988). By contrast, sinks are populations that have insufficient reproduction to balance local mortality and thus depend on immigration from sources to avoid local extinction or rescue them thereafter (Brown and Kodric-Brown 1977). The presence of source-sink dynamics in fragmented metapopulations has been used to explain the persistence of local populations in low-quality habitat (Foppen et al. 2000, Murphy 2001), argue for conservation of source areas (Robinson et al. 1995), and identify threats to population persistence (Balogh et al. 2011). For endangered species management in particular, the recognition of source-sink dynamics could have great impacts on conservation and recovery efforts. Populations of endangered species are frequently restricted in range and relatively small in size, forcing researchers concerned with the practicality of data collection to study only the largest or most densely inhabited locales. However, monitoring populations across a heterogeneous landscape may yield a more accurate representation of the overall status of the population. Distinguishing particular subpopulations as either sources or sinks may help highlight spatially-specific conservation needs and create more accurate long term predictions of population viability.

The establishment of source-sink dynamics results from heterogeneous landscapes where survival, reproduction, or both are spatially variable and where the movement of individuals from productive source populations at least temporarily sustains sink populations. Spatial heterogeneity may be driven by habitat fragmentation, which creates edges and often results in patches that vary in size and degree of isolation. Habitat variability along edges as well as within and between patches can impact risk of predation (Andrén 1992, Paton 1994, Heithaus and Dill 2006), brood parasitism (Paton 1994, Vasseur and LeBerg 2015), prey availability (O'Donnell 2000), and resource competition with con- and heterospecifics (Fagan et al. 1999, Amarasekare 2003, Piper and Caterall 2003). For birds that are able to fly long distances and are less likely to face physical impediments to dispersal, source-sink dynamics are often attributed to fluctuations in resource abundance (Bock and Bock 1974, Stacey and Taper 1992) or locally high predator or

[3] This work is in review as: Walker, L. E., J. M. Marzluff, and D. A. Cimprich. In Review. Source-sink population dynamics driven by a brood parasite: a case study of an endangered songbird. *Biological Conservation*.

brood parasite populations that reduce survival (Balogh et al. 2011) or nest success (Robinson et al. 1995, Vierling 2000, Wilson and Arcese 2006, Jewell and Arcese 2008) below what is necessary for the population to remain sustainable without immigration.

Drivers of source-sink dynamics may also be temporally variable (Brawn and Robinson 1996), particularly for species in actively changing landscapes due to environmental or climate change (Werner et al. 2009) or due to active management (McCoy et al. 1999, Kauffman et al. 2003, Burrell and Colwell 2012). Although a thorough understanding of the effects of temporal variability in the drivers of demographic change on source-sink population dynamics and long-term population viability is necessary for the design and implementation of effective management practices, this relationship remains poorly understood and under-studied. Here we investigate the source-sink population dynamics of an endangered songbird and the relationship between fluctuating demographics, population viability, and an evolving brood parasite management regime.

2.1.1.1 A Case Study

Vireos are small songbirds that breed locally throughout northeastern Mexico, Texas, and southern Oklahoma in early successional shrub habitat and winter along the western Mexican coast. In 1987, the species was listed as endangered by the U.S. Fish and Wildlife Service, which cited declines in breeding habitat due to the disruption of disturbance regimes (i.e. fire suppression), invasive vegetation (e.g., Ashe juniper; *Juniperus ashei*), and increased ranching, agriculture, and urbanization, which convert shrublands and increase brood parasitism by brown-headed cowbirds (cowbird; Ratzlaff 1987, USFWS 1991). Vireo reproductive success is limited by cowbird parasitism because vireos are generally unable to fledge their own young from parasitized nests and areas with high cowbird presence may represent lower quality or even sink habitat (Walker 2015). Today, the largest breeding population of vireos, approximately 6000 pairs, is located on the 88,478 hectare (ha) Fort Hood Military Installation (Fort Hood; Cimprich and Cimprich 2015), where cowbird populations are controlled to improve vireo productivity (Kostecke et al. 2005) and large patches of shrubland habitat remain undeveloped. Although the local population at the time of listing was estimated at only 85 male vireos (Tazik et al. 1993), base-wide cowbird trapping efforts (initiated in 1987 and ongoing; Kostecke et al. 2005, Kostecke and Cimprich 2008), as well as habitat management and concentrated intensive cowbird control in select study sites, have brought the total Fort Hood population to approximately 6000 males (Cimprich and Cimprich 2015). Today, the Fort Hood vireo population remains a relatively well-protected and well-studied “mainland” reserve surrounded by smaller “island” populations, separated by a matrix of development, farms, and ranchlands.

On Fort Hood and throughout central Texas, vireos exhibit differential reproductive success and survival between habitat types and parasitism regimes. Relative to habitats structured by military activity or mechanical disturbance, vireos are found in higher abundance and have greater nest success in natural shrublands with deciduous cover, perhaps due to reduced rates of parasitism (Bailey 2005, Noa et al. 2007). Across habitat types, vireo nests located higher above the ground also had greater daily survival probabilities (Noa et al. 2007), indicating that habitat structure may be an important factor in reproductive success. The annual survival of adult vireos on Fort

Hood varies between local breeding patches and may reflect differences in habitat quality (Kostecke and Cimprich 2008).

Although demographic factors may differ among populations, dispersal events between breeding populations are rarely observed and evidence for source-sink dynamics is inconclusive. Some genetic investigations into vireo population structure observed significant differences in genetic variation among subpopulations, effectively ruling out gene flow and the possibility of source-sink dynamics (Barr et al. 2008). However, other research does not exclude the possibility of a vireo metapopulation driven by source-sink dynamics (Fazio et al. 2004, Zink et al. 2010). In fact, populations with high heterozygosity may have immigrants from several source populations (Fazio et al. 2004). Ultimately, additional investigation into both genetic and demographic evidence remains important.

Successful management, conservation, and recovery of the black-capped vireo would benefit from a more complete understanding of the population dynamics across its expansive range. Substantial vireo population growth was the basis for a 2007 recommendation by the U.S. Fish and Wildlife Service to downgrade the species from endangered to threatened status (USFWS 2007). The presence of source-sink dynamics, however, could have repercussions for the stability of vireo metapopulations and the species as a whole. For example, if other small populations are largely sinks, it could indicate that the central Texas vireo metapopulation is highly dependent on the success of the Fort Hood subpopulation. Furthermore, the viability of individual populations and the metapopulation as a whole may be dependent on management, particularly cowbird control. To better understand vireo population dynamics across central Texas and its relationship with an evolving cowbird control regime, we measured vireo demography and survival on and around Fort Hood and assessed breeding sites across central Texas as sources or sink populations over a four-year period. We also ranked the relative importance of fecundity and adult and juvenile survival to identify the demographic processes driving vireo population dynamics. We predicted that the predominant driver of vireo population dynamics would be variable fecundity and areas with consistent cowbird control would most often serve as source populations. In general, we expected populations with relatively little cowbird control and high rates of cowbird parasitism to be sinks.

2.1.2 Methods

2.1.2.1 Study Sites

From 2011 through 2014, we surveyed vireo breeding sites on Fort Hood and in nearby areas to the south and west that vary in vegetative characteristics and cowbird control regimes (Figure 2.1.1). The habitat is largely characterized by shortgrass communities and cattle rangeland; many areas that were once grasslands are now woodlands due to fire suppression and the encroachment of the native evergreen Ashe juniper. The climate is semi-arid with an average of 838 mm of rainfall annually and average high temperatures between 14.4°C in January and 35.6°C in August. During the peak vireo breeding season (April through July), average precipitation and average high temperatures varied between study years, ranging between 38 and 95 mm per month and 30.6° and 34.4°C respectively.

Vireo demography has been studied on Fort Hood since 1987 (Tazik et al. 1993) and rigorous monitoring efforts across five study areas began in 1997 (Kostecke and Cimprich 2008). The Fort Hood Natural and Cultural Resources Management Branch (NRMB) consistently monitored four of these sites during the course of this study - East Range, Jack Mountain, Manning 2, and West Fort Hood, in total comprising approximately 318 hectares (ha) - and we include monitoring and nest data from these sites in our analyses (Figure 2.1.1). Sites managed by the NRMB had comprehensive cowbird control during all study years.

In addition to the long-term study sites monitored by the Fort Hood NRMB, we monitored three other sites on Fort Hood from 2011 through 2014 (Figure 2.1.1). We intentionally chose sites on Fort Hood that we expected to be relatively poor habitat in comparison with NRMB study sites. West Range, a 49-ha site, had comprehensive cowbird control until 2006 when Fort Hood began an experimental cessation of cowbird control in the northwest area of the base. Sixty-one ha Taylor Valley, like the NRMB sites, has had continuous cowbird control via both shooting and trapping since 1991. The Maxdale site is 101 ha and, although cowbirds are removed from the site when they are reported, there are no nearby traps and cowbird presence remains high.

Balcones Canyonlands National Wildlife Refuge is a 9638-ha reserve comprised of 65 individual tracts of land, located approximately 72 km southwest of Fort Hood near the intersection of Burnet, Williamson, and Travis Counties (Figure 2.1.1). We focused our monitoring efforts on three tracts along the northern edge of the refuge. In 2011, we monitored approximately 65 ha and, from 2012-2014, expanded our survey efforts to cover an additional 81 ha. Cowbird traps were present across the refuge, although they were not located directly on our study tracts.

From 2012 through 2014, we surveyed portions of two neighboring private ranches, San Saba, nearly 19 km southwest of San Saba, Texas, in San Saba County (Figure 2.1.1). There were no cowbird control efforts at the 25-ha San Saba property in either 2012 or 2013 but a cowbird trap was established mid-way through the 2014 breeding season.

Colorado Bend is a 2156-ha state park located along the west side of the Colorado River in San Saba County (Figure 2.1.1). From 2011 through 2014, we monitored vireo territories along the Tie Slide, Heller Brakes, and Gorman Falls trails, an area comprising approximately 121 ha. There was no effective cowbird control in the state park from 2011 through 2013 but trapping efforts began mid-way through the 2014 breeding season.

From 2012 through 2014, we monitored a privately owned ranch, Goldthwaite, approximately 15 km west of Goldthwaite, Texas in Mills County (Figure 2.1.1). There were no cowbird control efforts when we began monitoring the Goldthwaite site in 2012. However, in 2013, traps were placed near the study site mid-way through the breeding season and, in 2014, both traps and shooting were used to control local cowbird populations.

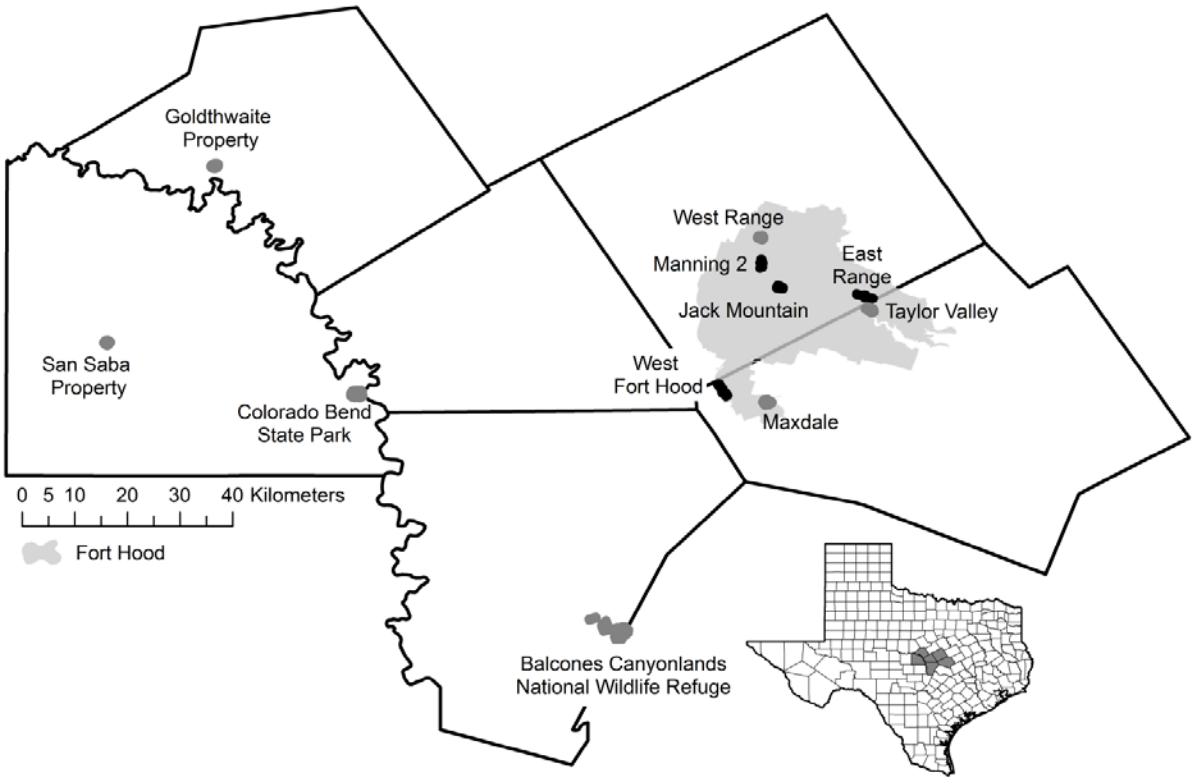


Figure 2.1.1. Black-capped vireo study sites in central Texas, 2011-2014. Reserve populations are located on the Fort Hood Military Installation (long-term NRMB sites are in black). Island populations are located off of Fort Hood, to the south and west.

2.1.2.2 Cowbird Control Efforts

In each study year, we classified each study site using a simplified measure of the level of cowbird control (Table 2.1.1). We designated sites with both trapping and shooting as having "complete" cowbird control. Although the implementation of trapping or shooting programs can alter their effectiveness (Summers et al. 2006a), we designated sites where cowbirds were either trapped *or* regularly removed by shooting as having "moderate" cowbird control. We labeled all other sites as having no cowbird control. For analyses of territorial adult survival, we used the cowbird control level at the site in the year that the bird was initially caught.

2.1.2.3 Monitoring Efforts

We visited study sites two to three days per week throughout the vireo breeding season, from late March through early July, and searched for all territorial males. We target-netted territorial vireos and banded them with U.S. Geological Survey aluminum bands and unique color band combinations. We visited each territory between one and three times per week, recording locations of territorial male vireos using a handheld GPS unit.

We monitored pairs and attempted to locate all nests. We visited known nest locations every three to four days until failure or fledging. During each visit, we recorded the number of vireo and cowbird eggs (if present), the number and approximate age of nestlings, and parental presence at the nest. If a nest survived to the nestling stage, we banded nestlings between 6 and 8 days post hatching with a U.S. Geological Survey aluminum band and a combination of plastic color bands unique to each study site. We considered a nest to be successful if we observed at least one fledgling with parents away from the nest or if we observed at least one vireo nestling in the nest on day 11 (average fledge day), and we observed behaviors by the adults to suggest they had fledglings (scolding, carrying food).

Table 2.1.1. Level of cowbird control at vireo breeding sites across central Texas from 2011-2014. At sites with complete control, managers used both shooting and trapping to remove cowbirds. At moderately controlled sites, cowbirds were controlled with either trapping or shooting.

	Year			
	2011	2012	2013	2014
Island Populations				
Balcones Canyonlands	Moderate	Moderate	Moderate	Moderate
Colorado Bend	None	None	None	Moderate
Goldthwaite[a]	---	None	Moderate	Complete
San Saba[a]	---	None	None	Moderate
Reserve Populations				
Maxdale	Moderate	Moderate	Moderate	Moderate
Taylor Valley	Complete	Complete	Complete	Complete
West Range	None	None	None	None
East Range	Complete	Complete	Complete	Complete
Jack Mountain	Complete	Complete	Complete	Complete
Manning 2	Complete	Complete	Complete	Complete
West Fort Hood	Complete	Complete	Complete	Complete

[a] Monitored in 2012-2014 only.

2.1.2.4 Analyses

2.1.2.4.1 Nest Success and Fecundity

Although we attempted to document all nesting attempts, we may have missed some nests that failed early in the nesting cycle or fledged before we were able to locate them. Additionally, these biases in nest detection were likely unbalanced between sites due to differences in nest success and habitat conditions. Therefore, to account for potential biases in nest detection, we calculated nesting success using the Mayfield (1975) method and fecundity following Donovan et al. (1995).

Based on exposure days, we calculated separate daily survival rates for nests in the egg-laying, incubation, and nestling stages, as well as the probability of surviving each individual nest stage (stage survival) and nest survival from egg-laying to fledging (overall nest survival; Mayfield 1975). Following standards used by Fort Hood Natural Resource biologists (Cimprich and Heimbuch 2011), we considered the egg-laying stage to begin in the middle of the first day an egg was observed in the nest, with a maximum exposure period of 2.5 days. Incubation, a period of 14 days, began at the beginning of the day the last egg was laid. We assumed the beginning of the nestling stage to be halfway between the last check with eggs alone and the first check with nestlings present. The nestling stage lasted 11 days. In parasitized nests where the cowbird hatched but the host eggs did not, we considered failure to occur on the day the cowbird nestling hatched. We considered nests to be successful if they fledged at least one vireo. We then evaluated the effects of level of cowbird control on both daily and nest stage survival using ANOVAs and used *post hoc* Tukey tests to further investigate the source of significant ANOVA results.

We calculated fecundity as the mean number of female offspring produced by each adult female each year based on nest survival estimates for each site and several assumptions of vireo breeding behavior (see Donovan et al. 1995). We assumed that vireo pairs would make up to three breeding attempts to fledge up to two successful broods. If the first breeding attempt is successful, a vireo pair will make one second brood attempt (Graber 1961, Grzybowski 1995). If the first breeding attempt was unsuccessful however, we assumed pairs would make up to three total nesting attempts to fledge a single brood. (Although we have observed pairs making up to seven nesting attempts, few pairs were ever successful beyond a third attempt.) We assumed that young produced exhibited a 50:50 male:female ratio and that nest success and fecundity were constant throughout the breeding season. Although nest success and fecundity likely vary throughout the nesting season along with parasitism rates (Boves et al. 2014), this is unlikely to affect our calculations of average annual fecundity.

2.1.2.4.2 Territorial Adult and Juvenile Survival

We used banding and resighting data from color-banded vireos to 1) calculate average dispersal distances (mean $\pm$ SE) of territorial adults and 2) estimate apparent survival (φ) and recapture probabilities (p) of territorial adults and juvenile vireos in separate analyses. We defined φ as the probability a vireo survived and returned to one of our sites in a subsequent breeding season and p as the probability of encountering a vireo given its survival and presence on one of our sites. To estimate territorial adult φ, we considered the unique effects of individual study site and study year and the combined effects of site and year. For adult recapture models, we considered single-variable models of study site, study year, and sex. Including null survival and recapture models, we considered 16 combinations of territorial adult vireo survival and recapture probabilities. In modeling juvenile vireo survival, we considered the effects of individual study year and study site on both φ and p. Because of a limited sample size, we could not consider the effects of sex or of combinations of variables that might interactively affect juvenile survival or recapture rate. Including null survival and recapture models, we considered 9 combinations of juvenile vireo survival and recapture probabilities. In both adult and juvenile analyses, we compared models using Akaike's Information Criterion adjusted for small sample size (AIC_c; Akaike 1974) and model weights (w_i). We used the package "RMark" (Laake 2013) in R v 3.1.1

(R Core Team 2014) for all survival analyses and assessed the goodness of fit for our top models using bootstrapping and median $\hat{c}$-hat implemented in program Mark (White and Burnham 1999, Cooch and White 2014).

2.1.2.4.3 Population Assessments and the Relative Importance of Survival and Reproduction

To determine the status of vireo populations in central Texas at each of our study sites, we followed methods outlined by Caswell (2001) and Pulliam (1988). We built simple two stage population matrices (Caswell 2001) for each individual site in each study year to calculate the deterministic population growth rate, λ_d, of each population in each study year and the stochastic growth rate, λ_s, of individual populations across study years as well as populations grouped by location (islands off of Fort Hood or reserve populations on Fort Hood) and cowbird control regime. Matrix elements were largely based on population-specific data from field observations. We calculated fecundity from nesting data collected from 2011 through 2014 (see 2.1.2.4.1 Nest Success and Fecundity) and estimated territorial adult and juvenile survival from an analysis of banding (2011-2014) and resighting data (2012-2015; see 1.2.4.2 Territorial Adult and Juvenile Survival). We assessed populations as sources or sinks using λ_s; populations with $\lambda_s > 1$ are sources and populations with $\lambda_s < 1$ are sinks.

Our intent was not to predict future population size but to demonstrate current rates of population decline or growth, highlighting the importance of immigration and stochasticity on future population viability. Thus, from our calculations of λ_s, we calculated the quasi-extinction probabilities (QEP) for all populations and for comparisons between years, locations, and cowbird control regimes given the observed demographics and ignoring the effects of immigration and emigration. For individual site QEPs, we used the average number of territories observed at each site over the four survey years as the starting population N_0. We used a starting population of 100 individuals in our comparisons of QEP between locations or levels of cowbird control. In tables and figures, we report the likelihood of extinction in the next 50 years (QEP_{50}).

To better define the relationship between matrix elements and stochastic population growth rates, we calculated the sensitivity for each demographic parameter (fecundity, territorial adult survival, and juvenile survival). Sensitivity is the rate of change in the population growth rate with respect to a numerical change in a matrix element (Caswell 2001). Survival and fecundity are measured on different scales; however, making comparisons between the sensitivity of fecundity and either measure of survival is uninformative. Therefore, we also calculated the elasticity, or *proportional* sensitivity, for fecundity and survival matrix elements. We compared the effects of individual demographic parameters across sites using sensitivity and compared the effects of different parameters within sites using elasticity. Additionally, to further evaluate the effects of varying demographic parameters, we modeled the relationship between deterministic population growth and a range of fecundity values (0 - 3.0 young fledged/year) and adult and juvenile survival rates (0 - 100%). We used the package “popbio” (Stubben and Milligan 2007) in R v 3.1.1 (R Core Team 2014) for all matrix calculations and population projections.

2.1.3 Results

2.1.3.1 Monitoring Efforts

Between 2011 and 2014, we banded 995 territorial adult black-capped vireos, including 581 males and 414 female vireos (Table 2.1.2). We monitored 821 vireo territories across eleven study sites and located and monitored 1709 vireo nests (Table 2.1.2). From those nests, we banded 2152 vireo nestlings (Table 2.1.2). Six hundred and eleven nests (36%) were successful in fledging at least one vireo nestling. Of 1098 unsuccessful nests, 69% (n = 753) were depredated, 23% (n = 256) were abandoned, and 6% (n = 61) failed or were destroyed (knocked down or ripped apart) by unknown causes.

Of 291 nests that were parasitized, most were at sites with no (n = 180) or only moderate cowbird control (n = 85; Table 2.1.2). In areas with complete cowbird control, only 26 out of 1081 nests were parasitized. Although only 10% of parasitized nests (n = 28) fledged a cowbird, no nests that fledged a cowbird were also able to successfully fledge any vireo young (Figure 2.1.2). The most common nest fate for parasitized nests was to be abandoned (42%, n = 121; Figure 2.1.2). Twenty parasitized nests (7%) were successful in fledging vireo young either because the cowbird egg failed to hatch (n = 18) or the cowbird nestling died shortly after hatching (n = 2). Successful parasitized nests fledged 2.50 young/nest (SE = 0.22), less than the average productivity of successful non-parasitized nests (3.27 young/nest, SE = 0.04; $t_{609} = 3.89$, $P < 0.001$).

Table 2.1.2. Summary of vireo banding and monitoring efforts across central Texas breeding sites, 2011-2014.

	Banded		Monitored	Total	Parasitism	Parasitism
	Adults	Nestlings	Territories	Nests	Rate	SE
Island Populations						
Balcones	41	100	44	56	0.16	0.03
Colorado Bend	48	82	68	181	0.64	0.07
Goldthwaite[a]	8	18	13	20	0.42	0.22
San Saba[a]	30	114	39	106	0.49	0.13
Reserve Populations						
Maxdale	63	153	74	140	0.29	0.05
Taylor Valley	69	240	78	126	0.01	0.01
West Range	69	200	68	133	0.21	0.08
East Range	311	471	180	387	0.02	0.01
Jack Mountain	69	83	57	75	0.06	0.01
Manning 2	164	430	106	287	0.02	0.02
West Fort Hood	123	261	94	198	0.03	0.01

[a] Monitored in 2012-2014 only.

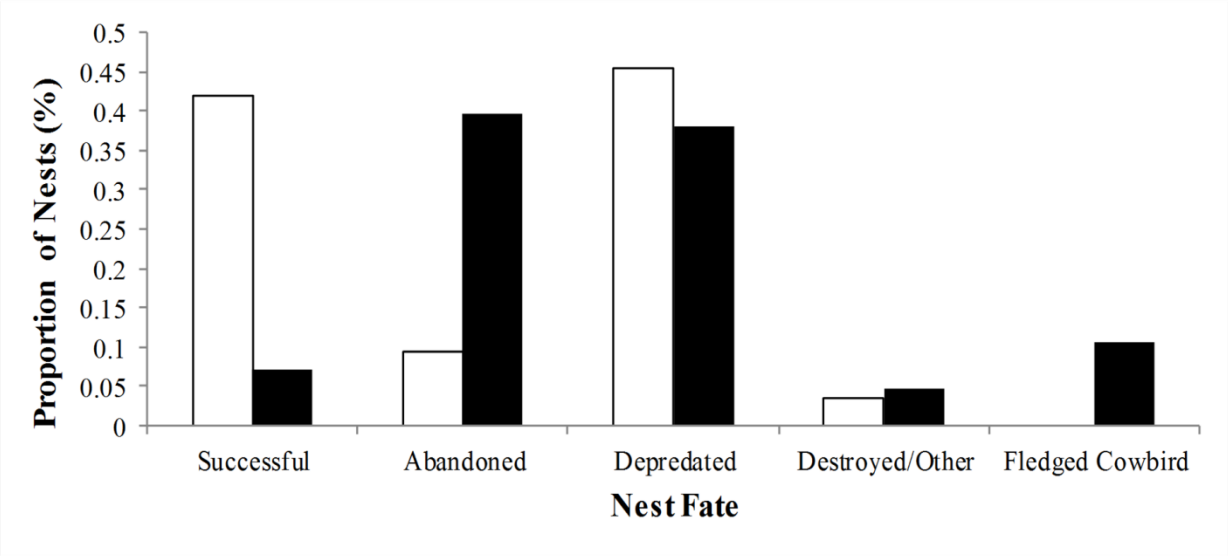


Figure 2.1.2. Nest fate of vireo nests (n = 1709) in central Texas, 2011-2014. Black bars represent the proportion of parasitized nests (n = 291) with different nest fates. Open bars represent non-parasitized nests (n = 1418).

2.1.3.2 Nest Survival

Overall nest survival at individual sites ranged between 0.08 at Colorado Bend and 0.42 at Manning 2 (Table 2.1.3) and averaged 0.30 (SE = 0.03). We observed no difference in average overall survival between study years ($F_{3,38}$ = 0.13, P = 0.94).

Both daily and nest stage survival varied by cowbird control regime (daily: $F_{2,123}$ = 3.10, P = 0.05; nest stage: $F_{2,123}$ = 3.85, P = 0.02). Differences in daily nest survival between cowbird control levels were driven by higher survival in areas with complete cowbird control compared with no cowbird control ($\bar{x}_{complete}$ = 0.95, $SE_{complete}$ = 0.004; $\bar{x}_{none}$ = 0.93, SE_{none} = 0.01, P = 0.04; Table 2.1.4). Similarly, nest stage survival was greater in areas with complete cowbird control compared with sites without cowbird control ($\bar{x}_{complete}$ = 0.72, $SE_{complete}$ = 0.02; $\bar{x}_{none}$ = 0.61, SE_{none} = 0.04, P = 0.02; Table 2.1.4).

Table 2.1.3. Daily, stage, and overall survival (Mayfield 1975) of vireo nests at breeding sites across central Texas from 2011-2014. The sample size, *n*, is the total number of nests from which survival estimates were calculated.

	n	Survival	Nest Stage			Overall Survival
			Egg Laying	Incubation	Nestling	
Island Populations						
Balcones Canyonlands	56	Daily	0.97	0.98	0.95	
		Stage	0.92	0.72	0.59	0.39
Colorado Bend	181	Daily	0.93	0.90	0.93	
		Stage	0.83	0.22	0.45	0.08
Goldthwaite[a]	20	Daily	0.88	0.96	0.96	
		Stage	0.72	0.55	0.64	0.26
San Saba[a]	106	Daily	0.93	0.95	0.95	
		Stage	0.84	0.47	0.54	0.21
All Islands	363	Daily	0.93	0.93	0.94	
		Stage	0.84	0.39	0.53	0.17
Reserve Populations						
Maxdale	140	Daily	0.93	0.95	0.93	
		Stage	0.84	0.50	0.46	0.19
Taylor Valley	126	Daily	0.96	0.98	0.96	
		Stage	0.89	0.72	0.63	0.41
West Range	133	Daily	0.96	0.96	0.97	
		Stage	0.91	0.58	0.68	0.36
East Range	387	Daily	0.93	0.97	0.95	
		Stage	0.83	0.70	0.59	0.34
Jack Mountain	75	Daily	0.93	0.96	0.96	
		Stage	0.83	0.55	0.62	0.28
Manning 2	287	Daily	0.93	0.98	0.97	
		Stage	0.83	0.75	0.68	0.42
West Fort Hood	198	Daily	0.93	0.97	0.96	
		Stage	0.83	0.66	0.64	0.35
All Reserves	1346	Daily	0.94	0.97	0.96	
		Stage	0.85	0.66	0.62	0.35

[a] Monitored in 2012-2014 only.

Table 2.1.4. Daily, stage, and overall survival (Mayfield 1975) of vireo nests at sites varying in level of cowbird control across central Texas from 2011-2014. Averages are calculated from the daily and stage survival of nests at individual study sites, in individual study years, with either complete (*n* = 20), moderate (*n* = 8), or no cowbird control (*n* = 14).

	Daily Survival		Stage Survival		Overall Survival
	Average	SE	Average	SE	
Complete					
Egg Laying	0.93	0.01	0.84	0.02	
Incubation	0.97	0.004	0.67	0.03	
Nestling	0.96	0.003	0.66	0.02	0.38
Moderate					
Egg Laying	0.93	0.02	0.83	0.04	
Incubation	0.97	0.01	0.63	0.05	
Nestling	0.95	0.01	0.61	0.09	0.24
None					
Egg Laying	0.91	0.03	0.82	0.06	
Incubation	0.94	0.01	0.45	0.05	
Nestling	0.93	0.02	0.57	0.07	0.18

2.1.3.3 Territorial Adult Survival

Of 995 territorial adult vireos banded from 2011 through 2014, we resighted 353 in at least one subsequent field season (2012-2015). Most resightings (*n* = 253) were of male vireos, but we also resighted 100 females. Site fidelity was high and we did not observe any dispersal of territorial adults between study sites.

The best model of territorial adult survival included the effects of study site and study year on survival and sex on recapture rate (Figure 2.1.3; Table 2.1.5; Table 2.1.6). This model had a weight > 0.99 and was substantially better than the second best model (φ(~site),p(~sex); ΔAIC_c = 21.57, w_i < 0.001; Table 2.1.6) and goodness of fit testing provided only limited evidence for lack of fit (bootstrap: p = 0.06; median $\hat{c}$-hat = 1.11). Thus, we used the estimates of territorial adult survival from the top model in our population assessments.

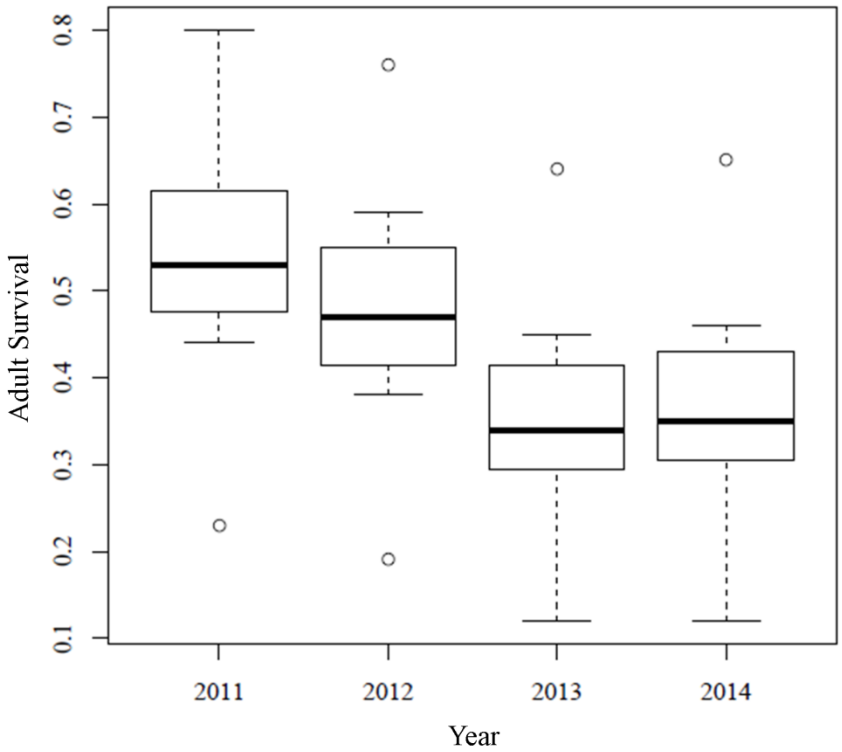


Figure 2.1.3. Variability in territorial adult vireo survival in central Texas across study years, 2011-2014.

Table 2.1.5. Parameter estimates from top model of territorial adult vireo survival, considering the effects of study site on survival (φ; probability of a territorial adult vireo surviving and returning to one of our study sites in a following breeding season) and sex on recapture probability (*p*; probability of encountering a territorial adult vireo given its survival and that it returned to one of our sites).

			95% Confidence Interval	
Parameter	Estimate	SE	Lower	Upper
φ (Balcones Canyonlands + 2011)	0.50	0.08	0.35	0.65
φ (Balcones Canyonlands + 2012)	0.44	0.07	0.30	0.58
φ (Balcones Canyonlands + 2013)	0.31	0.07	0.20	0.45
φ (Balcones Canyonlands + 2014)	0.32	0.07	0.21	0.46
φ (Colorado Bend + 2011)	0.61	0.07	0.47	0.73
φ (Colorado Bend + 2012)	0.54	0.06	0.42	0.66
φ (Colorado Bend + 2013)	0.41	0.06	0.30	0.53
φ (Colorado Bend + 2014)	0.42	0.07	0.30	0.55
φ (Goldthwaite + 2011)	0.62	0.14	0.34	0.84
φ (Goldthwaite + 2012)	0.56	0.14	0.29	0.80
φ (Goldthwaite + 2013)	0.42	0.14	0.19	0.70

φ (Goldthwaite + 2014)	0.44	0.14	0.20	0.70
φ (San Saba + 2011)	0.80	0.06	0.66	0.89
φ (San Saba + 2012)	0.76	0.06	0.61	0.86
φ (San Saba + 2013)	0.64	0.08	0.48	0.78
φ (San Saba + 2014)	0.65	0.08	0.49	0.79
φ (Maxdale + 2011)	0.49	0.07	0.37	0.62
φ (Maxdale + 2012)	0.43	0.06	0.32	0.56
φ (Maxdale + 2013)	0.31	0.05	0.21	0.42
φ (Maxdale + 2014)	0.32	0.06	0.22	0.43
φ (Taylor Valley + 2011)	0.53	0.06	0.41	0.65
φ (Taylor Valley + 2012)	0.47	0.06	0.36	0.59
φ (Taylor Valley + 2013)	0.34	0.05	0.24	0.45
φ (Taylor Valley + 2014)	0.35	0.06	0.25	0.47
φ (West Range + 2011)	0.44	0.07	0.31	0.57
φ (West Range + 2012)	0.38	0.06	0.26	0.51
φ (West Range + 2013)	0.26	0.05	0.17	0.37
φ (West Range + 2014)	0.27	0.05	0.18	0.39
φ (East Range + 2011)	0.46	0.04	0.38	0.54
φ (East Range + 2012)	0.40	0.04	0.33	0.47
φ (East Range + 2013)	0.28	0.03	0.22	0.35
φ (East Range + 2014)	0.29	0.03	0.23	0.36
φ (Jack Mountain + 2011)	0.23	0.06	0.14	0.36
φ (Jack Mountain + 2012)	0.19	0.05	0.11	0.30
φ (Jack Mountain + 2013)	0.12	0.03	0.07	0.20
φ (Jack Mountain + 2014)	0.12	0.04	0.07	0.21
φ (Manning 2 + 2011)	0.65	0.04	0.56	0.73
φ (Manning 2 + 2012)	0.59	0.04	0.50	0.67
φ (Manning 2 + 2013)	0.45	0.04	0.37	0.54
φ (Manning 2 + 2014)	0.46	0.04	0.38	0.55
φ (West Fort Hood + 2011)	0.53	0.05	0.43	0.62
φ (West Fort Hood + 2012)	0.47	0.05	0.38	0.56
φ (West Fort Hood + 2013)	0.34	0.04	0.26	0.43
φ (West Fort Hood + 2014)	0.35	0.05	0.26	0.44
p (Female)	0.67	0.07	0.53	0.79
p (Male)	1.00	< 0.001	0.99	1.00

Table 2.1.6. Models of territorial adult vireo survival and recapture rate. We compared 16 models in total, allowing survival (φ; probability of a territorial adult vireo surviving and returning to one of our study sites in a following breeding season) to vary by individual study year, study site, and the combination of year and site. We allowed recapture probability (*p*; probability of encountering a territorial adult vireo given its survival and that it returned to one of our sites) to vary by year, site, or sex (male or female).

Model	k	AIC_c	ΔAIC_c	w_i
φ (~site + year), *p* (~sex)	16	1785.98	0.00	1.00
φ (~site), *p* (~sex)	13	1807.85	21.87	< 0.001
φ (~site + year), *p* (~1)	15	1811.17	25.19	< 0.001
φ (~site + year), *p* (~year)	18	1812.40	26.42	< 0.001
φ (~site + year), *p* (~site)	25	1825.39	39.41	< 0.001
φ (~site), *p* (~year)	15	1826.62	40.63	< 0.001
φ (~year), *p* (~sex)	6	1829.23	43.24	< 0.001
φ (~site), *p* (~1)	12	1838.55	52.56	< 0.001
φ (~1), *p* (~sex)	3	1842.67	56.68	< 0.001
φ (~year), *p* (~site)	15	1846.50	60.52	< 0.001
φ (~site), *p* (~site)	22	1852.57	66.59	< 0.001
φ (~year), *p* (~1)	5	1854.76	68.77	< 0.001
φ (~year), *p* (~year)	8	1855.80	69.81	< 0.001
φ (~1), *p* (~year)	5	1861.28	75.29	< 0.001
φ (~1), *p* (~site)	12	1866.89	80.91	< 0.001
φ (~1), *p* (~1)	2	1873.04	87.06	< 0.001

2.1.3.4 Juvenile Survival

Across all study sites, we resighted 95 of 2152 juvenile vireos that we banded as nestlings (4.41%), including 56 males and 39 females, in at least one subsequent field season (2012-2015). Juveniles dispersed between 0.15 and 73.93 km from their natal territory ($\bar{x}$ = 3.62 km, SE = 0.92) and dispersal distance did not vary between sexes (t_{93} = 0.08, P = 0.93). The best model of juvenile survival included only the effects of study year on survival and study site on recapture rate, φ(~1),*p*(~site), and had a weight of 0.99 (Table 2.1.6). This model was considerably better than the second best model (φ(~1),*p*(~site); ΔAIC_c = 9.62, w_i = 0.01; Table 2.1.7) and assessments of goodness of fit revealed no evidence for lack of fit (bootstrap: p = 0.26; median $\hat{c}$-hat = 1.24). We used the estimates of juvenile survival from the top model in our calculations of population growth rates.

Table 2.1.7. Models of juvenile vireo survival and recapture rate. We compared 9 models in total, allowing survival (φ; probability of a juvenile vireo surviving and returning to one of our study sites in a following breeding season) and recapture probability (*p;* probability of encountering a juvenile vireo given its survival and that it returned to one of our sites) to vary by individual study site or study year.

Model	k	AICc	ΔAICc	*wi*
φ (~year), *p* (~site)	15	881.24	0.00	0.99
φ (~1), *p* (~site)	12	890.86	9.62	0.01
φ (~site), *p* (~year)	15	895.98	14.74	0.001
φ (~site), *p* (~1)	12	899.28	18.04	< 0.001
φ (~site), *p* (~site)	22	907.64	26.40	< 0.001
φ (~year), *p* (~1)	5	907.99	26.75	< 0.001
φ (~1), *p* (~year)	5	913.09	31.85	< 0.001
φ (~year), *p* (~year)	8	913.36	32.12	< 0.001
φ (~1), *p* (~1)	2	916.54	35.30	< 0.001

2.1.3.5 Population Assessment

2.1.3.5.1 Current Population Status and Likelihood of Population Persistence

Seven of eleven surveyed populations had negative stochastic population growth and we classified them as sinks (Table 2.1.8). Three sites on Fort Hood - Taylor Valley, Manning 2, and West Fort Hood - and the surveyed population at the San Saba property had positive population growth and could be defined as a source (Table 2.1.8). Sink populations varied substantially in their likelihood of going extinct (Table 2.1.8). Source populations all had less than 0.1% chance of extinction in the next 50 years while the QEP_{50} of sinks ranged between 4% and 100% (Table 2.1.8). Populations at Colorado Bend State Park, the Goldthwaite Property, and Maxdale and Jack Mountain on Fort Hood were all predicted to go extinct without an influx of breeding individuals via immigration (Table 2.1.8). In comparison, populations at West Range, East Range, and Balcones Canyonlands National Wildlife Refuge were relatively stable sinks and will likely persist even without immigration for many decades. The QEP for the population on West Range is unlikely to exceed 90% for 139 years and the populations on East Range and the National Wildlife Refuge are unlikely to exceed a QEP of 90% for 181 and 406 years respectively.

On average, island populations were sinks with a 34% chance of going extinct in the next 50 years without immigration (λ_s = 0.96; Figure 2.1.4A). In comparison, reserve populations on Fort Hood were relatively stable with a population growth rate of 0.98 and only a 14% chance of extinction in the next 50 years (Figure 2.1.4A).

Populations with complete cowbird control were sources (λ_s = 1.03) and were unlikely to go extinct in the next 50 years (QEP_{50} = 0.001; Figure 2.1.4B). In comparison, populations with relatively little cowbird control were sinks and will likely be dependent on immigration to

maintain them through the next 50 years (moderate cowbird control: $\lambda_s = 0.92$, $QEP_{50} = 0.92$; no cowbird control: $\lambda_s = 0.90$, $QEP_{50} = 0.99$; Figure 2.1.4B).

Population assessments using stochastic and deterministic models were largely consistent (Figure 2.1.5, Table 2.1.9). When we evaluated yearly deterministic population growth rates for individual sites, however, we determined that no site was a consistent source or a sink across all four years (Figure 2.1.5). Stochastic population growth across all populations was positive only in 2012 ($\lambda_{s\text{-}2012} = 1.23$) and substantially lower in other years ($\lambda_{s\text{-}2011} = 0.81$, $\lambda_{s\text{-}2013} = 0.90$, $\lambda_{s\text{-}2014} = 0.90$). We observed similar patterns in yearly population growth across locations and under different cowbird control regimes (Figure 2.1.6). Vireo populations on islands off of Fort Hood showed a much less dramatic increase in growth rate from 2011 to 2012 and the highest growth rates at these sites was in 2014 (Figure 2.1.6A). Overall, across the study, we observed a negative growth rate for the central Texas vireo population ($\lambda_s = 0.98$).

Table 2.1.8. Parameter estimates from top model of juvenile vireo survival, considering the effects of study year on survival (φ; probability of a vireo surviving and returning to one of our study sites in a following breeding season) and study site on recapture probability (*p*; probability of encountering a vireo given its survival and that it returned to one of our sites).

			95% Confidence Interval	
Parameter	Estimate	SE	Lower	Upper
φ (2011)	0.22	0.07	0.11	0.40
φ (2012)	0.82	0.18	0.29	0.98
φ (2013)	0.43	0.09	0.27	0.61
φ (2014)	0.42	0.11	0.23	0.63
p (Balcones Canyonlands)	0.03	0.02	0.006	0.10
p (Colorado Bend)	< 0.001	< 0.001	< 0.001	< 0.001
p (Goldthwaite)	0.12	0.13	0.01	0.57
p (San Saba)	0.04	0.02	0.01	0.12
p (Maxdale)	0.04	0.02	0.01	0.11
p (Taylor Valley)	0.02	0.01	0.005	0.05
p (West Range)	0.01	0.01	< 0.001	0.05
p (East Range)	0.10	0.03	0.06	0.17
p (Jack Mountain)	0.02	0.02	0.002	0.13
p (Manning 2)	0.08	0.02	0.05	0.14
p (West Fort Hood)	0.06	0.02	0.03	0.12

Table 2.1.9. Vireo population assessments at sites across central Texas from 2011-2014. QEP_{50} is the quasi-extinction probability for each study site in the next 50 years, averaged across 10 runs.

	Average Fecundity	SE	Stochastic Growth Rate (λ_s)	QEP_{50}	Population Assessment
Island Populations					
Balcones Canyonlands	1.27	0.11	0.99	0.04	Sink
Colorado Bend	0.64	0.23	0.82	1.00	Sink
Goldthwaite[a]	0.87	0.60	0.92	0.94	Sink
San Saba[a]	0.77	0.41	1.06	0.001	Source
Reserve Populations					
Maxdale	0.79	0.12	0.81	1.00	Sink
Taylor Valley	1.71	0.23	1.10	< 0.001	Source
West Range	1.37	0.20	0.96	0.40	Sink
East Range	1.32	0.17	0.96	0.15	Sink
Jack Mountain	1.21	0.07	0.83	1.00	Sink
Manning 2	1.59	0.10	1.16	< 0.001	Source
West Fort Hood	1.46	0.14	1.05	< 0.001	Source

[a] Monitored in 2012-2014 only.

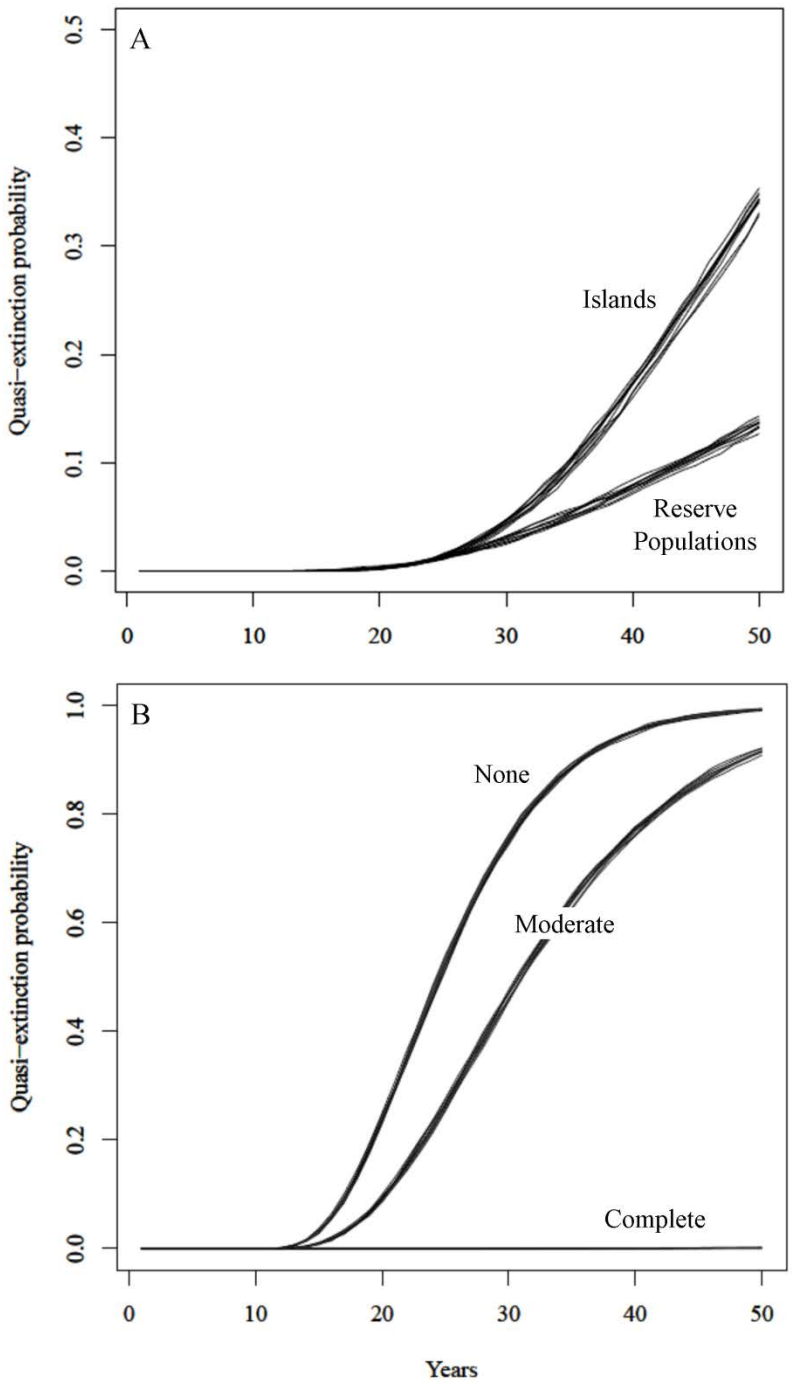


Figure 2.1.4. Quasi-extinction probabilities in the next 50 years for vireo populations in (A) different locations and (B) different cowbird control regimes. Extinction probabilities are based on averaged stochastic population growth models for individual sites and study years and considered a starting population of N_0 = 100 for each location or cowbird control group.

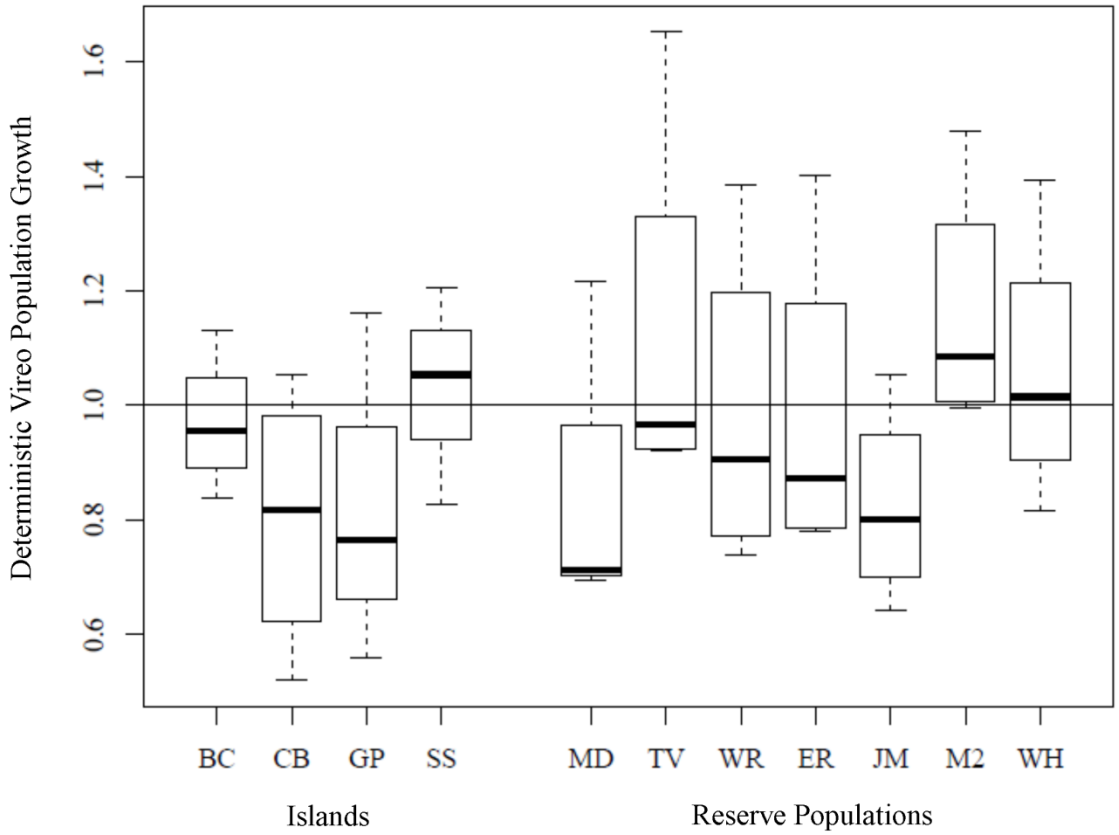


Figure 2.1.5. Deterministic vireo population growth rates calculated from population matrices (Caswell 2001) of demographic parameters, based on field observations from eleven study sites, 2011 - 2014. BC = Balcones Canyonlands National Wildlife Refuge, CB = Colorado Bend State Park, GP = Goldthwaite property, SS = San Saba Property, MD = Maxdale, TV = Taylor Valley, WR = West Range, ER = East Range, JM = Jack Mountain, M2 = Manning 2, and WH = West Fort Hood.

2.1.3.5.2 Effects of Survival and Fecundity on Population Growth Rates

In general, sites with the greatest rates of population decline (i.e. Colorado Bend, the Goldthwaite property, and Maxdale on Fort Hood) were most sensitive to changes in fecundity and territorial adult survival (Tables 2.1.9 and 2.1.10). We observed no significant trend between stochastic growth rates at individual sites and sensitivity to juvenile survival or elasticity of any demographic parameter (Tables 2.1.0 and 2.1.10). When we grouped sites by location, sites on Fort Hood were most sensitive to changes in juvenile survival ($F_{2,8}$ = 4.83, P = 0.04). Growth rates were also more elastic in response to changes in fecundity at sites on base ($F_{2,8}$ = 4.53, P = 0.05).

Holding both adult and juvenile survival at observed rates, populations on average would need a fecundity of 1.23 female young fledged/year to achieve positive growth (Figure 2.1.7). Island populations need a relatively low fecundity for positive growth (1.03) compared with reserve populations on Fort Hood (1.34).

We found that allowing juvenile survival to reach 52% enabled a positive growth rate on average across our study sites (Figure 2.1.7). On Fort Hood reserve sites, a juvenile survival rate of 50% would allow for positive growth while off of Fort Hood, juvenile survival would need to reach 56%.

Across all sites, an increase in adult survival to 44% would enable a positive growth rate and, on Fort Hood, adult survival rates of 37% would allow for positive growth (Figure 2.1.7). Off of Fort Hood, 58% adult survival would allow for positive growth rates across all sites on average and all individual sites except for Colorado Bend, which would require 83% adult survival.

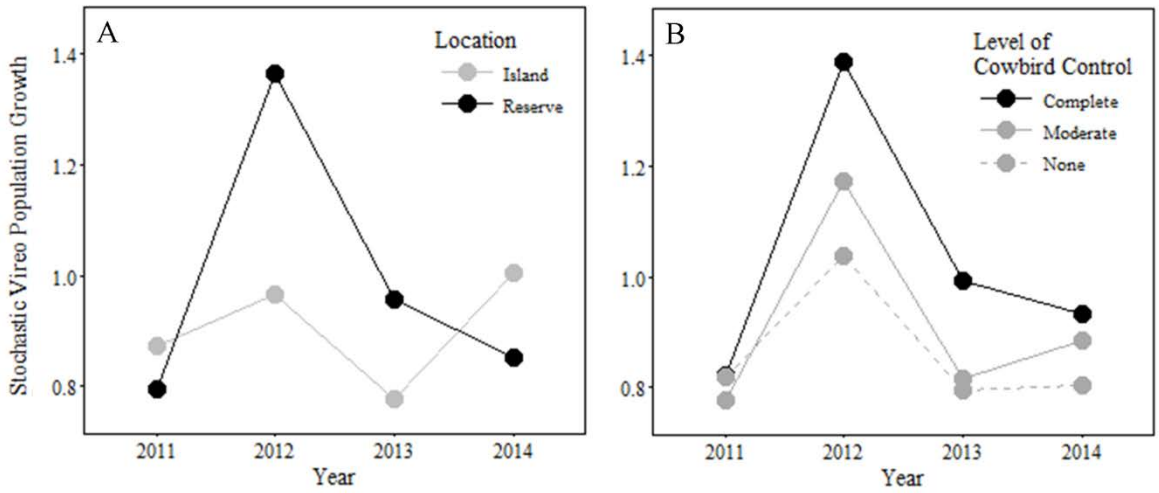


Figure 2.1.6. Stochastic vireo population growth rates across (A) locations and (B) different cowbird control regimes, from 2011 through 2014. Growth rates are calculated from population matrices (Caswell 2001) of demographic parameters, based on field observations from eleven study sites.

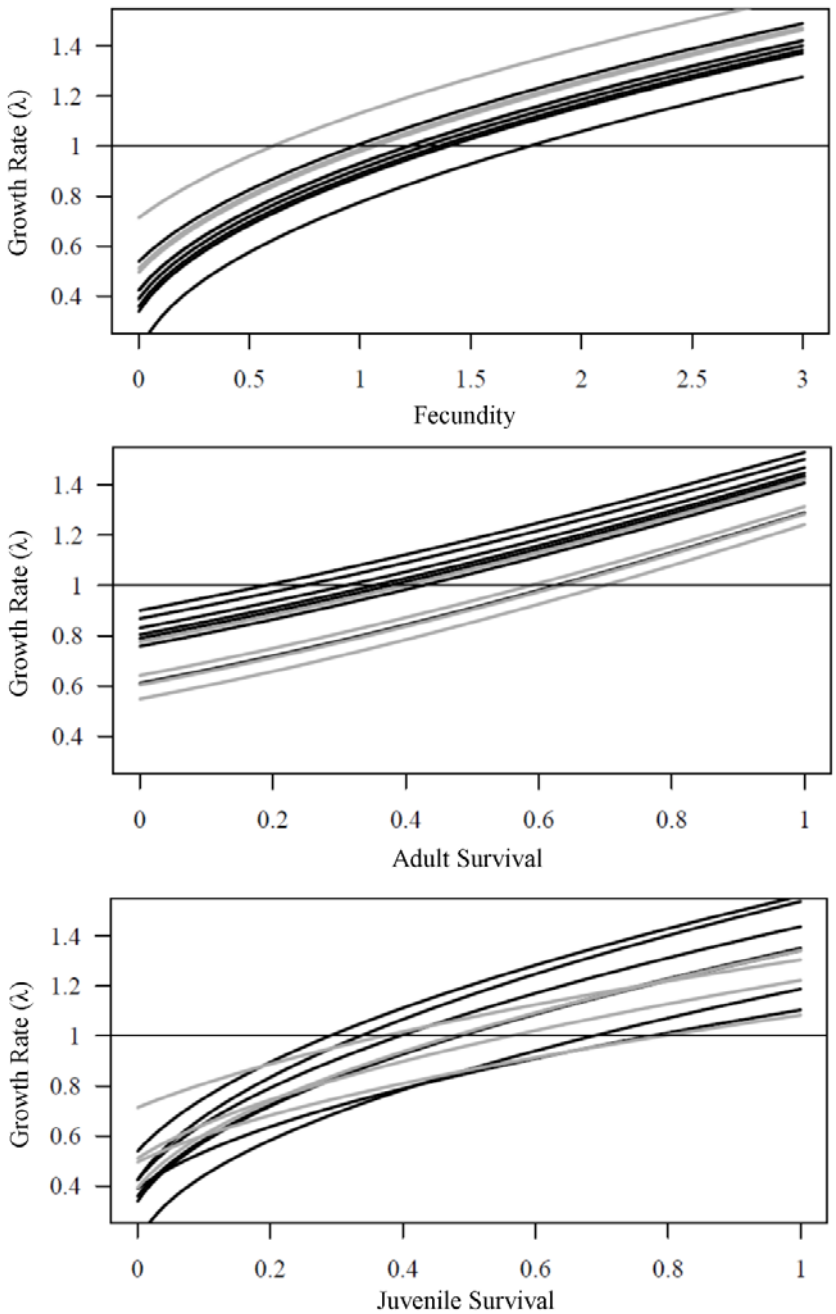


Figure 2.1.7. Variation in deterministic growth rate (λ) at vireo populations across central Texas considering a range of fecundity, adult survival, and juvenile survival. Black lines are projections for reserve sites on Fort Hood and gray lines are island sites located off of Fort Hood.

Table 2.1.10. Sensitivity and elasticity of demographic parameters at vireo populations across central Texas, 2011-2014. Sensitivity is the response of stochastic population growth rate, λ_s, to a numerical change in an individual parameter while elasticity reflects a proportional change. BC = Balcones Canyonlands National Wildlife Refuge, CB = Colorado Bend State Park, GP = Goldthwaite property, SS = San Saba Property, MD = Maxdale, TV = Taylor Valley, WR = West Range, ER = East Range, JM = Jack Mountain, M2 = Manning 2, and WH = West Fort Hood.

	Sensitivity			Elasticity		
	Fecundity	Juv. Surv.	Adult Surv.	Fecundity	Juv. Surv.	Adult Surv.
Island Populations						
BC	0.29	0.85	0.64	0.37	0.37	0.26
CB	0.62	0.62	0.96	0.28	0.27	0.45
GP[a]	0.58	0.53	0.77	0.31	0.31	0.38
SS[a]	0.35	0.52	0.7	0.26	0.27	0.47
Reserve Populations						
MD	0.46	0.78	0.83	0.35	0.34	0.31
TV	0.23	0.91	0.59	0.38	0.37	0.25
WR	0.3	0.92	0.64	0.39	0.39	0.21
ER	0.33	0.96	0.71	0.38	0.37	0.25
JM	0.38	0.95	0.66	0.45	0.44	0.1
M2	0.23	0.76	0.56	0.35	0.34	0.31
WH	0.26	0.78	0.6	0.37	0.37	0.26

[a] Monitored in 2012-2014 only.

2.1.4 Discussion

We documented a spatially and temporally variable source-sink system where the contribution of specific populations to the metapopulation changes between study years. Inter-annual variability in demographic rates and population growth is a long recognized phenomenon in the ecological literature across a broad range of taxa (e.g., Boughton 1999, Saether et al. 1999, Perkins et al. 2003, Schmidt 2003, Palstra et al. 2007, Werner et al. 2009), and understanding differences in population growth is fundamental to the evaluation of source-sink dynamics (Pulliam 1988). However, the implications of temporal variability in source-sink dynamics on long-term metapopulation viability are less often considered and are poorly understood (Runge et al. 2006). Populations with greater inter-annual variability may be more susceptible to extinctions (Runge et al. 2006) and future theoretical work on source-sink metapopulation dynamics should take this empirical realization into account.

Understanding the mechanisms driving both spatial and temporal variability in population performance also is crucial for effective application of ecological theory to conservation. By examining the dynamics of black-capped vireo populations across central Texas and beyond those on Fort Hood, a large mainland reserve, we have revealed broad-scale patterns that will

inform both management and long-term conservation of this endangered species. Although previous research found inconsistent evidence for source-sink dynamics in vireo populations (Fazio et al. 2004, Barr et al. 2008, Zink et al. 2010), we identified seven of eleven vireo populations as sinks. Of four source populations, three are located on Fort Hood and these reserve populations likely produce individuals that help sustain populations on nearby habitat islands. Yearly variation in population dynamics, however, suggests a complex system dependent on evolving cowbird control regimes.

Populations at sites with some degree of cowbird control were more likely to be sources and were unlikely to go extinct compared to populations without cowbird control. When looking at yearly variation, habitat islands had their greatest population growth in 2014, likely because many off Fort Hood sites initiated cowbird control programs later in our study. These results reinforce previous findings that cowbird parasitism is a primary factor in vireo population growth across central Texas (e.g., Kostecke et al. 2005, Wilsey et al. 2014), even when considering a larger spatial scale that includes a mainland-island metapopulation. However, not all sites with complete cowbird control were consistent sources, and other habitat differences may secondarily drive fluctuations in population growth rates. Importantly, cowbird control did not benefit vireo population growth equally across all years; for example, in 2011, there was no difference in the average population growth at sites with complete cowbird control compared to sites without cowbird control. Additionally, the most important demographic driver of population growth varied across individual breeding sites between adult and juvenile survival and fecundity, further highlighting the need for informed land management.

2.1.4.1 Demographic Drivers of Population Dynamics

In general, vireo populations at sites with high parasitism rates were more sensitive to increases in fecundity compared to sites with relatively low parasitism rates. Sensitivity to fecundity was lowest at Taylor Valley and Manning 2, where cowbirds parasitized only one of 126 and 6 of 287 monitored nests respectively. Proportional responses to fecundity, however, decreased with increasing parasitism rates. Thus, growth rates increased with increasing fecundity but fecundity had a greater impact on population growth at sites with little parasitism.

Our estimates of territorial adult vireo survival were generally in agreement with earlier estimates both on and off of Fort Hood that range between 36 and 75% (Graber 1961, Tazik et al. 1993, Grzybowski 1995, USFWS 1996, Weinberg et al. 1998, Grzybowski 2005; see Kostecke and Cimprich 2008 for summary). Kostecke and Cimprich (2008) estimated adult survival rates on NRMB sites on Fort Hood between 45% and 56%, which were notably higher than the average territorial adult survival we observed across Fort Hood from 2011 through 2014 (38%). This was true of the average survival across both new study sites (38%) and NRMB sites on Fort Hood (37%). Kostecke and Cimprich (2008) also found, however, that survival varied significantly between years and in some years was as low as 36% (i.e. 1999). Thus, our survival estimates could simply reflect survey years with relatively poor territorial adult survival on Fort Hood. Our estimates of survival may also be biased by relatively small sample sizes, although this bias would likely have the greatest effect on island sites off of Fort Hood (notably the Goldthwaite Property).

Territorial adult survival estimates may also be biased low in general because of incomplete breeding site-fidelity (Marshall et al. 2004), but this bias might differ between sites that vary in habitat quality if birds more frequently disperse away from low-quality sites in favor of better breeding habitat. Furthermore, biases in our estimates of territorial adult survival may have the greatest impact on population projections for sites with high parasitism and low nest success. Limited availability of breeding habitat, regardless of quality, may explain why we observed higher survival at sites off of Fort Hood compared with sites on base. Although birds that breed on a mainland reserve like Fort Hood have considerable nearby habitat to choose from and may disperse outside our search areas between subsequent breeding seasons, birds breeding in relatively isolated island patches may simply have nowhere else to go. Age-specific analyses that compare territorial adult survival between the first and second breeding seasons with survival in subsequent seasons may help elucidate these patterns.

We found no evidence that juvenile survival differed between populations on or off of Fort Hood or between individual sites. Juvenile survival is notoriously difficult to estimate because it is often impossible to distinguish between dispersal and true mortality. To compensate, many researchers instead assign juvenile survival as a percentage, often 50%, of adult survival (Greenberg 1980, Temple and Cary 1988, Noon and Sauer 1992, Donovan et al. 1995). In contrast, our average estimate of 46% juvenile survival is relatively high, even greater than our estimates of territorial adult survival on some study sites, and is higher than previous estimates of juvenile survival on Fort Hood (Kostecke and Cimprich 2008). Our estimate is, however, consistent with juvenile vireo survival estimates from the Wichita Mountains (Grzybowski 2005) and is further bolstered by evidence of high survival of independent juvenile vireos from radio-telemetry during the post-breeding season (Walker 2015). In fact, high juvenile dispersal and low return rates may have resulted in underestimates of juvenile survival.

2.1.4.2 Dispersal

We were unable to quantify the amount of immigration and emigration between study populations and, ultimately, the role of dispersal in the persistence of these populations. Dispersal events between high- and low-quality habitat patches could help alleviate demographic pressures placed on less productive populations, and although we did not directly observe any adult dispersal between breeding sites, we know from our estimates of population growth that migration must occur for many of these populations to have persisted through the course of this study. Vireo dispersal events as far as 78 km have been rarely documented from the resighting of uniquely banded individuals (Cimprich et al. 2009).

2.1.4.3 Implications to Management

Differences in demographics between reserves and islands highlight the need to consider broad-scale population dynamics in management decisions. Furthermore, annual variability in the role of individual populations in overall metapopulation dynamics must be considered in designing effective management plans. For black-capped vireos, management informed by monitoring efforts on the Fort Hood NRMB sites alone may be inefficient or inappropriate for smaller or more isolated populations operating under inconsistent cowbird control regimes. Though efforts to conserve endangered and threatened species often focus on the creation and preservation of

large reserves of high-quality habitat, small islands or patches of low-quality habitat may also contribute to the stability and long-term survival of metapopulations (Foppen et al. 2000, Murphy 2001) and may buy time for management of declining populations (Heinrichs et al. 2015). Although sink populations may individually be more vulnerable to a poor reproductive year or catastrophic event, low-quality habitat is often found in greater abundance (Foppen et al. 2000). Additionally, reproduction in sink patches may still contribute to overall metapopulation size in years with exceptionally high reproduction or survival, especially if individuals eventually leave and disperse to higher-quality habitat (Howe et al. 1991, Gaona et al. 1998, Foppen et al. 2000). The occasional importance of sinks was most evident in 2014, when island populations on average were sources but reserve populations on Fort Hood were sinks. Moreover, every individual sink population in our study system was a source in at least one individual year, often coinciding with the initiation of cowbird control, and young produced during source years could be important in maintaining overall population stability.

Vireo populations with low nest success and high parasitism rates respond more to proportional changes in adult survival than fecundity or juvenile survival. Elasticity, however, does not necessarily translate directly to management, and in addition to evaluating measures of elasticity, managers must assess their ability to affect change on demographic parameters (Heppel 1998, Mills et al. 1999). Although we know predation, food availability, and climate are likely to influence adult songbird mortality during the breeding season (Sherry and Holmes 1995), specific drivers of adult vireo mortality are unknown and probably vary across breeding populations. By contrast, much research (including the results of this study) has suggested that effective cowbird control can dramatically impact nest success and fecundity (e.g., Kostecke et al. 2005, Kus and Whitfield 2005). Ultimately, management action to improve reproductive success is likely to be both more feasible and much more effective than attempts to improve adult survival, particularly at sites with high parasitism rates. Additionally, while improvements to habitat quality may take several years, cowbird control can be immediately implemented making it a necessary first step in managing vireo breeding habitat. Importantly, our results suggest that cowbird removal programs are most effective when they utilize both shooting and trapping strategies, although the relative contribution of each control method is difficult to tease out. Previous research on Fort Hood suggests that, early in the breeding season, trapping may be the more effective, as well as the most cost-efficient, method for reducing cowbird parasitism (Summers et al. 2006a). However, shooting may be an effective alternative to trapping, particularly in May and June, because managers can target cowbirds that are most likely to parasitize nests (Kostecke et al. 2005; Summers et al. 2006a, 2006b). Furthermore, shooting cowbirds may also be a more suitable option for private landowners who are unable to regularly maintain and monitor traps.

2.2 Habitat use by adult and juvenile black-capped vireos: natural selection and the importance of considering a broader definition of breeding habitat[4]

2.2.1 Introduction

Natural selection, the fundamental mechanism of evolution, favors heritable traits of individuals that enhance reproduction and survival. Although much avian research has focused on understanding the characteristics guiding success of the actual reproductive event (e.g., nest or territory success within a single breeding season; see Streby and Andersen 2011), natural selection operates on the timescale of an individual's entire reproductive life. Natural selection, therefore, may guide not only the qualities that successfully produce young but also the qualities that allow those young to survive long enough to reproduce themselves. Research that focuses on understanding the qualities of breeding sites alone (e.g., nest placement or territory composition) may not fully document the way in which natural selection fashions the choice of where a species nests.

Aspects of the breeding site that affect post-independence juvenile survival vary across species and life history strategies. For relatively wide-ranging species such as raptors and seabirds, juvenile survival may be limited by temporal and spatial variation in prey availability (Rohner and Hunter 1996, Wiens et al. 2006, Riotte-Lambert and Weimerskirch 2013), environmental conditions (Fay et al. 2015), and interactions with humans (Votier et al. 2008, Stoychev et al. 2014). Juvenile survival for many passerines, however, is limited primarily by the ability to avoid predators and forage effectively (Sullivan 1989, Kershner et al. 2004), and foraging proficiency might be particularly important for birds preparing for an arduous fall migration.

For many young songbirds, the greatest threats to survival are predation shortly after fledging (Anders et al. 1997, Yackel Adams et al. 2001, Rush and Stutchbury 2008, Vitz 2008, Ausprey and Rodewald 2011) and the myriad challenges of migration (Owen and Black 1989, Sillett and Holmes 2002, Menu et al. 2005). Thus, parents may increase their reproductive output by selecting breeding territories with both sufficient cover to protect young birds from predators (Vega Rivera et al. 1998) and food resources that enable juveniles to store sufficient fat reserve for migration (White et al. 2005, Vitz and Rodewald 2007, Streby et al. 2011). Shrublands or habitats with dense understory vegetation may meet those requirements for many species. Juvenile yellow-breasted chats (*Icteria virens*) and gray catbirds (*Dumetella carolinensis*) that fledged from shrublands remained in early-successional habitat after they became independent (Maxted 2001). Young ovenbirds (*Seiurus aurocapilla*; King et al. 2006, Vitz 2008, Streby and Andersen 2013), worm-eating warblers (*Helmitheros vermivorum*; Vitz 2008), and white-throated robins (*Turdus assimilis*; Cohen and Lindell 2004) used post-fledging habitat with relatively dense understory vegetation compared with typical breeding habitat for those species.

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[4]This work was submitted as: Walker, L. E., and J. M. Marzluff. In Review. Habitat use by adult and juvenile black-capped vireos: natural selection and the importance of considering a broader definition of breeding habitat. *Condor*.

However, Streby and Andersen (2013) found that juvenile ovenbirds remained in their nesting habitat (mature forest) when dense understory cover was also available.

Tensions between the selection of a breeding territory that optimizes the production of fledglings versus one that maximizes offspring survival prior to migration should be reflected in differential habitat use by adults and juveniles (Figure 2.2.1). Furthermore, nest-site selection that considers juvenile habitat requirements might result in sub-optimal nest success whereas habitat that optimizes nest success alone may endanger juveniles. Thus, a full understanding of how natural selection shapes the choice of a breeding site is necessary for both researchers aiming to fully understand the life history and ecology of a species and land managers wishing to properly conserve or restore appropriate breeding habitat. This is perhaps particularly important for the management of endangered species already limited by habitat loss or restricted breeding ranges. To evaluate the role of juvenile habitat requirements on breeding site selection, we surveyed habitat use by territorial and juvenile birds of an endangered shrubland species, the black-capped vireo (vireo; *Vireo atricapilla*).

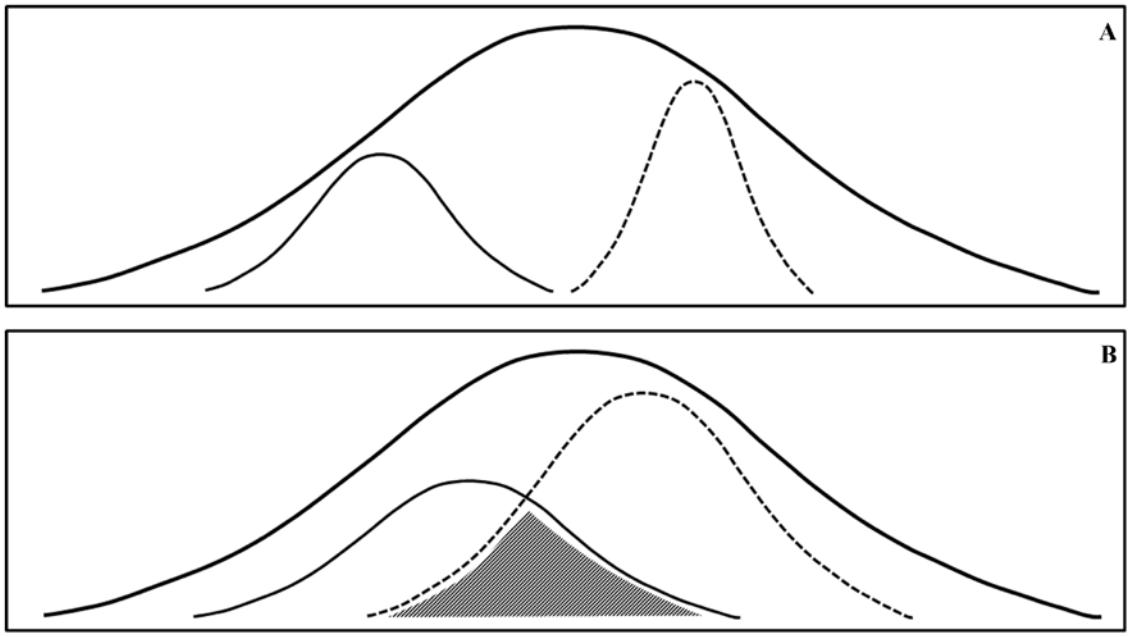

Figure 2.2.1. A hypothetical gradient of breeding habitat (large bold curve) with optimal nesting (area under thin solid line) and juvenile habitat (area under dashed line). In (A), habitat requirements for each reproductive stage are relatively narrow and breeding individuals must accept tradeoffs in selecting breeding habitat. In (B), overlap between nesting and juvenile habitat requirements prevents the need for tradeoffs in habitat selection.

Although the characteristics of vireo breeding habitat have been well documented (Grzybowski et al. 1994, Conkling et al. 2012), relatively little is understood about the habitat requirements for juvenile vireos or the tradeoffs, if any, between these requirements and those favored by nesting adults. Across their breeding range, adult vireos use habitats with high densities of deciduous shrub cover (Grzybowski et al. 1994). Vireo nest success is also higher in natural shrubland than in habitat modified by military activity (Bailey 2005, Noa et al. 2007). On Fort Hood, juveniles use riparian vegetation near water sources more than the shrub habitat characteristic of breeding territories (Dittmar et al. 2014). Young birds on Fort Hood also use areas with greater canopy cover and foliage density compared with random nearby locations (Dittmar et al. 2014). However, juvenile habitat use and survival has not been assessed across broader scales or in areas without nearby or easily accessible riparian vegetation.

We compared the use of vegetation by adult and juvenile vireos across central Texas during the breeding season and during the post-breeding/pre-migration period, respectively. We compared vegetative characteristics of nest sites, breeding territories, and places visited by juveniles using direct field measurements of structure as well as remotely sensed aspects of the landscape. We expected that both breeding and juvenile vireos would most frequently use areas with at least moderate shrub cover and dense cover near the ground because of previous observations of habitat associations for vireos (Grzybowski 1995, Bailey 2005, Dittmar et al. 2014). We predicted, however, that areas with relatively high amounts of low structural cover and high proportions of shrub and deciduous forest land cover would not necessarily benefit nest success (Bailey 2005, Chalfoun and Martin 2009) but would improve juvenile survival (Vitz 2008, Dittmar et al. 2014). We anticipated one important tradeoff in breeding site and juvenile habitat: to reduce risk of nest parasitism in areas without cowbird control – breeders may favor areas with less canopy cover relative to juveniles. Cowbirds may use perches within the canopy to survey and search for nest locations (Hauber and Russo 2000). In contrast, canopy cover may benefit juvenile birds by providing cover from predators (Streby et al. 2015). We also expected juveniles to concentrate habitat use and have greater survival in vegetation with abundant understory cover, including shrublands and mixed deciduous forest land covers. Finally, we predicted that juveniles would concentrate their use in wetland habitats, as found by Dittmar et al. (2014), but that there would be no association with wetlands in breeding territories.

2.2.2 Methods

2.2.2.1 Study Sites

We chose study sites on Fort Hood and in nearby areas to the south and west, all within the Hill Country of central Texas (Figure 2.1.1). The habitat is largely characterized by shortgrass communities and cattle rangeland. Many areas that were once native grass or shrublands have transitioned to woodlands due to fire suppression regimes and encroachment by the native evergreen Ashe juniper (*Juniperus ashei*).

Fort Hood Military Installation: We monitored three study sites on Fort Hood from 2011 through 2014 (Figure 2.1.1). West Range, approximately 50 ha, is dominated by mixed juniper

and deciduous woodlands. The Taylor Valley site, about 60 ha, and Maxdale, 100 ha, are both characterized by a mix of grasslands and deciduous woodlands.

Balcones Canyonlands National Wildlife Refuge: We focused our monitoring efforts on three tracts along the northern edge of the refuge, as described in Task 2.1. Vegetation cover varies between tracts from tall dense shin oak (*Quercus sinuata* var. *breviloba*) to juniper woodlands to open grasslands with scattered low shin oak and flame-leaf sumac (*Rhus lanceolata*).

San Saba: About 25 ha, the site is comprised of a northwest-facing hillside, largely covered in very dense persimmon (*Diospyros texana*), juniper, honey mesquite (*Prosopis glandulosa*), allthorn (*Koeberlinia spinosa*), and green condalia (*Condalia viridis*).

Colorado Bend State Park: The site was characterized by a mix of open grasslands and patchy juniper and live oak (*Quercus fusiformis*) woodlands.

Goldthwaite*:* We monitored vireo territories on 33 ha in the northeastern corner of the ranch, an area comprised of an open and patchy hilltop with densely vegetated south-facing slopes. Shrub and tree vegetation was primarily persimmon, juniper, elbow bush (*Forestiera pubescens*), and mesquite.

2.2.2.2 Effects of Cowbird Control

In each study year, we classified each study site using a simplified measure of the level of cowbird control (Table 2.2.1). We designated sites with both trapping and shooting as having "complete" cowbird control. Although the implementation of trapping or shooting programs can alter their effectiveness (Summers et al. 2006a, b), we designated sites where cowbirds were either trapped *or* regularly removed by shooting as having "moderate" cowbird control. We labeled all other sites as having no cowbird control.

2.2.2.3 Monitoring Efforts

2.2.2.3.1 Adults

We visited study sites two to three days per week throughout the vireo breeding season, from late March through early July, and searched for all territorial males. We identified males by individual color band combination and visited each territory from one to three times per week, recording locations of territorial male vireos using a handheld GPS unit. We recorded no more than five locations per day for each territory and each observation was separated by at least five minutes.

We monitored pairs to locate all nests. Although we attempted to document all nesting attempts, we likely missed some unsuccessful nests. We believe this happened infrequently, however, as relatively few nests were located post-fledging (2.0%) or post nest failure (1.4%). We visited known nest locations every three to four days until failure or fledging and recorded the number of vireo and cowbird eggs (if present), the number and approximate age of nestlings, and parental presence at the nest. We considered a nest to be successful (n = 223) if we observed at

least one fledgling with parents away from the nest (n = 150) or if we observed at least one vireo nestling in the nest on day 11 (average fledge day) and we observed behaviors by the adults to suggest they had fledglings (scolding, carrying food) (n = 73).

2.2.2.3.2 Juveniles

In late June through August of 2012-2014, we caught juvenile black-capped vireos and attached radio-transmitters weighing approximately 270 mg (or about 3% of a vireo's body weight) using leg loop harnesses. We aimed netting attempts at young vireos banded as nestlings so we could be certain of their exact age and natal location; we attached transmitters to 27 banded juveniles recaptured between 32 and 64 days post-fledging. However, we also attached transmitters to unbanded juvenile vireos (n = 86) that we caught incidentally. We assumed that all juveniles were fledged from breeding territories at their capture location. We followed and recorded locations of each radio-tagged bird daily until the bird could no longer be found. We lost contact with 51 birds that appeared to have moved beyond our search area (although their transmitters may have failed suddenly and earlier than expected) and 53 birds because the transmitter batteries died.

Table 2.2.1. Level of cowbird control at vireo breeding sites across central Texas from 2011-2014. At sites with complete control, managers used both shooting and trapping to remove cowbirds. At moderately controlled sites, cowbirds were controlled with either trapping or shooting. The properties in Goldthwaite and San Saba were not monitored in 2011.

	Year			
Site	2011	2012	2013	2014
Balcones Canyonlands	Moderate	Moderate	Moderate	Moderate
Colorado Bend	None	None	None	Moderate
Goldthwaite	---	None	Moderate	Complete
San Saba	---	None	None	Moderate
Maxdale	Moderate	Moderate	Moderate	Moderate
Taylor Valley	Complete	Complete	Complete	Complete
West Range	None	None	None	None

2.2.2.4 Home Range Estimation

We used a fixed-kernel density estimator in Geospatial Modeling Environment (GME 0.7.3.0; Beyer 2012) to create utilization distributions at 10-m resolution covering the points used by breeding adults and juveniles. We used the plug-in algorithm to estimate the optimal bandwidth and 1.5 as a starting point for the iterative smoothing factor algorithm for each home range. We then converted utilization distributions to percent volume contours and considered the home range equal to the area circumscribed by the 99 percent contour.

We obtained 4-86 locations on breeding adult males and 3-34 on juveniles. We estimated the home range area for all breeders (n = 377) and found a significant correlation between the number of location points and the size of the home range (r = 0.21, t_{376} = 4.18, P < 0.001). When we considered only territories represented by at least 40 location points (n = 121), however, the number of points and the size of the territory were no longer correlated (r = 0.14, t_{120} = 1.55, P = 0.12) and we considered only these territories in further analyses. Across all juveniles tracked (n = 113), juvenile range size was not correlated with the number of location points (r = 0.02, t_{112} = 0.20, P = 0.84). Thus, we compared range composition (land-cover area and proportion within the home range) among all juveniles. To balance kernel accuracy while achieving a sufficient sample size, however, we considered only juveniles with at least 15 location points (n = 73) in analyses of use (concentration of use and resource utilization functions) as well as structural vegetation plots.

2.2.2.5 Structural Vegetation Plots

2.2.2.5.1 Locations

We divided each home range into multiple strata reflecting relative use within which we established vegetation plots. For each territory, we split the utilization distribution into high (0-25% kernel density estimate), moderate (25-75%), and low-use (75-99%) strata. For each juvenile bird, we split the home ranges into high (0-25% kernel density estimate) and moderate/low-use (25-99%) strata. We used a random point generator in ArcGIS 10.0-10.2 (ESRI, Redlands, California) to establish vegetation plot locations (two per territory stratum and four per juvenile stratum) that were at least 30 m apart and at least 15 m from the stratum edge.

2.2.2.5.2 Field Measurements

We measured vegetation in plots centered on a survey point, with five additional points extending along axes in each of the four cardinal directions, each separated by 3 m. We measured four characteristics of vegetation structure that would together summarize the amount of low cover (foliage density from 0-1 m and 1-2 m), low woody plants (shrub cover), and high woody vegetation (canopy cover).

We measured foliage density in each plot using a 2 m cover pole divided into 10-cm sections, and we separately measured the foliage density within 1 m of the ground and between 1 and 2 m above the ground. At each of three points (the center point, 15 m north, and 15 m south) an

observer knelt and sighted the cover pole at a distance of 4 m in each of the cardinal directions. The observer noted the number of 10-cm sections which were at least 50% obscured in each of the height zones (0-1 m and 1-2 m). Thus, we collected 12 samples of foliage density in each height zone, and we considered the plot's foliage density in each zone to be the average percent of obscured pole segments.

To assess the presence of shrub cover, we placed a vertical 2-m pole at each survey point and marked shrub cover as present if any shrub branches or foliage were within 20 cm of the pole. We considered the canopy and shrub cover of the plot to be the percentage of points with canopy or shrub presence. Finally, to sample canopy cover at each point, we looked straight upward through an ocular tube (2 cm in diameter, 30 cm in length). We considered canopy cover to be present if we observed any branches or foliage at or above 3 m.

2.2.2.5.3 Analyses

We assessed differences between the vegetation structure in each use strata within breeding and juvenile home ranges across all study sites using ANOVAs. We also conducted an ANOVA to assess the impacts of vegetation structure and use-strata and their interaction on juvenile survival. We then conducted *post hoc* Tukey HSD tests and used the studentized range distribution (q) to determine specific differences between strata, age class, and success. We assessed the effects of vegetation characteristics on territory success using a generalized linear model including vegetation, strata, level of cowbird control, and all two-way interactions. We used *post hoc* chi-square tests to identify specific differences. For all tests, we used an alpha of 0.05 to indicate significance, but we additionally report results that approach significance (are within the 90% confidence interval).

2.2.2.6 Land Cover Classification

We determined the composition of adult and juvenile ranges with land-cover data from the 2011 National Land Cover Database (NLCD; Homer et al. 2015), a national dataset that classifies land cover in the conterminous United States into 16 categories at 30 m resolution. A 2011 NLCD layer also provided percent canopy cover at 30-m resolution (Homer et al. 2015). We identified 14 NLCD land-cover classifications within vireo territories that, to focus on habitat types biologically relevant to the black-capped vireo, we simplified into five land-cover types:

(1) Water/Wetlands: areas with perennial open water and woody wetlands where forest or shrubland vegetation is periodically saturated or covered by water;

(2) Open/Developed: areas with little structural vegetation, including developed areas, herbaceous grasslands and wetlands, pastures and agricultural land, and areas identified as barren;

(3) Mixed/Deciduous Forest: mix of deciduous and evergreen trees with a canopy height greater than 5 m tall and comprising greater than 20% of the total vegetative cover;

(4) Evergreen Forest: primarily evergreen forest (at least 75%), trees are greater than 5 m tall and comprise more than 20% of the vegetative cover;

(5) Shrubland: shrubs and early successional trees with a canopy less than 5 m in height and greater than 20% of the total vegetative cover.

2.2.2.6.1 Home-Range Composition

Within both breeding and juvenile home ranges, we calculated the area and the proportion of total area covered by each land-cover type (mean ± SE). Then, using ANOVAs and *post hoc* Tukey tests, we compared the area and land-cover composition of breeding home ranges with those of juvenile vireos. Finally, we assessed the effects of land-cover composition and the level of cowbird control on the reproductive success of territorial birds using a binomial generalized linear model. We assessed the importance of home range area and land-cover composition to juvenile survival using Cox proportional hazards regression and the package "coxph" in R (3.1.1; R Core Team 2014).

2.2.2.6.2 Nest Characteristics

For each vireo nest, we recorded the plant species supporting the nest and the height of the nest above ground level. We also overlaid nest locations onto land-cover maps (Homer et al. 2015) and identified the land-cover type surrounding the nest and the distance to the nearest edge using ArcGIS 10.2 (ESRI, Redlands, California). Finally, we determined the average canopy cover over the nest location using the NLCD canopy-cover dataset (Homer et al. 2015). Using a binomial generalized linear model, we compared the effects of cowbird control and each of four nest characteristics (nest height, distance to edge, canopy cover, and land-cover type), as well as their interaction, on nest success.

2.2.2.6.3 Concentration of Use

Using GME (Beyer 2012), we created a regular grid of points, each separated by 30 m, across the utilization distribution of each home range and sampled use and land-cover type at each point. We then used Fragstats (4.2.1; McGarigal et al. 2012) to evaluate the area of each land-cover type within each bird's home range. Finally, we calculated concentration of use for each habitat type within each vireo's home range for both territorial and juvenile birds. Concentration of use (COU), a measure of selectivity within the home range, is the ratio of the total volume of the utilization distribution within each land-cover type to the area of that land cover within the home range (Neatherlin and Marzluff 2004). We compared concentration of use among the five land-cover types and between breeding and juvenile birds using an ANOVA. Finally, we assessed the relationship between COU and territory success using a generalized linear model that considered success as a dependent binomial variable and the independent variables: COU, land-cover type, cowbird control effort, and all two-way interactions.

2.2.2.6.4 Resource Utilization Functions

We related territorial and juvenile vireo space use with spatial predictor variables, including land-cover type and canopy cover, using resource utilization functions (RUFs; Marzluff et al. 2004, Kertson and Marzluff 2011). Because low-use cells are more abundant in utilization distributions than high-use cells (Johnston 2013), we expected some problems with the fit of RUFs. Therefore, to evaluate model fit, we examined residual plots from univariate RUFs from a sample of five breeding and five juvenile birds and found, in many cases, that the response variable was right-skewed. We were able to improve residual normality in our test RUFs by log-transforming the response variable (use) and thereafter applied this transformation to all breeding and juvenile birds. We did not transform any predictor variables. We calculated all RUFs using the package "ruf" in R (2.13.1; Handcock 2004, R Core Team 2014).

2.2.3 Results

2.2.3.1 Home Range Composition

Of 121 territories with at least 40 location points, the average territory size was 6.96 ± 0.39 ha. Juvenile birds (n = 113) used much larger areas ($\bar{x}$ = 195.82 ± 27.56 ha) than were defended by adults.

Across all birds, home ranges differed in their relative composition of land-cover types ($F_{4,960}$ = 72.12, $P < 0.001$; Tables 2.2.2 and 2.2.3, Figure 2.2.2). Both breeding birds and juveniles had home ranges with proportionally more shrubland and evergreen forest than open or developed land (shrub: $q = 5.08$, $P = 0.003$; evergreen: $q = 4.35$, $P = 0.02$), mixed and deciduous forest (shrub: $q = 10.73$, $P < 0.001$; evergreen: $q = 10.00$, $P < 0.001$), or wetlands (shrub: $q = 20.55$, $P < 0.001$; evergreen: $q = 19.82$, $P < 0.001$; Tables 2.2.2 and 2.2.3). Home ranges also had relatively more open habitat than mixed forest ($q = 5.64$, $P < 0.001$) or wetlands ($q = 15.46$, $P < 0.001$) and more mixed forest than wetland habitat ($q = 9.82$, $P < 0.001$; Tables 2.2.2 and 2.2.3).

Breeding territories differed in land-cover composition from juvenile home ranges ($F_{4,960} = 6.31$, $P < 0.001$; Tables 2.2.2 and 2.2.3, Figure 2.2.2). Breeding birds used areas with proportionally more shrubland ($q = 4.83$, $P < 0.001$), less open or developed areas ($q = 3.73$, $P = 0.01$), and less wetland habitat ($q = 3.29$, $P = 0.02$) than in juvenile home ranges (Tables 2.2.2 and 2.2.3, Figure 2.2.2). Average canopy cover in home ranges, however, did not differ between breeding and juvenile vireos ($t_{192} = 0.09$, $P = 0.93$). Juvenile home ranges had a smaller variance in the proportion of each land-cover type, as well as canopy cover, compared with breeding birds (Bartlett Test of Homogeneity of Variance; water: $k = 414.38$, $P < 0.001$; open: $k = 5.88$, $P = 0.02$; mixed forest: $k = 38.41$, $P < 0.001$; evergreen forest: $k = 3.62$, $P = 0.06$; shrub: $k = 40.04$, $P < 0.001$; canopy cover: $k = 5.75$, $P = 0.02$; Figure 2.2.2).

2.2.3.2 Nest Sites

Over four breeding seasons, we located and monitored 784 vireo nests. Canopy cover over nests averaged 42.5 ± 0.89% and nests were located 1.10 ± 0.02 m off the ground. On average, nests were located 15.59 ± 0.55 m from the nearest patch edge.

We found nests in all land-cover types, although most were located in shrublands (32.4%; Table 2.2.4). Nests in different land-cover types differed in distance to edge ($F_{4,779} = 3.83$, $P = 0.004$), height off the ground ($F_{4,770} = 3.90$, $P = 0.004$), as well as canopy cover ($F_{4,779} = 142.59$, $P < 0.001$; Table 2.2.5). Nests in mixed forests were located closer to the patch edge than nests in either evergreen forest ($q = 4.72$, $P = 0.007$) or open habitat ($q = 4.73$, $P = 0.007$). Nests in evergreen forests were higher off the ground than nests in either shrublands ($q = 4.73$, $P = 0.007$) or open land cover ($q = 3.82$, $P = 0.05$).

2.2.3.3 Concentration of Use

Breeding pairs ($n = 121$) and juveniles ($n = 73$) varied their concentration of use in five land-cover types ($F_{4,960} = 40.84$, $P < 0.001$; Table 2.2.6). Birds within both reproductive stages used forests and shrublands more than open or developed areas (mixed/deciduous forest: $q = 4.17$, $P = 0.03$; evergreen forest: $q = 4.33$, $P = 0.02$; shrubland: $q = 5.59$, $P < 0.001$) and more than water/wetlands (mixed/deciduous forest: $q = 14.14$, $P < 0.001$; evergreen forest: $q = 14.31$, $P < 0.001$; shrubland: $q = 15.56$, $P < 0.001$), even after considering availability. Vireos also used open or developed areas more than wetlands (open/developed: $q = 9.97$, $P < 0.001$).

Breeding birds, but not juveniles, also used shrub more than mixed forests although the difference was not quite significant ($q = 3.55$, $P = 0.09$). There was no significant interaction between concentration of use in a particular land-cover type and reproductive stage ($F_{4,960} = 1.59$, $P = 0.17$).

2.2.3.4 Resource Utilization Functions

We found no consistent association between canopy cover or any land-cover type and juvenile use of the landscape, although a negative association with open and developed areas was nearly significant (Table 2.2.7). Relative use of areas within the home range of breeding vireos was positively associated (95% CI around RUF coefficients did not include zero) with both deciduous and evergreen forest as well as shrublands (Table 2.2.7).

Table 2.2.2. Average area and proportion of total area of five land-cover types within the home ranges of breeding vireos that were (*n* = 63) and were not successful in fledging young (*n* = 58), 2011-2014.

	All Territories				Non-Successful				Successful			
Land Cover	Area (ha)	SE	Prop.	SE	Area (ha)	SE	Prop.	SE	Area (ha)	SE	Prop.	SE
Water/Wetland	0.02	0.006	0.003	< 0.001	0.02	0.01	0.003	0.002	0.009	0.006	0.002	0.001
Open/Developed	1.24	0.15	0.2	0.02	0.9	0.18	0.15	0.03	1.56	0.23	0.24	0.03
Mixed/Deciduous Forest	1	0.08	0.17	0.01	0.88	0.12	0.14	0.02	1.12	0.11	0.19	0.02
Evergreen Forest	2.2	0.25	0.29	0.02	2.77	0.44	0.33	0.03	1.68	0.24	0.26	0.03
Shrubland	2.5	0.2	0.34	0.02	2.93	0.32	0.38	0.03	2.11	0.24	0.3	0.02

Table 2.2.3. Average area and proportion of total area of five land-cover types within the home ranges of independent juvenile vireos that did (*n* = 104) and did not survive the tracking period (*n* = 9), 2011-2014.

	All Juveniles				Did Not Survive				Survived			
Land Cover	Area (ha)	SE	Prop.	SE	Area (ha)	SE	Prop.	SE	Area (ha)	SE	Prop.	SE
Water/Wetland	7.84	2.18	0.05	0.01	15.22	14.69	0.03	0.02	4.93	1.71	0.03	0.008
Open/Developed	58.05	10.08	0.25	0.02	33.39	23	0.25	0.08	60.18	10.77	0.25	0.01
Mixed/Deciduous Forest	25.04	3.38	0.16	0.01	15.87	7.97	0.31	0.1	25.79	3.59	0.15	0.007
Evergreen Forest	55.58	8.78	0.29	0.02	25.22	17.13	0.23	0.06	60.52	9.61	0.32	0.01
Shrubland	49.33	7.29	0.25	0.01	24.31	17.12	0.18	0.03	51.49	7.77	0.25	0.01

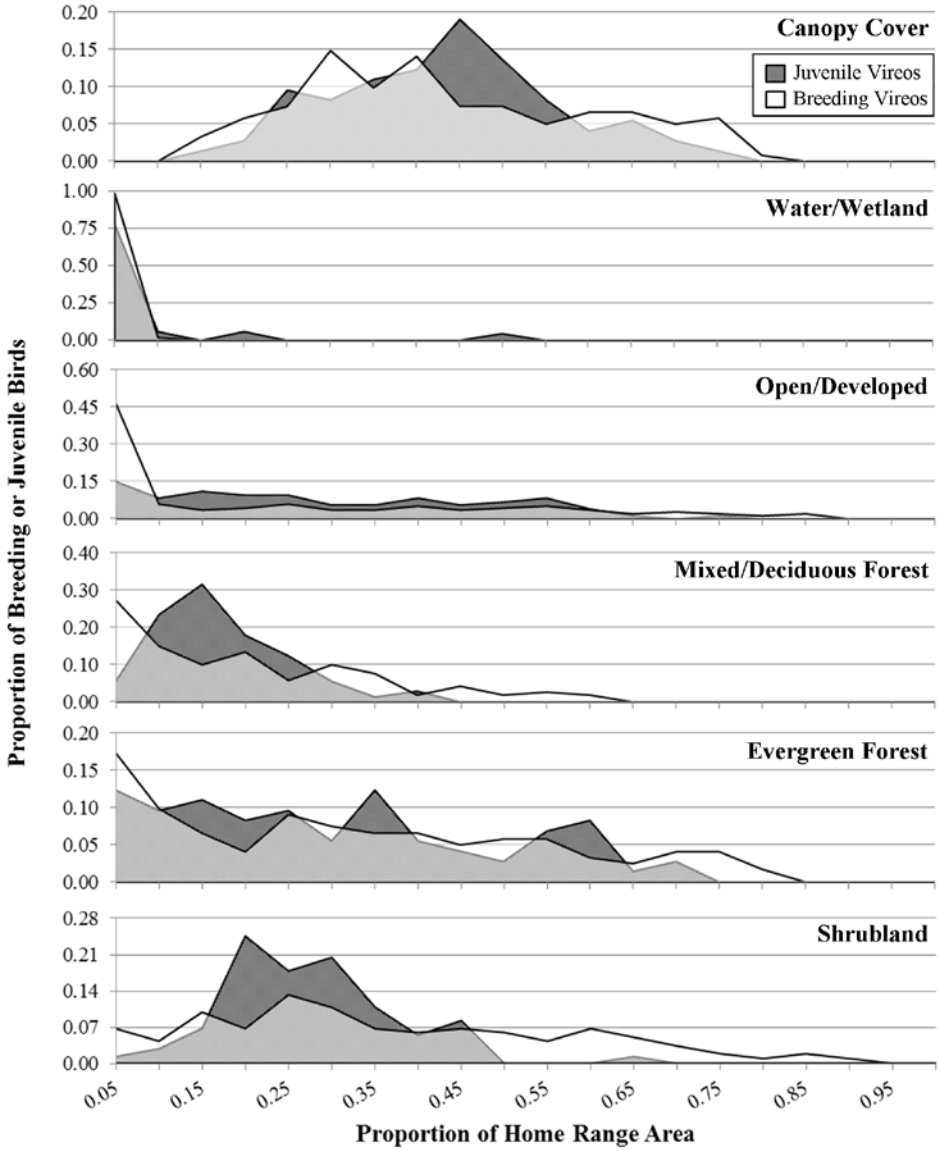

Figure 2.2.2. Canopy cover and land-cover composition of juvenile and breeding vireo home ranges in central Texas, 2011-2014.

Table 2.2.4 Success and associated land cover of black-capped vireo nests in central Texas, 2011-2014.

Land Cover	n_{total}	Proportion of Total Nests	$n_{successful}$	Percent Successful
Water/Wetland	2	0.03%	0	0%
Open/Developed	160	20.4%	60	37.5%
Mixed/Deciduous Forest	158	20.2%	50	31.6%
Evergreen Forest	210	26.8%	56	26.7%
Shrubland	254	32.4%	57	22.4%

Table 2.2.5 Characteristics of black-capped vireo nests across five land-cover types in central Texas, 2011-2014.

	Canopy Cover (%)		Distance to Edge (m)		Height (m)	
Land Cover	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Water/Wetland	86.00	5.00	6.16	2.00	1.08	0.16
Open/Developed	24.96	1.69	17.48	1.28	1.07	0.03
Mixed/Deciduous Forest	60.55	0.96	11.78	0.67	1.13	0.04
Evergreen Forest	58.40	1.46	17.13	1.16	1.21	0.03
Shrub	28.82	1.19	15.57	1.03	1.04	0.03

Table 2.2.6 Concentration of use (COU) by breeding (n = 121) and juvenile (n = 73) vireos across five land-cover types in central Texas, 2011-2014.

	Breeding Territory COU		Juvenile COU	
Land Cover	$\bar{x}$	SE	$\bar{x}$	SE
Water/Wetland	5.01	3.26	166.30	28.90
Open/Developed	132.33	13.14	321.78	30.83
Mixed/Deciduous Forest	191.38	13.14	380.85	33.46
Evergreen Forest	195.17	11.79	381.84	34.51
Shrubland	253.17	11.10	359.33	29.75

2.2.3.5 Vegetation Structure

From 2012-2014, we measured vegetation in 113 vireo territories with greater than or equal to 40 location points, totaling 671 vegetation plots. Additionally, we measured vegetation at 477 plots representing areas used by 62 juvenile vireos. Across all study sites, we observed similar patterns in vegetation characteristics in breeding territories and in areas used by juveniles (Table 2.2.8).

Comparing reproductive stage and use level together, we found that both breeding and juvenile vireo high-use areas of the home range had greater shrub cover ($F_{1,1144} = 19.63$, $P < 0.001$) as well as areas with greater foliage density between 0 and 1 m ($F_{1,1140} = 25.38$, $P < 0.001$; Table 2.2.8). Canopy cover differed between breeding and juvenile birds but not between strata; juveniles had home ranges with greater canopy cover than territorial birds ($F_{1,1144} = 48.70$, $P < 0.001$). Foliage density from 1 to 2 m differed between both breeding and juvenile birds and use strata; breeding birds used areas with greater foliage density from 1 to 2 m than juvenile birds ($F_{1,1144} = 5.05$, $P = 0.03$), but both breeding birds and juveniles concentrated use in areas of their home ranges with relatively high foliage density from 1-2 m ($F_{1,1144} = 26.82$, $P < 0.001$).

2.2.3.6 Correlates of Reproductive Success

Of pairs with home ranges represented by at least 40 location points, 52% ($n = 63$) successfully fledged at least one vireo. Cowbird control had a strong relationship with territory success ($\chi^2 = 36.35$, df = 2, $P < 0.001$). Even after accounting for cowbird control, however, territory success was also related to the area and proportion of land-cover types (area: $\chi^2 = 10.26$, df = 4, $P = 0.04$; proportion: $\chi^2 = 9.41$, df = 4, $P = 0.05$; Table 2.2.2). *Post hoc* tests, however, found no specific differences in the amount (area or proportion) of individual land-cover types between successful and unsuccessful territories.

Territory success was not related to any measure of vegetation structure within the home range (canopy: $\chi^2 = 0.04$, df = 1, $P = 0.83$; shrub: $\chi^2 = 1.91$, df = 1, $P = 0.17$; foliage density 0-1 m: $\chi^2 = 2.40$, df = 1, $P = 0.12$; foliage density 1-2 m: $\chi^2 = 0.07$, df = 1, $P = 0.79$), even when considering differences between use-strata (canopy: $\chi^2 = 3.21$, df = 2, $P = 0.20$; shrub: $\chi^2 = 1.74$, df = 2, $P = 0.42$; foliage density 0-1 m: $\chi^2 = 2.45$, df = 2, $P = 0.29$; foliage density 1-2 m: $\chi^2 = 0.001$, df = 2, $P = 0.99$). Territory success was, however, affected by interactions between the level of cowbird control and both canopy cover ($\chi^2 = 6.60$, df = 2, $P = 0.04$) and shrub cover ($\chi^2 = 6.23$, df = 2, $P = 0.04$). The effect of canopy cover on territory success varied between areas with moderate levels of cowbird control and those with none ($\chi^2 = 6.73$, df = 1, $P = 0.03$). At sites with moderate cowbird control, successful territories had less canopy cover than territories which failed to fledge any young ($\bar{x}$successful = 0.25 ± 0.02; $\bar{x}$failed = 0.29 ± 0.02). Successful territories in areas without cowbird control, however, had more canopy cover than unsuccessful territories ($\bar{x}$successful = 0.31 + 0.02; $\bar{x}$failed = 0.27 ± 0.01). Territories in areas without cowbird control were also more likely to successfully fledge young when they contained more shrub cover ($\bar{x}$successful = 0.62 + 0.02; $\bar{x}$failed = 0.56 ± 0.02).

Of the 784 nests we monitored, only 28.3% ($n = 223$) were successful. The success of individual nests was not related to the nearby canopy cover ($\chi^2 = 0.57$, df = 1, $P = 0.45$), nest height ($\chi^2 = 0.001$, df = 1, $P = 0.97$), or distance from the nest to the nearest patch edge ($\chi^2 = 0.33$, df = 1, $P = 0.56$). Nest success nearly differed between land-cover types ($\chi^2 = 8.98$, df = 4, $P = 0.06$; Table 2.2.4) and there was a significant interaction with the degree of cowbird control ($\chi^2 = 24.84$, df = 7, $P < 0.001$). In areas with moderate cowbird control, nest success was greater in evergreen forests than in mixed forests ($z = 1.98$, $P = 0.05$) or in shrublands ($z = 2.72$, $P = 0.01$). At sites with no cowbird control, nests in open areas were more likely to succeed than nests in forests (evergreen: $z = 4.46$, $P < 0.001$; mixed/deciduous: $z = 2.19$, $P = 0.03$) and shrublands ($z = 4.03$, $P < 0.001$); nest success was also greater in mixed forests than in evergreen forests ($z = 2.43$, $P = 0.02$).

Table 2.2.7. Means and standard errors of unstandardized maximum likelihood coefficients of juvenile and breeding vireo resource utilization functions.

	Juveniles			Breeding		
Habitat Measure	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE
Canopy	72	3.8E-04	2.1E-04	121	-6.9E-05	0.001
Water/Wetland	37	-0.02	0.09	8	-0.26	0.29
Open/Developed	71	-0.12	0.07	69	0.06	0.09
Mixed/Deciduous Forest	72	-0.11	0.07	103	0.26	0.11
Evergreen Forest	69	-0.10	0.07	106	0.33	0.12
Shrubland	72	-0.12	0.06	120	0.20	0.09

Table 2.2.8. Structural characteristics of vegetation in breeding and juvenile vireo home ranges in central Texas, 2011-2014.

		Canopy		Shrub		Foliage Density (0-1 m)		Foliage Density (1-2 m)	
	n	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Juveniles									
High Use	233	0.40	0.02	0.66	0.02	0.48	0.02	0.44	0.02
Low Use	244	0.37	0.02	0.59	0.02	0.41	0.02	0.37	0.02
Breeding Birds									
High Use	219	0.28	0.01	0.65	0.01	0.51	0.02	0.48	0.02
Moderate Use	226	0.29	0.01	0.62	0.02	0.48	0.02	0.44	0.01
Low Use	226	0.28	0.02	0.55	0.02	0.39	0.01	0.36	0.01

2.2.3.7 Correlates of Juvenile Survival

Excluding birds that immediately moved beyond our search area or whose transmitters malfunctioned shortly after attachment, we tracked 113 recently fledged, independent black-capped vireos during the pre-migration periods of 2012, 2013, and 2014. Excluding transmitters on birds that were lost immediately and one transmitter that obviously malfunctioned (failed almost immediately upon release), the transmitters lasted on average 17 days. The longest we were able to track a vireo was 40 days. Nine birds died during tracking.

Based on observations of tracked juveniles, we calculated daily survival probabilities (Kaplan and Meier 1958) and found that juvenile vireos had a 91.3% chance of surviving two weeks or more of independence (Figure 2.2.3). Juvenile survival was not correlated with total home range size (Cox Proportional Hazards Regression, Wald $\chi^2 = 0.83$, df = 1, $P = 0.36$) or with the area of individual land-cover classes (Wald $\chi^2 = 3.47$, df = 5, $P = 0.63$). However, survival was positively related to the proportion of mixed deciduous forest (Wald $\chi^2 = 11.02$, df = 1, $P < 0.001$) in the juvenile's home range and negatively related to the proportion of shrub therein (Wald $\chi^2 = 4.96$, df = 1, $P = 0.03$; Table 2.2.3).

2.2.4 Discussion

Across a diversity of wildlife taxa, researchers recognize numerous potential tradeoffs in the selection of an optimal breeding location that consider successful reproduction, adult survival, and survival of dependent young (Pianka 1976). Despite acknowledging these tradeoffs, it is

often difficult to find habitat characteristics that are good predictors of breeding success, particularly for birds (Chalfoun and Schmidt 2012). We propose that, for some species, survival of independent young may also shape selection of breeding habitat and may help explain some apparent discrepancies between the selection of breeding locations and ultimate reproductive success. Tradeoffs between breeding success and independent juvenile survival may exist when habitat features benefit either success or survival but not both (Streby et al. 2014a, 2014b).

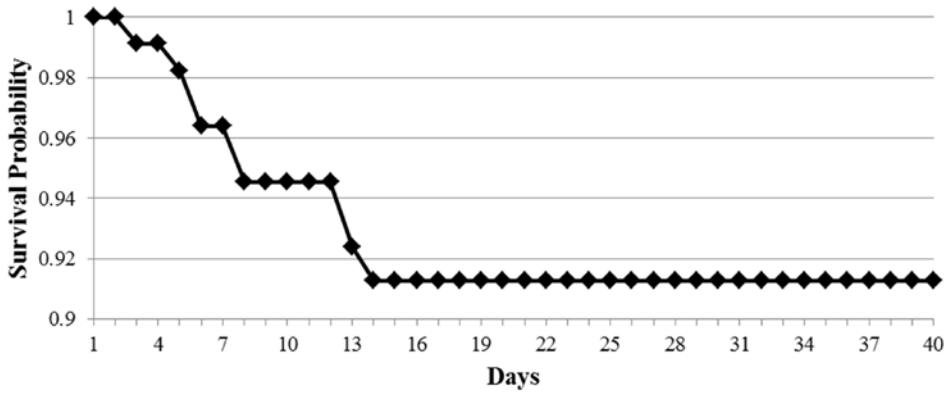

Figure 2.2.3 Post-independence daily survival probabilities of juvenile vireos across central Texas from 2012-2014.

Independent juveniles may face periods of high mortality risk before they reach reproductive age, a risk that for some species might be mediated by selection of breeding habitat. Among species that provide no parental care, for example, juveniles are highly vulnerable when leaving the nest and nest site selection may have a great impact on juvenile survival (e.g., sea turtles; Whelan and Wyneken 2007). For migratory avian taxa, juveniles face a stressful migration shortly after independence that is thought to be a period of high mortality (Sillett and Holmes 2002), and habitat that enables juveniles to adequately prepare for their first migration may benefit overall juvenile survival. Adult migratory songbirds may improve their genetic legacy by selecting breeding areas that include or are adjacent to habitat that will provide their independent offspring with cover from predators to improve immediate survival and abundant food resources to better prepare them for stressful migration.

2.2.4.1 Breeding and Juvenile Habitat Selection and Use

Breeding habitat selection must optimize a variety of factors to maximize an individual's lifetime reproductive success. Breeding birds specifically must ultimately balance numerous factors that influence nest success, survival of young fledglings, and survival of independent juveniles as well as themselves. Home ranges of breeding and juvenile vireos, although similar in many characteristics, differed in several aspects of land-cover composition and vegetation structure, indicating a complicated relationship between territory and nest site selection and juvenile survival. It is also possible that, due to habitat loss, vireos have only limited availability of optimal breeding sites and this might be particularly true at breeding sites off of Fort Hood that

are relatively small and isolated. First time breeders arrive on the breeding grounds later than older birds and, if optimal habitat is limited, may be forced to choose territories that do not match juvenile habitat needs.

2.2.4.1.1 Tradeoffs in Nest Success

Similarities in breeding and juvenile home ranges that were not in congruence with higher nest success may exist as a tradeoff to improve juvenile survival. Both juvenile and breeding vireos concentrated use in deciduous and evergreen forests, perhaps due to the association between forest land cover and the presence of canopy cover. Juveniles with greater proportions of mixed forest were more likely to survive and, matching our predictions, juveniles also used areas with more canopy cover than breeding birds. Although we also predicted that breeding birds would avoid areas with canopy cover, high use areas within breeding territories had greater canopy cover than low use areas in general. Additionally, in areas with some cowbird control, neither nest success nor territory success were affected by canopy cover or the presence of forest. In accordance with our predictions, however, territories and nests at sites without cowbird control, and thus with greater risk of parasitism, were more successful in areas with less canopy cover. Although canopy provides perches for cowbirds and increases rates of parasitism among some host species (Hauber and Russo 2000), abundant canopy may also provide cover for nests (Fiorini et al. 2012, Vasseur and Leberg 2015). Thus, for breeding vireos, selection against canopy cover may be relatively weak in areas with less parasitism risk, allowing adult birds to select areas that better reflect juvenile habitat requirements.

Selection for breeding territory characteristics that do not appear to benefit either nest success or independent juvenile survival may instead reflect habitat features that optimize the survival of adults or of very young dependent fledglings. Both breeding and independent juvenile vireos in central Texas used shrublands more than other land-cover types and open areas relatively infrequently, a result that closely followed expectations set by previous research (Grzybowski 1995). These habitat associations, however, proved detrimental to nest and territory success as well as independent juvenile survival. Thus, shrub cover might present an alternative tradeoff with either adult survival or survival of young dependent fledglings. We did not track habitat use by young fledglings or family groups, and so the selective forces behind use of shrublands are difficult to tease out from our data. We suspect, however, that fledgling survival may benefit from habitat with shrubby understory based on research of other songbird species (e.g., King et al. 2006).

2.2.4.1.2 Juvenile Habitat Selection

Although adults must select breeding habitats that present multiple tradeoffs in reproductive success that might vary across their breeding range, juveniles can choose from available habitats to optimize only their own survival. We predicted that juveniles would focus on particular habitat features that provide the right balance of cover and food availability. Juvenile vireos selected habitats with a relatively narrow range of shrubland availability compared with breeding adults and, while low levels of shrubland may not provide enough cover, landscapes dominated by shrublands alone may not have enough food resources to support birds preparing for migration. Similarly, juvenile home ranges contained a narrower range of forest proportion and

canopy cover than breeding territories. Home ranges dominated by forested areas may not provide the understory vegetation for sufficient refuge from predators but some canopy cover may be necessary to supply juveniles with sufficient food availability. Additionally, older juveniles are less vulnerable to predation than young fledglings and may risk exposure in favor of finding additional food resources (Jenkins et al. 2013, Small et al. 2015). Independent juvenile Swainson's thrush (*Catharus ustulatus*) in Oregon selected habitats with abundant ants and beetles without regard to shrub cover (Jenkins et al. 2013). Similarly, independent juvenile grasshopper sparrows (*Ammodramus savannarum*) used relatively open areas with more bare ground and easier foraging opportunities compared with dependent fledglings that stayed in areas with more shrubby cover (Small et al. 2015). We observed no evidence of disproportionate use of wetlands by juvenile vireos across a broad range of central Texas although past research on Fort Hood indicated that juvenile vireos spent the most time in riparian habitats due to increased insect availability (Dittmar et al. 2014).

2.2.4.1.3 Habitat Prospecting by Juveniles

We assumed that juvenile vireo habitat use was driven by survival pressures such as the availability of food and cover from predators, an assumption bolstered by the results of previous juvenile habitat selection observations on Fort Hood (Dittmar et al. 2014). For many juvenile birds, however, the post-breeding period may also be used to prospect for potential future breeding sites (Schjorring et al. 1999, Nicolaus et al. 2012). For some species, prospecting birds assess the quality of a potential breeding site based on the success of local breeding pairs (Part and Doligez 2003). Although no studies have evaluated black-capped vireos for post-breeding season prospecting behavior, we often observed juvenile vireos in association with adults and other hatch year birds. Additionally, there is evidence that first time breeders are thought to be attracted to conspecific vocalizations after spring migration during the early breeding season (Ward and Schlossberg 2004). This tendency toward conspecific attraction suggests that our observations of juvenile habitat use may reflect a need to balance survival with potential future breeding success. This may also partially explain why we observed similarity between juvenile and breeding habitat selection of shrub and forest land-cover types.

2.2.4.2 Juvenile Survival

We observed high survival of juvenile vireos during the post-breeding/pre-migration period, making associations between habitat selection and juvenile survival difficult to interpret. For many migratory songbirds, much of post-independence juvenile mortality may occur during migration itself (Sillett and Holmes 2002). Thus, it is not surprising that survival might be relatively high during the pre-migration period, and this pattern has been observed in other neotropical migrants (Vitz 2008, Whittaker and Marzluff 2009, Jenkins et al. 2013, Streby et al. 2015). Our study of juvenile mortality was limited by the lifespan of small transmitter batteries, however, and it is possible we were simply unable to track juvenile vireos long enough to capture many pre-migration mortality events. With the advent of new technologies, longer tracking periods would enable researchers to better define overall juvenile mortality as well as associate patterns of survival with land-cover availability and use.

2.2.4.3 Management Implications

Management guidelines for vireo breeding habitat maintenance and restoration often focus on the provision of moderate shrub cover needed to provide sufficient nesting sites and nest cover (e.g., Reemts and Cimprich 2014). Restoration guidelines pay little attention, however, to the provision of optimal habitat requirements for young vireos after they have become independent from their parents. To most benefit this endangered species, land managers should conserve and even restore habitats vital for reproduction and survival throughout the annual cycle, not just during periods of active breeding.

Our results suggest that, in addition to low vegetative cover, abundant canopy cover may be the most important structural feature relevant to juvenile habitat selection. Deciduous and mixed deciduous and evergreen forest may provide habitat with both good understory cover and high canopy, thus providing both sufficient food availability and cover from predators. Although vireo reproductive success was inversely related to the availability of evergreen forest in territories, breeding sites that provide nearby or adjacent forested areas with abundant canopy cover may improve juvenile survival and aid in the establishment of larger breeding populations.

2.2.4.4 What is Breeding Habitat?

For all wildlife species, the ideal breeding habitat is based on a combination of factors that contribute to the successful passing on of the parent's genes. Although wildlife researchers often characterize breeding habitat based on areas used by actively breeding individuals, the availability of habitats used by family groups or independent juveniles in the post-breeding season might be just as vital for offspring survival. In fact, sites that provide good habitat for nesting or denning, but do not also offer sufficient habitat for dependent and newly independent young, may act as ecological traps (see Dwernychuk and Boag 1972). The redefinition of breeding habitat to include these additional habitat considerations would expand the requirements on land managers and stake-holders seeking to provide quality breeding habitat for a given wildlife species but might ultimately improve breeding success, juvenile survival, and population persistence (Battin 2004).

2.3 Reticence or vigilance at the nest: a cruel bind for the endangered black-capped vireo[5]

2.3.1 Introduction

Animal communication is critical for locating conspecifics, establishing territories, obtaining a mate, and coordinating social activities (Bradbury and Vehrencamp 2011). Breeding birds in particular use songs and calls to attract mates and repel rivals (Catchpole 1987, Kroodsma and Byers 1991), and song quality can directly contribute to mating success as well as mate quality (Nowicki and Searcy 2005). Additionally, vocalizations of a particular frequency or quality, such as scold calls, may attract neighboring birds for group defense or social learning (Cornell et al. 2012). Frequent or loud vocalizations near the nest, however, may also cue nest predators or brood parasites to the location of the caller's nest. Avian brood parasites rely on pairs of other breeding birds to incubate their eggs and raise their young, often inducing reproductive and energetic costs on their hosts (Rothstein 1975, Payne 1977). Thus, although defense strategies could favor increased communication between pairs, risk of predation or parasitism might induce alternative selective pressures on vocalization near the nest. Nesting birds might benefit from secretive behavior with fewer vocalizations in proximity to their developing clutch (Skutch 1976, Marzluff and Balda 1992). The need to remain attentive and coordinated without attracting undo attention puts nesting birds in a cruel bind. Natural selection presumably solves this bind by considering the combined influence of communication on parental actions that benefit the development of their young while enabling detection and appropriate responses to the threats of parasites and predators.

The strength and direction of selection on vocalization frequency during the breeding season may depend on a variety of community features, including the predator guild or the presence of brood parasites such as the brown-headed cowbird (cowbird; *Molothrus ater*). Avian predators and brood parasites cue in to auditory and other behavioral signals to locate nests (McLean et al. 1986, Uyehara and Narins 1995, Clotfelter 1998, Banks and Martin 2001, Haff and Magrath 2011), whereas many mammalian or reptilian nest predators are more reliant on olfaction (Conover 2007). For example, loud vocalizations by American robins (*Turdus migratorius*) during the breeding season attract crows (McLean et al. 1986) and begging calls by nestlings attract a wide variety of avian predators (Skutch 1976, McDonald et al. 2009, Haff and Magrath 2011). In a comparison of four songbird species, Banks and Martin (2001) also found that the frequency of cowbird parasitism increased among species with males that were more vocal and active near their nests during the nest-building period. By contrast, some species may benefit from remaining vigilant and actively defensive of their nests. Bell's vireos (*Vireo bellii*) that vocalized more during nest building and incubation were parasitized less by cowbirds than relatively quiet pairs (least Bell's vireo, *V. b. pusillus*: Sharp and Kus 2006; Arizona Bell's vireo, *V. b. arizonae*: Steckler and Conway 2012).

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[5]This work was submitted as: Walker, L. E., and J. M. Marzluff. In Review. Reticence or vigilance at the nest: a cruel bind for the endangered black-capped vireo. *Avian Conservation and Ecology*.

A temporal shift in vocalizations could allow for a combination of behavioral adaptations that would accommodate both sexual selection and natural selection to reduce parasitism or predation risk. Cowbirds present a particularly challenging and unique threat to nesting songbirds because the risk they present at nests may shift throughout the nesting cycle. Cowbirds often locate nests while the host is building and generally return to parasitize the nest early in the morning during the host's laying stage (Scott 1991, Davies 2000, Banks and Martin 2001). In later nesting stages, however, cowbirds may also be nest predators, removing eggs or nestlings from unparasitized host nests to encourage the parents to re-nest (Arcese et al. 1996, Dubina and Peer 2013). Thus, depending on the local suite of brood parasites and nest predators, nesting songbirds may minimize parasitism or predation risk through stage-specific vocalization behaviors (e.g., being relatively secretive during building but vigilant in nest defense in laying or incubation stages). Likewise, many songbirds are able to adjust vocalizations to minimize interference from singing males of other species (Ficken et al. 1974, Barclay et al. 1985, Lougheed and Handford 1989) or in response to increases in urban noise (Warren et al. 2006, Fuller et al. 2007), and plasticity in the timing of social behaviors may also help some birds avoid temporally-specific threats (Ghalambor and Martin 2000, Eggers et al. 2005). For example, in areas with high predator presence, Siberian jays (*Perisoreus infaustus*) visited their nests less frequently during the afternoon, when their nest predators were more active, and compensated by making more frequent visits when predators were less active (Eggers et al. 2005).

The black-capped vireo is threatened by habitat loss as well as high rates of brood parasitism by cowbirds (Ratzlaff 1987). Management of vireo recovery to date has largely focused on the removal of cowbirds from vireo breeding habitat, creating several large, managed populations, including the Fort Hood Military Installation (Fort Hood) in central Texas (Kostecke et al. 2005, Cimprich and Cimprich 2015). Nest parasitism, however, continues to significantly contribute to the ongoing low reproductive rate of vireos in many areas without cowbird control (Walker 2015). Vireo nests are also susceptible to a broad suite of nest predators across the breeding range (Stake and Cavanagh 2001, Stake and Cimprich 2003, Conkling et al. 2012). Although the most frequent predators are Texas rat snakes (*Elaphe obsoleta lindheimeri)* and fire ants (*Solenopsis* spp.), avian nest predators are also common and include western scrub-jays (*Aphelocoma californica*) and hawks (*Accipiter* spp., *Buteo* spp.), as well as cowbirds (Stake and Cavanagh 2001, Stake and Cimprich 2003, Conkling et al. 2012). In contrast to other nest predators in central Texas, however, cowbirds often only partially depredate vireo nests, leaving one or more eggs or nestlings in the nest, and do not always cause nest failure (Stake and Cavanaugh 2001, Stake and Cimprich 2003). Thus, vireo populations on and around Fort Hood provide a unique opportunity to investigate vocalization behavior at the nest across a gradient of parasitism risk, as they weigh potential trade-offs with a relatively stable risk of predation.

We investigated the vocal response of vireos to predation and parasitism risk across different nesting stages and times of day using two hypotheses: the predator-attraction hypothesis (Aviles et al. 2006, Steckler and Conway 2012) and the parasite-assessment hypothesis (Forsman and Martin 2009, Steckler and Conway 2012). The predator-attraction hypothesis assumes that nest predators use auditory cues to locate nests and that brood parasites use information on perceived predation risk to make decisions about which nests to parasitize (Aviles et al. 2006, Steckler and Conway 2012). This hypothesis predicts that individuals who vocalize frequently near their

nests should have a greater probability of incurring nest predation and a lower probability of brood parasitism (Aviles et al. 2006, Steckler and Conway 2012). In contrast to the predator-attraction hypothesis, the parasite-assessment hypothesis predicts that nesting individuals perceive parasitism risk based on local parasite densities and that host vocalization rate will be inversely correlated with local parasite density (Forsman and Martin 2009, Steckler and Conway 2012).

We expected the impact of parental vocalizations on vireo nest fate to vary throughout the nesting cycle. Nest predation, in general, is not likely to be affected by vocalizations in the building stage, but selection to reduce predation pressure may affect vocalization rate in later nesting stages, particularly as the threat cowbirds pose at vireo nests shifts from brood parasite to nest predator (Arcese et al. 1996, Stake and Cavanaugh 2001, Stake and Cimprich 2003, Conkling et al. 2012, Dubina and Peer 2013). We expected that vireos would lower their risk of brood parasitism by being relatively quiet and secretive during the building and laying stages, especially in areas with high cowbird densities. We also hypothesized that vireos breeding in areas where cowbirds are common may make fewer nesting vocalizations in the morning and more in the afternoon or evening relative to vireos breeding in areas with lower parasitism risk.

2.3.2 Methods

2.3.2.1 Study Sites

We chose five study sites in central Texas on Fort Hood and in nearby areas to the west that represent a range of cowbird control efforts and offer vireos a range of tradeoffs relevant to nest communication. The habitat within the Hill Country of central Texas is semi-arid and largely characterized by shortgrass communities and cattle rangeland. Many ungrazed areas that were once grass or deciduous shrublands are now woodlands due to fire suppression and encroachment by the native evergreen Ashe juniper (*Juniperus ashei*). The San Saba study site is comprised of portions of two neighboring private ranches southwest of San Saba, Texas, nearly 100 km west of Fort Hood (Figure 2.1.1). Moderate cowbird control efforts began at San Saba in 2014, but cowbirds remained common on the site throughout this study. Colorado Bend State Park is located almost 60 km west of Fort Hood along the west side of the Colorado River in San Saba County, Texas (Figure 2.1.1). The study site, along the northeastern boundary of the park, consists of a mix of grassland and patchy juniper and live oak woodlands (*Quercus fusiformis*). During the course of this study, there was no effective cowbird control in the state park except for minimal trapping efforts in 2014.

On Fort Hood, we chose three study sites that represented a range of cowbird control: Taylor Valley, West Range, and Maxdale (Figure 2.1.1). West Range, dominated by mixed juniper and deciduous woodlands, had comprehensive cowbird control until 2006 when Fort Hood began an experimental cessation of cowbird control in the northwest area of the base. Taylor Valley is located on the eastern side of the installation where cowbirds have been continually controlled via shooting and trapping since 1991. Maxdale is located near the southern edge of the Fort Hood installation, and although cowbirds are removed from the site when they are reported, there

are no nearby traps and cowbird presence remains high. A mix of grasslands and deciduous woodlands characterizes Taylor Valley and Maxdale.

2.3.2.2 Cowbird Density Estimation

Cowbird density may be reliably estimated using point counts (Miles and Buehler 2000). Thus, to assess the relative level of cowbird presence, we conducted 10-minute, variable distance point counts across each study site. We based the number of point count locations roughly on the relative area of each site and spaced count locations at least 200 m apart. We conducted counts at seven locations on Taylor Valley, nine on Maxdale, five on West Range, five on San Saba, and 13 on Colorado Bend. At each location, we conducted three rounds of 10-minute counts in 2013 and three in 2014, noting the distance to any cowbirds we detected. Using our point-count observations, we conducted detection-dependent density modelling using the packages "Distance" and "mrds" in R v.3.1.1 (Laake et al. 2014, Miller 2014, R Core Team 2014). We compared detection models with half-normal or hazard-rate key functions, cosine or simple polynomial adjustment functions with an optimized number of adjustment terms, and variations in data truncation using Akaike's Information Criterion (AIC; Akaike 1974, Table 2.3.1). We compared models with no truncation of the data, left truncation only, right truncation only, and both right and left data truncation. In several cases, adjustment functions did not improve the model. The best detection model estimated cowbird density using the hazard-rate key function, no adjustment terms, and both left and right truncation of the data (Table 2.3.1). In total, we compared 19 detection models using AIC (Akaike's Information Criterion; Akaike 1974) and model weights (Table 2.3.1).

After evaluating the best model (Table 2.3.1) for goodness of fit (Kolmogorov-Smirnov = 0.09, $P = 0.39$), we estimated cowbird density on each study site (Table 2.3.2). The standard errors for cowbird density estimates were quite large, however, and at best these estimates gave us an indication of the relative level of cowbird abundance. Thus, based on our knowledge of cowbird control efforts and our estimates of relative cowbird abundance across our study sites, we classified sites into two categories of relative cowbird density (Table 2.3.2). We placed Taylor Valley in the low cowbird density category; the other four sites had high cowbird density (Table 2.3.2).

Table 2.3.1 Detection models used to evaluate cowbird density at five black-capped vireo breeding sites, comparing half-normal or hazard-rate key functions, cosine or simple polynomial adjustment functions, and variations in data truncation (truncation distances are in km).

Cowbird Detection Model	AIC	ΔAIC	w_i
Hazard-Rate, No adjustments, Left Truncation at 0.01, Right Truncation at 0.091	-558.64	0.00	0.37
Hazard-Rate, No adjustments, Left Truncation at 0.01, Right Truncation at 0.097	-558.39	0.25	0.32
Hazard-Rate, No adjustments, Left Truncation at 0.01, Right Truncation at 0.087	-557.80	0.83	0.24
Half-Normal, Cosine (2) adjustments, Left Truncation at 0.01, Right Truncation at 0.087	-552.60	6.04	0.02
Half-Normal, No adjustments, Left Truncation at 0.01, Right Truncation at 0.087	-552.24	6.40	0.02
Half-Normal, No adjustments, Left Truncation at 0.01, Right Truncation at 0.091	-551.97	6.67	0.01
Half-Normal, No adjustments, Left Truncation at 0.01, Right Truncation at 0.091	-551.97	6.67	0.01
Hazard-Rate, No adjustments, No Left Truncation, Right Truncation at 0.091	-550.00	8.64	0.005
Half-Normal, No adjustments, Left Truncation at 0.01, Right Truncation at 0.097	-549.92	8.72	0.005
Hazard-Rate, No adjustments, No Left Truncation, Right Truncation at 0.097	-549.71	8.93	0.004
Half-Normal, Cosine (2) adjustments, No Left Truncation, Right Truncation at 0.091	-542.09	16.54	< 0.001
Half-Normal, No adjustments, No Left Truncation, Right Truncation at 0.091	-540.90	17.74	< 0.001
Half-Normal, No adjustments, No Left Truncation, Right Truncation at 0.097	-539.39	19.24	< 0.001
Hazard-Rate, No adjustments, Left Truncation at 0.01, No Right Truncation	-536.64	22.00	< 0.001
Hazard-Rate, No adjustments, No Left Truncation, No Right Truncation	-527.91	30.72	< 0.001
Half-Normal, Cosine (2) adjustments, Left Truncation at 0.01, No Right Truncation	-520.94	37.70	< 0.001
Half-Normal, Cosine (2) adjustments, No Left Truncation, No Right Truncation	-512.09	46.54	< 0.001
Half-Normal, No adjustments, Left Truncation at 0.01, No Right Truncation	-487.62	71.02	< 0.001
Half-Normal, No adjustments, No Left Truncation, No Right Truncation	-480.27	78.37	< 0.001

Table 2.3.2. Cowbird density (birds/km^2), level of cowbird control, and categorical cowbird abundance at black-capped vireo breeding sites in central Texas.

	Cowbird Density		Level of Cowbird Control	Categorical Cowbird Abundance
Site	Estimate	SE		
Colorado Bend	69.47	15.99	None	High
Maxdale	89.79	18.63	Moderate	High
San Saba	57.04	20.63	None	High
Taylor Valley	10.19	4.97	Complete	Low
West Range	66.55	20.82	None	High

2.3.2.3 Nest Monitoring

We monitored black-capped vireos at each study site in 2013 and 2014. We visited study sites three times a week throughout the breeding season, from late March through mid-July, and searched for territorial males. Upon identifying territories, we visited each territory two or three times a week to identify nesting behavior and locate nests. We visited known nest locations every three to four days until the nest either failed or fledged. During each visit, we recorded the number of host eggs and cowbird eggs (if present) and the number and approximate age of nestlings.

2.3.2.4 Audio Recordings

2.3.2.4.1 Nest Recordings and Site Selection

In central Texas, cowbirds may parasitize vireo nests throughout the breeding season; however, the probability of brood parasitism is relatively low for nests initiated in the first few weeks of April compared with nests initiated in later weeks (Boves et al. 2014). Thus, to avoid biases in the likelihood of nest parasitism, we recorded vireo vocalizations at nests between sunrise and sunset from mid-April through late June during multiple nest stages: building, egg-laying, and early incubation (days 1-4 of incubation). Parasitism events typically occur during the egg-laying or early incubation stages, so to avoid unnecessary disruption of the nesting cycle, we did not record vocalizations at nests during later periods of vireo incubation or after eggs hatched. We also avoided recording on days with rain or high wind. Minimizing disturbance of the nest, we attached a Sennheiser condenser microphone to a branch at the approximate height of the nest three to five meters away and, using a Sony digital voice recorder, recorded vocalizations for the battery life of the recorder (about 23 hours). We concealed recorders in vegetation below the microphone.

We selected nests to record at random within each site. We located most nests we recorded during the building stage (88%, n = 46) but 12% (n = 6) were located during egg-laying. Taylor Valley was the only site with low cowbird density, and we recorded nests at this site in both

2013 and 2014 (n = 17). In 2013, we also conducted nest recordings at Maxdale (n = 10) and Colorado Bend (n = 11) and, in 2014, nests at West Range (n = 8) and San Saba (n = 6).

2.3.2.4.2 Vocalization Rates

To calculate vocalization rates, we divided each day's recording into morning (sunrise to 9 am), midday (noon to 3 pm), and evening (6 pm to sunset) time periods and randomly selected one 30 minute section from each time period. We then counted the number of male song vocalizations in each 30-minute section, categorizing the singer's approximate distance from the nest as "near" (within approximately 15 m of the nest) or "far" (greater than 15 m from the nest) based on the relative volume of vocalizations, and totaled "near nest" vocalizations. Vocalizations distant from the nest are unlikely to cue a cowbird or predator to the nest location and, in some cases, may represent a vocalization from a neighboring male. Therefore, we discarded vocalizations determined to be "far from the nest" and they were not included in further analyses. A single observer listened to all recordings and categorized all vocalization distances. Across nests, we also calculated average vocalization rates (mean ± SE songs/minute).

2.3.2.4.3 Analyses

To test the predator-attraction (Aviles et al. 2006, Steckler and Conway 2012) and parasite-assessment hypotheses (Forsman and Martin 2009, Steckler and Conway 2012), we conducted three analyses of "near nest" vocalizations using poisson log-linear models. To assess the predator-attraction hypothesis, we compared models defined *a priori* considering combinations of nest stage, time of day, and (1) depredation fate (whether the nest was eventually depredated or not) and (2) parasitism fate (whether the nest was eventually parasitized or not). To analyze the parasite-assessment hypothesis, we compared models considering nest stage, time of day, and (3) estimated cowbird density.

To explain observed vocalizations at vireo nests, we compared seven models in each of three analyses including a null model, a model considering only nest stage, time of day, and their interaction, and additional analysis-specific models that considered either parasitism fate, depredation fate, or cowbird density. We ranked candidate models defined *a priori* using AIC_c (AIC adjusted for small sample sizes; Akaike 1974) and assigned a relative probability to each model (Burnham and Anderson 1998). We compared model weights (w_i), which measure relative support for a particular model within the model set, and considered a model to be competitive if its ΔAIC_c was less than 2 (Burnham and Anderson 1998).

After defining our best model for each analysis, we conducted *post hoc* tests of factor interactions to determine the relationship between nest stage, time of day, and measures of nest fate and cowbird density. All analyses were conducted in R v.3.1.1 (R Core Team 2014); we used the packages "AICcmodavg" (Mazerolle 2015) to calculate AIC_c (Akaike 1974) and "phia" for all *post hoc* evaluations (De Rosario-Martinez 2015).

2.3.3 Results

We recorded vocalizations at 52 nests during the 2013 and 2014 seasons (Table 2.3.3). Fifteen nests (28.8%) were eventually parasitized and 19 (36.5%) were depredated. Four parasitized nests (26.7%) were also eventually depredated. On average, males at nests which were eventually parasitized and depredated were more vocal (1.13 + 0.56 songs/minute) than nests which were only depredated (0.59 + 0.17 songs/minute), only parasitized (0.59 + 0.14 songs/minute), or were neither depredated nor parasitized (0.62 + 0.12 songs/minute); but these differences were not significant ($F_{3,151} = 0.84$, $P = 0.47$).

Table 2.3.3. Male black-capped vireo vocalization rates (songs/minute) near nests in central Texas, 2013-2014. Standard errors are in parentheses.

	Nest Stage							
Time of Day	Building	*N*	Laying	*N*	Incubation	*N*	Total	*N*
Morning	0.75 (0.26)	23	0.67 (0.19)	18	0.65 (0.32)	10	0.70 (0.15)	51
MidDay	1.19 (0.19)	23	0.27 (0.08)	19	1.71 (0.82)	10	0.95 (0.19)	52
Evening	0.27 (0.09)	23	0.31 (0.21)	19	0.27 (0.15)	10	0.28 (0.09)	52
Total	0.73 (0.12)	69	0.41 (0.10)	56	0.88 (0.31)	30	0.64 (0.09)	155

2.3.3.1 Predator-attraction Hypothesis

2.3.3.1.1 Depredation Fate

Nests belonging to vocal males were more likely to be depredated than nests belonging to quiet males in general ($\chi^2 = 21.84$, $P < 0.001$) and in the early incubation stage ($\chi^2 = 31.29$, $P < 0.001$; Figure 2.3.1). Conversely, nests were less likely to be depredated when males vocalized more during building ($\chi^2 = 51.60$, $P < 0.001$) and in the laying stage ($\chi^2 = 45.72$, $P < 0.001$; Figure 2.3.1). Depredation was also most likely when males vocalized less in the evening ($\chi^2 = 54.27$, $P < 0.001$) and more during the middle of the day ($\chi^2 = 7.24$, $P = 0.01$; Figure 2.3.2). After comparing seven models relating vocalization rate to combinations of nest stage, time of day, and depredation fate, the best supported model included all main effects and two-way interactions (Tables 2.3.4 and 2.3.5); there were no other competitive models (Table 2.3.4).

2.3.3.1.2 Parasitism Fate

Near nest vocalizations by male vireos were not associated with risk of nest parasitism in general ($\chi^2 = 0.01$, $P = 0.94$), but relationships within specific nest stages and periods of the day were evident (Figure 2.3.2). During the laying period, eventual nest parasitism was associated with less frequent vocalizations ($\chi^2 = 96.61$, $P < 0.001$), and conversely, in the building and early incubation stages and during the midday parasitism was positively associated with male vocalizations (building: $\chi^2 = 29.76$, $P < 0.001$; incubation: $\chi^2 = 144.89$, $P < 0.001$; midday: $\chi^2 = 8.17$, $P = 0.01$; Figure 2.3.2). The best model of vocalization rate considering parasitism fate included all three main effects (nest stage, time of day, and parasitism fate) and all two-way interactions (Tables 2.3.6 and 2.3.7).

2.3.3.2 Parasite-assessment Hypothesis

2.3.3.2.1 Cowbird Density

Male vireos vocalized more at sites with high cowbird density in general ($\chi^2 = 78.20$, $P < 0.001$) and across most individual nest stages (building: $\chi^2 = 150.37$, $P < 0.001$; incubation: $\chi^2 = 101.28$, $P < 0.001$) and periods of the day (morning: $\chi^2 = 129.14$, $P < 0.001$; midday: $\chi^2 = 47.97$, $P < 0.001$; evening: $\chi^2 = 4.90$, $P = 0.03$; Figure 2.3.3). During the laying stage, however, male vireos were quieter in areas with relatively high cowbird densities (laying: $\chi^2 = 116.03$, $P < 0.001$; Figure 2.3.3). The best and only competitive model of "near nest" vocalizations considering cowbird density included all three main effects (nest stage, time of day, and level of cowbird density) as well as all two-way interactions (Tables 2.3.8 and 2.3.9).

2.3.3.2.2 Importance of Nest Stage and Time of Day

Nest stage, time of day, and their interaction were important in all analyses described above and better explained patterns in vireo vocalizations than depredation fate, parasitism fate, or cowbird density alone (Tables 2.3.4, 2.3.6, and 2.3.8). In the midday, male song rate at nests was greatest in the incubation and building stages and relatively low during laying (Table 2.3.3). During building and incubation, vocalization rates were lowest in the evening and highest in the midday. Song rates in the morning were moderate but significantly greater than in the evening and less than in midday. During the laying stage, "near nest" vocalizations were most frequent in the morning. These vocalization patterns in response to nest stage and time of day were consistent across all final models that tested the predator-attraction and parasite-assessment hypotheses (although χ^2 values varied between analyses, all $P < 0.001$).

Table 2.3.4. Models used to evaluate the predator-attraction hypothesis and the role of nest stage (Stage), time of day (Time), and depredation fate (Depr) on "near nest" vocalizations by male vireos.

Parameters	ΔAIC_c	w_i
Stage + Time + Depr + Stage*Time + Stage*Depr + Time*Depr	0.00[†]	1.00
Stage + Time + Depr + Stage*Time + Stage*Depr	69.23	< 0.001
Stage + Time + Depr + Stage*Time + Time*Depr	126.04	< 0.001
Stage + Time + Stage*Time	223.53	< 0.001
Stage + Time + Depr + Stage*Time	225.80	< 0.001
Depr	1409.56	< 0.001
(null)	1421.39	< 0.001

[†] $AIC_c = 4934.35$

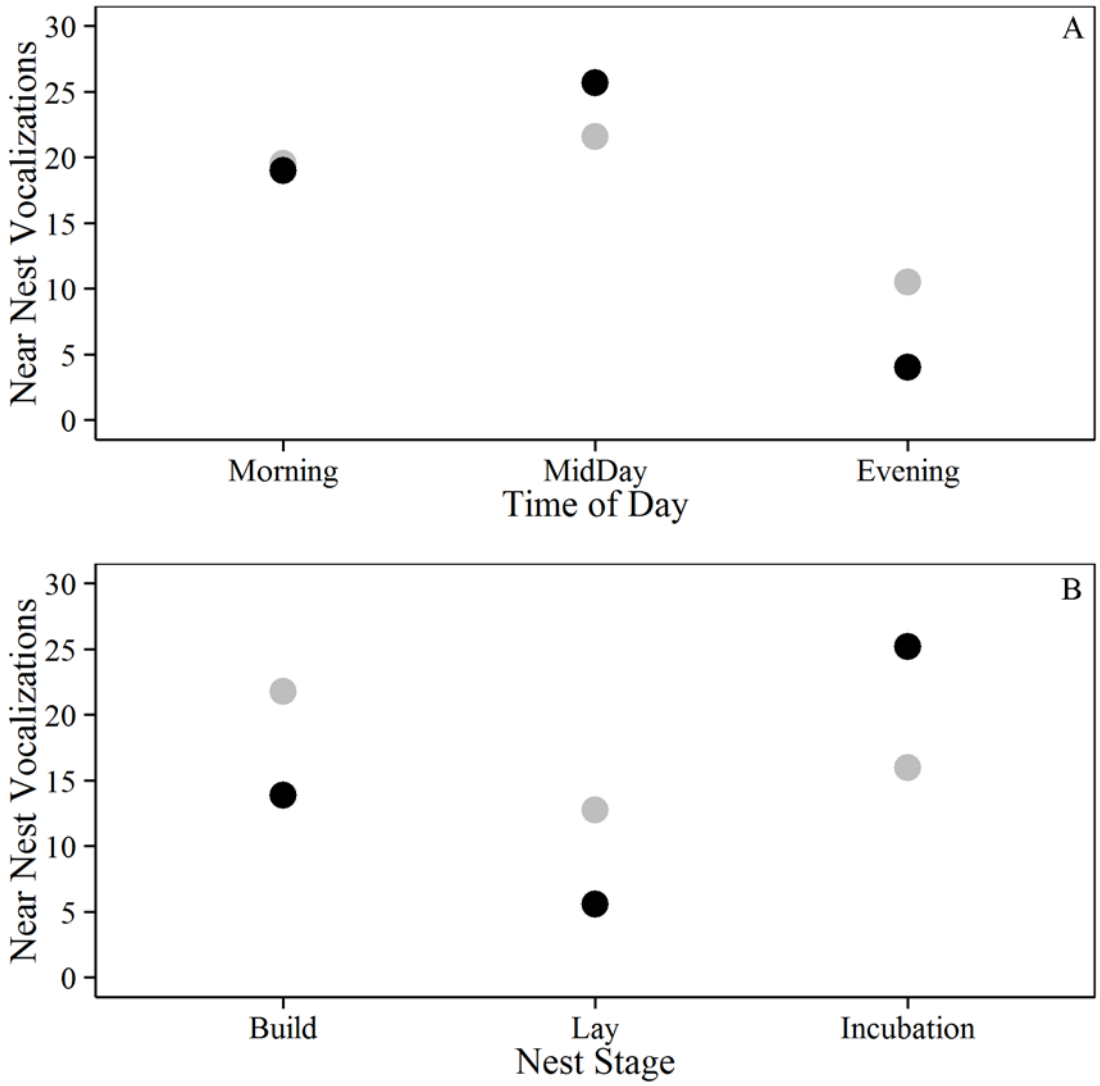

Figure 2.3.1. Interaction means from the best model of "near nest" vocalizations by male vireos in central Texas, 2013-2014, considering depredation fate and (A) time of day and (B) nest stage. Vocalizations at nests that were eventually depredated are indicated in black; vocalizations at non-depredated nests are in grey. Standard errors are all too small to display accurately (all SE are < 0.12).

Table 2.3.5. Parameter estimates for best model of "near nest" vocalizations considering nest stage, time of day, and depredation fate.

β	Estimate	SE	*z*	*P*
Intercept	-0.20	0.06	-3.65	< 0.001
Nest Stage (Lay)	-0.10	0.08	-1.30	0.20
Nest Stage (Incubation)	-0.57	0.10	-5.86	< 0.001
Time of Day (MidDay)	0.37	0.07	5.40	< 0.001
Time of Day (Evening)	-0.72	0.10	-7.52	< 0.001
Depredation Fate	-0.20	0.08	-2.64	0.008
Nest Stage (Lay)*Time of Day (MidDay)	-1.32	0.12	-11.45	< 0.001
Nest Stage (Incubation)*Time of Day (MidDay)	0.50	0.10	4.93	< 0.001
Nest Stage (Lay)*Time of Day (Evening)	0.01	0.13	0.12	0.91
Nest Stage (Incubation)*Time of Day (Evening)	0.28	0.16	1.76	0.08
Nest Stage (Lay)*Depredation Fate	-0.38	0.13	-2.88	0.004
Nest Stage (Incubation)*Depredation Fate	0.91	0.09	9.96	< 0.001
Time of Day (MidDay)*Depredation Fate	0.20	0.09	2.27	0.02
Time of Day (Evening)*Depredation Fate	-0.94	0.15	-6.43	< 0.001

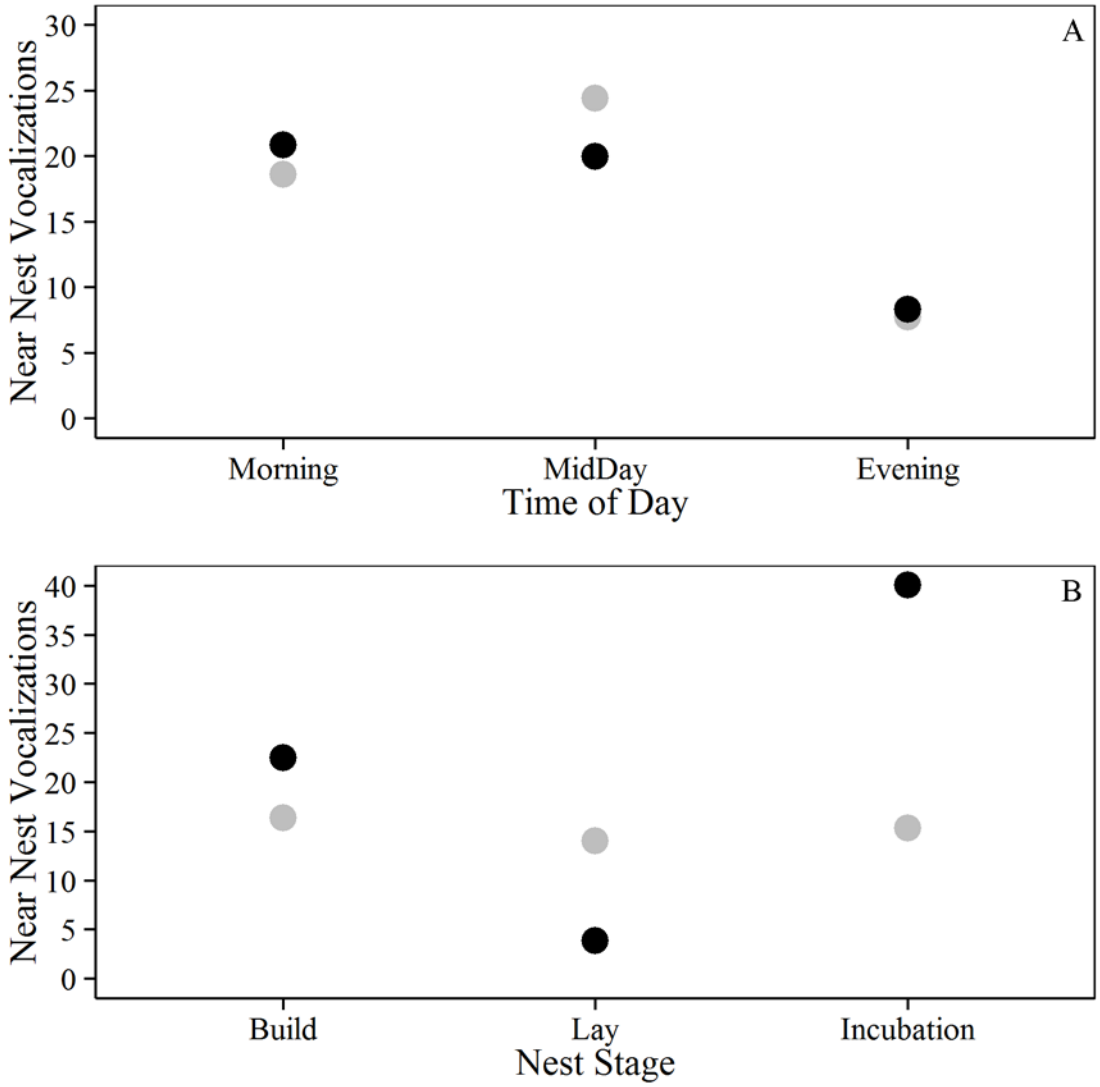

Figure 2.3.2. Interaction means from the best model of "near nest" vocalizations by male vireos in central Texas, 2013-2014, considering parasitism fate and (A) time of day and (B) nest stage. Vocalizations at nests that were eventually parasitized are indicated in black; vocalizations at non-parasitized nests are in grey. Standard errors are all too small to display accurately (all SE are < 0.13).

Table 2.3.6. Models used to evaluate the predator-attraction hypothesis and the role of nest stage (Stage), time of day (Time), and parasitism fate (Para) on "near nest" vocalizations by male vireos.

Parameters	ΔAIC_c	w_i
Stage + Time + Para + Stage*Time + Stage*Para + Time*Para	0.00[†]	0.99
Stage + Time + Para + Stage*Time + Stage*Para	8.54	0.01
Stage + Time + Para + Stage*Time	264.60	< 0.001
Stage + Time + Para + Stage*Time + Time*Para	266.89	< 0.001
Stage + Time + Stage*Time	283.68	< 0.001
Para	1459.86	< 0.001
(null)	1481.54	< 0.001

[†] AIC_c = 4874.20

Table 2.3.7. Parameter estimates for best model of "near nest" vocalizations considering nest stage, time of day, and parasitism fate.

β	Estimate	SE	*z*	*P*
Intercept	-0.47	0.06	-8.32	< 0.001
Nest Stage (Lay)	0.28	0.08	3.60	< 0.001
Nest Stage (Incubation)	-0.29	0.09	-3.15	0.002
Time of Day (MidDay)	0.59	0.07	8.71	< 0.001
Time of Day (Evening)	-1.00	0.10	-9.66	< 0.001
Parasitism Fate	0.44	0.08	5.68	< 0.001
Nest Stage (Lay)*Time of Day (MidDay)	-1.50	0.12	-12.90	< 0.001
Nest Stage (Incubation)*Time of Day (MidDay)	0.53	0.10	5.27	< 0.001
Nest Stage (Lay)*Time of Day (Evening)	0.21	0.13	1.60	0.11
Nest Stage (Incubation)*Time of Day (Evening)	0.15	0.16	0.96	0.34
Nest Stage (Lay)*Parasitism Fate	-1.61	0.14	-11.26	< 0.001
Nest Stage (Incubation)*Parasitism Fate	0.64	0.09	7.09	< 0.001
Time of Day (MidDay)*Parasitism Fate	-0.32	0.09	-3.46	0.001
Time of Day (Evening)*Parasitism Fate	-0.04	0.13	-0.31	0.76

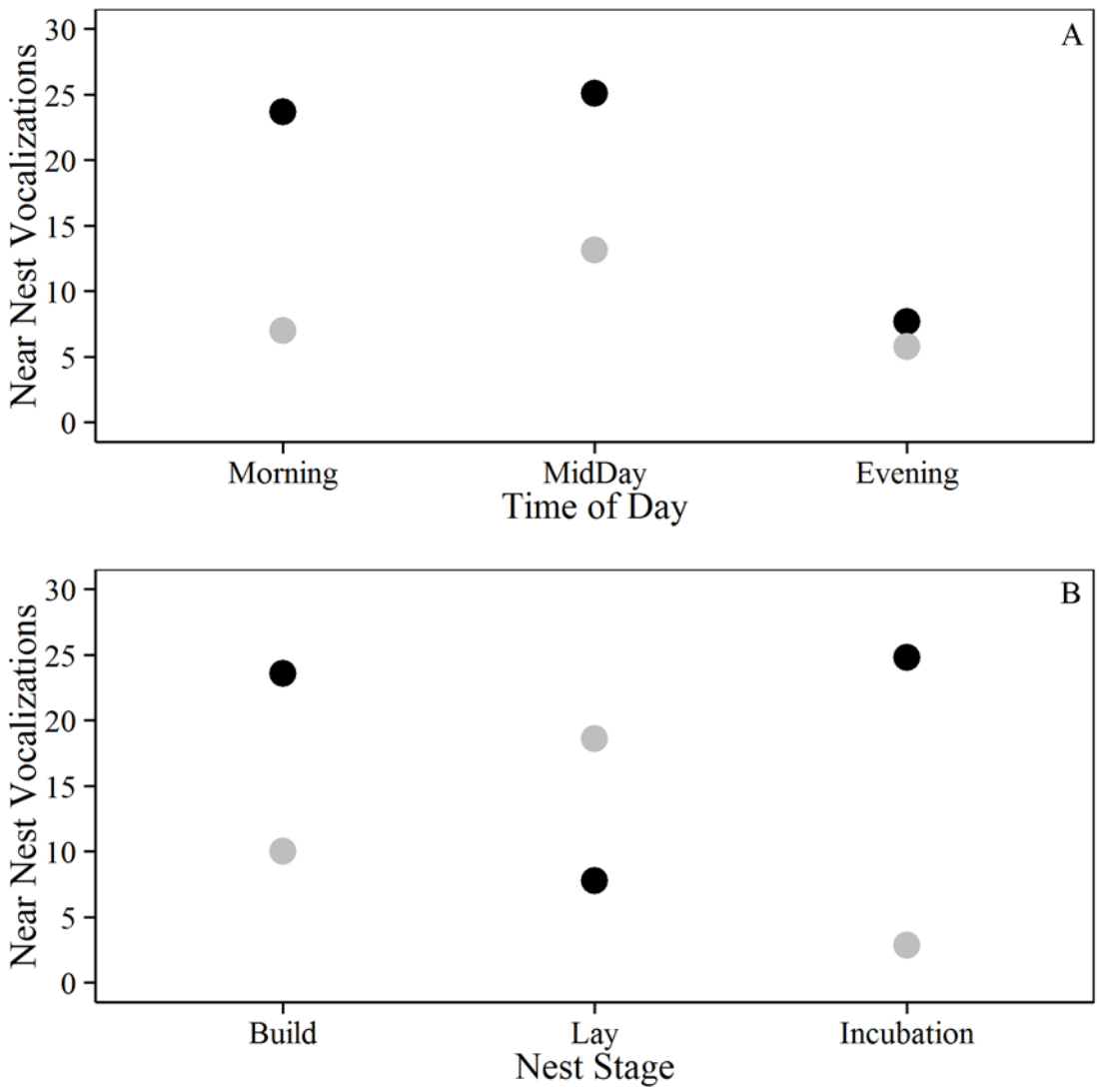

Figure 2.3.3. Interaction means from the best model of "near nest" vocalizations by male vireos in central Texas, 2013-2014, considering cowbird density and (A) time of day and (B) nest stage. Vocalizations in areas with high cowbird density are indicated in black, low cowbird density in grey. Standard errors are all too small to display accurately (all SE are < 0.22).

Table 2.3.8. Models used to evaluate the parasite-assessment hypothesis and the role of nest stage (Stage), time of day (Time), and local cowbird density (Cowbird) on vocalizations by male vireos near their nests.

Parameters	ΔAIC_c	w_i
Stage + Time + Cowbird + Stage*Time + Stage*Cowbird + Time*Cowbird	0.00[†]	1.000
Stage + Time + Cowbird + Stage*Time + Stage*Cowbird	48.79	< 0.001
Stage + Time + Cowbird + Stage*Time + Time*Cowbird	373.41	< 0.001
Stage + Time + Cowbird + Stage*Time	438.18	< 0.001
Stage + Time + Stage*Time	591.25	< 0.001
Cowbird	1631.13	< 0.001
(null)	1789.10	< 0.001

[†] AIC_c = 4566.63

Table 2.3.9. Parameter estimates for best model of vireo vocalizations considering nest stage, time of day, and local cowbird density.

β	Estimate	SE	*z*	*P*
Intercept	0.05	0.05	1.12	0.26
Nest Stage (Lay)	-0.57	0.08	-7.58	< 0.001
Nest Stage (Incubation)	-0.28	0.09	-3.25	0.001
Time of Day (MidDay)	0.36	0.06	6.01	< 0.001
Time of Day (Evening)	-1.22	0.09	-13.15	< 0.001
Cowbird Density (Low)	-1.36	0.10	-13.33	< 0.001
Nest Stage (Lay)*Time of Day (MidDay)	-1.56	0.12	-13.16	< 0.001
Nest Stage (Incubation)*Time of Day (MidDay)	0.66	0.10	6.37	< 0.001
Nest Stage (Lay)*Time of Day (Evening)	-0.06	0.13	-0.45	0.65
Nest Stage (Incubation)*Time of Day (Evening)	0.33	0.16	2.03	0.04
Nest Stage (Lay)*Cowbird Density (Low)	1.73	0.11	16.03	< 0.001
Nest Stage (Incubation)*Cowbird Density (Low)	-1.31	0.22	-5.91	< 0.001
Time of Day (MidDay)*Cowbird Density (Low)	0.58	0.12	4.97	< 0.001
Time of Day (Evening)*Cowbird Density (Low)	0.94	0.14	6.85	< 0.001

2.3.4 Discussion

Vocalizations near nests are known to attract predators and brood parasites for some host species (Uyehara and Narins 1995, Clotfelter 1998, Banks and Martin 2001) and reduce rates of parasitism for others (Sharp and Kus 2006, Steckler and Conway 2012). For the endangered black-capped vireo, we found only limited, stage-specific evidence for both the predator-attraction and parasite-assessment hypotheses across landscapes that vary in parasitism risk. Thus, we suggest that neither hypothesis adequately captures the selection pressures that shape vireo vocalization patterns. Black-capped vireos face a cruel bind in navigating the risks of

predation and brood parasitism risk, a bind that they solve, in part, through temporal plasticity in vocalization frequency near the nest.

2.3.4.1 Predator-attraction Hypothesis

Patterns in black-capped vireo vocalizations near their nests do not support the predictions outlined by the predator-attraction hypothesis. Across all recordings, the relationships observed between song rate and depredation and parasitism fate were in contrast to the expectations of this hypothesis; namely, nests with more vocal males were less likely to be depredated and there was no relationship between parasitism and song rate. Additionally, although we found some temporal variation between vireo defense strategies, patterns relating vocalization frequency and depredation or parasitism fate were generally consistent suggesting that vireos experience minimal trade-offs in mediating parasitism or predation risk through vocalizations.

We suspect that, during the early stages of the nesting cycle, selection for an optimal frequency of vocalizations at the nest might focus most on minimizing the threat of cowbird parasitism. Although the predator-attraction hypothesis assumes that important nest predators cue in to parental behaviors such as vocalizations, this may not be true for vireos, particularly during the early nesting stages. Vireos' most common nest predators, snakes and ants (Stake and Cavanagh 2001, Stake and Cimprich 2003, Conkling et al. 2012), are not known to respond to aural cues such as vocalizations (Conover 2007). Additionally, although many of the vireo's avian predators do likely cue into vocalizations (e.g., western scrub-jays; Curry et al. 2002), predation events by birds other than cowbirds are relatively uncommon (Stake and Cimprich 2003). Cowbirds are most likely to depredate nests that are later in the nesting cycle (Conkling et al. 2012), in some cases forcing the host pair to re-nest and giving the cowbird another parasitism opportunity (Arcese et al. 1996, Stake and Cavanaugh 2001, Dubina and Peer 2013). Thus, had we observed nests during nestling development, we may have garnered more support for the predator-attraction hypothesis.

2.3.4.2 Parasite-assessment Hypothesis

In central Texas, the frequency of black-capped vireo vocalizations is strongly correlated with local cowbird density, although generally not in the direction predicted by the parasite-assessment hypothesis. During the building and incubation stages, vireo vocalizations near the nest were most frequent at sites with higher cowbird densities. Thus, while cowbirds may be attracted to singing vireos, it does not appear that vireos adjust song to counter this threat. During the laying stage, however, vocalization rates were highest in areas where cowbird density was low, perhaps providing some stage-specific evidence for the parasite-assessment hypothesis. Cowbirds typically parasitize nests near the end of the laying stage (Davies 2000), and vireos may vocalize less frequently in response to increases in perceived parasitism risk during this nest stage (Forsman and Martin 2009). Alternatively, high cowbird densities may induce nest vigilance by vireos during the building or early incubation stages, although the mechanism for this phenomenon is not obvious.

2.3.4.3 Reticence versus Vigilance: Alternative Strategies for Nest Success

We observed little evidence of trade-offs between the mediation of risk for predators and brood parasites, yet some stage-specific patterns provide clues as to how vireos balance the risks and benefits of social communication. Temporally-specific behavioral adaptations by vireos may alleviate some conflicts in nest defense strategy and ultimately optimize nest success. Cowbirds often locate nests while hosts are building and then return to parasitize the nest during the host's laying period (Davies 2000, Banks and Martin 2001). Vireos may minimize their risk of eventual nest parasitism by remaining quiet during the building stage to prevent cowbirds from finding the nest location. Nests that are discovered by cowbirds may be abandoned before laying occurs because vireos are less invested in the particular nest location. Once laying begins, however, vireos are more invested in their nest and benefit by remaining vigilant to ward off potential brood parasites. Previous studies found that vireo nests suffer higher rates of predation during the nestling stage compared with incubation (Stake and Cimprich 2003, Conkling et al. 2012), but these studies did not evaluate predation rates during laying or early incubation periods. In general, avian predators of vireo nests on Fort Hood, including cowbirds, act diurnally (Stake and Cimprich 2003). Stake and Cavanagh (2001) observed that cowbirds depredating vireo nests during the nestling stage most frequently acted during the midday between 10 am and 3 pm. Scrub-jays and other corvids are generally active throughout the day although the specific timing of predation events is unreported (Luginbuhl et al. 2001, Eggers et al. 2005). Thus, vireos may minimize depredation threat by being relatively quiet during the middle of the day when avian predators are most active; this proved an especially effective strategy during early incubation.

In general, patterns demonstrate that parasitism and predation risks do not require conflicting defense strategies during the early nesting stages. However, some differences in risk mediation suggest that, in cases of conflict, vireos minimize loss by optimizing behavior to defend against nest predation. During the building stage, for example, vigilant and more vocal vireos reduced their susceptibility to eventual nest depredation while increasing their risk of parasitism, even in the face of high cowbird densities. In the evenings, vireos that remained vigilant did not increase their risk of nest parasitism but were able to reduce their probability of nest depredation.

Although vireos demonstrate some flexibility in the timing of vocalizations, selection pressures for pair bonding and territory defense may limit plasticity in social communication. In areas with high cowbird densities, vireos became more vigilant during the building stage, when cowbirds typically locate nests (Banks and Martin 2001), and more secretive while they were laying, when brood parasitism generally occurs (Davies 2000). These were not, however, effective defense strategies against parasitism; birds that vocalized more during building and less during the laying stage were also more often parasitized. Additionally, these patterns may amplify one another; if cowbirds are able to follow aural cues and locate a nest during the building stage (Davies 2000, Banks and Martin 2001), vireo reticence during laying may inadvertently aid cowbirds by allowing them more uninterrupted access to the nest. Although vigilance during building may reflect a trade-off with predation risk, we did not observe evidence for such a trade-off during the laying stage. During laying, frequent vocalizations near the nest increased the likelihood of both parasitism and depredation. Instead, vireo territory density and trade-offs with territory defense may help explain these apparent conflicts. High

host density may favor selection for territory defense and increased vocalization rates. Indeed, previous studies have positively correlated vireo densities with parasitism rates (Barber and Martin 1997). Thus, at sites with high cowbird densities, vocalization rates may reflect selection for territory defense rather than parasitism risk. Alternatively, at high cowbird densities, building vireos may be more likely to become incidentally discovered by a cowbird, regardless of vocalization rate. Under those circumstances, mate communication may outweigh reticence as an effective defense against parasitism.

In contrast to our results, nest parasitism in a similar species, Bell's vireo, was negatively correlated with vigilance and increased vocalization near the nest during the building and incubation stages but not during laying (Steckler and Conway 2012). Bell's vireo vocalizations during laying were positively correlated with eventual parasitism, although the difference was not significant. This contrast between two very similar species may suggest that, in some cases, parasitism is affected by variables or behaviors not captured well by audio recordings (e.g. female presence on the nest; Neudorf and Sealy 1994). Alternatively, trade-offs with predation risk may differ across habitat types and predator guilds (e.g., Kotler et al. 1991), resulting in different vocalization patterns in response to risk of brood parasitism.

Vocalization behavior and parasitism risk have an interactive relationship that is made increasingly complex by the additional consideration of nest predation. Although in many species, more vocal individuals suffer higher rates of brood parasitism (Uyehara and Narins 1995, Clotfelter 1998, Banks and Martin 2001); adaptation of vocalization behaviors that minimize parasitism risk may be outweighed by selection for behaviors that enable individuals to maintain important conspecific bonds or minimize risk of nest predation. Species that do not have nest predators cued by auditory signals, however, may be able to more readily adapt vocalization patterns that minimize parasitism risk. Without the complications of additional trade-offs with predation, some species may develop more temporal flexibility and avoid vocalizing during periods of the day or stages of the nesting cycle when they are most vulnerable to brood parasitism.

2.4 Simultaneous polygyny by a male black-capped vireo in central Texas[6]

2.4.1 Introduction

Avian species exhibit a wide variety of mating systems. Birds that produce altricial young are most often socially monogamous because both parents are required for proper care of the young. However, approximately 5% of North American passerines practice regular simultaneous polygyny (hereafter polygyny; Verner and Willson 1966), whereby a male maintains pair bonds with more than one female at the same time. Additionally, several passerine groups are known to occasionally or rarely practice polygyny, including hummingbirds (Batchelder et al. 2012), flycatchers (Prescott 1986, Sedgwick and Knopf 1989, Newell et al. 2013), sparrows (Petrinovich and Patterson 1978, Smith et al. 1982, Wheelwright et al. 1992), warblers (Barg et al. 2006, Peak et al. 2010), and wrens (Verner 1964, Leonard 1990). Here, we report an observation of polygyny in the endangered black-capped vireo, to our knowledge only the second instance of polygyny within the Vireonidae (see Mountjoy 1997).

Black-capped vireos are small Neotropical migrants that winter along western Mexico and breed locally from northeastern Mexico through Texas and southern Oklahoma (Graber 1961, Grzybowski 1995). Males begin arriving on the breeding grounds in late March, followed shortly by females (Graber 1961; LEW, pers. obs.). Their mating system is typically socially monogamous: males establish territories and pair with a single female (Graber 1961, Grzybowski 1995). Females and males build nests together and share incubation duties, and both parents care for nestlings and young fledglings (Graber 1961, Grzybowski 1995). On average, eggs are incubated for 14-17 days and nestlings generally fledge after 11 days (Graber 1961, Grzybowski 1995). Clutch size is typically four eggs (three is regular, five is rare), and pairs may re-nest several times if their initial efforts are unsuccessful (Graber 1961, Grzybowski 1995). Cup-shaped nests are generally located along forked branches of low vegetation (often below 2 m; Graber 1961, Grzybowski 1995) and, once found, are often easy to access and monitor.

2.4.2 Methods

We observed simultaneous polygyny in the black-capped vireo while conducting a broad-scale investigation of vireo population dynamics across central Texas from 2011-2014. We visited study sites throughout the vireo breeding season, from late March through early July, and searched for all territorial males. We caught and banded adult vireos using individual color band combinations, looked for molt limits to determine age (second year or after second year), and took several measurements of body size, including mass, tarsus length, and wing chord length. We visited each territory at least once a week (often more), recording locations of territorial male vireos using a handheld GPS unit. We recorded no more than five locations a day for each

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territory and each observation was separated by at least five minutes. We then delineated territories using fixed-kernel density estimation and the 99% utilization distribution (van Winkle 1975, Worton 1989; see Walker 2015 for detailed methods).

When nesting activity was observed, we carefully monitored pairs and attempted to locate all nests. We visited known nest locations every three to four days until failure or fledging and recorded the number of host eggs and cowbird eggs (if present), the number and approximate age of nestlings, and parental presence at the nest. We considered a nest to be successful if we observed evidence that at least one vireo nestling had fledged.

2.4.3 Results

On 19 May 2014, we located a vireo nest with four eggs incubated by an unbanded female paired with a color-banded male. The nest was located on the Mullen tract of Balcones Canyonlands National Wildlife Refuge, 0.48 meters off the ground in a low patch of shin oak (*Quercus sinuata* var. *breviloba*; Figure 2.4.1). Although male vireos typically help incubate their nests, we checked this nest four times and never observed this male incubate or brood. We were, however, scolded by the male when we discovered the nest on 19 May and when we banded the nestlings on 28 May. On 30 May, we found the nest empty and presumably depredated. On 2 June, we discovered a nearby vireo nest (178 meters away), 1.28 meters off the ground in a tall shin oak under high live oak canopy. An unbanded female and the same color-banded male were brooding this second nest with three eggs and a single 1-day-old nestling. Four fledglings successfully fledged from this second nest on 14 June 2014. Because we carefully monitored and spotmapped all territories, we were able to identify both nests as solidly within the male's territory (Figure 2.4.1). Although we did not locate the male's second nest until after the first had been depredated, the presence of nestlings on 2 June allows us to reconstruct a timeline; the second nest was initiated (first egg likely laid around 17 May) while the first nest was still active. As both nests were being incubated simultaneously, we believe the nests were likely laid by two separate females.

There was only one adjacent territory (Figure 2.4.1) and that male was not paired during these observations. Although we did not directly assess paternity, we never observed this second male within the primary male's territory during 15 visits. We monitored 377 territories across four breeding seasons and seven study sites in central Texas and this was the only observed case of polygyny.

2.4.4 Discussion

Occasional polygyny has been observed in a number of otherwise monogamous species and is thought to be associated with a variety of species-specific, or perhaps case-specific, drivers. While the benefits of polygyny are obvious for the male (he may be able to produce more young), benefits to the females are less apparent and the shift to polygyny may be explained by the presence of unbalanced sex ratios (Liker et al. 2014), asynchronous settlement (Leonard 1990), uneven distribution of resources such as nesting sites or food availability (the polygyny-

threshold model; Verner 1964, Verner and Willson 1966, Orians 1969), or individual male quality (the sexy son hypothesis; Weatherhead and Robinson 1979).

We suspect that differences in habitat quality between the two adjacent territories were drivers in this instance of polygyny among black-capped vireos. During the 2014 breeding season, we found two territorial males and two females on the Mullen tract of Balcones Canyonlands National Wildlife Refuge. Thus, we did not observe any unbalance in the sex ratio of the breeding population at this site, a pattern consistent with observations across other local breeding areas (D. Cimprich, pers. comm.). Although we do not know the settlement date for each of the females in 2014, the timing of their nests overlapped significantly and thus asynchronous settlement seems unlikely. We have only limited means of comparing the quality of individual males. Both males were second year birds in 2014, in their first breeding season. We observed small differences in body condition metrics including mass/wing chord or mass/tarsus length (the polygynous male had a 2% larger mass/wing and a 3% larger mass/tarsus ratio), but these metrics are not always a reliable measure of fitness (Schamber et al. 2008). Thus, territory quality seems the most likely driver. The territory of the polygynous male had more open land cover and less canopy cover than the adjacent male. These habitat features may be associated with territory success (Walker 2015). Anecdotally, the location of the polygynous territory was also occupied in the 2011-2013 breeding seasons and successfully produced young each year. The other territory was occupied in 2011 and 2012, but not 2013, and fledged young only in 2011.

This is the first documented occurrence of simultaneous polygynous nesting in the endangered songbird, the black-capped vireo. Simultaneous nesting has implications at multiple scales. Individual birds that produce simultaneous nests may be able to successfully fledge more young. This phenomenon may also boost productivity at the population level, potentially aiding in long term viability and population persistence. Although polygyny appears rare in this species, this example demonstrates flexibility in mating strategy that may be important in the face of potential habitat changes due to land management or climate change. Such flexibility in individuals may aid in the persistence of populations, which may be especially important for endangered species with limited population strongholds.

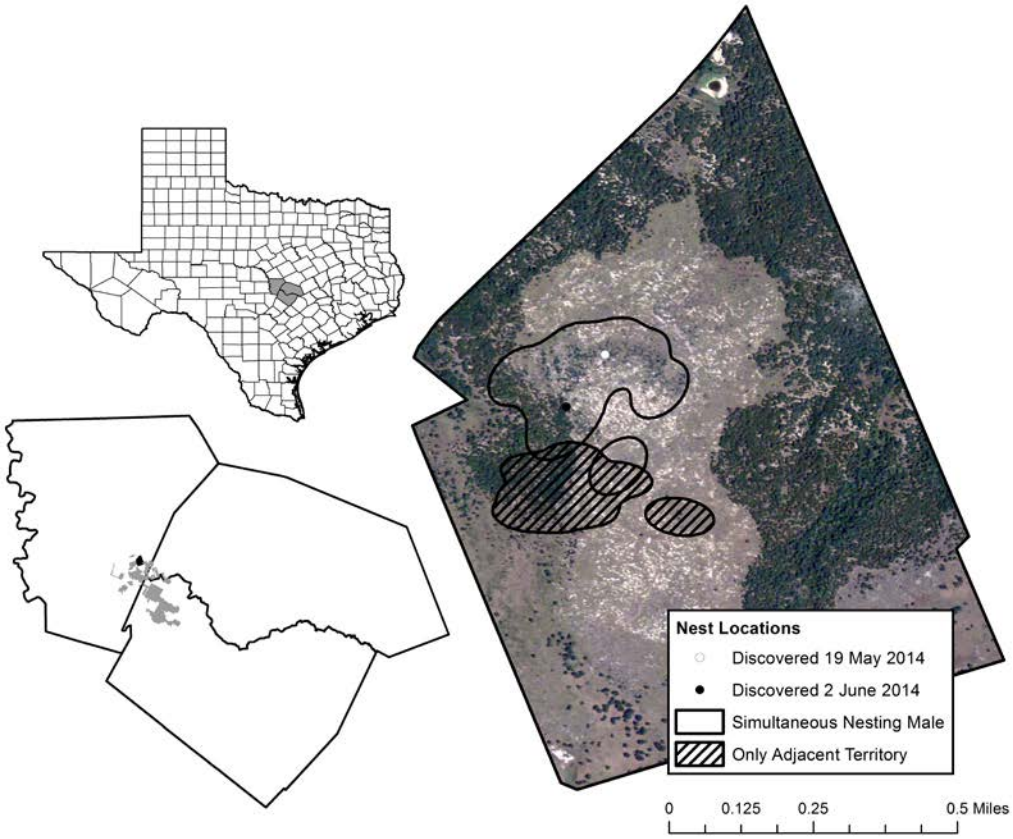

Figure 2.4.1. Location of polygynous black-capped vireo territory on the Mullen tract of Balcones Canyonlands National Wildlife Refuge in 2014.

Phase 2 References

Akaike, H. 1974. A new look at the statistical model identification. Institute of Electrical and Electronics Engineers Transactions on Automatic Control 19:716-723.

Amarasekare, P. 2003. Competitive coexistence in spatially structured environments: a synthesis. Ecology Letters 6:1109-1122.

Anders, A. D., D. C. Dearborn, J. Faaborg, and F. R. Thompson. 1997. Juvenile survival in a population of neotropical migrant birds. Conservation Biology 11:698-707.

Andrén, H. 1992. Corvid density and nest predation in relation to forest fragmentation: A landscape perspective. Ecology 73:794–804.

Arcese, P., J. N. M. Smith, and M. I. Hatch. 1996. Nest predation by cowbirds and its consequences for passerine demography. Proceedings of the National Academy of Sciences 93:4608-4611.

Ausprey, I. J., and A. D. Rodewald. 2011. Postfledging survivorship and habitat selection across a rural-to-urban landscape gradient. Auk 128:293-302.

Aviles, J. M., B. G. Stokke, and D. Parejo. 2006. Relationship between nest predation suffered by hosts and brown-headed cowbird parasitism: a comparative study. Evolutionary Ecology 20:97-111.

Bailey, J. W. 2005. Hierarchical nest-site selection and the effects of habitat characteristics on black-capped vireo nest survival. Thesis. University of Missouri, Columbia, Missouri, USA.

Balogh, A. L., T. B. Ryder, and P. P. Marra. 2011. Population demography of gray catbirds in the suburban matrix sources, sinks and domestic cats. Journal of Ornithology 152:717-726.

Banks, A. J., and T. E. Martin. 2001. Host activity and the risk of nest parasitism by brown-headed cowbirds. Behavioral Ecology 12:31-40.

Barber, D. R., and T. E. Martin. 1997. Influence of alternate host densities on brown-headed cowbird parasitism rates in black-capped vireos. Condor 99:595-604.

Barclay, R. M. R., M. L. Leonard, and G. Friesen. 1985. Nocturnal singing by marsh wrens. Condor 87:418-422.

Barg, J. J., J. Jones, M. K. Girvan, and R. J. Robertson. 2006. Within-pair interactions and parental behavior of cerulean warblers breeding in eastern Ontario. Wilson Journal of Ornithology 118:316–325.

Barr, K. R., D. L. Lindsay, G. Athrey, G., R. F. Lance, T. J. Hayden, S. A. Tweddale, and P. L. Leberg. 2008. Population structure in an endangered songbird: maintenance of genetic differentiation despite high vagility and significant population recovery. Molecular Ecology 17:3628-3639.

Batchelder, N., G. Batchelder, D. A. Livezey, and J. S. Marks. 2012. Simultaneous multiple nests of calliope hummingbird and rufous hummingbird. Wilson Journal of Ornithology 124:640-643.

Battin, J. 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. Conservation Biology 18:1482-1491.

Beyer, H.L. 2012. Geospatial Modelling Environment (Version 0.7.3.0). http://www.spatialecology.com/gme

Bock, C. E., and J. H. Bock. 1974. Geographical ecology of the acorn woodpecker: diversity versus abundance of resources. American Naturalist 108:694-698.

Boughton, D. A. 1999. Empirical evidence for complex source-sink dynamics with alternative states in a butterfly population. Ecology 80:2727-2739.

Boves, T. J., J. H. Sperry, K. Comolli, and P. J. Weatherhead. 2014. Brood parasitism of black-capped vireos: frontline and post-laying behavioral responses and effects on productivity. Journal of Field Ornithology 85:364-378.

Bradbury, J. W., and S. L. Vehrencamp. 2011. Principles of animal communication, 2nd edition. Sinauer, Sunderland, Massachusetts, USA.

Brawn, J. D., and S. K. Robinson. 1996. Source-sink population dynamics may complicate the interpretation of long-term census data. Ecology 77:3-12.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58:445-449.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information theoretic approach. Springer-Verlag, New York, New York, USA.

Burrell, N. S., and M. A. Colwell. 2012. Direct and indirect evidence that productivity of snowy plovers *Charadrius nivosus* varies with occurrence of a nest predator. Wildfowl 62:204-223.

Caswell, H. 2001. Matrix population models: Construction, analysis, and interpretation, Second edition. Sinauer, Sunderland, Massachusetts, USA.

Catchpole, C. K. 1987. Bird song, sexual selection and female choice. Trends in Ecology and Evolution 2:94-97.

Chalfoun, A. C., and T. E. Martin. 2009. Habitat structure mediates predation risk for sedentary prey: experimental tests of alternative hypotheses. Journal of Animal Ecology 78:497-503.

Chalfoun, A. D., and K. A. Schmidt. 2012. Adaptive breeding-habitat selection: is it for the birds? Auk 129:589-599.

Cimprich, D. A., and M. Heimbuch. 2011. Monitoring of the black-capped vireo during 2011 on Fort Hood, Texas. *In* Endangered species monitoring and management at Fort Hood, Texas: 2011 annual report. Fort Hood Natural and Cultural Resources Management Branch, Fort Hood, Texas, USA.

Cimprich, D. A., and P. M. Cimprich. 2015. Monitoring of the black-capped vireo (*Vireo atricapilla*) during 2014 on Fort Hood Military Installation, Fort Hood, Texas. *In* 2015 United States Fish and Wildlife Service Annual Report: Endangered Species Monitoring and Management on Fort Hood Military Installation, Fort Hood, Texas. Fort Hood, Directorate of Public Works, Natural and Cultural Resources Management Branch, Fort Hood, Texas, USA.

Cimprich, D. A., C. W. Sexton, P. K. McDowell, G. Lasley, and W. S. Simper. 2009. Long-distance dispersal records for the black-capped vireo. Bulletin of the Texas Ornithological Society 42:44-47.

Clotfelter, E. D. 1998. What cues do brown-headed cowbirds use to locate red-winged blackbird host nests? Animal Behaviour 55:1181-1189.

Cohen, E. B., and C. A. Lindell. 2004. Survival, habitat use, and movements of fledgling white-throated robins (*Turdus assimilis*) in a Costa Rican agricultural landscape. Auk 121:404-414.

Conkling, T. J., T. L. Pope, K. N. Smith, H. A. Mathewson, M. L. Morrison, R. N. Wilkins, and J. W. Cain, III. 2012. Black-capped vireo nest predator assemblage and predictors for nest predation. Journal of Wildlife Management 76:1401-1411.

Conover, M. R. 2007. Predator–prey dynamics: the use of olfaction. Taylor and Francis, Boca Raton, Florida, USA.
Cooch, E., and G. White. 2014. Using Mark – a gentle introduction. www.phidot.org/software/mark/docs/book/mark-book.exe.
Cornell, H. N., J. M. Marzluff, and S. Pecoraro. 2012. Social learning spreads knowledge about dangerous humans among American crows. Proceedings of the Royal Society B 279:499-508.
Curry, R. L., A. T. Peterson, and T. A. Langen. 2002. Western scrub jay (*Aphelocoma californica*). Account 712 *in* A. Poole, editor. Birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA. http://bna.birds.cornell.edu/bna/species/712
Davies, N.B. 2000. Cuckoos, cowbirds and other cheats. T & AD Poyser Ltd, London, UK.
De Rosario-Martinez, H. 2015. Phia: post-hoc interaction analysis. R package version 0.2-0. http://CRAN.R-project.org/package=phia
Dittmar, E. M., D. A. Cimprich, J. H. Sperry, and P. J. Weatherhead. 2014. Habitat selection by juvenile black-capped vireos following independence from parental care. Journal of Wildlife Management 78:1005-1011.
Donovan, T. M., F. R. Thompson, J. Faaborg, and J. R. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. Conservation Biology 9:1380-1395.
Dubina, K. M., and B. D. Peer. 2013. Egg pecking and discrimination by female and male brown-headed cowbirds. Journal of Ornithology 154:553-557.
Dwernychuk, L. W., and D. A. Boag. 1972. Ducks nesting in association with gulls: an ecological trap? Canadian Journal of Zoology 50:559-563.
Eggers, S., M. Griesser, and J. Ekman. 2005. Predator-induced plasticity in nest visitation rates in the Siberian jay (*Perisoreus infaustus*). Behavioral Ecology 16:309-315.
Fagan, W. E., R. S. Cantrell, and C. Cosner. 1999. How habitat edged change species interactions. American Naturalist 153:165-182.
Fay, R., H. Weimerskirch, K. Delord, and C. Barbraud. 2015. Population density and climate shape early-life survival and recruitment in a long-lived pelagic seabird. Journal of Animal Ecology 84:1423-1433.
Fazio, V. W., D. B. Miles, and M. M. White. 2004. Genetic differentiation in the endangered black-capped vireo. Condor 106:377-385.
Fiorini, V. D., D. T. Tuero, and J. C. Reboreda. 2012. Dense canopy cover over house wren (*Troglodytes aedon*) nests increases latency of brood parasitism by shiny cowbirds (*Molothrus bonariensis*). Emu 112:55-59.
Foppen, R. P. B., J. P. Chardon, and W. Liefveld. 2000. Understanding the role of sink patches in source-sink metapopulations: reed warbler in an agricultural landscape. Conservation Biology 14:1881-1892.
Forsman, J. T., and T. E. Martin. 2009. Habitat selection for parasite-free space by hosts of parasitic cowbirds. Oikos 118:464-470.
Ficken, R. W., M. S. Ficken, and J. P. Hailman. 1974. Temporal pattern shifts to avoid acoustic interference in singing birds. Science 183:762–763
Fuller, R. A, P. H. Warren, and K. J. Gaston. 2007. Daytime noise predicts nocturnal singing in urban robins. Biology Letters 3:368-370.
Gaona, P., P. Perreras, and M. Delibes. 1998. Dynamics and viability of a metapopulation of the endangered Iberian lynx (*Lynx pardinus*). Ecological Monographs 68:349-370.

Ghalambor, C. K., and T. E. Martin. 2000. Parental investment strategies in two species of nuthatch vary with stage-specific predation risk and reproductive effort. Animal Behaviour 60:263-267.

Graber, J. W. 1961. Habitat requirements and life history of the black-capped vireo (*Vireo atricapilla*). Ecological Monographs 31:313-336.

Greenberg, R. 1980. Demographic aspects of long-distance migration. Pages 493-504 in A. Keast and E. S. Morton, editors. Migrant birds in the neotropics: ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Washington, D.C., USA.

Grzybowski, J. A., D. J. Tazik, and G. D. Schnell. 1994. Regional-analysis of black-capped vireo breeding habitats. Condor 96:512–544.

Grzybowski, J. A. 1995. Black-capped vireo (*Vireo atricapilla*). Account 181 *in* A. Poole, editor. Birds of North America Online. Cornell Laboratory of Ornithology, Ithaca, New York, USA. http://bna.birds.cornell.edu/bna/species/181

Grzybowski, J. A. 2005. An estimate of juvenile survival in black-capped vireos and its implications to source-sink analyses of songbirds. USDA Forest Service General Technical Report PSW-GTR-191.

Haff, T. M., and R. D. Magrath. 2011. Call at a cost: elevated nestling calling attracts predators to active nests. Biology Letters 7:493-495.

Handcock, M. S. 2004. Ruf: an R package for the estimation of the resource utilization function. http://csde.washington.edu/~handcock/ruf

Hauber, M. E., and S. A. Russo. 2000. Perch proximity correlates with high cowbird parasitism of ground nesting song sparrows. Wilson Bulletin 112:150-153.

Heinrichs, J. A., D. J. Bender, D. L. Gummer, and N. H. Schumaker. 2015. Effects of landscape and patch-level attributes on regional population persistence. Journal for Nature Conservation 26:56-64.

Heithaus, M. R., and L. M. Dill. 2006. Does tiger shark predation risk influence foraging habitat use by bottlenose dolphins at multiple spatial scales? Oikos 114:257-264.

Heppel, S. S. 1998. Application of life-history theory and population model analysis to turtle conservation. Copeia 2:367-375.

Homer, C. G., J. A. Dewitz, L. Yang, S. Jin, P. Danielson, G. Xian, J. Coulston, N. D. Herold, J. D. Wickham, and K. Megown. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States-representing a decade of land cover change information. Photogrammetric Engineering and Remote Sensing 81:345-354.

Howe, R. W., G. J. Davis, and G. J. Mosca. 1991. The demographic significance of sink populations. Biological Conservation 57:239-255.

Jenkins, S. R., M. G. Betts, M. M. Huso, and J. C. Hagar. 2013. Habitat selection by juvenile Swainson's thrushes (*Catharus ustulatus*) in headwater riparian areas, Northwestern Oregon, USA. Forest Ecology and Management 305:88-95.

Jewell, K. J., and P. Arcese. 2008. Consequences of parasite invasion and land use on the spatial dynamics of host populations. Journal of Applied Ecology 45:1180-1188.

Johnston, A. N. 2013. Eastern gray squirrel ecology and interactions with western gray squirrel. Dissertation. University of Washington, Seattle, WA, USA.

Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53:457-481.

Kauffman, M. J., W. F. Frick, and J. Linthicum. 2003. Estimation of habitat-specific demography and population growth for peregrine falcons in California. Ecological Applications 13:1802-1816.

Kershner, E. L., J. W. Walk, R. E. Warner, and D. A. Haukos. 2004. Postfledging movements and survival of juvenile eastern meadowlarks (*Sturnella magna*) in Illinois. Auk 121:1146-1154.

Kertson, B. N., and J. M. Marzluff. 2011. Improving studies of resource selection by understanding resource use. Environmental Conservation 38:18-27.

King, D. I., R. M. Degraaf, M. L. Smith, and J. P. Buonaccorsi. 2006. Habitat selection and habitat-specific survival of fledgling ovenbirds (*Seiurus aurocapilla*). Journal of Zoology 269:414-421.

Kostecke, R. M., S. G. Summers, G. H. Eckrich, and D. A. Cimprich. 2005. Effects of brown-headed cowbird (*Molothrus ater*) removal on black-capped vireo (*Vireo atricapilla*) nest success and population growth at Fort Hood, Texas. Ornithological Monographs 57:28-37.

Kostecke, R. M., and D. A. Cimprich. 2008. Adult and juvenile survival of black-capped vireos within a large breeding population in Texas. Condor 110:251-259.

Kotler, B. P., J. S. Brown, and O. Hasson. 1991. Factors affecting gerbil foraging behavior and rates of owl predation. Ecology 72:2249-2260.

Kroodsma, D. E., and B. E. Byers. 1991. The function(s) of bird song. American Zoologist 31:318-328.

Kus, B. E., and M. J. Whitfield. 2005. Parasitism, productivity, and population growth: response of least Bell's vireos (*Vireo bellii pusillus*) and southwestern willow flycatchers (*Empidonax traillii extimus*) to cowbird (*Molothrus* spp.) control. Ornithological Monographs 57:16-27.

Laake, J. L. 2013. RMark: an R interface for analysis of capture-recapture data with Mark. AFSC Processed Rep 2013-01, Alaska Fisheries Science Center, NOAA, National Marine Fisheries Service, Seattle, WA, USA.

Laake, J., D. Borchers, L. Thomas, D. Miller, and J. Bishop. 2014. Mrds: mark-recapture distance sampling (mrds). R package version 2.1.10. http://CRAN.R-project.org/package=mrds

Leonard, M. L. 1990. Polygyny in marsh wrens: asynchronous settlement as an alternative to the polygyny-threshold model. American Naturalist 136:446–458.

Liker, A., R. P. Freckleton, and T. Szekely. 2014. Divorce and infidelity are associated with skewed adult sex ratios in birds. Current Biology 24:880-884.

Lougheed S. C., and P. Handford. 1989. Night songs of the rufous-collared sparrow. Condor 91:462-465.

Luginbuhl, J. M., J. M. Marzluff, J.E. Bradley, M. G. Raphael, and D. E.Varland. 2001. Corvid techniques and the relationship between corvid relative abundance and nest predation. Journal of Field Ornithology 72:556-572.

Marshall, M. R., D. R. Diefenbach, L. A. Wood, and R. J. Cooper. 2004. Annual survival estimation of migratory songbirds confounded by incomplete breeding site-fidelity: study designs that may help. Animal Biodiversity and Conservation 27:59-72.

Marzluff, J. M., and R. P. Balda. 1992. The pinyon jay, behavioural ecology of a colonial and cooperative corvid. T & AD Poyser Ltd, London, UK.

Marzluff, J. M., J. Millspaugh, P. Hurvitz, and M. S. Handcock. 2004. Resource utilization by an avian nest predator: relating resources to a probabilistic measure of animal space use. Ecology 85:1411-1427.

Maxted, A. M. 2001. Post-fledging survival, dispersal, and habitat use in two migratory shrubland bird species. Thesis. Purdue University, West Lafayette, Indiana, USA.

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456-466.

Mazerolle, M. J. 2015. AICcmodavg: model selection and multimodel inference based on (Q)AIC©. R package version 2.0-3. http://CRAN.R-project.org/package=AICcmodavg

McCoy, T. D., M. R. Ryan, E. W. Kurzejeski, and L. W. Burger. 1999. Conservation reserve program: source or sink habitat for grassland birds in Missouri? Journal of Wildlife Management 63:530-538.

McDonald, P. G., D. R. Wilson, and C. S. Evans. 2009. Nestling begging increases predation risk, regardless of spectral characteristics or avian mobbing. Behavioral Ecology 20:821-829.

McGarigal, K., S. A. Cushman, and E. Ene. 2012. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. University of Massachusetts, Amherst, USA. http://www.umass.edu/landeco/research/fragstats/fragstats.html

McLean, I. G., J. N. M. Smith, and K. G. Stewart. 1986. Mobbing behaviour, nest exposure, and breeding success in the American robin. Behaviour 96:171-185.

Menu, S., G. Gauthier, and A. Reed. 2005. Survival of young greater snow geese (*Chen caerulescens atlantica*) during fall migration. Auk 122:479-496.

Miles, R. K., and D. A. Buehler. 2000. An evaluation of point counts and playbacks as techniques for censusing brown-headed cowbirds. Pages 63-68 *in* J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, editors. Ecology and management of cowbirds and their hosts: studies in the conservation of North American passserine birds. University of Texas Press, Austin, Texas, USA.

Miller, D. L. 2014. Distance: a simple way to fit detection functions to distance sampling data and calculate abundance/density for biological populations. R package version 0.9.2. http://CRAN.R-project.org/package=Distance

Mills, L. S., D. F. Doak, and M. J. Wisdom. 1999. Reliability of conservation actions based on elasticity analysis of matrix models. Conservation Biology 13:815-829.

Mountjoy, D. J. 1997. A probable case of polyterritorial polygyny in the red-eyed vireo, *Vireo olivaceus*. Canadian Field-Naturalist 1114:628-630.

Murphy, M. T. 2001. Source-sink dynamics of a declining eastern kingbird population and the value of sink habitats. Conservation Biology 15:737-748.

Neatherlin, E. A., and J. M. Marzluff. 2004. Responses of American crow populations to campgrounds in remote native forest landscapes. Journal of Wildlife Management 68:708-718.

Neudorf, D. L., and S. G. Sealy. 1994. Sunrise nest attentiveness in cowbird hosts. Condor 96:162-169.

Newell, F. L., A. N. K. Haiman, D. L. Narango, J. M. Elder, L. D. Leonhard, J. Philhower-Gillen, A. M. Johnson, and A. D. Rodewald. 2013. Occurrence of polygyny and double brooding in the eastern wood-pewee. Wilson Journal of Ornithology 125:251-259.

Nicolaus, M., S. P. M. Michler, K. M. Jalvingh, R. Ubels, M. van der Velde, J. Komdeur, C. Both, and J. M. Tinbergen. 2012. Social environment affects juvenile dispersal in great tits (*Parus major*). Journal of Animal Ecology 81:827-837.

Noa, L. A., D. H. Hirth, T. M. Donovan, and D. Cimprich. 2007. Demographic differences of black-capped vireos in two habitat types in central Texas. Journal of Wildlife Management 71:1042-1049.

Noon, B. R., and J. R. Sauer. 1992. Population models for passerine birds: structure, parameterization, and analysis. Pages 441-464 *in* D. R. McCullough, and R. H. Barrett, editors. Wildlife 2001: populations. Elsevier Applied Science, New York, USA.

Nowicki, S., and W. A. Searcy. 2005. Song and mate choice in birds: how the development of behavior helps us understand function. Auk 122:1-14.

O'Donnell, C. F. J. 2000. Influence of season, habitat, temperature, and invertebrate availability on nocturnal activity of the New Zealand long-tailed bat (*Chalinolobus tuberculatus*). New Zealand Journal of Zoology 27:207-221.

Orians, G. H. 1969. On the evolution of mating systems in birds and mammals. American Naturalist 103:589-603.

Owen, M., and J. M. Black. 1989. Factors affecting the survival of barnacle geese on migration from the breeding grounds. Journal of Animal Ecology 58:603-617.

Palstra, F. P., M. F. O'Connell, and D. E. Ruzzante. 2007. Population structure and gene flow reversals in Atlantic salmon (*Salmo salar*) over contemporary and long-term temporal scales: effects of population size and life history. Molecular Ecology 16:4504-4522.

Part, T., and B. Doligez. 2003. Gathering public information for habitat selection: prospecting birds cue on parental activity. Proceedings of the Royal Society of London B 270:1809-1813.

Paton, P. W. C. 1994. The effect of edge on avian nest success – how strong is the evidence. Conservation Biology 8:17-26.

Payne, R. B. 1977. The ecology of brood parasitism in birds. Annual Review of Ecological Systems 8:1-28.

Peak, R. G., D. J. Lusk, and J. D. Peppers. 2010. Polygyny in the golden-cheeked warbler. Bulletin of the Texas Ornithological Society 43:44–47.

Perkins, D. W., P. D. Vickery, and W. G. Shriver. 2003. Spatial dynamics of source-sink habitats: effects on rare grassland birds. Journal of Wildlife Management 67:588–599.

Petrinovich, L., and T. L. Patterson. 1978. Polygyny in the white-crowned sparrow (*Zonotrichia leucophrys*). Condor 80:99-100.

Pianka, E. R. 1976. Natural selection of optimal reproductive tactics. American Zoologist 16:775-784.

Piper, S. D., and C. P. Caterall. 2003. A particular case and a general pattern: hyperaggressive behavior by one species may mediate avifaunal decreases in fragmented Australian forests. Oikos 101:602-614.

Prescott, D. R. C. 1986. Polygyny in the willow flycatcher. Condor 88:385-386.

Pulliam, H. P. 1988. Sources, sinks, and population regulation. American Naturalist 132:652-661.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Ratzlaff, A. 1987. Endangered and threatened wildlife and plants: determination of the black-capped vireo to be an endangered species. Federal Register 52:37420-37423.

Reemts, C. M., and D. A. Cimprich. 2014. Restoring early-successional shrubland habitat for black-capped vireos using mechanical mastication. Natural Areas Journal 34:400-407.

Riotte-Lambert, L., and H. Weimerskirch. 2013. Do naïve juvenile seabirds forage differently from adults? Proceedings of the Royal Society of London B 280: 20131434.
Robinson, S. K., F. R. Thompson, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987-1990.
Rohner, C., and D. B. Hunter. 1996. First-year survival of great horned owls during a peak and decline of the snowshoe hare cycle. Canadian Journal of Zoology 74:1092-1097.
Rothstein, S. I. 1975. Evolutionary rates and host defenses against avian brood parasitism. American Naturalist 109:161-176.
Runge, J. P., M. C. Runge, and J. D. Nichols. 2006. The role of local populations within a landscape context: defining and classifying sources and sinks. American Naturalist 167:925-938.
Rush, S. A., and B. J. M. Stutchbury. 2008. Survival of fledgling hooded warblers (*Wilsonia citrina*) in small and large forest fragments. Auk 125:183-191.
Saether, B-E., T. H. Ringsby, O. Bakke, and E. J. Solberg. 1999. Spatial and temporal variation in demography of a house sparrow metapopulation. Journal of Animal Ecology 68:628-637.
Schamber, J. L., D. Esler, and P. L. Flint. 2008. Evaluating the validity of using unverified indices of body condition. Journal of Avian Biology 40:49-56.
Schjorring, S., G. Gregersen, and T. Bregnballe. 1999. Prospecting enhances breeding success of first time breeders in the great cormorant, *Phalacrocorax carbo sinensis*. Animal Behavior 57:647-654.
Schmidt, K. A. 2003. Linking frequencies of acorn masting in temperate forests to long-term population growth rates in a songbird: the veery (*Catharus fuscescens*). Oikos 10:548-558.
Scott, D. M. 1991. The time of day of egg laying by the brown-headed cowbird and other icterines. Canadian Journal of Zoology 69:2093-2099.
Sedgwick, J. A., and F. L. Knopf. 1989. Regionwide polygyny in willow flycatchers. Condor 91:473-475.
Sharp, B. L., and B. E. Kus. 2006. Factors influencing the incidence of parasitism of least Bell's vireos. Journal of Wildlife Management 70:682-690.
Sherry, T. W., and R. T. Holmes. 1995. Summer versus winter limitation of populations: what are the issues and what is the evidence? Pages 85-120 *in* T. E. Martin, and D. M. Finch, editors. Ecology and management of neotropical migratory birds. Oxford University Press, New York, USA.
Sillett, T. S., and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296-308.
Skutch, A. F. 1976. Parent birds and their young. University of Texas Press, Austin, Texas, USA.
Small, D.M., P. J. Blank, and B. Lohr. 2015. Habitat use and movement patterns by dependent and independent juvenile grasshopper sparrows during the post-fledging period. Journal of Field Ornithology 86:17-26.
Smith, J. N. M., Y. Yom-Tov, and R. Moses. 1982. Polygyny, male parental care, and sex ratio in song sparrows: an experimental study. Auk 99:555-564.
Stacey, P. B., and M. Taper. 1992. Environmental variation and the persistence of small populations. Ecological Applications 2:18-29.

Stake, M. M., and P. M. Cavanagh. 2001. Removal of host nestlings and fecal sacs by brown-headed cowbirds. Wilson Bulletin 113:456-459.
Stake, M. M., and D. A. Cimprich. 2003. Using video to monitor predation at black-capped vireo nests. Condor 105:348-357.
Steckler, S. E., and C. J. Conway. 2012. Frequent vocalizing is negatively associated with brood parasitism in a host of the brown-headed cowbird. Condor 114:219-226.
Stoychev, S., D. Demerdzhiev, S. Spasov, B-U. Meyburg, and D. Dobrev. 2014. Survival rate and mortality of juvenile and immature eastern imperial eagles (*Aquila heliaca*) from Bulgaria studied by satellite telemetry. Slovak Raptor Journal 8:53-60.
Streby, H. M., and D. E. Andersen. 2011. Seasonal productivity in a population of migratory songbirds: why nest data are not enough. Ecosphere 2(78):1-15.
Streby, H. M., and D. E. Andersen. 2013. Movements, cover-type selection, and survival of fledgling ovenbirds in managed deciduous and mixed coniferous-deciduous forests. Forest Ecology and Management 287:9-16.
Streby, H. M., S. M. Peterson, and D. E. Andersen. 2011. Invertebrate availability and vegetation characteristics explain use of non-nesting cover types by mature-forest songbirds during the postfledging period. Journal of Field Ornithology 82:406-414.
Streby, H. M., J. M. Refsnider, and D. E. Andersen. 2014a. Redefining reproductive success in songbirds: moving beyond the nest success paradigm. Auk 131:718-726.
Streby, H. M., J. M. Refsnider, S. M. Peterson, and D. E. Andersen. 2014b. Retirement investment theory explains patterns in songbird nest-site selection. Proceedings of the Royal Society B 281: 20131834.
Streby, H. M., S. M. Peterson, G. R. Kramer, and D. E. Andersen. 2015. Post-independence fledging ecology in a migratory songbird: implications for breeding-grounds conservation. Animal Conservation 18:228-235.
Stubben, C. J., and B. G. Milligan. 2007. Estimating and analyzing demographic models using the popbio package in R. Journal of Statistical Software 22:11.
Sullivan, K. 1989. Predation and starvation: age-specific mortality in juvenile juncos *Junco phaenotus*. Journal of Animal Ecology 58:275-286.
Summers, S. G., R. M. Kostecke, and G. I. Norman. 2006a. Efficacy of trapping and shooting in removing breeding brown-headed cowbirds. Wildlife Society Bulletin 34:1107-1112.
Summers, S. G., M. M. Stake, G. H. Eckrich, R. M. Kostecke, and D. A. Cimprich. 2006b. Reducing cowbird parasitism with minimal-effort shooting: a pilot study. Southwestern Naturalist 51:409-411.
Tazik, D. J., J. D. Cornelius, and C. Abrhamson. 1993. The black-capped vireo on the lands of Fort Hood, Texas, Volume 1: distribution and abundance. Technical Report EN-94/01, US Army Corps of Engineers, CERL, Champaign, Illinois, USA.
Temple, S. A., and J. R. Cary. 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. Conservation Biology 2:340-347.
U.S. Fish and Wildlife Service. 1991. Black-capped vireo (*Vireo atricapillus*) recovery plan. Austin, Texas, USA.
U.S. Fish and Wildlife Service. 1996. Black-capped vireo population and habitat viability assessment report. Page 57 *in* C. Beardsmore, J. Hatfield, and J. Lewis, editors. Report of a September 18-21, 1995 workshop, U.S. Fish and Wildlife Service, Austin, Texas, USA.
U.S. Fish and Wildlife Service. 2007. Black-capped vireo (*Vireo atricapilla*) 5-year review: summary and evaluation. Arlington, Texas, USA.

Uyehara, J. C., and P. M. Narins. 1995. Nest defense by willow flycatchers to brood-parasitic intruders. Condor 97:361-368.
van Winkle, W. 1975. Comparison of several probabilistic home-range models. Journal of Wildlife Management 39:118-123.
Vasseur, P. L., and P. L. LeBerg. 2015. Effects of habitat edges and nest-site characteristics on painted bunting nest success. Journal of Field Ornithology 86:27-40.
Vega Rivera, J. H., J. H. Rappole, W. J. McShea, and C. A. Haas. 1998. Wood thrush postfledging movements and habitat use in northern Virginia. Condor 100:69-78.
Verner, J. 1964. Evolution of polygamy in the long-billed marsh wren. Evolution 18:252-261.
Verner, J., and M. F. Willson. 1966. The influence of habitats on mating systems of North American passerine birds. Ecology 47:143-147.
Vierling, K. T. 2000. Source and sink habitats of red-winged blackbirds ina rural/suburban landscape. Ecological Applications 10:1211-1218.
Vitz, A. C. 2008. Survivorship, habitat use, and movements for two species of mature forest birds. Dissertation. The Ohio State University, Columbus, Ohio, USA.
Vitz, A. C., and A. D. Rodewald. 2007. Vegetative and fruit resources as determinants of habitat use by mature-forest birds during the postbreeding period. Auk 124:494-507.
Votier, S. C., T. R. Birkhead, D. Oro, M. Trinder, M. J. Grantham, J. A. Clark, R. H. McCleery, and B. J. Hatchwell. 2008. Recruitment and survival of immature seabirds in relation to oil spills and climate variability. Journal of Animal Ecology 77:974-983.
Walker, L. E. 2015. Population dynamics of the endangered black-capped vireo (*Vireo atricapilla*). Dissertation. University of Washington, Seattle, Washington, USA.
Ward, M. P., and S. Schlossberg. 2004. Conspecific attraction and the conservation of territorial songbirds. Conservation Biology 18:519-525.
Warren, P. S., M. Katti, M. Ermann, and A. Brazel. 2006. Urban bioacoustics: it's not just noise. Animal Behaviour 71:491-502.
Weatherhead, P. J., and R. J. Robertson. 1979. Offspring quality and the polygyny threshold: "the sexy son hypothesis". American Naturalist 113:201-208.
Weinberg, H. J., T. J. Hayden, and J. D. Cornelius. 1998. Local and installation-wide black-capped vireo dynamics on the Fort Hood, Texas Military Reservation. Technical Report 98/54, U.S. Army Construction Engineering Research Laboratories, Champaign, Illinois, USA.
Werner, E. E., R. A. Relyea, K. L. Yurewicz, D. K. Skelly, and C. J. Davis. 2009. Comparative landscape dynamics of two anuran species: climate-driven interaction of local and regional processes. Ecological Monographs 79:503-521.
Wheelwright, N. T., C. B. Schultz, and P. J. Hodum. 1992. Polygyny and male parental care in savannah sparrows: effects on female fitness. Behavioral Ecology and Sociobiology 31:279-289.
Whelan, C. L., and J. Wyneken. 2007. Estimating predation levels and site-specific survival of hatchling loggerhead seaturtles (*Caretta caretta*) from south Florida beaches. Copeia 2007:745-754.
White, G. C., and K. P. Burnham. 1999. Program Mark: survival estimation from populations of marked animals. Bird Study 46:S120-S139.
White, J. D., T. Gardali, F. R. Thompson, and J. Faaborg. 2005. Resource selection by juvenile Swainson's thrushes during the postfledging period. Condor 107:388-401.

Whittaker, K. A., and J. M. Marzluff. 2009. Species-specific survival and relative habitat use in an urban landscape during the postfledging period. Auk 126:288-299.

Wiens, J. D., B. R. Noon, and R. T. Reynolds. 2006. Post-fledging survival of northern goshawks: the importance of prey abundance, weather, and dispersal. Ecological Applications 16:406-418.

Wilsey, C. B., J. J. Lawler, D. Cimprich, and N. H. Schumaker. 2014. Dependence of the endangered black-capped vireo on sustained cowbird management. Conservation Biology 28:561-571.

Wilson, S., and P. Arcese. 2006. Nest depredation, brood parasitism and reproductive variation in island populations of song sparrows (*Melospiza melodia*). Auk 123:784-94.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164-168.

Yackel Adams, A. A., S. K. Skagen, and R. D. Adams. 2001. Movements and survival of lark bunting fledglings. Condor 103:643-647.

Zink, R. M., A. W. Jones, C. C. Farquhar, M.. C. Westberg, and J. I. Gonzales Rojas. 2010. Comparison of molecular markers in the endangered black-capped vireo (*Vireo atricapilla*) and their interaction in conservation. Auk 127:797-806.

Phase 3: Modeling Black-capped Vireo Regional Source-sink Dynamics

Phase 3 Overview

In Phase 3, we modeled the regional source-sink dynamics of black-capped vireos in Texas by coupling site and demographic information gathered in phase 2, with the source-sink modeling framework used in Task 1 (HexSim modeling platform). In a data-driven vireo model, we combined a habitat suitability model (from RC-1541, "Forecasting the Relative and Cumulative Effects of Multiple Stressors on Populations") with location-specific demography, territory sizes, and life history information to model the current and potential future abundance and dynamics of vireos across Fort Hood and surrounding counties. We explored the impact of alternative rates of exchange among regional breeding populations as well as the potential differential contributions of different sources and sinks to regional vireo viability. Further, we explored the effects of increased off-base cowbird control and habitat restoration on public lands in altering regional source-sink dynamics and population trajectories. In Task 2, we assessed how climate change, through its effects on survival and reproduction could affect vireo abundance and source-sink dynamics using results from a climate-demography analysis. We found that most habitats off of Fort Hood behaved like population sinks, and rates of exchange among on- and off-base populations can measurably alter regional population outcomes and source-sink dynamics. The stability of source-sink characterizations differed with the type of system change. Management actions may need to weigh interventions that improve regional abundance against those that alter regional source-sink dynamics as abundance and source-sink states are sensitive to different kinds of system changes. Climate change may result in general population increases, suggesting that future source-sink dynamics may be driven more by density-dependence and inter-population dispersal than contemporary populations.

3.1 Modeling Black-capped vireo regional source-sink dynamics

3.1.1 Introduction

Seven study sites on Fort Hood have been the focus of past vireo monitoring efforts including territory mapping, mark and re-sight efforts and associated demographic analyses. Four of these sites represent higher quality vireo habitat (East Range - ER, West Fort Hood - WF, Manning 2 - M2, Jack Mountain - JM; Kostecke and Cimprich 2008a; 1997-2006) with long time-series of data (>10 years). Lower quality sites (Maxdale - MX, Taylor Valley - TV, West Range - WR; 2011-2014; Task 2) were intensively studed from 2011-2014 by the University of Washington. Beyond Fort Hood, we evaluated four much smaller populations (Balcones Canyonlands National Wildlife Refuge – BC, San Saba – SS, Colorado Bend State Park – CB, and Goldwaite – GW) amidst the largely inhospitable matrix of agriculture, ranchland, developed, and urban areas in the surrounding counties. These sites were evaluated for the same duration and using the same methods as on-base lower quality sites (see Phase 2).

Although areas of the base function as population sources (Phases 1 and 2), the Fort Hood population is reliant on continued trapping and shooting of cowbirds (Wilsey et al. 2014). Off of Fort Hood, cowbird control was more recently enacted. Yet many of these populations still function as population sinks (Phase 1). Although site-specific populations have been well studied, the interactions and population dynamics among on- and off-base populations are poorly understood. Limited banding data (Phase 1; Cimprich, *unpublished data)* indicate that there are birds moving among on- and off-base breeding populations. However, the degree to which long-distance dispersal could impact regional population dynamics has not been investigated. Due to its large area and population size (>90% of vireos in the study population), the Fort Hood population is akin to a mainland population, with off-base 'island' populations separated by more than 30 km (mean 60 km) of largely inhospitable matrix. Hence, regional population sizes are expected to be primarily a product of mainland population conditions. However, island populations may contribute to regional outcomes, particularly if they behave like strong sinks or if exchange rates among mainland-island populations are high.

To examine the degree to which regional vireo abundance and source-sink dynamics depend on mainland-island interactions, we simulated site-specific habitat use and demography under alternative movement, cowbird control, habitat restoration, and climate scenarios within a spatially explicit individual-based modeling framework (HexSim version 4.0). We also evaluated the contribution of key source, sink, and high abundance sites using habitat/population removal experiments. In doing so, we assessed the degree to which emergent source-sink dynamics changed with system alterations and evaluated the stability of current source-sink categorizations.

3.1.2 Methods

3.1.2.1 Approach

We used the spatially explicit individual-based modeling framework, HexSim, to construct a simulation model of vireo habitat use, movement, and demography. In this mechanistic model, source-sink dynamics were an emergent function of multiple interacting conditions including location-specific habitat conditions, demography, territory sizes and density, and local and distant movements. Variation in local conditions gave rise to differential population states (i.e., sources and sinks) when summed across individuals through time. We used this simulation framework to evaluate both the current and future possible states of this source-sink system using a range of alternative movement, management, and landscape changes.

3.1.2.2 Habitat

Black-capped vireos generally breed in patchy shrublands, using areas that vary in structure and species composition (Wilkins et al. 2006, Wilsey et al. 2012). As this habitat information was not consistently available across our study area, we used a hybrid spatial approach to combine the best available information in each location within a common habitat-population framework.

On Fort Hood, we used a continuous habitat suitability model (SERDP grant RC-1541; Wilsey et al. 2012; 75 m pixel resolution) to indicate habitat 'quality' throughout the military base. The habitat suitability model used vireo location data (2002-2003 surveys; Cimprich and Kostecke 2006), vegetation type and height, soil depth, and edge-density maps (Wilsey et al. 2012) to estimate the suitability of areas for vireo use. Pixels with habitat suitability probabilities in the upper two tertile bins (≥ 0.36) indicated likely habitat (Wilsey et al. 2014), and were used to build exclusive multi-pixel territories. In high densities, individuals without territories could temporarily occupy areas below this threshold.

Study populations away from Fort Hood are comparatively small, isolated, and lacked habitat suitability characterizations (i.e., given the lack of available LiDAR and stratified presence location sampling, the habitat suitability model could not be applied to the off-base sites). To delineate habitat from non-habitat (matrix) we created minimum convex polygons (MCP) for each of the sites to encompass mapped territories from 2011-2014. Homogeneous habitat within the MCPs was used by individuals to construct shared or exclusive territories, depending on their location and measured territory sizes.

3.1.2.3 Population model

We constructed a three-stage habitat-population model in the HexSim modeling platform, explicitly modeling only males (similar to Wilsey et al. 2014). We made this simplification because adults (in their second breeding season) and juveniles (in their first breeding season) establish and defend territories that generally include a paired female. Further, Fort Hood count data and fecundity estimates also reflect successful male territories (Cimprich and Heimbuch 2012), and a males-only model reduces computation time. Adult males (5478) were placed in habitat according to their 2012 abundance and distribution among sites (Cimprich and Heimbuch

2012; Task 2 data). Birds on Fort Hood, but outside of the demographic study sites were preferentially placed in higher suitability pixels and were given multiple opportunities to move and locate a suitable territory, until virtually all had successfully established a territory. Simulated vireos then underwent an annual flow of events including juvenile local and long-distance dispersal, territory selection, reproduction and survival (Figure 3.1.1).

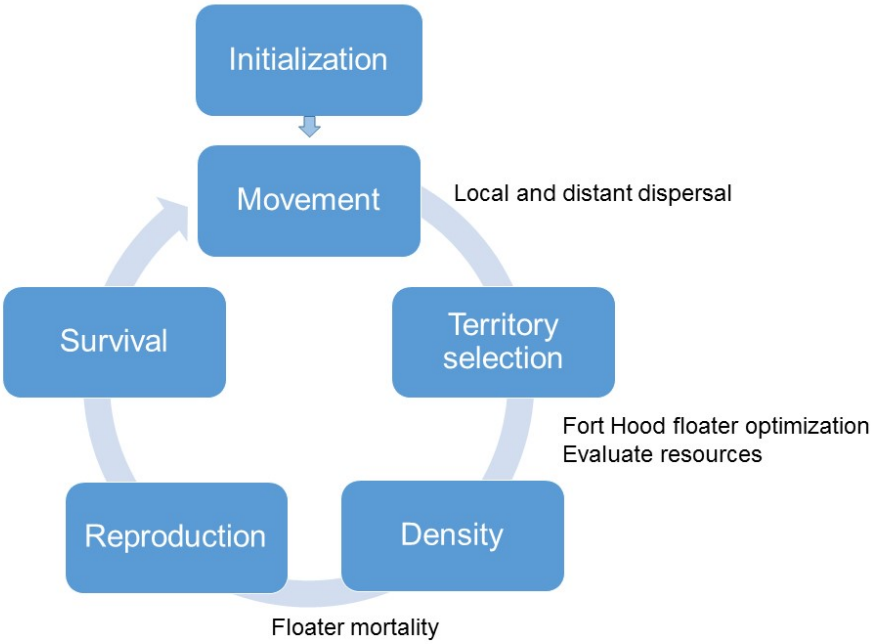

Figure 3.1.1. Annual series of events in the black-capped vireo life cycle as implemented in HexSim.

3.1.2.3.1 Movement

Black-capped vireos migrate away from their Texas breeding range to their winter range in Mexico (Graber 1961, Vega Rivera et al. 2011); however, surviving adults often return to the same breeding territory after migration (Phase 2 data). As our focus was on breeding population dynamics, our model assumed that surviving adults remained on their territories. Similarly, many juvenile black-capped vireos return to their natal area after migration to establish territories a short distance away (Phase 2 data). These local juvenile dispersals (along with floaters i.e., birds without territories) took place on Fort Hood by drawing a path length from a uniform distribution with a minimum path length of 3.75 km (50 pixels) to a maximum of > 30 km. Individuals would then move up to their maximum path distance, but could prematurely stop if they encountered 3 consecutive pixels of habitat after 5.6 km (75 pixels). Simulated birds were attracted to higher habitat suitability scores (above the habitat threshold) and moved with forward momentum (80% autocorrelation in path direction over the previous 5 pixels). In combination, these rules resulted in simulated juveniles moving a mean of 2.5 km (with a population lognormal distribution of path lengths) from their natal nest to their selected territory (described below), matching natal dispersal records (mean 2.6 km, range 0-30 km, SD = 4.4 km; lognormal distribution of dispersal distance records; Cimprich, *unpublished data*; Task 2

dispersal data, excluding inter-patch distance records). The few individuals that became 'lost' in the matrix were placed back in habitat prior to territory establishment. Simulated birds in off-base habitat patches were able to move and occupy any vacant pixel in the habitat patch, without search limitations.

Dispersal events between Fort Hood and off-base breeding sites occur but are rarely observed (Task 2 data, Cimprich *unpublished data;* Cimprich et al. 2009). As there are few tracked birds relative to the overall population size and only a few years of data collected outside of Fort Hood, the frequency and patterns of movements among Fort Hood and more distant populations are poorly understood. We used natal dispersal data (1992 – 2015) and inter-patch distances to infer distance-based rates of exchange among breeding populations. We divided the 5 inter-patch dispersal records (≥ 30 km, minimum inter-patch distance) by the total natal dispersal records (324) to estimate the proportion of vireos dispersing within- (0.985) versus among-patches (0.015). As the recorded inter-patch dispersals were primarily to the closest off-base site (Balcones Canyonlands National Wildlife Refuge), we constructed an inverse distance-based matrix of inter-patch dispersal probabilities to move simulated birds from one breeding population to another. Alternative inter-patch movement probabilities were also evaluated (see movement scenarios below).

3.1.2.3.2 Territory Selection

After moving, individuals in study sites explored an area equivalent to their entire study site and selected the best location to establish their territory (Figure 3.1.2 – red and orange). Simulated bird on Fort Hood but outside of demographic study sites explored an equivalent area (e.g., radius of 7 pixels; Figure 3.1.2 – white, gray). Territory selection criteria differed among vireo locations, reflecting site-specific territory sizes and heterogeneous Fort Hood habitat suitability (Table 3.1.1). As male territories overlap to some extent, minimum observed territory sizes (Cimprich, *unpublished data*, Phase 2 data) were used to construct maximum, non-overlapping territories (Table 3.1.2). Where territory sizes were smaller than a single pixel, multiple male territories could be established in the same pixel. Conversely, where territory sizes spanned multiple pixels, simulated birds were required to piece together a minimum number of pixels. Simulated birds on Fort Hood also considered the habitat suitability of pixels when constructing their territory, requiring a minimum territory condition to establish a territory (territory size in pixels * mean site habitat suitability value; Table 3.1.1). Outside of study areas on Fort Hood, birds also sought to build territories with a target condition (i.e., level of resources; mean territory size* mean habitat suitability). Individuals were given multiple territory selection opportunities to ensure that simulated birds could occupy proximate suitable territories, minimizing the number of floaters (i.e., without territories). Any remaining floaters on Fort Hood were given another opportunity to move (locally, with similar but shorter movement distances) and establish a territory (as previously described) before a 50% mortality penalty was applied to birds without territories.

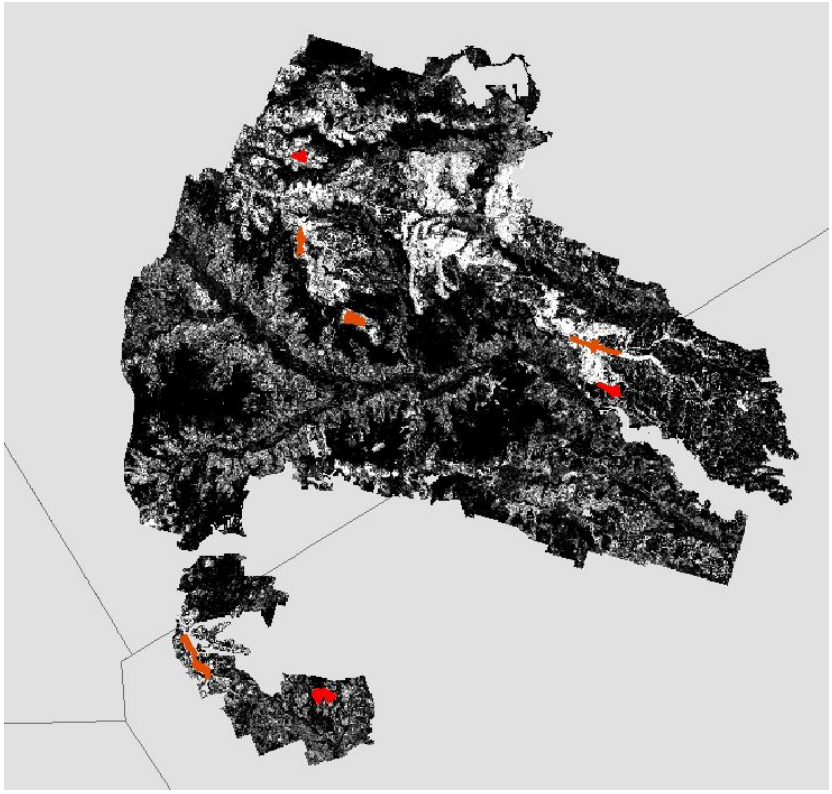

Figure 3.1.2. Black-capped vireo study sites (red and orange) superimposed on the Fort Hood habitat suitability map.

Table 3.1.1. Simulated black-capped vireo group sizes, habitat selection search areas, territory sizes and conditions for territory establishment across the study area in Texas

Site	Empirical min territory size (ha)	Max. territory size (pixels; ha)	Number of coinciding males (max)	Mean site habitat suitability	Min. territory condition	Explored area (pixels)
SS	0.24	1.0; 0.49	2	1*	1	65
BC	0.44	1.0; 0.49	1	1*	1	275
GW	1.41	2.9; 1.41	1	1*	2	39
TV	0.44	1.0; 0.49	1	44.3	40	144
CB	0.95	2.0; 0.95	1	1*	1	214
MP	2.22	4.6; 2.22	1	1*	4	31
MX	0.60	1.2; 0.60	1	36.0	44	179
WR	0.54	1.1; 0.54	1	61.2	68	121
ER	0.14	1.0; 0.49	3	94.8	27	179
JM	0.28	1.0; 0.49	2	85.8	49	114
M2	0.18	1.0; 0.49	2	90.5	33	95
WF	0.10	1.0; 0.49	5	78.3	16	185
FH	0.3 (min), 0.43 (mean)	1.0; 0.49	1	58.0	17 (min), 51 (target)	179

*Off-base sites with binary habitat characterizations are indicated by pixel scores of 1

3.1.2.3.3 Reproduction

Simulated birds were assigned a location-specific probability of having a successful territory that produced at least one fledgling (through one or more broods) in a given year. Individual success probabilities were drawn from a Bernoulli distribution using site-specific empirical territory success probabilities (Phase 2 data; Cimprich, *unpublished data*). Birds with successful territories were then assigned a number of male fledglings (assuming an equal sex ratio at birth) based on the mean number of fledglings per total successful territory in a given site (Table 3.1.2). Simulated birds on Fort Hood outside of the demographic study areas were assigned interpolated territory success and number of fledglings based on the resource condition of their territory. Site-specific habitat suitability values were used to fit a linear relationship to predict territory success and number of fledglings in lower quality habitats (up to mean suitability values of 0.44, and 0.61 respectively), where an increasing relationship with higher habitat suitability pixels was evident. Habitats similar to higher suitability study sites were assigned the mean territory success rates and mean number of fledglings of high quality study sites. Site-specific fledgling data included 2005-2015 for military study sites ER, JM, M2, WF (Cimprich, *unpublished data*), and 2011-2014 for non-military study sites (Task 2 data) and 2011-2014 for territory success rates.

Table 3.1.2. Black-capped vireo territory success and number of fledglings assigned to simulated birds based on their location within a study site or resource condition of their territory (Fort Hood).

Site	Territory success Mean	Territory success SD	Male fledglings/ successful territory	Adult survival mean; (SE)
SS	0.54	0.33	1.98	0.52 (0.05)
BC	0.46	0.16	1.50	0.36 (0.05)
GW	0.54	0.28	1.79	0.46 (0.14)
ER	0.64	0.14	1.78	0.33 (0.04)
CB	0.34	0.14	1.70	0.46 (0.05)
MP	0.29	0.23	1.25	0.45 (0.07)
MX	0.43	0.10	1.52	0.41 (0.04)
WR	0.69	0.13	1.77	0.35 (0.04)
ER	0.62	0.12	1.66	0.37 (0.03)
JM	0.53	0.07	1.76	0.27 (0.04)
M2	0.74	0.13	1.80	0.54 (0.03)
WF	0.63	0.13	1.69	0.44 (0.04)
FH	0.43-0.64	0.12	1.52-1.79	0.41 (0.04)

3.1.2.3.4 Survival

The annual survival of adult vireos on Fort Hood differs among study sites (Kostecke and Cimprich 2008b; Phase 2 data) and simulated birds were assigned the corresponding empirical surival rates measured in their site. As a robust relationship between habitat suitability values

and adult survival rates on Fort Hood was not evident, individuals outside of the study sites were given a mean survival rate that averaged survival across all Fort Hood study sites (excluding JM which was not grouped with other sites in the Phase 2 analysis). Empirical means and variances (Phase 2 data) were used to create site-specific normal distributions, from which survival rates were pulled each year. Location-specific annual draws from distributions were correlated in space on Fort Hood to represent 'local' environmental stochasticity and uncorrelated among off-base breeding populations. Hatcher (young of the year) survival was defined as the probability of a vireo banded as nestling surviving and returning to a study site following migration (Phase 2 data). As resighting probabilities were low (<2.6% of males; Phase 2 data) and confidence intervals of estimates are large, we explored two alternative hatcher survival rates to account for possible under-estimates of survival resulting from incomplete site fideltiy (Cilimburg et al. 2002, Kostecke and Cimprich 2008a). We simulated population dynamics using the empirically-estimated hatcher survival rate (0.46 +- 0.07; Phase 2 data), as well as a higher rate of 0.54 (within the 95% CI), chosen to produce a largely stable population and approximate the range of abundance estimates from 2005-2015 (Cimprich and Heimbuch 2011, 2012; Cimprich, *unpublished data*).

3.1.2.4 Simulations

In baseline simulations, we simulated population dynamics for the regional system over 50 years, and summarized population outcomes across 25-50 replicate simulations. In addition to assessing location-specific popualtion sizes through time, we also tracked individual births, deaths, immigration, and emigrations through space. We evaluated two source-sink metrics: 1) Productivity (births – deaths), and BIDE (births + immigration) – (deaths + emigration), tallied for for each study site and each pixel on Fort Hood. Sources were inferred in locations with positive source-sink metric values. Negative values indicated sinks.

To assess the impact of juvenile dispersal on source-sink outcomes, we constructed alsternative movement scenarios by implementing different rates of exchange among discrete breeding populations. We assumed that empirical estimates underestimated exchanges of birds and additionally evaluated scenarios with higher proportions (3 or 10 times) of hatcher dispersal.

To evaluate which areas have the largest effect on Fort Hood population viability (i.e., source and sink contributions), we iteratively removed study sites representing the strongest source and sink populations as indicated by the BIDE metric. We also simulated the persistence and source-sink status of off-base study sites in the absence of Fort Hood as it is the primary source of inter-breeding popualtion dispersers.

3.1.2.4.4 Cowbird control scenario

In efforts to improve conditions for black-capped vireo persistence, nest parasitizing cowbirds are controlled using trapping and/or shooting in the majority habitat on Fort Hood (excepting West Range and surrounding area). More recent cowbird control efforts in satellite/island popualtions (BC: 2011-2014) have also been initiated (e.g., 2013 or 2014 in CB, SS) but the intensity of control varies among sites. To examine how further increases in off-base cowbird control could affect source-sink dynamics, we simulated the impact of increased cowbird control

effort on territory success and number of fledglings. We quantified the difference in territory success and fledglings before versus after cowbird control was implemented at off-base sites and used this difference to indicate the degree to which increased cowbird control intensity could further improve reproductive success. To do so, we averaged annual measures of reproductive success before cowbird control (CB and SS sites from 2012/2012-2013), subtracted these from 2014 values, and averaged the resulting differences among sites to result in a 0.28 increase in territory success, and 0.24 increase in the number of males fledged from successful territories.

3.1.2.4.5 Habitat restoration scenario

To examine the degree to which habitat restoration actions in off-base breeding populations could change regional source-sink dynamics, we digitally expanded and restorated possible vireo habitats and simulated emergent source-sink dynamics. We identified public lands in the counties of study populations that: 1) were composed of likely vireo habitat types including deciduous, coniferous, mixed forest, or shrub vegetation classes (NLCD, 2011), 2) were at least 15 ha in size (Figure 3.1.3 - blue), 3) and excluded extreme topographical features. Simulations began with an additional 100 males randomly distributed among new habitats. Demographic conditions and territory sizes in restored sites were equivalent to the mean off-base conditions, with similar territory sizes, survival, and reproduction rates to the Balcones population. Distance-based dispersal was also updated to include restored patches and distribute dispersing individuals among all patches.

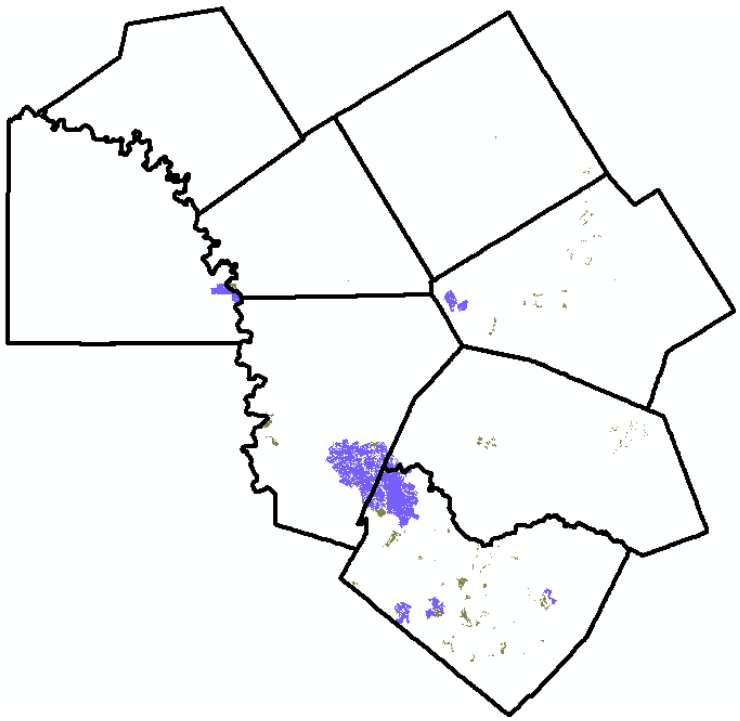

Figure 3.1.3. Habitat restoration locations (blue/purple) evaluated in the off-base habitat restoration scenario for black-capped vireos near Fort Hood, Texas.

3.1.3 Results

3.1.3.1 Population trajectories

Using field-measured demographic parameters, the modeled regional population declined throughout the fifty-year simulation period. Declines in the first decade of simulations resulted in an abundance equivalent to 2008, and continued declines yielded a small (<1000 male) population by 2060 (Figure 3.1.4). Using the 'steady' scenario with elevated hatcher survival rates, the population was relatively stable over the fifty-year period with a slight decreasing trend, approximating the expected population trajectory. The population size was within the range of variation observed between 2005 and 2012 and resulted in a final population size that exceeded 2008 and 2011 empirical estimates.

The degree to which breeding populations exchanged juveniles via long-distance dispersal impacted regional population outcomes. When we tripled the proportion of juveniles moving among breeding populations increased, mean population sizes were substantively lower. With ten times higher inter-population dispersal, abundance approximated that of the empirical scenario, offsetting the increased juvenile survival of the steady scenario (Figure 3.1.4) and turning some sources (i.e., M2) into sinks (Table 3.1.4).

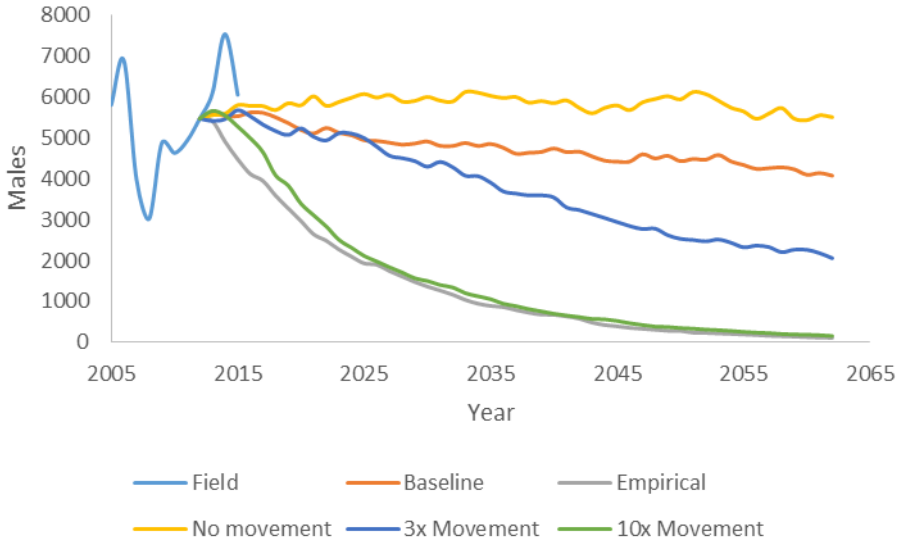

Figure 3.1.4. Simulated black-capped vireo abundance under alternative baseline and movement scenarios relative to field abundance estimates, using both empirical demographic estimates and increased hatcher survival rates (baseline) to produce a comparatively steady population.

Table 3.1.3. Simulated black-capped vireo source-sink dynamics using empirical demographic rates and higher hatcher survival rates (steady scenario). Source-sink dynamics are characterized using productivity and BIDE metrics during the first and last years of simulations. Sources are indicated by positive metric values, sinks by negative values.

Site	Empirical years 5-10 (rapid decline)		Empirical years 45-50 (near extinction)		Steady years 5-10 (slow decline)		Steady years 45-50 (slow decline)	
	Prod.	BIDE	Prod.	BIDE	Prod.	BIDE	Prod.	BIDE
SS	-268	-114	-18	-1	-204	**64**	-116	-20
BC	-800	-307	-46	-29	-976	-229	-615	-113
GW	-541	-306	-45	-32	-777	-560	-527	-367
CB	-733	-303	-39	-10	-939	-230	-611	-165
TV	-121	-95	0	**8**	-75	-130	-40	-46
MP	-973	-862	-41	-23	-1474	-1346	-965	-877
MX	-27	-31	-4	-6	-34	-26	-28	-17
WR	-65	-24	-1	**1**	-24	-19	**44**	**3**
ER	-229	-274	-10	-15	-130	-156	-47	**6**
JM	-214	-196	-18	-10	-210	-100	-165	-136
M2	213	-56	5	-9	**508**	**132**	**276**	**204**
WF	-19	-89	-2	-2	-7	-102	-2	-15
FH	-33334	-34634	-1423	-1524	**7809**	**5854**	**166**	-1374

Scenarios with rapidly declining or small dwindling populations (i.e., empirical scenario years 5-10 and 45-50) primarily resulted in sink populations throughout the landscape (Productivity and BIDE metrics; Table 3.1.3). In the steady population scenario, the majority of sites still functioned as sinks with MP acting as the strongest off-base breeding population sink. Fort Hood and M2 served as the strongest sources, and ER, WR, and BB functioned as weaker sources during the early or late evaluation periods.

To evaluate the contribution of key sources and sinks to regional population abundance and the stability of source-sink classifications, we iteratively removed FH, M2, ER, and MP patches. Relative to the baseline (steady) scenario, the removal of the strongest source, M2, had little effect on the regional population size (Figure 3.1.5) and a minor effect on the source-sink status of breeding populations (SS, ER patches; Table 3.1.4). Removing the weak source ER and the strong sink MP had larger effects on regional population size. When ER was removed, FH acted more as a source population, and WR became a population sink. The removal of the strongest off-base sink (MP) resulted in slight changes in the balance of demography and movements changing the source-sink status for 3 patches (WR, ER, SS). Expectedly, the absence of the Fort Hood military base reduced the population to a very small population size (less than 100 males), causing local off-base extinctions and vireos being sustained in SS and BC breeding populations.

In scenarios of increased cowbird control in off-base sites, increased territory success and number of fledglings had little impact on the overall population but resulted in substantive improvements for many off-base breeding populations. San Saba, Balcones, and Colorado Bend populations all became sources, but the most central population (MP) remained a sink.

The restoration of non-habitat to create new patches, with conditions similar to those on Balcones (BC), did not result in the expected net population increase (Figure 3.1.6). Restored

habitats acted as population sinks (Table 3.1.5) and all populations performed more poorly (i.e., lower BIDE scores).

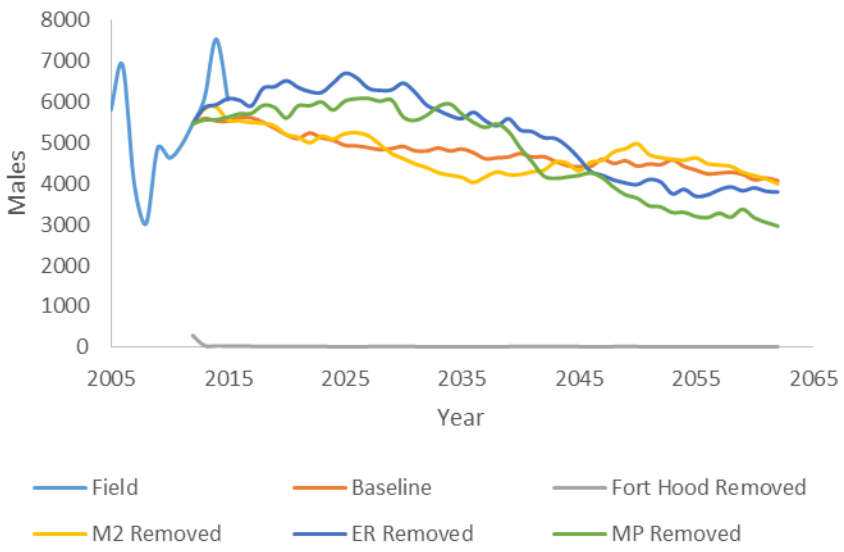

Figure 3.1.5. The effect of habitat removals on simulated black-capped vireo abundance and population trajectories, relative to field estimates and baseline predictions

Table 3.1.4. Source-sink status of breeding black-capped vireo populations under alternative habitat removal and inter-population dispersal scenarios, as characterized by positive or negative BIDE values (years 45-50).

	No M2	No MP	No ER	No FH	3x Dispersal	10x Dispersal	Baseline
SS	**So**	**So**	Si	**So**	Si	Si	Si
BC	Si	Si	Si	**So**	Si	Si	Si
GW	Si	Si	Si	Si	Si	Si	Si
CB	Si	Si	Si	0	Si	Si	Si
TV	Si	Si	Si	0	Si	Si	Si
MP	Si	NA	Si	Si	Si	Si	Si
MX	Si	Si	Si	0	Si	Si	Si
WR	**So**	Si	Si	0	Si	Si	**So**
ER	Si	Si	NA	0	Si	**So**	**So**
JM	Si	Si	Si	0	Si	Si	Si
M2	NA	**So**	**So**	0	**So**	Si	**So**
WF	Si	Si	Si	0	**So**	Si	Si
FH	Si	Si	**So**	NA	Si	Si	**Si**

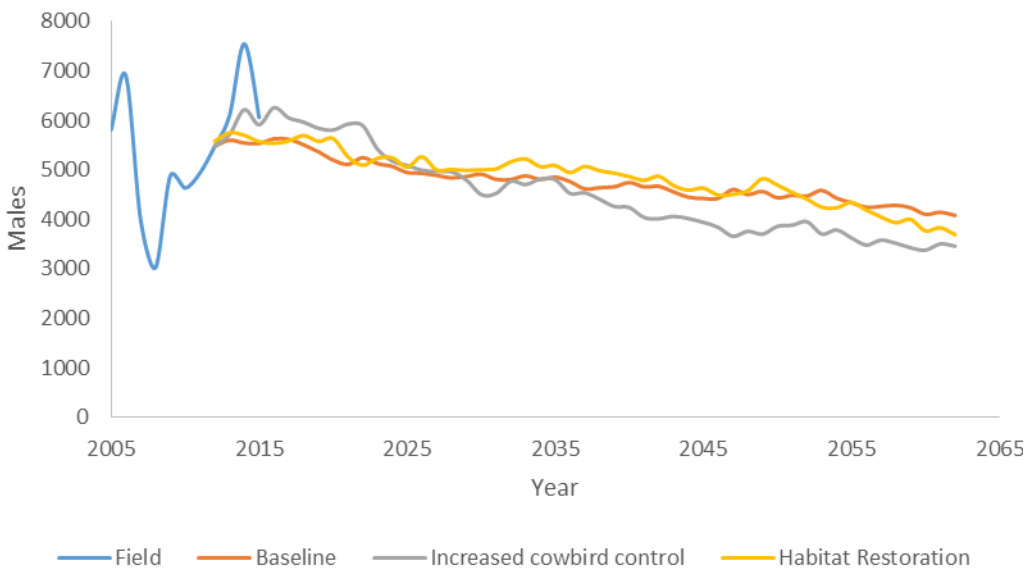

Figure 3.1.6. The relative influences of simulated off-base management actions of regional population abundance of black-capped vireos

Table 3.1.5. Source-sink of breeding black-capped vireo populations under alternative off-base cowbird control and habitat restoration scenarios, as characterized by positive or negative BIDE values (years 45-50).

	Increased cowbird control	Habitat restoration	Baseline
SS	**244**	-1	-20
BC	**683**	0	-113
GW	-414	0	-367
CB	**413**	0	-165
TV	-36	-165	-46
MP	-1085	0	-877
MX	-32	-30	-17
WR	-25	-37	**3**
ER	-60	-161	**6**
JM	-102	-280	-136
M2	**112**	**48**	**204**
WF	-20	-45	-15
FH	**2073**	-6495	-1374
Restored		-23	

3.1.4 Discussion

3.1.4.1 Effects of system changes

Distant dispersal: By virtue of Fort Hood's large population size, breeding population movement flows were primarily from Fort Hood to off-base sink populations. The re-distribution of juveniles to suboptimal locations resulted in a greater number of deaths in off-base locations, with fewer individuals on Fort Hood to move shorter distances into source areas. Although more complete movement data are required to characterize the frequency and patterns of distant dispersal, our results indicate that actions aimed at increasing the dispersal to off-base locations may be detrimental to regional population persistence when off-base sites act as sink populations and territory site fidelity is high.

Habitat removals: Population responses to the removal of key habitats revealed the contribution of individual sites and the degree of inter-dependency among sites. Removing small individual study sites (i.e., strong sources or sinks) had little effect on system-wide abundance, indicating that the loss of small sites is not likely to cause lasting population effects. By contrast, removing the mainland Fort Hood changed the entire system indicating the dependency of vireos on the high abundance of birds on the military base.

Cowbird control: Increased cowbird control in off-base areas resulted in the conversion of most sinks to sources, although some sinks actually strengthened. The most central off-base patch (MP) had a large number of immigrants relative to emigrants and an isolated patch (GW) had a higher population size with low emigration, but a large number of local deaths. These results indicate that cowbird control may be more or less effective depending on the rates and patterns of immigration, emigration, and local density limitations. Although increases in off-base cowbird control affected local and region-wide source-sink dynamics, there was little impact on regional abundance. Large population size differentials among on- and off-base populations make Fort Hood a more responsive target if actions can be applied to a larger number of birds. However, improvements to off-base sinks may be an important objective if long-distance movements to off-base sites are more frequent than our baseline conditions.

Habitat restoration: Adding new off-base habitat with conditions similar to the largest off-base site (Balcones) did not measurably improve vireo abundance through time. This indicates that off-base habitat restoration may be most effective if coupled with improvements in cowbird control or other means of improving demography.

3.1.4.2 Stability of source-sink dynamics

3.1.4.2.1 Methods of evaluation

Source-sink modeling results largely agree with field-based classifications from Task 2, with both approaches classifying the off-base Balcones, Colorado Bend, and Goldthwaite sites as sinks, as well as the on-base Maxdale, Manning 2, and Jack Mountain populations as long-term sinks. However, some amount of disagreement was expected as our field and modeling approaches to source-sink characterizations fundamentally differ. Field-based approaches focus

on the balance of birth and death rates with limited consideration of movement among populations resulting from a lack of inter-population dispersal data. By contrast, the modeling approach explicitly considered the exchange of individuals among populations in source-sink calculations and tracked every individual in the population through time. Baseline source-sink predictions were made using long-term population data (time steps 45-50), and were the product of several stochastic simulation repetitions that included a broader range of population conditions than experienced during field data collection and calculation of associated stochastic growth rates. The simulation model also included additional data describing habitat, territory sizes, and territory success to represent the influences of source-sink dynamics throughout Fort Hood on regional population dynamics. Despite differences in field and modeling approaches, short-term modeling results (years 5-10; but not long-term results) support the field source status of San Saba and the sink status of East- and West Range. However, differences in long-term modeling predictions may indicate that these sites may not always behave as sources. At all time periods of evaluation, Taylor Valley and West Fort Hood behaved as sinks in the simulation model, albeit West Fort Hood was a relatively weak sink. High emigration, in part, resulted in the classification of West Fort Hood and Taylor Valley as sinks.

The comparison of field and modeling results indicates that some source-sink signals are strong enough to be detected and predicted by multiple approaches, affording a greater degree of confidence in managing populations based on transcendent source-sink signals. Yet, other source-sink signals may be a product of transient environmental conditions or influenced by analysis or modeling constructs. Sites with weaker source-sink signals may require additional data collection and analysis to understand the factors driving local population dynamics and make appropriate management decisions.

3.1.4.2.2 System alterations

Beyond stochastic variability, directional system changes in the landscape or the way in which individuals use the landscape, have the potential to dramatically change regional population dynamics. We conducted experiments that altered movement-based rates of exchange among breeding populations, habitat removals and additions, and management of nest parasitizing cowbirds. Our results indicate that system changes involving small study site removals and movement (via increased probability of distance-based exchanges) are likely to result in fewer changes (~20%) in source-sink status than management actions involving cowbird control and habitat restoration (~45% of sites). This suggests that managing individual breeding populations based on their predicted source-sink states is likely to be less risky when changes to the habitat footprint are small or if the propensities of movement, rather than the patterns of exchange of birds is altered. By contrast, management actions that change local demographic conditions (e.g., off-base cowbird control) or changing the population distribution by adding birds to new places in the landscape (i.e., habitat restoration), are likely to change the source-sink status of many populations, necessitating re-evaluation of source-sink dynamics.

In addition to source-sink considerations, management actions also need to consider the abundance and stability of the regional population size, which is affected by different factors than those influencing source-sink stability. For example, regional abundance was much more responsive to changes in the proportion of birds emigrating from Fort Hood, and impacted little

by off-base cowbird control efforts. Hence, effective management actions are likely to require the simultaneous consideration of factors that support regional abundance as well as local and system-wide source-sink dynamics.

3.2 Climate-demographic analysis

3.2.1 Introduction

To assess the role of climate in shaping the past demography of the black-capped vireo, we 1) statistically evaluated a range of historical climate variables against time series of territory success, mean fledglings per successful territory (Cimprich, *unpublished data*), and adult survival (Table 3.2.1; Kostecke and Cimprich 2008b) on the Fort Hood military installation in Texas. We then 2) assessed the degree to which climate change could alter future demography over the next half-century (2050s) by applying historical climate-demography relationships to future climate conditions using ClimateNA predictions (Hamann et al. 2013; https://sites.ualberta.ca/~ahamann/data/climatena.html). We then 3) used future demographic conditions to simulate population dynamics and examine the degree to which abundance and population dynamics could be altered in the future using the vireo (HexSim) population model described in the previous task.

3.2.2 Methods

3.2.2.1 Historical Climate-demography Relationships

We used historical climate data (temperature, precipitation, drought metrics; Table 3.2.2) along with time series of demography (territory success, fledglings per successful territory, and adult survival; Table 3.2.1) to construct statistical climate-demography relationships.

We downloaded monthly historical climate data (PRISM) for 1995-2013 from ClimateNA and downscaled the spatial climate data (from 4-km PRISM resolution) using an input digital elevation model (90 m DEM). We selected and evaluated a range of predictor variables including temperature, precipitation and drought-related climate metrics (Table 3.2.2) calculated over the breeding seasons (spring and summer) and associated breeding months (March – August). We limited our evaluation to temperature, precipitation, and drought variables as these impacts were considered more directly and imminently related to vireo demography during the months that they resided on Fort Hood.

To evaluate past relationships between climatic conditions and demography, we constructed multi-variate generalized linear models for each of our response variables: adult survival, territory success, and number of fledglings.

As many climate variables are related, we first reduced the number of candidate variables by testing each response variable with each predictor variable in univariate generalized linear models (GLMs; Table 3.2.1). All statistical models were implemented in R (version 3.2.0; R Core Team, 2015) using the “stats” and “betareg” packages. We retained only the variables that were significant in univariate models ($p \leq 0.1$) or the variables with the lowest three p-values in non-significant models for subsequent evaluation. We further reduced our climate variable set by assessing pairwise correlations among predictor variables. When predictor variables were

highly correlated (> 0.5), we retained the climate variable with the lower univariate p-value. This two-step procedure resulted in multivariate models with up to 10 variables.

The remaining climate variables were used to create alternative multivariate models. All variables were standardized (scaled), and the full model for each response variable was reduced in a step-wise fashion (stepAIC R package) until the AIC_c (Akaike Information Criterion corrected for small sample size; AIC_c) value was optimized. The highest ranking models were evaluated for overfitting and the most parsimonious model was selected for use in future climate-demography projections. To account for cowbird variability through time, the number of cowbirds that were removed annually was evaluated as a model covariate.

Table 3.2.1. Black-capped vireo demographic data used in the climate-demography analysis.

Demographic variable	Data structure	GLM Distribution	Years	Fort Hood Sites
Territory success (%)	Success/Failure	Binomial	2000 – 2013	ER/M2/WF/JM
Mean fledglings per successful territory	Mean count	Lognormal	2005 – 2013	ER/M2/WF/JM
Adult survival (%)	Percent survival	Beta	1998 – 2006, 2011 – 2013	ER/M2/WF

Table 3.2.2. ClimateNA climatic variables evaluated in the historical climate-demography analysis. Monthly variables were evaluated individually for March, April, May, June, July, and August. Spring refers to the average conditions during March through May. Summer refers to June through August. Nesting refers to mean conditions during March to August.

Time periods	Temperature	Precipitation	Drought
Monthly, Spring, Summer, Nesting	Tmax	PPT	CMD (climatic moisture deficit)
Monthly, Spring, Summer, Nesting	Tmin		
Monthly, Spring, Summer, Nesting	Tave		

3.2.2.2 Climate-demography Projections

We downloaded predicted (future) climate data from ClimateNA (Hamann et al. 2013; https://sites.ualberta.ca/~ahamann/data/climatena.html), including projections from several global climate models (GCMs from CMIP5; Table 3.2.3) for the 2050s (which averages the years 2041-2070) and 2080s (2071-2100), and two different representative concentration pathways (RCPs 4.5 and 8.5) for each GCM. We similarly downscaled the spatial climate data (from 4-km PRISM resolution) using an input digital elevation model (90 m DEM). The eight GCMs were used to provide a range of demographic responses to projected climate change. GCMs spanned a range of climate conditions from “hot/dry” (e.g., IPSL-CM4), “middle-of-the-road” climate condition (CCSM-4), to “cool/wet” scenarios (e.g., INM-CM4). For each GCM, two different representative concentration pathway scenarios (RCPs) 4.5 and 8.5 were also evaluated.

The most parsimonious historical climate-demography equations were then 'updated' with future climate data for each GCM and RCP, creating 16 new predictive equations for each response variable (adult survival, territory success, and number of fledglings and time period). Each equation was then 'solved' for the predicted future demographic rate by multiplying the Beta/regression coefficient value from the historical climate-demography equation with the updated future climate variable value.

Table 3.2.3. Global circulation models evaluated in the black-capped vireo climate-demography analysis.

Model	Model expansion	Origin	Type
CanESM2	Second Generation Canadian Earth System Model	Canada	Earth System Model
CCSM4	Community Climate System Model, version 4	U.S.A.	Atmosphere-ocean coupled
CNRM-CM5	Centre National de Recherches Météorologiques Coupled Global Climate Model, version 5.1	France	Atmosphere-ocean coupled
GFDL-CM3	Geophysical Fluid Dynamics Laboratory Climate Model, version 3	U.S.A	Atmosphere-ocean coupled
HadGEM2-ES	Hadley Centre Global Environment Model, version 2–Earth System	UK	Earth system model chemistry coupled
INM-CM4	Institute of Numerical Mathematics Coupled Model, version 4.0	Russia	Atmosphere-ocean coupled
IPSL-CM5A-MR	L'Institut Pierre-Simon Laplace Coupled Model, version 5, coupled with NEMO, mid resolution	France	Earth system model chemistry coupled
MPI-ESM-LR	Max Planck Institute Earth System Model, low resolution	Germany	Earth System model

3.2.2.3 Future Climate-demography Simulations

To assess the degree to which climate change could affect the future outcome of vireos on Fort Hood, we integrated predicited changes in each demographic variable into a common population framwork to simulate their combined influences on abundance and population dynamics. For each response variable and RCP 4.5 and 8.5 scenarios, we averaged the 8 future demographic rates from the 8 GCMs. We then used the mean percent change in each demographic rate to modify baseline adult survival, territory success, and the number of fledglings in the habitat-population model framework from Task 1 (Phase 3). We then simulated population dynamics through time and evaluated ensuing population sizes and growth rates.

3.2.3 Results

3.2.3.1 Historical Climate-demography Relationships

The climate variables considered in historical multivariate models included primarily temperature and precipitation metrics (Table 3.2.4); however, some of the top models included drought indicators and cowbird removal (Table 3.2.5). The most parsimonious adult survival model included the effects of minimum temperature in April and moisture deficit in the summer. Historical territory success was best explained by June precipitation, minimum spring temperature, and cowbird removal; and increased number of fledglings was associated with higher minimum spring temperatures.

In RCP 4.5 scenarios, the minimum spring and April temperatures were projected to increase across all GCMs in both the 2050s and 2080s (Table 3.2.6). Precipitation was predicted to decrease in most scenarios, and moisture deficit was expected to increase in most, but not all, scenarios. RCP 8.5 scenarios yeilded similar patterns.

Table 3.2.4. Climate variables included in alternative multivariate climate-demography models for the black-capped vireo in Texas, calculated with historical climate data for North America (ClimateNA).

Territory success	Adult Survival	Average # of Fledglings
PPT04	PPT_sp	PPT07
PPT05	Tmax03	PPT08
PPT06	Tmin04	PPT_sp
PPT07	Tave05	Tmin05
PPT08	CMD03	Tmin06
Tmax07	CMD07	CMD03
Tmin05	CMD_sm	PPT06
Tave03	Number of cowbirds removed	Number of cowbirds removed
Tave06		
Tmax_sp		
Tmin_sp		
CMD03		
Number of cowbirds removed		

Table 3.2.5. Highest ranking multivariate models for climate influences on adult survival, territory success, and number of black-capped vireo fledglings on Fort Hood, Texas.

Adult Survival Models	AICc
survival ~ -0.0731 +(0.1802)Tmin04 – (0.199)CMD_sm	**-18.04**
survival ~ PPT_sp, Tmin04, Tave05, CMD_sm	-7.44
survival ~ PPT_sp, Tmin04, Tave05, CMD03, CMD_sm	3.87
Territory Success Models	
tsuccess ~ 0.1767 +(0.2801)PPT06 + (0.1965)Tmin_sp – (0.2495)cowbirds	**82.16**
tsuccess ~ PPT06, Tmin_sp	84.13
tsuccess ~ PPT06, PPT08, Tmin_sp	86.33
Fledgling Models	
fledglings ~ 1.2404 + (0.0443)Tmin_sp	**5.18**
fledglings ~ cowbirds	7.51
Fledglings ~ Tmin_sp, cowbirds	8.21
Fledglings ~ Tmin_sp, CMD03	10.26

Table 3.2.6. Historical (1995-2013) and future climatic conditions for variables selected in GLM climate-demography models for RCP 4.5 in the 2050s (top) and 2080s (bottom). CMD_sm refers to the Hargreaves climatic moisture deficit (mm), with higher values indicating more severe moisture deficits/drought as measured in the summer (sm). Tmin04 describes the minimum temperature in April (°C). Similarly, Tmin_sp describes the minimum temperature in spring. PPT06 indicates June precipitation (mm).

		CGM Predictions for RCP 4.5 (2050s)							
	Historic	CanESM2	CCSM4	CNRM	GFDL	HadGEM2	INM	IPSL	MPI
CMD_sm	377.8	390.3	430.8	369.7	422	523.3	185.5	460.2	415.2
Tmin04	12.38	15.8	14.2	14.6	14.6	17.7	14.25	14.8	14.8
PPT06	99.53	91.2	88.9	102.0	95.9	42.0	94.6	45.1	87.5
Tmin_sp	12.25	14.9	13.9	13.9	14.1	15.6	13.3	14.8	14.2

		CGM Predictions for RCP 4.5 (2080s)							
	Historic	CanESM2	CCSM4	CNRM	GFDL	HadGEM2	INM	IPSL	MPI
CMD_sm	377.8	393.5	424.5	401.6	492.1	530.8	359	426.7	423.6
Tmin04	12.38	16.4	14.81	15.4	15.4	18.14	15.1	15.1	15.1
PPT06	99.53	96.3	87.8	91.2	84.0	47.1	107.6	58.4	106.2
Tmin_sp	12.25	15.5	14.0	14.5	14.7	17.0	14.1	14.3	14.5

3.2.3.2 Climate-demography Projections

When the top historical climate-demography models were applied to future climate data, increases in adult survival, territory success, and fledglings resulted for the 2050s and for both RCP 4.5 and 8.5 scenarios. Mean GCM predictions yielded increases of 5.89% and 9.12% from current adult survival rates for 2050 RCP 4.5 and 8.5 projections, respectively (Table 3.2.7). Territory success projections for 2050 yielded increases of 11.63% (RCP 4.5) and 17.58% (RCP

8.5; Table 3.2.8), and the number of fledglings per successful territory increased by 7.45% (RCP 4.5) and 10.19% (RCP 8.5; Table 3.2.9). Demographic improvements for the 2080s were greater than for the 2050s, with adult survival expected to increase by 7.86% and 12.61%, territory success by 14.94% and 28.75%, and number of fledglings by 8.82% and 16.89% (for RCP 4.5 and 8.5 scenarios, respectively).

Table 3.2.7. Projected changes in adult survival in the 2050s under RCP 4.5 and 8.5 scenarios.

	Adult Survival	
GCM Model	**RCP 4.5**	**RCP 8.5**
CanESM2 4.5	0.55	0.56
CCSM4 4.5	0.50	0.52
CNRM 4.5	0.53	0.53
GFDL 4.5	0.50	0.49
HadGEM2 4.5	0.52	0.53
INM 4.5	0.51	0.54
IPSL 4.5	0.47	0.52
MPI 4.5	0.51	0.52
Multimodel average	*0.51*	*0.53*
Difference from historical	*0.0284*	*0.044*
% difference from historical	*+5.89%*	*+9.12%*

Table 3.2.8. Projected changes in territory success in the 2050s under RCP 4.5 and 8.5 scenarios.

	Territory Success	
GCM Model	**RCP 4.5**	**RCP 8.5**
CanESM2 4.5	0.64	0.67
CCSM4 4.5	0.60	0.62
CNRM 4.5	0.61	0.63
GFDL 4.5	0.61	0.64
HadGEM2 4.5	0.67	0.69
INM 4.5	0.57	0.62
IPSL 4.5	0.60	0.64
MPI 4.5	0.60	0.65
Multimodel average	*0.61*	*0.64*
Difference from historical	*0.0637*	*0.0962*
% difference from historical	*+11.63%*	*+17.58%*

Table 3.2.9. Projected number of fledglings per successful territory in the 2050s under RCP 4.5 and 8.5 scenarios.

	Number of Fledglings	
GCM Model	**RCP 4.5**	**RCP 8.5**
CanESM2 4.5	3.77	3.87
CCSM4 4.5	3.65	3.73
CNRM 4.5	3.65	3.74
GFDL 4.5	3.67	3.79
HadGEM2 4.5	3.99	4.08
INM 4.5	3.58	3.67
IPSL 4.5	3.76	3.85
MPI 4.5	3.68	3.78
Multimodel average	*3.72*	*3.81*
Difference from historical	*0.26*	*0.35*
% difference from historical	*7.45%*	*10.19%*

3.2.3.3 Future Climate-demography Simulations

Using the mean percent change in future demographic rates, baseline survival and reproduction rates were modified to reflect future climatic projections. When population dynamics were simulated through time, future demography yielded positive growth rates for both RCP 8.5 and 4.5 scenarios in both the 2050s (Figure 3.1.2) and 2080s. Growth rates were high (lambda > 1) during the first twenty years of simulation before the population stabilized at a higher population size. In the 2050s scenario, the 'future' population size was nearly ten times the starting population size in the year 2012. The much larger populations also contained strong source populations that sustained vireo abundance into the future.

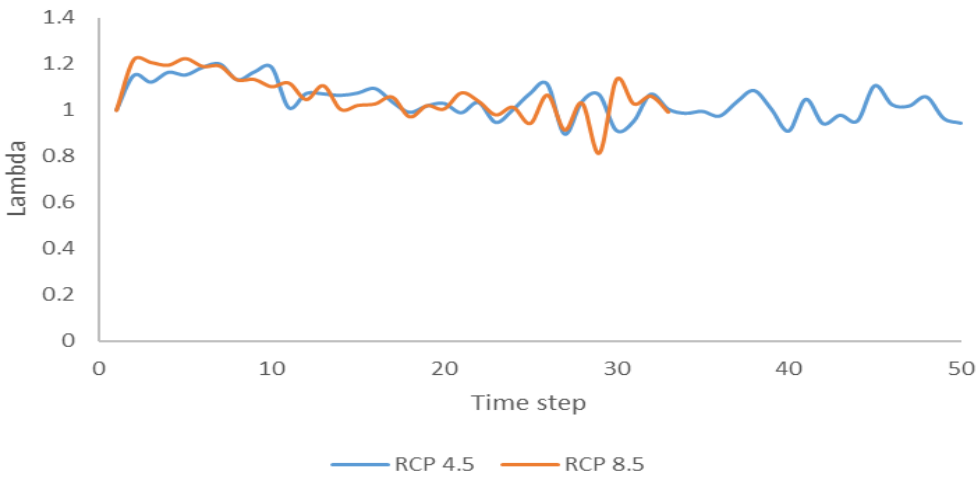

Figure 3.2.1. The influences of climate-induced changes in adult survival, territory success, and number of fledglings on regional black-capped vireo population growth for the 2050s.

3.2.3 Discussion

Historical climate-demography results indicate that vireo survival and reproduction are particularly responsive to low spring temperatures. Cold temperatures can be energetically challenging, impacting thermoregulation and reducing survival. Similarly, low minimum temperatures early in the breeding season were inversely associated with vireo territory success and number of fledglings per successful territory, suggesting reduced survival for hatchers or modified adult breeding or parenting success during cold temperature events. Survival and territory success were also related to precipitation and drought conditions, with greater territory success expected with higher June precipitation and higher survival resulting from lower drought conditions. Vireo sensitivity to drought is supported by previous field observations of lower survival and abundance during drought years.

Future climate projections indicate that minimum spring temperatures are generally expected to increase, bolstering expected future survival, territory success, and number of fledglings. Conversely, June precipitation is expected to generally decrease in most future circulation models, and climateNA projections generally indicate and increase in climatic moisture deficit (CMD) during future summer months. Despite poorer future precipitation and drought conditions, increases in April or spring temperatures result in net improvements for all demographic variables. In turn, demographic increases resulted in larger future population sizes in all climate scenarios, indicating possible improvements in persistence as the climate changes. Although simulated future populations equilibrated at a 10-fold larger population size (2050s scenarios), it is unclear how vireos are likely to behave and respond to ensuing high density conditions. Density-induced changes in territoriality, movement, and demography could substantively alter predicted population increases. Similarly, density-dependent demography and movement may become a key driver of future source-sink patterns.

Despite our results, climate change could still pose important challenges to vireo demography and persistence. Future inferences were based on limited historical data and our ability to characterize the impacts of under-represented and extreme events was limited. The historical climate-demography relationships were built on a limited times series (8-14 years of data) and included a range of responses to climatic events, but the time series is likely too short to well-characterize demographic responses to extreme climate conditions. As the frequency and magnitude of extreme and catastrophic events can greatly impact population sizes and persistence, simulated ‘future’ population sizes are likely to be optimistic. Realized future population sizes are also likely to depend on vireo responses to novel climate conditions that challenge physiological limits, and change community dynamics and ecosystem function. Further, our climate-demography analysis investigated climatic variables with direct (potential) impacts on vireo survival and reproduction during the breeding season. We did not assess climatic variables with more indirect or time-lagged effects on vegetation, food availability, predators, or cowbirds. Similarly, we did not test climatic variables measured during the non-breeding season when vireos migrate away from Fort Hood as the causal mechanisms become difficult to infer. Our climate-demography predictions do not consider climate-induced changes in cowbird parasitism pressure or habitat gains and losses due to vegetation dynamics. Although these limitations are common in such studies, their acknowledgement supports the need for

continued data collection and re-analysis to detect shifts in vireo demography, creation of more robust future predictions, and observation of new climate-responses as climate changes.

Phase 3 References

Cilimburg, A. B., M. S. Lindberg, J. J. Tewksbury, S. J. Hejl, and F. Thompson Iii. 2002. Effects of Dispersal on Survival Probability of Adult Yellow Warblers (Dendroica Petechia). The Auk 119:778–789.

Cimprich, D. A., and M. Heimbuch. 2011. Monitoring of the black capped vireo during 2011 on Fort Hood, Texas. In Endangered species monitoring and management at Fort Hood, Texas: 2011 annual report. Fort Hood Natural and Cultural Resources Management Branch.

Cimprich, D. A., and M. Heimbuch. 2012. Monitoring of the black-capped vireo during 2012 on Fort Hood, Texas. Endangered Species monitoring and management at Fort Hood, Texas: 2012 annual report.

Cimprich, D. A., and R. M. Kostecke. 2006. Distribution of the Black-capped vireo at Fort Hood, Texas. Southwestern Naturalist 51:94–102.

Cimprich, D. A., C. W. Sexton, P. K. Mcdowell, G. Lasley, and W. S. Simper. 2009. Long-distance dispersal records for the Black-capped vireo. Bulletin of the Texas Ornithological Society 42:44–47.

Graber, J. W. 1961. Habitat requirements and life history of the black-capped vireo (Vireo atricapilla). Ecological Monographs 31:313–336.

Kostecke, R. M., and D. A. Cimprich. 2008a. Adult and Juvenile Survival of Black-Capped Vireos Within a Large Breeding Population in Texas. The Condor 110:251–259.

Kostecke, R. M., and D. a. Cimprich. 2008b. Adult and Juvenile Survival of Black-Capped Vireos Within a Large Breeding Population in Texas. The Condor 110:251–259.

R Core Team (2015). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/. Version 3.2.0.

Ratzlaff, A. 1987. Endangered and threatened wildlife and plants: determination of the black-capped vireo to be an endangered species. Federal Register 52:37420–37423.

Vega Rivera, J. H., M. a. Ortega-Huerta, S. Sarkar, and J. H. Rappole. 2011. Modelling the potential winter distribution of the endangered Black-capped Vireo (Vireo atricapilla). Bird Conservation International 21:92–106.

Wilkins, N., R. A. Powell, A. A. T. Conkey, and A. G. Snelgrove. 2006. Population status and threat analysis for the black-capped vireo. Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX.

Wilsey, C. B., J. J. Lawler, and D. A. Cimprich. 2012. Performance of habitat suitability models for the endangered black-capped vireo built with remotely-sensed data. Remote Sensing of Environment 119:35–42.

Wilsey, C. B., J. J. Lawler, D. Cimprich, and N. H. Schumaker. 2014. Dependence of the Endangered Black-Capped Vireo on Sustained Cowbird Management. Conservation Biology 28:561–571.

Phase 4: White-eyed Vireo Monitoring

4.1 White-eyed and black-capped vireos—how two songbirds respond to the challenges of life in Texas

4.1.1 Introduction

To better manage the black-capped vireo, it is important to have an understanding of its population dynamics across its range. The white-eyed vireo, a closely related species, occupies the same habitat across most of the black-capped vireo's range yet appears to have an opposite population trajectory. Understanding the differences in habitat use, behavior, and demography among these species will provide insight into the challenges that are unique to the black-capped vireo, informing their differential management. In Phase 4, we collected white-eyed vireo data to support comparisons among the closely related species and identified important differences among them that may account for their differential success and management needs.

4.1.2 Methods

In 2014 and 2015, we monitored white-eyed vireos at seven study sites across central Texas: four sites on the Fort Hood military installation in Bell and Coryell Counties—Cow House Creek (CH), Taylor Valley (TV), Maxdale (MD), and West Range (WR; Figure 4.1.1); the northwestern portion of the Eckhardt tract of the Balcones Canyonlands National Wildlife Refuge (BC) in Burnet County; Colorado Bend State Park (CB) in San Saba County; and two adjacent private properties in San Saba County (SS). During the 2015 field season, BC was not intensively monitored due to habitat modifications performed to restore black-capped vireo habitat; BC was surveyed multiple times, however, for returning white-eyed vireos from previous seasons.

During the 2015 field season, black-capped vireos were monitored at six study sites across central Texas, including all sites monitored for white-eyed vireos. This monitoring was conducted to supplement intensive black-capped monitoring efforts that concluded in 2014 and so that parasitism and nest success rates between both vireo species could be compared within the 2015 season.

4.1.2.1 Monitoring Efforts

Adult male and female white-eyed and black-capped vireos were captured using mist nests and banded with combination of U.S. Geological Survey (USGS) aluminum bands and a unique arrangement of colored leg bands to make birds individually identifiable. After the breeding season, we netted juvenile white-eyed vireos and adults that remained un-banded throughout the breeding season. Biologists visited study sites approximately two to three times per week to monitor territories of adult males. White-eyed vireos were resighted with binoculars and territory

locations were collected with a handheld GPS unit. No more than five territory locations were collected in a single day and locations were recorded a minimum of five minutes apart. Territory locations were used to establish territory sizes; we used fixed-kernel density estimation to create probability contours from territory locations.

White-eyed vireo nesting behavior was observed, and when possible, nests were located and monitored. We visited nests two to three times per week and recorded the number of host eggs and brown-headed cowbird eggs (if present), number and estimated age of nestlings, and parental presence/absence at the nest. When nestlings were between 6-8 days old, they were banded with a USGS band and nestling color-band combination unique to the study site. To confirm fledging, we looked for fledglings and listened for fledgling begging calls. Behavioral observations were also used to confirm fledging; we considered nests successful if we observed adults carrying food post-fledging or observed persistent and intense adult scolding for more than one-day post-fledging. Daily mortality and survival, period survival, and total survival were then calculated using the 'Mayfield method' (Mayfield 1975). During the 2015 field season, black-capped vireo nests were also monitored following identical protocols and methods as described above for white-eyed vireos.

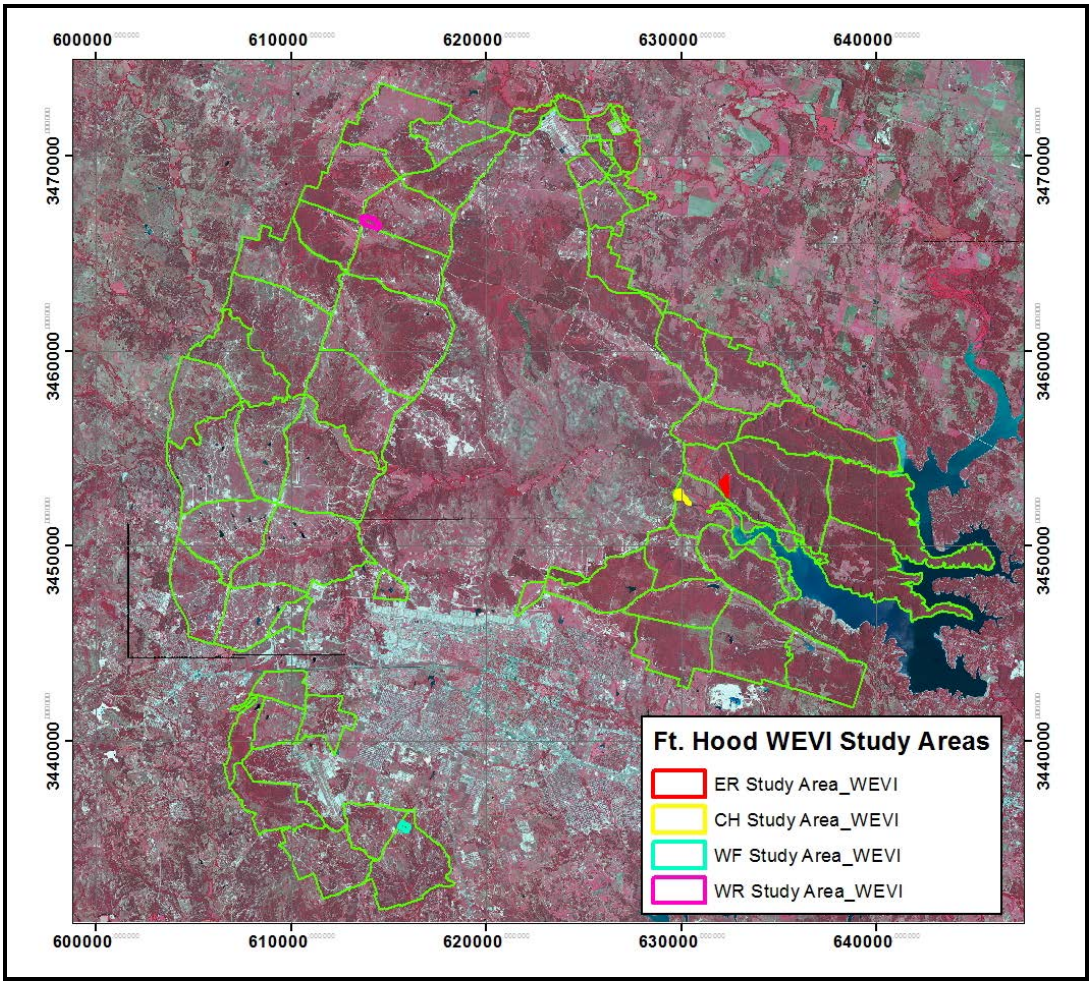

Figure 4.1.1. Locations of white-eyed vireo study sites on Ft. Hood, TX

4.1.2.2 Radio Telemetry

To help understand juvenile survival and dispersal, radio telemetry was used to track independent juvenile white-eyed vireos during the 2014 and 2015 field seasons. In July and August, juvenile white-eyed vireos were captured with mist nets and banded with a USGS aluminum band and unique combination of colored leg bands. A radio transmitter was then attached to a leg-loop harness affixed to the bird. The harness was made of cotton, designed to degrade and fall off within several months to decrease the impact on the bird. The average mass of a juvenile white-eyed vireo in central Texas is 10.6g (n = 30); the transmitters had an average mass of 270 mg, which is 2.5% of the white-eyed vireo's body mass (less than the standard requirement of 3% of the bird's mass).

Netting attempts targeted territories with banded fledglings of monitored nests. Due to difficulties capturing banded juvenile vireos, transmitters were also affixed to un-banded juveniles captured incidentally. Birds were then tracked daily using radio telemetry until their transmitter batteries died or they could no longer be found. Birds were resighted when possible and their location was collected using a handheld GPS unit. If a bird moved to a location that could not be accessed (e.g. private property), the bird's location was estimated using triangulation with GPS locations and compass bearings.

4.1.2.3 Nest Observations

Nest observations were performed on black-capped vireo (n = 18) and white-eyed vireo (n = 21) nests during the 2014 and 2015 field seasons to collect behavioral information during the nest building stage. Nests were observed from a concealed location for 1-1.5 hours, time began with the first observation of an adult at the nest. Duration of building events, time between building events, vocalizations at/around the nest, and other behaviors were recorded during the observation period. When possible, male and female adults were distinguished and their behaviors recorded separately. Observations were recorded for behaviors occurring within 15m of the nest.

4.1.2.4 Presence-Absence Surveys

Presence-absence surveys were conducted for white-eyed and black-capped vireos in a selection of habitat types across Fort Hood in 2014 and 2015. Five land-cover classes were identified as potential vireo breeding habitat using the 2011 National Land Cover Database (NLCD 2011): herbaceous (grassland), deciduous forest, evergreen forest, scrub, and woody wetlands (Homer et al. 2015). The herbaceous habitat type was not surveyed in 2015 as no detections of white-eyed or black-capped vireos occurred during 2014 surveys in this habitat class.

Survey locations were selected at random using the 'random point' tool of ESRI ArcMap 10.2 and 10.3 (ESRI, Redlands, California); 10 survey locations were selected in each of the habitat types. Survey start points were excluded if the habitat patch was too small completely contain

the survey route. A line transect survey was conducted using the random starting point and following and triangular path with one vertex established 100 m north and another 100 m east of the starting location. Surveys lasted 30 minutes or ended when both black-capped and white-eyed vireos were detected during the survey time, only birds observed within the count triangle were considered present. The habitat classification of surveys were ground-truthed to ensure that the actual land-cover class was consistent with the NLCD habitat designation. If habitat modifications changed the classification of a survey, the survey was not conducted and a new survey was conducted using spare points.

4.1.2.5 Foraging Observations

Foraging observations were conducted on male white-eyed vireos in July and August of 2015 (no foraging observations were made during the 2014 field season). Observations were performed on males within study areas that were part of the intensive territory monitoring. Vireos were followed a minimum of 5 minutes before beginning a foraging observation to ensure the bird's behavior and location were not influenced by the observer. Birds were resighted before beginning a foraging observation to confirm the correct individual was observed. Observations were recorded using a hand-held recording device so the observer could maintain visual contact with the subject throughout the observation, observations ended when visual contact was lost. During observations, details of each foraging attempt were recorded: the species of foraging substrate, location of foraging attempt on the substrate (e.g. end of branch, glean from the air, etc.), structure of foraging substrate (e.g. leaf, dead branch, trunk, etc.), and estimated height of the foraging attempt.

4.1.3 Results

4.1.3.1 Banding

Between March 18th and August 28th, 2014, we banded 619 white-eyed vireos in central Texas. Of the 182 adults banded, 114 were confirmed males and 68 confirmed females. We banded 198 white-eyed vireo nestlings (of which 134 fledged) and 230 juveniles (Table 4.1.1). Between March 30th and August 5th, 2015, we banded 302 white-eyed vireos. Of the 64 adults banded, 31 were confirmed males and 19 confirmed females (we could not confirm sex on 14 adults). We banded 180 white-eyed vireo nestlings (of which 38 fledged) and 57 juveniles (Table 4.1.2). Biologists also banded 213 black-capped vireos in 2015. Of the 126 adults banded, 76 were confirmed males and 50 confirmed females. We banded 86 black-capped vireo nestlings and 4 juveniles (Table 4.1.3).

4.1.3.2 Territories

During the 2014 field season, we monitored 95 white-eyed vireo territories across seven study sites. Forty-seven territories (49.47%) were successful at producing at least one fledgling. White-eyed vireo territories produced 134 fledglings with an average of 1.41 fledglings produced per territory and 0.86 fledglings per nest. The average territory size was 2.74 acres (Table 4.1.4).

Table 4.1.1. Summary of 2014 white-eyed vireo banding effort, territory monitoring, and nest monitoring.

	Total	SS	BC	CB	CH	TV	MD	WR
Total Banded	619	57	69	45	50	191	60	92
Males Banded	114	16	15	14	10	18	14	26
Females Banded	68	7	8	4	8	25	7	8
Nestlings Banded	198	28	30	23	15	48	24	30
(Fledged)	(134)	(22)	(29)	(18)	(9)	(30)	(6)	(20)
Terr. Monitored	95	12	12	17	9	16	12	17
# Succ. Territories	47	7	11	6	4	11	2	6
% Terr. Success	49.47%	58.33%	91.67%	35.29%	44.44%	68.75%	16.67%	35.29%
# Parasitized	26	3	2	10	0	0	5	6
Fledged/Terr.	1.41	1.83	2.41%	1.06	1.00	1.88	0.50	1.18
Nests	155	14	17	32	18	30	24	20
# Succ. Nests	43	6	8	6	3	11	2	7
% Nest Success	27.74%	36.49%	60.66%	15.80%	10.97%	29.00%	8.09%	38.77%
% Parasitism	16.77%	23.08%	13.33%	32.26%	0.00%	0.00%	20.83%	35.29%
Young Fledged	134	22	29	18	9	30	6	20
Fledged/Nest	0.86	1.57	1.71	0.56	0.50	1.00	0.25	1.00

Table 4.1.2. Summary of 2015 white-eyed vireo banding effort, territory monitoring, and nest monitoring.

	Total	SS	BC*	CB	CH	TV	MD	WR
Total Banded	302	50	4	23	32	80	49	52
Males Banded	31	3	1	2	7	7	5	6
Females Banded	19	1	1	0	2	6	2	6
Nestlings Banded (Fledged)	180 (133)	42 (34)	-- --	21 (21)	11 (11)	47 (27)	31 (19)	28 (21)
Terr. Monitored	69	9	--	12	14	12	9	13
# Succ. Territories	41	7	--	9	5	9	7	4
% Terr. Success	59.42 %	77.78%	--	75.00 %	35.71 %	75.00 %	77.78 %	30.77 %
Fledged/Terr.	2.43	4.00	--	2.75	1.00	3.25	2.56	1.77
Nests	150	20	--	33	21	30	20	26
# Succ. Nests	54	11	--	12	5	12	7	7
% Nest Success	34.84 %	55.00%	--	36.36 %	23.81 %	29.27 %	35.00 %	26.92 %
# Parasitized	25	1	--	8	8	0	0	8
% Parasitism	16.13 %	5.00%	--	24.24 %	38.10 %	0.00%	0.00%	30.77 %
Young Fledged	168	36	--	33	14	39	23	23
Fledged/Nest	1.10	1.71	--	1.00	0.67	1.30	1.10	0.85

*BC was not intensively monitored in 2015.

Table 4.1.3. Summary of 2015 black-capped vireo banding effort, territory monitoring, and nest monitoring.

	Total	SS	BC*	CB	CH	TV	MD	WR
Total Banded	213	36	14	21	2	25	49	42
Males Banded	76	10	10	11	1	7	13	12
Females Banded	50	8	4	7	1	1	8	9
Nestlings Banded	86	18	--	3	0	17	28	20
(Fledged)	(38)	(8)	--	(3)	(0)	(10)	(8)	(9)
Terr. Monitored	33	9	--	1	1	8	7	8
# Succ. Territories	18	3	--	1	0	7	3	4
% Terr. Success	54.55%	33.33%	--	100%	0.00%	87.50%	42.86%	50.00%
Fledged/Terr.	1.55	1.33	--	1.00	0.00	2.25	1.14	1.50
Nests	73	16	--	4	2	14	18	19
# Succ. Nests	21	4	--	2	1	7	3	4
% Nest Success	28.77%	25.00%	--	50.00%	50.00%	50.00%	16.67%	21.05%
# Parasitized	10	3	--	1	0	0	0	6
% Parasitism	13.70%	18.75%	--	25.00%	0.00%	0.00%	0.00%	31.58%
Young Fledged	58	16	--	2	2	18	8	12
Fledged/Nest	0.79	1.00	--	0.50	1.00	1.29	0.44	0.63

* The BC study site was not intensively monitored in 2015.

Table 4.1.4. Average size of white-eyed vireo territories, in acres, monitored across study sites during 2014 field season.

Study Area	Average Territory Size (Acres)	SE
BB	4.395	1.283
CB	1.587	0.208
CH	1.880	0.206
ER	1.047	0.146
WF	4.194	0.640
WR	3.337	0.573

In 2015, we monitored 69 white-eyed vireo territories across six study sites. Forty-one territories (59.42%) were successful at producing at least one fledgling and a total of 168 young white-eyed vireos fledged. On average, white-eyed vireo territories produced an average of 2.43 fledglings per territory and 1.10 fledglings per nest (Table 4.1.2). The average territory size was 2.65 acres (Table 4.1.5).

We also monitored 33 black-capped vireo territories across six study sites in 2015. Eighteen territories (54.55%) were successful at producing at least one fledgling. Fifty-eight fledglings were produced with an average of 1.55 fledglings produced per territory and 0.79 fledglings per nest (Table 4.1.3).

Table 4.1.5. Average size of white-eyed vireo territories, in acres, monitored across study sites during 2015 field season.

Study Area	Average Territory Size (Acres)	SE
CH	1.849	1.212
ER	2.251	1.279
WF	3.539	1.524
WR	2.957	1.869

4.1.3.3 Nests

Of the 92 white-eyed vireo nests intensively monitored on Fort Hood in 2014, 23 (25.00%) were successful, 59 (64.13%) were depredated, six (6.52%) were abandoned, and three (3.26%) were destroyed. Eleven nests were parasitized with an overall parasitism rate of 11.96%. From 23 successful nests, 65 white-eyed vireos fledged (mean = 2.83 fledglings per successful nest). In 2014, white-eyed vireo nests were found in 18 substrates across central Texas (Tables 4.1.1 and 4.1.6). Of the 150 white-eyed vireo nests intensively monitored during the 2015 field season, 54 (34.83%) were successful, 84 (56.00%) were depredated, six (4.00%) were abandoned, and two (1.33%) were destroyed. 25 nests were parasitized with an overall parasitism rate of 16.13%. From 54 successful nests, 168 white-eyed vireos fledged (mean = 3.11 fledglings per successful nest). White-eyed vireo nests were found in 23 different substrates in 2015 (Tables 4.1.2 and 4.1.7).

Of the 73 black-capped vireo nests intensively monitored during the 2015 field season, 21 (28.77%) were successful, 36 (49.32%) were depredated, nine (12.33%) were abandoned, and one (1.37%) was destroyed. 10 nests were parasitized with an overall parasitism rate of 13.70%. Fifty-eight black-capped vireos fledged, averaging 2.76 fledglings per successful nest. In 2015, black-capped vireo nests were found in 13 different substrates (Table 4.1.3 and Table 4.1.8).

Table 4.1.6. Summary of nest substrates for white-eyed vireos nests monitored on Fort Hood 2014.

Common Name	Scientific Name	Nests	Percentage
Texas Red Oak	*Quercus buckleyi*	29	32.22%
Cedar Elm	*Ulmus crassifolia*	16	17.78%
Texas White Ash	*Fraxinus texensis*	9	10.00%
Carolina Buckthorn	*Frungula caroliniana*	5	5.56%
Texas Redbud	*Cercis canadensis*	5	5.56%
Mexican Plum	*Prunus mexicana*	4	4.44%
Elbow Bush	*Forestiera pubescens*	3	3.33%
Green Ash	*Fraxinus pennsylvanica*	3	3.33%
Ashe Juniper	*Juniperus ashei*	3	3.33%
Rough-leaf Dogwood	*Cornus drummondii*	3	3.33%
American Elm	*Ulmus americana*	2	2.22%
Hackberry	*Celtis laevigata*	2	2.22%
Boxelder	*Acer negundo*	1	1.11%
Button Bush	*Cephalanthus occidentalis*	1	1.11%
Live Oak	*Quercus fusiformis*	1	1.11%
Rusty Blackhaw	*Viburnum rufidulum*	1	1.11%
Shin Oak	*Quercus sinuata* var. *breviloba*	1	1.11%
Skunk Bush	*Rhus trilobata*	1	1.11%

Table 4.1.7. Summary of white-eyed vireo nest substrates of nests monitored during the 2015 field season.

Common Name	Scientific Name	Nests	Percentage
Texas Red Oak	*Quercus buckleyi*	33	21.43%
Ashe Juniper	*Juniperus ashei*	17	11.04%
Cedar Elm	*Ulmus crassifolia*	15	9.74%
Texas Persimmon	*Diospyros texana*	14	9.09%
Hackberry	*Celtis laevigata*	13	8.44%
Green Ash	*Fraxinus pennsylvanica*	9	5.84%
Texas White Ash	*Fraxinus texensis*	9	5.84%
Mexican Buckeye	*Ungnadia speciosa*	7	4.55%
Gum Bumelia	*Sideroxylon lanuginosum*	5	3.25%
Texas Redbud	*Cercis canadensis*	5	3.25%
Carolina Buckthorn	*Frungula caroliniana*	4	2.60%
Mexican Plum	*Prunus mexicana*	4	2.60%
Shin Oak	*Quercus sinuata* var. *breviloba*	4	2.60%
Pecan	*Carya illinoinensis*	3	1.95%
Deciduous Holly	*Ilex vomitoria*	2	1.30%
Elbow Bush	*Forestiera pubescens*	2	1.30%
Mulberry Spp.	*Morus* spp.	2	1.30%
American Elm	*Ulmus americana*	1	0.65%
Rough-leaved Dogwood	*Cornus drummondii*	1	0.65%
Fig	*Ficus carica*	1	0.65%
Live Oak	*Quercus fusiformis*	1	0.65%
Mustang Grape	*Vitis musrangensis*	1	0.65%
Texas Mulberry	*Morus microphylla*	1	0.65%

Table 4.1.8. Summary of black-capped vireo nest substrates monitored during the 2015 field season.

Common Name	Scientific Name	Nests	Percentage
Texas Red Oak	*Quercus buckleyi*	31	42.47
Ashe Juniper	*Juniperus ashei*	11	15.07
Texas Persimmon	*Diospyros texana*	8	10.96
Texas Redbud	*Cercis canadensis*	5	6.85
Texas White Ash	*Fraxinus texensis*	5	6.85
Cedar Elm	*Ulmus crassifolia*	3	4.11
Shin Oak	*Quercus sinuata* var. *breviloba*	3	4.11
Mexican Buckeye	*Ungnadia speciosa*	2	2.74
Burr Oak	*Quercus macrocarpa*	1	1.37
Carolina Buckthorn	*Frungula caroliniana*	1	1.37
Live Oak	*Quercus fusiformis*	1	1.37
Mexican Plum	*Prunus mexicana*	1	1.37
Rusty Blackhaw	*Viburnum rufidulum*	1	1.37

4.1.3.4 Site-Specific Nest Survival

4.1.3.4.1 White-eyed Vireo

In 2014, 18 white-eyed vireo nests were monitored on the Cow House study site (Table 4.1.1); three (10.97%) were successful, 14 (77.78%) were depredated, one (5.56%) was abandoned, and no nests were parasitized. Nine fledglings were produced with 0.50 fledglings per nest (Table 4.1.1). Period survivals were 69% for the egg-laying, 56% for incubation, and 28% for nestlings (Table 4.1.9). Total survival was 10.97%.

Nineteen nests were monitored on the Cow House study site in 2015; five (26.32%) were successful, 13 (68.42%) were depredated, one (5.26%) was destroyed due to flooding, and eight nests were parasitized (42.11%). Fourteen fledglings were produced with 0.74 fledglings per nest (Table 4.1.2). Period survivals were 87% for the egg-laying, 54% for incubation, and 48% for nestlings (Table 4.1.10). Total survival was 22.51%.

Table 4.1.9. Daily mortality, daily survival, and period survival for white-eyed vireo nests on Fort Hood in 2014, calculated using Mayfield method (Mayfield 1975).

Site	Nests		Egg-laying Period	Incubation Period	Nestling Period
		Daily Mortality	0.14	0.04	0.11
CH	18	Daily Survival	0.86	0.96	0.89
		Period Survival	0.69	0.56	0.28
		Daily Mortality	0.10	0.03	0.05
TV	30	Daily Survival	0.90	0.97	0.95
		Period Survival	0.78	0.66	0.57
		Daily Mortality	0.00	0.07	0.13
MD	24	Daily Survival	1.00	0.93	0.87
		Period Survival	1.00	0.36	0.23
		Daily Mortality	0.00	0.01	0.07
WR	20	Daily Survival	1.00	0.99	0.93
		Period Survival	1.00	0.83	0.47

Table 4.1.10. Daily mortality, daily survival, and period survival for white-eyed vireo nests on Fort Hood in 2015, calculated using Mayfield method (Mayfield 1975).

Site	Nests		Egg-laying Period	Incubation Period	Nestling Period
		Daily Mortality	0.05	0.04	0.06
CH	19	Daily Survival	0.95	0.96	0.94
		Period Survival	0.87	0.54	0.48
		Daily Mortality	0.13	0.02	0.05
TV	30	Daily Survival	0.87	0.98	0.95
		Period Survival	0.70	0.77	0.54
		Daily Mortality	0.15	0.04	0.03
MD	20	Daily Survival	0.85	0.96	0.97
		Period Survival	0.67	0.58	0.73
		Daily Mortality	0.08	0.04	0.07
WR	26	Daily Survival	0.92	0.96	0.93
		Period Survival	0.82	0.59	0.47

Thirty nests were monitored on the Taylor Valley study site in 2014 (Table 4.1.1); 11 (29.00%) were successful, 15 (50.00%) were depredated, two (6.67%) were abandoned, two (6.67%) were destroyed, and no nests were parasitized. Thirty fledglings were produced with 1.00 fledglings per nest (Table 4.1.1). Period survivals were 78% for the egg-laying, 66% for incubation, and 57% for nestlings (Table 4.1.9). Total survival was 29.00%.

In 2015, 30 nests were monitored on Taylor Valley (Table 4.1.2); Twelve (40.00%) were successful, 17 (56.67%) were depredated, two (3.33%) were abandoned, and no nests were parasitized. Thirty-nine fledglings were produced with 1.30 fledglings per nest (Table 4.1.2).

Period survivals were 70% for the egg-laying, 77% for incubation, and 54% for nestlings (Table 4.1.10). Total survival was 29.27%.

Twenty-four nests were monitored on Maxdale in 2014 (Table 4.1.1); Two (8.09%) were successful, 21 (87.50%) were depredated, one (4.16%) was abandoned, and five nests (20.83%) were parasitized. Six fledglings were produced with 0.25 fledglings per nest (Table 4.1.1). Period survivals were 100% for the egg-laying, 36% for incubation, and 23% for nestlings (Table 4.1.9). Total survival was 8.09%.

In 2015, 20 nests were monitored on the Maxdale study site (Table 4.1.2); Seven (35.00%) were successful, 13 (65.00%) were depredated, no nests were parasitized. Twenty-two fledglings were produced with 1.1 fledglings per nest (Table 4.1.2). Period survivals were 67.33% for the egg-laying, 58.10% for incubation, and 72.59% for nestling (Table 4.1.10). Total survival was 28.39%.

Twenty nests were monitored on the West Range study site in 2014 (Table 4.1.1); Seven (38.77%) were successful, nine (45.00%) were depredated, two (1.00%) were abandoned, one (1.00%) was destroyed, and six nests (35.29%) were parasitized. Twenty fledglings were produced with 1.00 fledglings per nest (Table 4.1.1). Period survivals were 100% for the egg-laying, 83% for incubation, and 47% for nestlings (Table 4.1.9). Total survival was 38.77%.

Twenty-six nests were monitored on the West Range study site in 2015 (Table 4.1.2); seven (26.92%) were successful, 13 (50.00%) were depredated, three failed (11.53%; two failed due to a fledged cowbird), two (7.69%) were abandoned, one (3.85%) was destroyed, and eight nests (30.77%) were parasitized. Twenty-one fledglings were produced with 0.81 fledglings per nest (Table 4.1.2). Period survivals were 81.86% for the egg-laying, 59.02% for incubation, and 46.82% for nestlings (Table 4.1.10). Total survival was 22.62%.

4.1.3.4.2 Black-capped Vireo

Only two black-capped vireo nests were found on the Cow House study site during the 2015 field season (Table 4.1.3). One was successful, producing two fledglings and the other nest was depredated. Due to small sample size, a survival analysis could not be conducted.
Fourteen nests were monitored on the Taylor Valley study site in 2015 (Table 4.1.3); seven (50.00%) were successful, six (43.00%) were depredated, one (7.00%) were abandoned, and no nests were parasitized. Eighteen fledglings were produced with 1.29 fledglings per nest (Table 4.1.3). Period survivals were 83% for the egg-laying, 74% for incubation, and 69% for nestlings (Table 4.1.11). Total survival was 42.43%.

Eighteen nests were monitored on the Maxdale study site (Table 4.1.3); Three (15.79%) were successful, 13 (68.42%) were depredated, two nests failed (10.53%), and no nests were parasitized. Eight fledglings were produced with 0.44 fledglings per nest (Table 4.1.3). Period survivals were 100% for the egg-laying, 57% for incubation, and 45% for nestling (Table 4.1.11). Total survival was 25.56%.

Nineteen nests were monitored on the West Range study site (Table 4.1.3); Four (21.05%) were successful, six (31.58%) were depredated, six (31.58%) were abandoned, two (15.79%) failed, and six nests (31.58%) were parasitized. Twelve fledglings were produced with 0.63 fledglings per nest (Table 4.1.3). Period survivals were 58.11% for the egg-laying, 29.31% for incubation, and 43.17% for nestlings (Table 4.1.11). Total survival was 9.86%.

Table 4.1.11. Daily mortality, daily survival, and period survival for black-capped vireo nests on Fort Hood in 2015, calculated using Mayfield method (Mayfield 1975).

Site	Nests		Egg-laying Period	Incubation Period	Nestling Period
		Daily Mortality	0.07	0.02	0.03
TV	14	Daily Survival	0.93	0.98	0.97
		Period Survival	0.83	0.74	0.69
		Daily Mortality	0.00	0.04	0.07
MD	18	Daily Survival	1.00	0.96	0.93
		Period Survival	1.00	0.57	0.45
		Daily Mortality	0.20	0.06	0.07
WR	19	Daily Survival	0.80	0.94	0.93
		Period Survival	0.58	0.39	0.43

* Too few nests (n = 2) were monitored on CH in 2015 to conduct survival analyses.

4.1.3.5 Recaptures

In 2015, four white-eyed vireos that had been initially banded in 2014 were recaptured, three on Fort Hood and one on Balcones Canyonlands National Wildlife Refuge (Tables 4.1.12 and 4.1.13). The average dispersal of the four vireos was over 1.17 km (Tables 4.1.12 and 4.1.13).

4.1.3.6 Radio Telemetry

We tracked 25 recently fledged, independent white-eyed vireos during the pre-migration periods of 2014 and 2015. Of the 25 white-eyed vireos with transmitters, 6 were lost soon (less than 10 days) after the start of tracking by either moving beyond our search area or had transmitter malfunctions. 18 birds were tracked over 20 days and one bird died during tracking. Excluding birds with transmitters that failed or were lost soon after the start of tracking; transmitters lasted an average of 27 days. Using tracking data for vireos fitted with transmitters, we calculated daily survival probabilities (Kaplan and Meier 1958) and found that juvenile white-eyed vireos had a 95% probability of surviving more than four weeks of independence (Figure 4.1.2). We compared the survival of independent black-capped vireos and white-eyed vireos using a log rank test and found there was no significant difference in their survival ($\chi^2 = 0.2$, df = 1, P = 0.66) during the tracking period (Rich et al. 2010).

Table 4.1.12. Recapture summary for white-eyed vireos on Fort Hood study sites. Easting and Northing UTMs are in the WGS 1984 coordinate system.

Band Number	Color Combination	Age[a]	Sex	Initial Capture Year	Recapture Year	Dispersal Distance
1710-77617	DG/BL:RD/SI	ATY	M	2012	2014	0.00
1710-77640	PI/PI:MV/SI	ATY	M	2012	2014	1254.73
2270-37492	YE/PI:DB/SI	A4Y	M	2012	2014	359.49
2270-38216	WH/OR:PI/SI	A4Y	M	2012	2014	22.80
2270-38218	BL/YE:DB/SI	5Y	F	2012	2014	524.87
2270-38242	OR/OR:DG/SI	4Y	U	2012	2014	11.40
2650-89822	DG/SI:PI/WH	A4Y	M	2012	2014	85.98
2710-13113	GR/RD:DG/SI	ATY	M	2013	2014	172.54
2710-13126	BL/MV:OR/SI	ATY	M	2013	2014	76.16
2710-13368	MV/YE:YE/SI	TY	U	2013	2014	263.74
2710-13432	YE/PI:YE/SI	ATY	M	2013	2014	120.42
2710-13510	BK/WH:PI/SI	ATY	M	2013	2014	633.82
2710-14976	PI/DB:BL/SI	TY	F	2013	2014	1447.51
2720-57386	WH/RD:RD/SI	ATY	F	2014	2015	166.90
2730-08064	RD/RD:PI/SI	TY	M	2014	2015	2107.10
2730-07658	RD/SI:BK/BK	TY	U	2014	2015	2042.90

[a] Age at initial capture: SY- Second Year, ASY- After Second Year, ATY- After Third Year, 4Y- Fourth Year

Table 4.1.13. Recapture summary for white-eyed vireos on Balcones Canyonlands National Wildlife Refuge. Easting and Northing UTMs are in the WGS 1984 coordinate system.

Band Number	Color Combination	Age[a]	Sex	Initial Capture Year	Recapture Year	Dispersal Distance
2270-37542	PI/MV:PI/SI	ATY	M	2012	2014	113.76
2710-13531	YE/PI:WH/SI	ASY	M	2013	2014	52.35
2720-57274	NB/NB:NB/SI	TY	M	2014	2015	371.46

[a] Age at initial capture: SY- Second Year, ASY- After Second Year, ATY- After Third Year, 4Y- Fourth Year

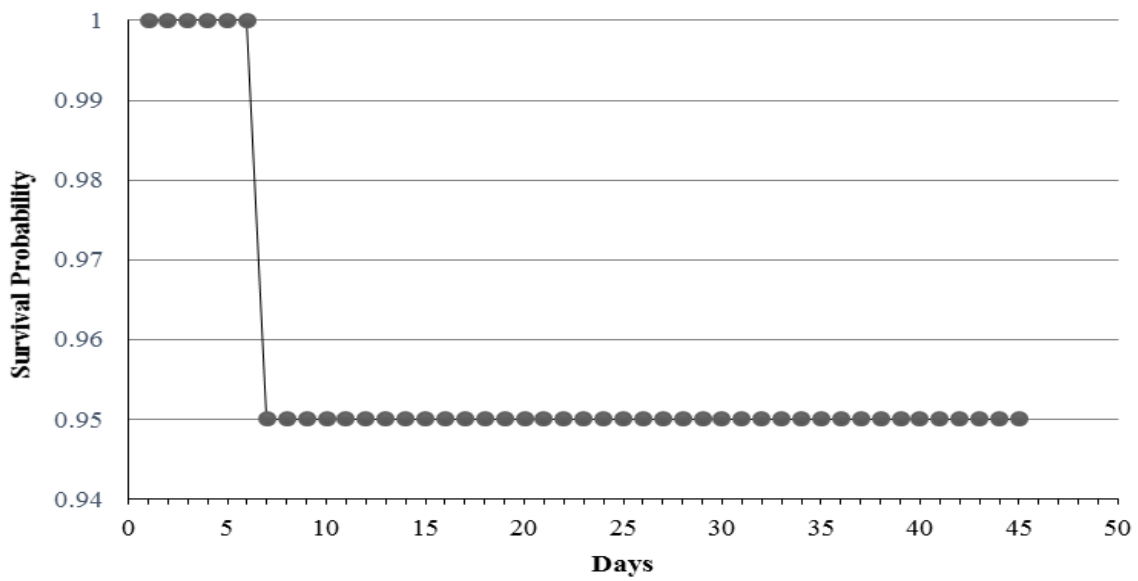

Figure 4.1.2. Post-independence daily survival probabilities of juvenile white-eyed vireos across central Texas in 2014 and 2015.

4.1.3.7 Presence/Absence Surveys

White-eyed vireos were found in each of the four habitat classes surveyed in both 2014 and 2015. No black-capped or white-eyed vireos were detected during the 10 surveys conducted in herbaceous (grassland) habitat class in 2014. Black-capped vireos were not detected in any of the 20 surveys conducted in the woody wetland habitat, while white-eyed vireos were detected in

Table 4.1.14. Summary of 2014 black-capped (BCVI) and white-eyed vireo (WEVI) presence-absence surveys. Numbers indicate detections of each species in each habitat type out of the 10 surveys conducted in each habitat type. All surveys were conducted on Fort Hood.

	Deciduous Forest	Evergreen Forest	Herbaceous	Scrub	Woody Wetlands
WEVI	10	7	0	7	10
BCVI	7	5	0	9	0

Table 4.1.15. Summary of 2015 black-capped (BCVI) and white-eyed vireo (WEVI) presence-absence surveys. Numbers indicate detections of each species in each habitat type out of the 10 surveys conducted in each habitat type. All surveys were conducted on Fort Hood.

	Deciduous Forest	Evergreen Forest	Scrub	Woody Wetlands
WEVI	9	5	6	10
BCVI	6	6	5	0

Table 4.1.16. Combined results of 2014 and 2015 black-capped (BCVI) and white-eyed vireo (WEVI) presence-absence surveys across the four habitat classes surveyed in both years. Numbers indicate detections of each species in each habitat type out of the 20 total surveys conducted in each habitat type. All surveys were conducted on Fort Hood.

	Deciduous Forest	Evergreen Forest	Scrub	Woody Wetlands
WEVI	19	12	13	20
BCVI	13	11	14	0

4.1.4 Discussion

Through this research, we found substantive differences in habitat use, return dates, reproductive behaviors and vocalizations that may help explain the opposite population trajectories of black-capped and white-eyed vireos. White-eyed vireos use a wider variety of habitat types than black-capped vireos, which may confer survival and reproductive advantages over more limited habitat selection. In particular, white-eyed vireos used deciduous forest and woody wetland habitat to a greater extent than black-capped vireos. These habitats are characterized by fewer edges and greater canopy cover, both of which are associated with lower rates of brown-headed cowbird brood parasitism. Tracking of white-eyed vireo fledglings also showed that birds tended to select riparian habitats, possibly due to increased foraging opportunities. In general, the use of a broader range of habitat types may result in greater connectivity among habitats. In turn, this may increase the survivorship of independent fledgling white-eyed vireos by providing cover during movement, and aid in the persistence of sink populations by connecting sources to sinks.

White-eyed vireos arrived on the breeding grounds and initiated nests earlier than black-capped vireos. During the 2015 field season, we observed several white-eyed vireo territories that successfully fledged three broods of nestlings. By initiating nests earlier, white-eyed vireos may be avoiding brown-headed cowbird parasitism and reducing the risk of nest depredation by snakes, which become more abundant as the breeding season progresses. White-eyed vireos also continued to breed later in the season allowing for additional nesting attempts. While not observed in this study, the larger size of the white-eyed vireo may allow for the successful fledgling of both brown-headed cowbird and host from parasitized nests.

White-eyed vireo nest building behavior may also reduce the risk of brown-headed cowbird parasitism compared to black-capped vireos. During nest observations, white-eyed vireos tended to vocalize less frequently near their nest than black-capped vireos; Vocalizations and movement near a nest are used by cowbirds to find nests during the nest building stage. White-eyed vireos also tended to have a faster rate of nest building, making more trips to the nest during nest observations, a shorter duration of nest building may lead to reduced detection by cowbirds and decrease parasitism. Our results indicate that a number of habitat, life history, and behavioral factors may important in defining differential outcomes for vireo species on Fort Hood.

Phase 4 References

Homer, C. G., J. A. Dewitz, L. Yang, S. Jin, P. Danielson, G. Xian, J. Coulston, N. D. Herold, J. D. Wickham, and K. Megown. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States-representing a decade of land cover change information. Photogrammetric Engineering and Remote Sensing 81:345-354.

Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53:457-481.

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456-466.

Rich, J. T., J. G. Neely, R. C. Paniello, C. C. J. Voelker, B. Nussenbaum, and E. W. Wang. 2010. A practical guide to understanding Kaplan-Meier curves. Otolaryngology – Head and Neck Surgery 143:331-336.

Management Implications

In this project, we used a range of approaches to develop a better understanding of the emergence, stability, effective measurement and strength, and management implications of source-sink dynamics. Our explorations yielded general and transferrable insights into source-sink theory by extending source-sink concepts to explicitly address the population conditions faced by species at risk of decline or extinction. For example, Phase 1 (Task 1.1) results highlighted the conditions and systems under which, source-sink dynamics may emerge and result in strong dynamics that can influence the outcome of management actions. Department of Defense (DoD) managers can use the relative importance of variables to indicate how changes in the system could alter the strength of source-sink dynamics and seek alternatives that do not polarize habitat quality, increase periodic demographic variation through disturbance, or avoid creating or strengthening sinks that are in close proximity to sources.

Beyond theoretical abstractions, we also constructed and made extensive use of targeted case studies to explore the generality of source-sink concepts, such as the contribution of sinks to population persistence (Tasks 1.2 and 1.3) and the ability of source-sink and related metrics to identify the habitats and populations required for population persistence (Task 1.3). In framing the case studies in terms of their population and system attributes, case-study results can be used as testable hypotheses for analogous systems in which source-sink dynamics are either suspected or confirmed. For instance, results from Phase 1 (Task 1.2) indicate that sinks can be beneficial in systems with rapid population decline but superfluous in stable, robust source-sink systems. Sinks can also compromise regional population persistence if they are black-hole sinks (with little or no emigration), and make variable contributions in systems with pseudo-sinks and complex dynamics. DoD managers can use these insights to avoid the false assumption that sinks are always detrimental to populations, and weigh case-specific factors such as population size and volatility, rate of decline, inter-population movement, landscape configuration, and density dependence to make targeted and adaptive management decisions regarding different kinds of sink habitats and populations.

Phase 1 (Task 3) results also highlight the need for thorough assessments of sources and sinks before habitats are prioritized for protection. Our results indicate that although sources are generally needed for long-term persistence, protecting high abundance sinks can make more substantive contributions to the short-term conservation of declining populations, avoiding imminent extinction. Our results also indicate that the source-sink and population metrics by which habitats are prioritized matter most for species with gradual rates of decline and those inhabiting large proportions of sink habitat. Hence, managers should invest the most effort in characterizing source-sink dynamics for species that are gradually, rather than precipitously, declining and consider the benefits of protecting high abundance sinks.

In addition to the general insights gained in Phase 1, the modeling approach used to examine source-sink dynamics and management consequences can be applied to other species and contexts to generate case-specific results as we have done for the black-capped vireo in Phase 3. The data-driven models were created with a freely available modeling platform (HexSim) that

DoD managers can similarly use to investigate the implications of system-specific conditions for other species on other ranges.

The results from our black-capped vireo field study (Phase 2) provide valuable information on the relative states and stability of sources and sinks on and near Fort Hood. These data can be used to guide the differential management of vireo populations on and off Fort Hood to optimize vegetation conditions and control brown-headed cowbirds. Because improvements in nest success and productivity (e.g,. Kostecke et al. 2005) and vireo population growth in "source years" (Phase 2) are directly related to the implementation of cowbird control, effective management of nest parasitism will remain a key management strategy for black-capped vireos. The absence of vocalization strategies to minimize detection and nest parasitism (Phase 2, Task 3) further increases vireo reliance on continued cowbird control. Land managers currently control cowbirds through shooting and trapping methods on and off the base. Yet, our results (Phase 2, Task 1) suggest that cowbird removal programs are most effective when they use both shooting and trapping strategies. Despite the general effectiveness of cowbird control, the current level of shooting and trapping efforts are likely to be insufficient to prevent years of exceptionally poor or declining population growth ("sink years", e.g., 2011; Phase 2, Task 1). Hence, augmented or complementary management strategies will be required during periods of extended low population growth.

In addition to efforts to improve vireo productivity via cowbird control, land managers may also support vireo survival through improvements to habitat conditions (Tasks 2.1 and 2.2). Although little is known about the factors that affect survival during migration or during the non-breeding season, our results in Task 2.2 identify habitat characteristics that may benefit juvenile vireos in central Texas in the post-breeding season. Maintaining areas of deciduous and mixed deciduous/evergreen forest, including low shrub cover, on the landscape will better provide important cover from predation and food resources for juvenile vireos. In Task 2.2, we also observed that breeding sites located near or adjacent to forested areas with abundant canopy cover may improve juvenile survival and aid in the establishment of larger breeding populations. As the factors affecting adult survival during the breeding season are still largely unknown, actions that improve habitat for juvenile survival may be a key first step towards achieving sustainable populations (Tasks 2.1 and 2.2).

Maintaining high quality breeding habitat and pro-actively controlling cowbirds within these sites is likely to aid in creating and strengthening source populations, ultimately improving regional abundance and viability. However, as in Phase 1, we found that sink populations can play a vital role in the central Texas metapopulation (Task 2.1). Sink habitats are more abundant than high-quality source habitats in this landscape, and sinks may support a relatively large portion of the overall population. Additionally, reproduction in sink patches may still contribute to overall metapopulation size in years with exceptionally high reproduction or survival, especially if vireos eventually leave and disperse to higher-quality habitat. That is, populations that are sinks on average may still be occasional sources and thus may be valuable contributors to the overall central Texas population. Furthermore, evidence of flexibility in vireo mating strategy (i.e. the adoption of polygyny) suggests that vireos may be adaptable to habitat changes that result in low population densities (Task 2.4). Such behavioral flexibility in breeding individuals may aid in the persistence of vireo populations in sink habitats beyond the

predictions of our models in Task 2.1. Although land managers may be forced to focus resources on areas of high-quality habitat, areas of relatively low-quality habitat should not be disregarded and allowed to degrade into non-habitat.

Comparisons of black-capped and white-eyed vireos on and near Fort Hood yielded insights into the unique challenges faced by black-capped vireos. Because black-capped vireos use a narrower range of habitats than white-eyed vireos, maintaining sufficient availability of the successional habitats preferred by black-capped vireos is important for abundance and persistence. Specifically, protecting the riparian and woody wetland habitat that provides important refuges for juvenile vireos and preferentially protecting or proactively managing black-capped vireo habitats with higher degrees of cover may result in greater survival and reproductive success. Our work on black-capped and white-eyed vireos also highlights the importance of continued cowbird management on Fort Hood, as both species are vulnerable to nest parasitism.

Forecasting the impacts of uncertainties and system change is an important planning action, which supports effective management of species at risk of decline and extinction. In Phase 3 (Task 3.1), we integrated disparate sources of information into a spatially-explicit population model to create a predictive framework for examining the degree to which current and future uncertainties and system changes could change our conception of source-sink dynamics and population outcomes in the black-capped vireo regional population network in and around Fort Hood military base. As one of the most influential uncertainties was the frequency of inter-population dispersal events, better characterization of the pattern and extent to which vireos are moving among populations will be important for effectively prescribing on- and off-base management actions. Because the very small off-base populations tend to function as stronger sinks than the larger on-base sites, conservation efforts are best focused on-base. Even with augmented off-base cowbird control, the large population size differential and low rates of exchange among on- and off-base populations result in a low level of dependency of Fort Hood populations on off-base sites. Off-base habitat restoration actions are unlikely to substantively improve regional vireo persistence (under the tested conditions) unless they can support a large population size, accompanied by augmented cowbird control, and in a strategic location to maximize the benefits of source-sink exchanges. Hence, these results underscore the importance of managing for large, robust vireo populations on-base, without relying on the contributions of nearby off-base populations to support regional persistence.

Our assessment of potential demographic responses to future climatic conditions highlighted the likelihood of overall increases in vireo abundance on Fort Hood resulting from higher minimum spring temperatures. Yet, projected increases in future abundance and persistence may be mediated by density-induced changes in territoriality, movement, and demography. Continued monitoring of behavior, movement, demography, cowbirds, and climate-induced vegetation shifts will improve our understanding of vireo responses to extreme events and gradual shifts in climate. Although this analysis is specific to vireos on Fort Hood, a similar approach can be undertaken for other species and other DoD lands to assess how climate change may impact populations on other installations. Through the coupling of statistical climate-demography analysis and spatially explicit population modeling, explorations of the impacts of climate

change can be integrated with other important system considerations to provide the integration of system conditions, stressors, and alternative future scenarios.

Conceptualizing spatially structured populations as sources and sinks brings awareness to the need for management actions that are based on integrated knowledge of habitat, demography, and movement conditions. We found the source-sink paradigm to be a useful construct around which management actions for declining and at-risk species can be prescribed. Furthermore, our results highlight the potential for meaningfully adverse consequences of ignoring the spatial structure inherent in many populations. Our findings also indicate that the specific characteristics of source-sink systems are important in discerning effective management actions. It may often be insufficient to manage local populations based on their current source-sink status as strong sources are not always the most important elements of the source-sink system, and sinks can be integral to population persistence. Further, accurately classifying sources and sinks is challenging, particularly in variable and directionally changing systems. Decisions of which sources and sinks to protect or alter are best informed by the simultaneous consideration of current and future population sizes and variability, rates of decline, potential for population growth, differential habitat quality, rates and patterns of inter-population exchange, behavior, type of sink, strength of source-sink dynamics, and landscape configuration. In conclusion, this project highlights the importance of understanding source-sink dynamics for the successful management of at-risk populations as well as the need for the continued development of source-sink theory, methods, and best practices that target species at risk in complex and changing landscapes.

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