

Informing management of rare species with an approach combining scenario modeling and spatially explicit risk assessment

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Abstract. Wildlife managers are tasked with identifying and managing stressors that threaten persistence of populations. We demonstrate an approach to land-use planning that combines scenario modeling and ecological risk assessment to map and quantify risk to population persistence for three rare prairie species in Washington State, USA. Following corroboration of model output, we found that of the management scenarios considered, only a scenario with year-round restrictions on use of off-road vehicles, digging, and camping enforced in all potential habitat reduces risk to the species. Decreased risk is focused primarily in two patches of prairie habitat in our study area, indicating stringent restrictions need not be applied broadly. However, one area is not easily accessed by two of the three species considered, suggesting reintroductions to suitable but inaccessible habitat may play an important role in management of these species. Our analyses suggest changes in land use and management that might improve habitat for rare species, with options for minimizing monetary and social costs. Because the proposed approach relies on hypothetical management scenarios and uses a model flexible in data requirements to provide spatially explicit output, it can be used to inform adaptive management of rare species in diverse land-planning processes and will be especially useful when management decisions must be made under time or cost constraints.

Key words: *adaptive management; land-use planning; Mazama pocket gopher (Thomomys mazama); military training; Puget Sound prairie; rare species management; risk assessment; scenario modeling; Scotch broom (Cytisus scoparius); spatially explicit model; Streaked Horned Lark (Eremophila alpestris strigata); Taylor's checkerspot butterfly (Euphydryas editha taylori).*

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Introduction

Many species face multiple, often interacting threats to persistence (Wilcove et al. 1998, Lawler et al. 2002). Wildlife managers must identify stressors that threaten persistence of populations and then try to reduce risk posed to population viability (Burgman et al. 1993, Bakker and Doak 2008). Unfortunately, when managing a species in a heterogeneous environment with multiple stressors, it is not always clear which stressors pose the greatest risk to a population, how that risk varies spatially and temporally, and how stressors can be

managed to mitigate risk (Pressey et al. 2007). Experimental field research provides clear evidence connecting management actions to outcomes. However, field research can be challenging when working with species of conservation concern. Difficulties include permitting issues and fear of doing harm to endangered populations (MacKenzie et al. 2005), sampling issues and lack of statistical power (Gaston 1994), or time limitations when a population is rapidly decreasing or decisions regarding protection status are pending (Soule 1985, Scott et al. 2010). A quick, low-cost approach to quantifying and mapping risk to a population that could be used to explore potential effects of management on risk would be a welcome addition to a wildlife manager's toolbox.

Risk assessment can be defined as the process of assigning probabilities and magnitudes to the effects of an activity or event to guide decision-making in the face

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of uncertainty (Burgman 2005, Suter 2007). The risk assessment approach includes the identification of stressors resulting from an initiating event (e.g., human activity or natural catastrophe) and quantification of the relationship between the initiating event and consequences for a subject of interest (Suter 2007). Given the history of risk assessment in diverse business and governmental settings, the approach is generally supported and readily adopted by regulatory agencies charged with implementing policies and guidelines (e.g., U.S. Environmental Protection Agency; Burgman 2005, Suter 2007, 2008).

Increasingly, approaches using ecological risk assessment in a conservation context are combined with scenario modeling (Harwood 2000, Linkov et al. 2006, Hobday et al. 2011). Scenario modeling offers a method for describing outcomes of alternative management actions while potentially avoiding issues encountered with experimental field research. Because scenario modeling considers a variety of alternative futures with uncertainty about links between management and outcomes built into the model, it is useful when system manipulations are difficult or impossible and when uncertainty is high (Peterson et al. 2003). Indeed, the inclusion of uncertainty in scenario modeling allows use of data collected from surveys of expert opinion when empirical data are lacking. Whereas methods linking management actions directly to population viability via demographic analyses are ideal (Bakker and Doak 2008), local knowledge and expert opinion have proven useful in guiding conservation decisions in data-poor settings (Donland et al. 2010, Castellanos-Galindo et al. 2011). Furthermore, scenario modeling allows wildlife managers to assess threats to species populations and examine potential trade-offs associated with alternative management actions while integrating socioeconomic factors into management decisions (Kerns and Ager 2007). Including socioeconomic interests in management decisions can be used to garner much-needed public support and funding (Kerns and Ager 2007). Despite the many benefits of combining ecosystem risk assessment with scenario modeling to conservation management, the approach is still employed predominantly in marine systems (Harwood 2000, Linkov et al. 2006, Hobday et al. 2011).

We describe an approach that combines a spatially explicit risk assessment model with scenario modeling to map effects of alternative land-uses and management actions on risk to population persistence for terrestrial animals. We demonstrate application of our approach to guide adaptive management of three rare prairie species on Joint Base Lewis-McChord, a 37 000-ha military base in western Washington State, USA. Our study included three specific objectives: (1) to quantify and map risk to the three study species at Joint Base Lewis-McChord under current conditions, (2) following corroboration of current risk estimates with maps of species distribution,

to quantify and map risk to the three study species under four alternative future management scenarios, and (3) to compare differences in predicted risk to the three study species between current conditions and alternative future scenarios.

Methods

A scenario-based risk assessment approach

Our scenario-based risk assessment approach (Fig. 1) begins with identification of stressors and potential actions for managing the risk posed by stressors. After developing scenarios that explore the effects of changed land-use and management on risk, data is compiled and risk is mapped for each scenario using a spatially explicit risk assessment model. We use a habitat risk assessment model packaged in open-source software developed by the Natural Capital Project (see *Habitat risk assessment model description*) to map cumulative impacts to a species or its habitat. The model combines information about the degree to which the habitat of a given species is exposed to stressors with information about consequences to the species for exposure to the stressors. In this model, the consequence of exposure is a function not only of the change in habitat caused by the stressor, but also resilience of the species based on attributes, such as natural rates of dispersal, maturity, reproduction, and mortality (Folke et al. 2004, De Lange et al. 2010). When possible, we suggest risk should be mapped under current conditions and compared to maps of species distribution, habitat quality, or a proxy for habitat quality, such as forage quality. Additional stressors may be added or model parameters may be modified until a satisfactory match between maps of current risk and maps of species distribution or habitat quality is achieved. Discrepancies may also be investigated empirically. Once model output is corroborated, the outcomes of potential management scenarios can be compared. These outcomes, combined with species-specific details (e.g., risk threshold for persistence, potential for successful reintroduction), as well as economic and social data (e.g., monetary costs of alterations in land use and management, public support for alterations) can be used to guide management decisions. Outcomes of enacted management decisions can, and should, be monitored so that management can be adapted to changes in stressors, exposure, or with other updated information. Despite the inclusion of potentially nuanced species-specific information, the risk assessment model is quite flexible in data requirements and can use coarse categorical data based on expert opinion. Furthermore, the model is part of an open-source software package, making the approach transparent and repeatable, and allowing its application in a wide array of settings. For example, the approach could help federal agencies conducting Environmental Impact Statements as required by the Nation-

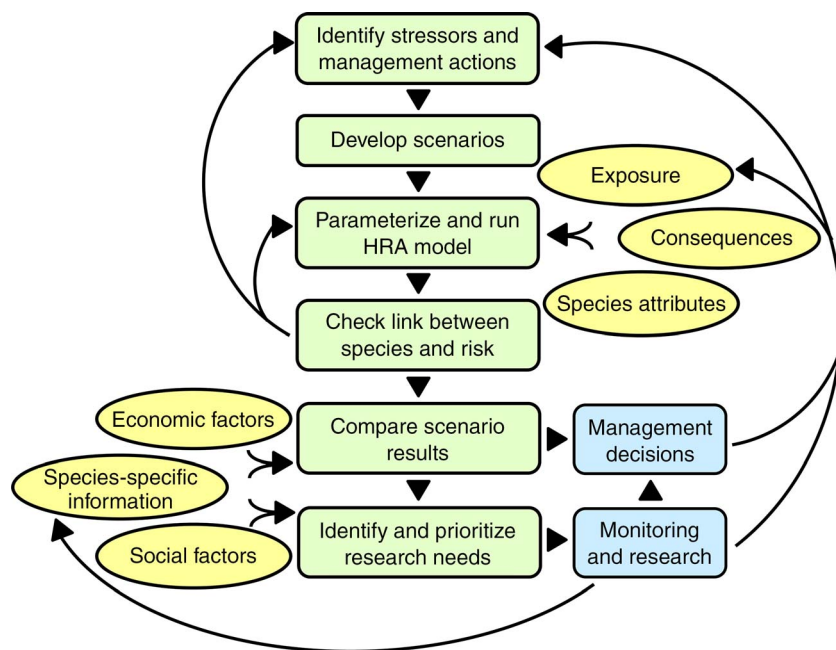


Fig. 1. Overview of an approach that combines a spatially explicit habitat risk assessment (HRA) model with scenario modeling to map effects of alternative land-uses and management actions on risk to population persistence for terrestrial animals. Green backgrounds indicate steps taken in our approach, yellow backgrounds indicate information/inputs used in our approach, and blue backgrounds indicate final outcomes/actions resulting from use of our approach. Model parameterization can be corroborated by checking if species persistence (e.g., species distribution, habitat quality) is linked with spatially explicit risk output under current conditions. Once model parameterization is corroborated, model results for alternative management scenarios can be compared and combined with species-specific information (e.g., risk threshold for persistence, potential for successful reintroduction), as well as economic and social data (e.g., monetary costs of alterations in land use and management, public support for alterations) to guide management, as well as identify and prioritize research filling data gaps to further inform management. Outcomes of management decisions should be monitored and adapted to changes in stressors, exposure, or other updated information.

al Environmental Policy Act when proposing plans that would change land use and management. It could also be used by planners in less traditional, stakeholder-driven planning processes. Indeed, the proposed approach could provide a valuable addition to planning projects for which formal analyses examining potential effects of changed land-use and management of terrestrial species are lacking.

Habitat risk assessment model description

The Natural Capital Project recently developed a habitat risk assessment (HRA) model to assist in the evaluation of biodiversity and habitat quality (Tallis et al. 2011, Guerry et al. 2012, Arkema et al. 2014, Sharp et al. 2014). The HRA model is included in an open-source software suite called Integrated Valuation of Environmental Services and Tradeoffs (InVEST), and similar to other recently developed risk assessment tools, uses a geographic information system (GIS) to map cumulative impacts to a species or its habitat (Andersen et al. 2004, Halpern et al. 2008, Grech et al. 2011). The InVEST HRA model combines two dimensions of information to calculate risk to a species or its habitat (Fig. 2; Arkema et al. 2014, Sharp et al. 2014). The first dimension is

exposure; it represents the degree to which the habitat of a given species experiences stressors, typically due to a human activity. Exposure is a function of the degree of spatial and temporal overlap between habitat and a stressor, stressor intensity, and effectiveness of management strategies mitigating stressor impacts (Fig. 2). The second dimension is consequence; it reflects the habitat- or species-specific responses to stressors associated with various human activities. Consequence to the species for exposure to a stressor is a function of sensitivity (i.e., the extent of change due to exposure) and resilience to its effects (i.e., recovery following exposure; Folke et al. 2004, De Lange et al. 2010). Sensitivity includes the extent of change in habitat area and structure due to the stressor and the frequency of disturbance relative to the historical disturbance regime (e.g., a fire-adapted habitat such as prairie would be less sensitive to burning than a habitat that rarely experiences fire). Resilience includes attributes of the species either comprising or residing in the habitat that influence the likelihood of its recovery (Folke et al. 2004, De Lange et al. 2010) from effects of the stressor (i.e., natural rates of dispersal, maturity, reproduction, and mortality; Fig. 2). Previous studies differ in how they combine exposure and consequence information; whereas cumulative impact-mapping stud-

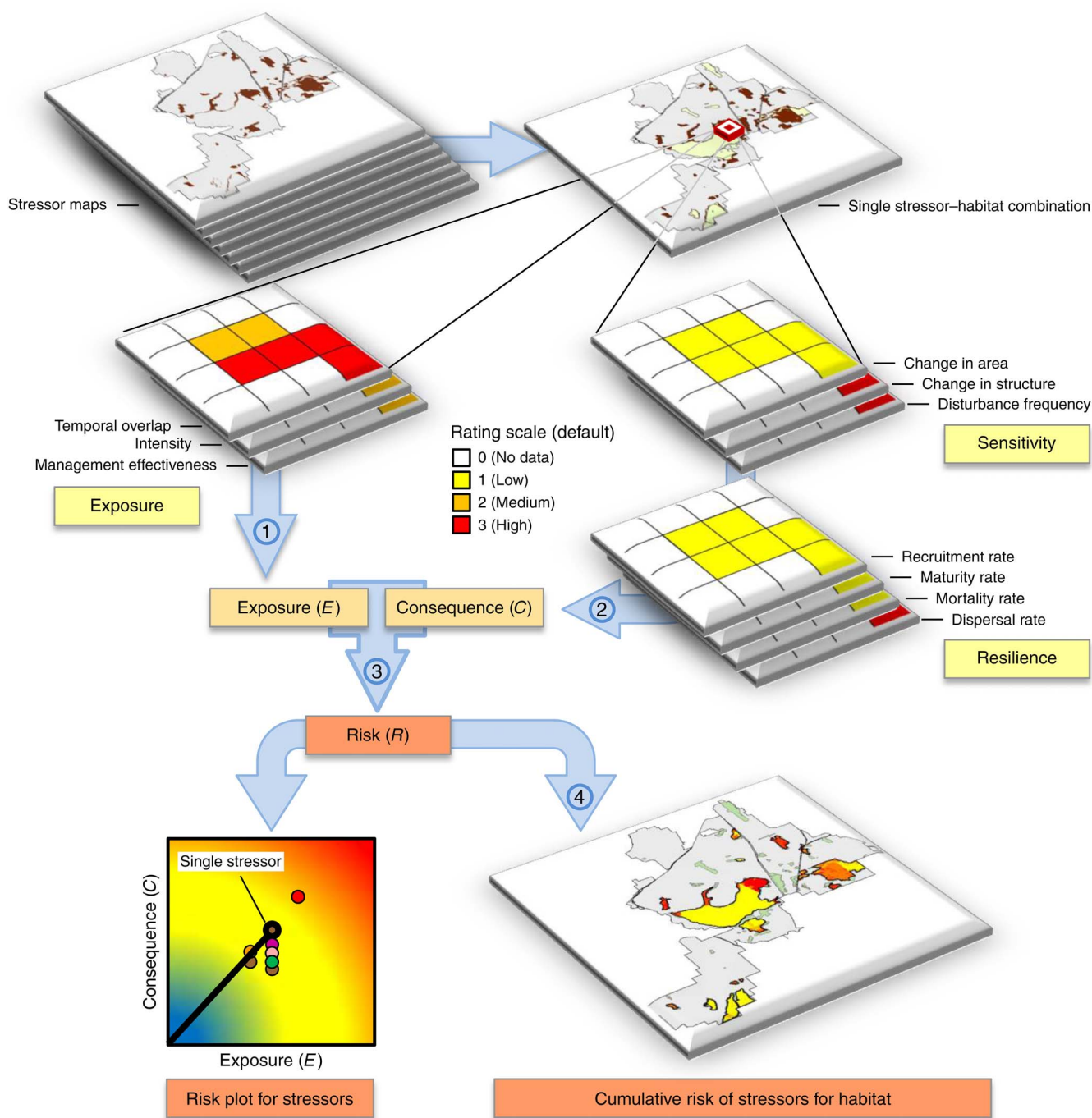


Fig. 2. Conceptual diagram depicting the primary inputs and outputs of the InVEST HRA model. Circles found on blue arrows indicate use of Eqs. 1–4, described in detail in *Methods: HRA model description*. Spatial exposure of habitat to stressors (i.e., a stressor-habitat combination) is determined using habitat and stressor maps (see Figs. 3 and 4 for habitat and stressor maps used in this study). For each stressor-habitat combination, the user rates each exposure and consequence attribute; ratings are stored in a data table and applied to each pixel within a stressor-habitat combination. The model can accommodate any rating scale, but the default is 1–3, where 1 is low (yellow), 2 is medium (orange), 3 is high (red), and 0 is no data (white). Exposure attributes include temporal overlap, intensity, and management effectiveness. Consequence attributes include information about sensitivity of habitat to stressors (change in area, change in structure, disturbance frequency) and resilience of habitat/species (rates of recruitment, maturity, mortality, and dispersal). For each pixel within a stressor-habitat combination, overall exposure (E) to a stressor is calculated as a weighted average of all exposure attributes (Eq. 1), and overall consequence (C) for habitat/species is calculated as a weighted average of all consequence attributes (Eq. 2). Overall E and C are combined to calculate and illustrate risk (R) for each pixel within a stressor-habitat combination (Eq. 3). Relative levels of exposure and consequence averaged across pixels for each habitat-stressor combination are illustrated in risk plots, and cumulative risk of all stressors to a habitat is calculated (Eq. 4) and mapped by pixel for each habitat.

ies primarily use a multiplicative approach to estimate risk, ecosystem risk assessment studies typically use an additive approach (Arkema et al. 2014). The most recent InVEST HRA model can accommodate either approach (Sharp et al. 2014).

The InVEST HRA model allows the user to indicate the quality of data used to score exposure and consequence criteria and to weigh the importance of each criteria relative to other criteria (Tallis et al. 2011, Sharp et al. 2014). Overall exposure (E) and consequence (C) are calculated as weighted averages of exposure values e_i and consequence values c_i for each criterion i where d_i represents the data quality rating, w_i represents the weight of importance for each criterion i , and N is the number of criteria evaluated for each habitat

$$E = \frac{\sum_{i=1}^N \frac{e_i}{d_i w_i}}{\sum_{i=1}^N \frac{1}{d_i w_i}} \quad (1)$$

$$C = \frac{\sum_{i=1}^N \frac{c_i}{d_i w_i}}{\sum_{i=1}^N \frac{1}{d_i w_i}} \quad (2)$$

We used an additive, or Euclidean, approach to estimate risk (R), which can be visualized by plotting habitat–stressor combinations along exposure and consequence axes (Fig. 2). The model produces E and C scores on a scale of 1–3 (low to high risk), but the approach is flexible and can be adapted to any range of risk categories appropriate to the context. Here, risk to habitat i caused by stressor j is the Euclidean distance to the origin for this habitat–stressor combination (Fig. 2; Tallis et al. 2011, Arkema et al. 2014, Sharp et al. 2014)

$$R_{ij} = \sqrt{(E - 1)^2 + (C - 1)^2} \quad (3)$$

Model output includes risk plots depicting relative levels of exposure and consequence for each habitat–stressor combination. Risk plots allow visualization of risk and efficient selection of actions most effective in managing each stressor. For example, whereas stressors with high levels of both exposure and consequence, such as invasive Scotch broom (*Cytisus scoparius*; red circle in Fig. 2 risk plot) may require intensive intervention, stressors with high consequence but lower exposure, such as digging (brown circle with black outline in Fig. 2 risk plot) may be managed more effectively with monitoring and preparation for treatment following exposure (Dawson et al. 2011, Tallis et al. 2011, Sharp et al. 2014).

Last, to assess the influence of multiple activities, the cumulative risk of all stressors on each habitat i is

calculated as the sum of all risk scores for each combination of habitat and activity j as R_i

$$R_i = \sum_{j=1}^J R_{ij} \quad (4)$$

Cumulative risk for habitat i is the sum of all risk scores for that habitat (Fig. 2). Model outputs include maps illustrating cumulative risk summed for each habitat in each pixel within a study region (Fig. 2). Given the simplistic scoring of the exposure and consequence dimensions used to calculate risk, cumulative risk to a habitat is most useful for comparing relative levels of risk under varied scenarios rather than as a precise estimate of risk at any time or location. Detailed information describing the InVEST HRA model and additional capabilities not described here can be found in the user manual (Tallis et al. 2011, Sharp et al. 2014) and in Arkema et al. (2014).

Study system

Less than 10% of pre-European Puget Sound prairie ecosystem remains in Washington, USA, two-thirds of which occurs as grassland patches within a matrix of Douglas fir (*Pseudotsuga menziesii*) forest at Joint Base Lewis-McChord (Crawford and Hall 1997; Fig. 3). Native prairies are disappearing due to land development, invasion of exotic plants, and encroachment by conifer forest in the absence of fire (Chappell and Crawford 1997). The remaining prairie on the base supports a number of species that have experienced population declines due to loss of habitat. At the time we conducted analyses, our three study species, Streaked Horned Lark (*Eremophila alpestris strigata*), Taylor's checkerspot butterfly (*Euphydryas editha taylori*), and Mazama pocket gopher (*Thomomys mazama*) were candidates for federal listing. Since completion of the study, the lark has been listed as threatened, the butterfly as endangered, and the gopher is proposed for listing (USFWS 2013a, b). Populations of these species are generally restricted to prairie patches within the forest matrix. Whereas forests are uninhabitable by these species, prairie varies in its ability to support populations, so that areas bearing few stressors present little risk to population persistence and areas with many stressors present high risk. Long-term population viability for each species is unlikely without either expansion from currently occupied areas or recolonization of suitable, low-risk habitat (Camfield et al. 2011, Schultz et al. 2011, Stinson 2013). Similar to wildlife managers on nonmilitary land, managers on the base strive to protect native biodiversity and to promote population persistence of rare species, but they are additionally tasked with ensuring military training and testing objectives are met (Cohn 1996, Stein et al. 2008, Lee Jenni et al. 2012). Methods for managing prairie on

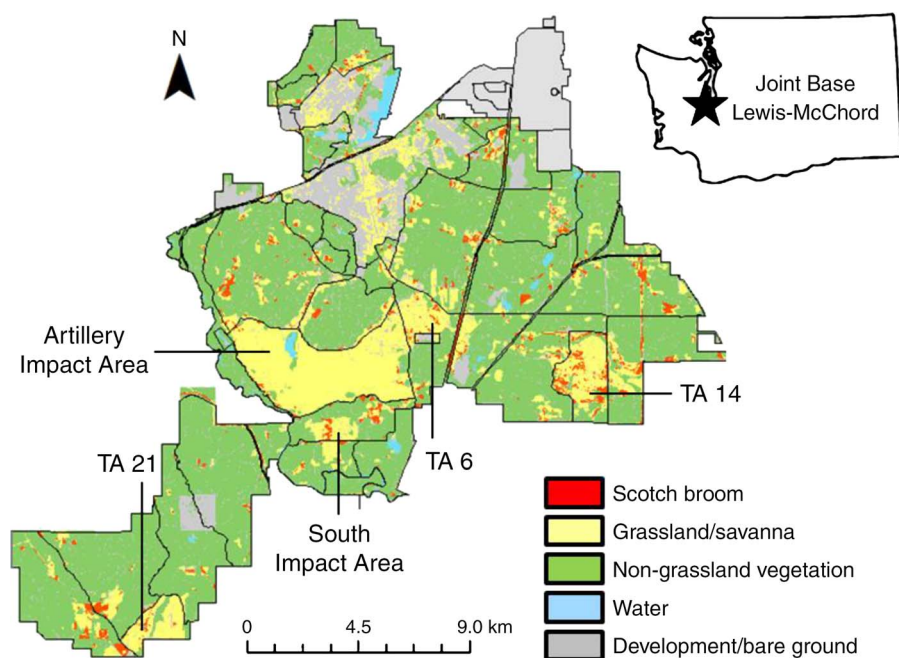


Fig. 3. Current cover by Scotch broom (*Cytisus scoparius*), grassland/savanna, non-grassland vegetation, water, and development/bare ground across Joint Base Lewis-McChord in western Washington State, USA. The largest grassland areas occur within the Artillery Impact Area, South Impact Area, and Training Areas (TAs) 21, 6, and 14. All training and impact areas are outlined in black.

the base are similar to those used on nearby ecological reserves. Prescribed burning is typically used to prevent encroachment by shrubs, trees, and invasive vegetation, primarily Scotch broom, in grasslands of the Puget Sound area; however, the largest grassland patch on the installation also experiences fires ignited during gunnery practices within an Artillery Impact Area (Fig. 3). Management also includes removal of invasive species using hand pulling, mowing, and herbicide treatments, and restoration following soil disturbance (JBLM 2007). The constant management necessary to maintain prairie can be labor-intensive and costly. Joint Base Lewis-McChord currently spends US\$1.86 million per year on resource management for prairie and other habitats (J. Foster, *personal communication*).

Model inputs

Habitat and stressors

We used a detailed installation vegetation map (Chastain 2008) to map current cover by Scotch broom, grassland/savanna, non-grassland vegetation, water, and development/bare ground at a 30-m resolution across Joint Base Lewis-McChord; we included all vegetative cover as habitat input for HRA models (Fig. 3). Stressors, defined as any factor that might threaten the existence of species inhabiting prairie on the base, were identified during creation of a draft Candidate Conservation Agreement and Candidate Conservation Agreement with Assurances for Puget Sound Prairie

Species (G. Reub, *personal communication*). The process of creating the two agreements included both interviews with biological experts and literature reviews investigating relationships between potential stressors and the study species (G. Reub, *personal communication*). We included seven training-activity stressors in HRA models identified during creation of the agreements (digging, off-road vehicles, camping, flight operations, foot training, ordnance, firing range training), as well as an eighth stressor (invasive Scotch broom) identified during our consultation with biological experts on the base (Fig. 4).

Exposure

We used maps of training areas and training restrictions, training manuals, and interviews with base personnel to determine which training-activity stressors occurred in prairie on each training area on the base. We classified temporal overlap between training-activity stressors and prairie by the frequency of training per year (high, medium, low, or no overlap; Appendix: Table A1). We assumed year-round overlap between Scotch broom and prairie, except in scenarios including treatment of 100% of Scotch broom. We considered stressor intensity (i.e., number of soldiers·d⁻¹·ha⁻¹) equal for all training-activity stressors and scenarios (Table 1), but see a related study for examples of scenarios with varied training-activity intensity at Joint Base Lewis-McChord (Daily et al. 2015). We scored stressor intensity for Scotch broom higher than training activities (Table 1)

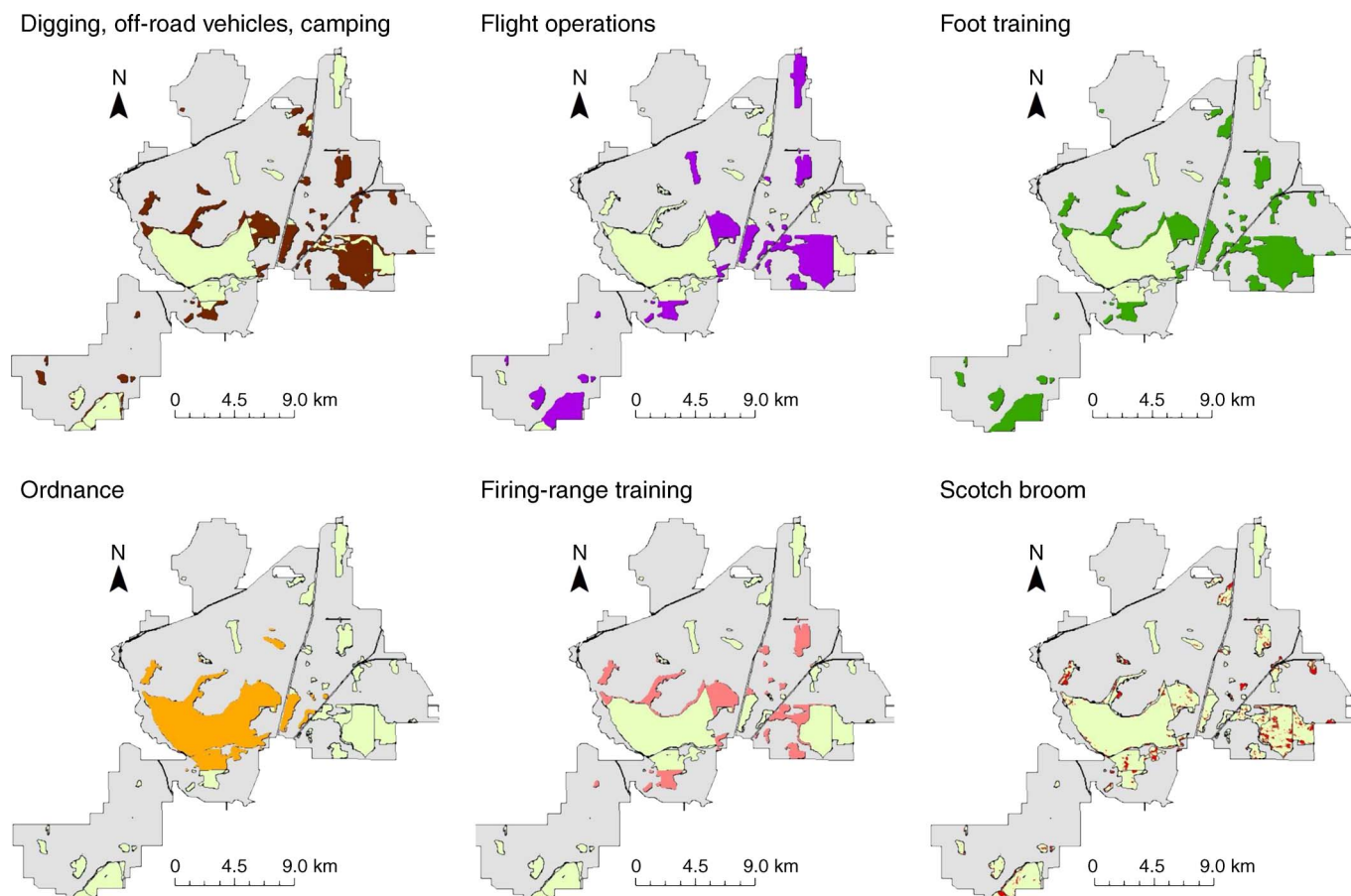


Fig. 4. Overlap of eight stressors with grassland habitat (light green) under current conditions at Joint Base Lewis-McChord (non-grassland habitat shown in gray). Stressors include digging (brown), off-road vehicles (brown), camping (brown), flight operations (purple), foot training (green), ordnance (orange), firing range training (pink), and Scotch broom (red). Note that digging, off-road vehicles, and camping share identical overlap with grassland habitat.

because detrimental effects of the shrub on the study species are well documented (USFWS 2013a, b). For all scenarios, we considered management more effective for off-road vehicles and ordnance training than other stressors (Table 1), because periodic disturbance by these activities is managed to provide openings in prairie beneficial to nesting and movement of the study species (Pearson et al. 2005, JBLM 2007).

Consequences

Given the history of ecosystem risk assessment in marine systems, criteria for evaluating consequences have been developed primarily to assess risk to fisheries and have relied on information about fecundity, breeding, and reproductive strategies (Patrick et al. 2010, Hobday et al. 2011, Samhouri and Levin 2012). Criteria appropriate for a wider range of habitats were developed by the Natural Capital Project and are described in the InVEST HRA model user manual (Tallis et al. 2011, Sharp et al. 2014) and in Arkema et al. (2014). Users with data relating a terrestrial species/habitat’s resistance to, or recovery from, exposure to a

Table 1. Exposure for the three study species, Streaked Horned Lark (*Eremophila alpestris strigata*), Taylor’s checkerspot butterfly (*Euphydryas editha taylora*), and Mazama pocket gopher (*Thomomys mazama*), at Joint Base Lewis-McChord, Washington, USA.

Stressor	Exposure (all study species)	
	Intensity	Management effectiveness
Digging	2	2
Off-road vehicles	2	1
Camping	2	2
Flight operations	2	2
Foot training	2	2
Ordnance	2	1
Fire-range training	2	2
Scotch broom	3	2

Notes: Exposure is the same for all three species and includes the intensity of each stressor (1–3; low to high intensity) and effectiveness of management actions used to mitigate stressors (1–3; highly effective to not effective). All inputs are classified from 1 to 3 (low to high risk), based on literature (Pearson et al. 2005, JBLM 2007, USFWS 2013a, b).

Table 2. Estimates for effects of stressors on changes in area and structure (G. Reub, *personal communication*), as well as historic and current frequency of disturbances (Chappell and Crawford 1997, Crawford and Hall 1997, Dunn 1998, Whitecotton et al. 2000, Quist et al. 2003, JBLM 2007, Dunwiddie and Bakker 2011) and scores representing species-specific consequences of a stressor, as experienced by lark, butterfly, and gopher.

Stressor	Change in area			Change in structure			Change in frequency (type) All species
	Lark	Butterfly	Gopher	Lark	Butterfly	Gopher	
Estimates							
Digging	L	T	M	T	H	L	H (digging by humans)
Off-road vehicles	L	L	T	T	M	L	M (foot traffic)
Camping	L	L	T	T	L	T	H (digging by humans)
Flight operations	L	T	T	L	H	T	M (foot traffic)
Foot training	L	T	T	T	L	T	M (foot traffic)
Ordnance	L	M	M	T	L	L	H (fire frequency)
Fire-range training	T	T	M	T	M	L	M (fire frequency)
Scotch broom	H	H	H	H	H	H	H (conifer encroachment)
Scores							
Digging	1	1	2	1	3	1	3
Off-road vehicles	1	1	1	1	2	1	2
Camping	1	1	1	1	1	1	3
Flight operations	1	1	1	1	3	1	2
Foot training	1	1	1	1	1	1	2
Ordnance	1	2	2	1	1	1	3
Fire range training	1	1	2	1	2	1	2
Scotch broom	3	3	3	3	3	3	3

Notes: Change in frequency is for all species, from historic to current conditions. Changes are trace (T), low (L), moderate (M), and high (H). Consequence scores are categorized from 1 to 3 (low to high risk) based on broad criteria developed by the Natural Capital Project (Tallis et al. 2011, Sharp et al. 2014).

stressor may develop their own criteria and classification thresholds (Briske et al. 2006, Sharp et al. 2014). Additionally, the most recent release of the HRA model can support spatially explicit criteria (Sharp et al. 2014). In this study, however, we did not have such data available, and instead we demonstrate the first application of broad criteria developed by the Natural Capital Project (Tallis et al. 2011, Sharp et al. 2014) to a terrestrial system. We corroborate resulting estimates of risk under current conditions with maps of species distribution for the three study species at Joint Base Lewis-McChord.

We used data from a draft Candidate Conservation Agreement and Candidate Conservation Agreement with Assurances for Puget Sound Prairie Species estimating the effect of stressors on loss of prairie area and structure, as experienced by a species, as trace, low, medium, and high (G. Reub, *personal communication*) to classify consequences from 1 to 3 (low to high risk; Table 2). In the InVEST user manual, 1 is 0–19% loss, 2 is 20–49% loss, and 3 is 50–100% loss (Tallis et al. 2011, Sharp et al. 2014). We conducted a literature review to determine sources and frequency of historical disturbance levels in Puget Sound prairie and classified the effect of a stressor as 3 (high) when analogous historical disturbances (e.g., digging, foot traffic or fires by Native Americans, conifer encroachment) occurred either much more or much less frequently than stressor disturbance, 2 (medium) when historical disturbances occurred slightly more or slightly less frequently, and 1 (low) when disturbance frequencies were similar (Chappell and Crawford 1997, Crawford and Hall 1997, Dunn

1998, Whitecotton et al. 2000, Quist et al. 2003, Dunwiddie and Bakker 2011; Table 2).

We reviewed literature to assess the resilience of each study species to both historical disturbances and current stressors on the basis of natural rates of mortality, recruitment, maturity, and dispersal (Folke et al. 2004, De Lange et al. 2010). We assigned scores of 1–3 to indicate stressor impact (low–high), given the resilience of each species (Table 3). The InVEST HRA model assumes species with rapid life cycles (i.e., high mortality and recruitment rates and short times until maturity) and frequent dispersal between populations should be those most resilient to the effects of stressors (Folke et al. 2004, De Lange et al. 2010). Therefore, species least impacted by stressors have annual mortality rates >80%, annual recruitment, maturity rates <1 yr, and dispersal distances >100 km, and species highly impacted by stressors have annual mortality rates <20%, recruitment rates >2 yr, maturity rates >10 yr, and dispersal distances <10 km (Tallis et al. 2011, Sharp et al. 2014). Consequences are habitat- and species-specific and do not vary among scenarios (Tallis et al. 2011, Sharp et al. 2014).

In this study, all three study species experience high rates of natural mortality and annual recruitment (USFWS 2013a, b) and received scores indicating low stressor impact based on naturally high rates of turnover (Table 3). Whereas all three study species reach sexual maturity in ~1 yr, butterflies can lay up to 1200 eggs/season in clusters of 20–350 (Scott 1986) and thus received a lower stressor impact score based on greater

Table 3. Estimates from literature for natural rates of mortality, recruitment, maturity, and connectivity (Erlich et al. 1975, Scott 1986, Pearson et al. 2008, Schapaugh 2009, Camfield et al. 2011, Kaye et al. 2011, Bennett et al. 2013, Stinson 2013, USFWS 2013a, b) and scores representing species-specific consequences, for lark, butterfly, and gopher, given resilience based on biological attributes.

Natural rates influencing consequences	Lark	Butterfly	Gopher
Estimates			
Mortality	~80% juveniles/yr	~90% larvae/yr	~85% juveniles/yr
Recruitment	annual (~3 eggs)	annual (20–350 eggs)	annual (~5 young)
Maturity	1 yr	1 yr	1 yr
Connectivity	adult dispersal uncommon, high site fidelity	~15% cross forest–grassland edges	dispersal up to 160 m observed
Scores			
Mortality	1	1	1
Recruitment	1	1	1
Maturity	2	1	2
Connectivity	3	3	3

Note: Consequence scores are categorized from 1 to 3 (low to high impact) based on broad criteria developed by the Natural Capital Project (Tallis et al. 2011, Sharp et al. 2014).

reproductive capacity than the lark and gopher, which produce <10 young/yr (Camfield et al. 2011, Stinson 2013; Table 3). All three study species received high stressor impact scores based on low natural rates of dispersal (Table 3). Whereas dispersal distance for gopher is limited by its fossorial lifestyle (USFWS 2013b), dispersal of butterfly is limited by its resistance to crossing non-grassland habitat, particularly forests (Kaye et al. 2011). Dispersal of lark is limited by behavioral attributes; adults display extremely high site fidelity to nesting sites and juvenile dispersal to new nesting sites appears likely only during periods of population growth (Pearson et al. 2008).

Management scenarios

Wildlife biologists and resource managers identified two important policy drivers influencing management practices on the base: training activities and the budget for resource management. Training activities causing frequent or extensive soil disturbance (digging, off-road vehicle use, and camping) can change prairie area and structure (JBLM 2007) and therefore are restricted either seasonally (4–6 months during breeding/nesting seasons) or year-round in some areas. The budget for resource management is allocated largely to Scotch

broom control, but also includes habitat maintenance and restoration. In the scenarios we developed, we varied levels of Scotch broom control and locations of training restrictions to depict effects of policy drivers on the risk to population persistence of the study species under simple, but reasonable, alternative management scenarios. The five management scenarios included current management conditions, a drastic year-round restriction scenario deemed possible if one or more study species was listed as endangered, and three intermediate scenarios with less severe management actions (Table 4, Fig. 5).

Mapping and quantifying risk

We mapped and quantified risk to population persistence within all occupied and potential habitat for each study species at Joint Base Lewis-McChord under current conditions and alternative future management scenarios. We ran all models at a 30-m resolution, the finest resolution possible given our land-use and -cover input data and one which staff find relevant to the scale at which they conduct management at Joint Base Lewis-McChord. We summarized risk to each species by calculating total and mean risk within areas classified as verifiably occupied or unoccupied potential habitat by

Table 4. Five alternative management scenarios for which policy drivers are altered to vary the percentage of invasive Scotch broom treated and the area restricting training activities in potential habitat of three prairie species at Joint Base Lewis-McChord.

Scenario	Policy drivers		
	Scotch broom treated annually (%)	Seasonal training restrictions (ha)	Year-round training restrictions (ha)
Current conditions	40	1474	2390
Scotch broom removal	100	1474	2390
Additional seasonal restrictions	40	6628	2390
Scotch broom removal and additional seasonal restrictions	100	6628	2390
Additional year-round restrictions	40	1474	7544

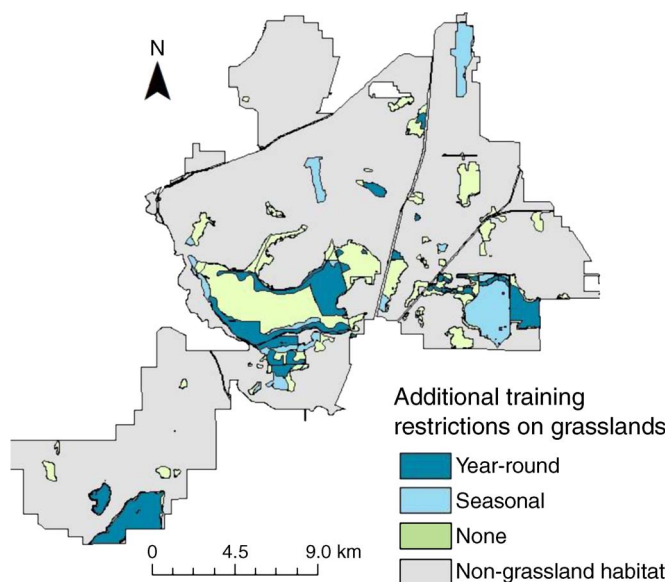


Fig. 5. Additional areas of year-round and seasonal training restrictions on grassland habitat at Joint Base Lewis-McChord. Training activities restricted in these areas include digging, off-road vehicle use, and camping.

wildlife biologists at Joint Base Lewis-McChord (Fig. 6, Table 5). In addition to verified occupied areas, the species have recolonized edges of the Artillery Impact Area and undocumented occurrences within the area are likely; however, the presence of undetonated ordnances prevents surveys providing verification (J. Foster, *personal communication*). Thus, we included the Artillery Impact Area as potential habitat for each of the species where occupancy cannot be verified, but designate potential habitat as either in or outside the Artillery Impact Area (Fig. 6). The area designated as potential habitat for each species ranges from 3264 ha for lark to 5428 ha for butterfly and 5825 ha for gopher (Fig. 6). The butterfly occupies 2% of its potential habitat, occurring only within the Artillery Impact Area (Fig. 6). By contrast, of the potential habitat occupied by lark (23%) and gopher (22%), most is outside the Artillery Impact Area (lark, 18%; gopher, 13%; Fig. 6).

Potential management of the study species at Joint Base Lewis-McChord may include not only maintenance

of occupied habitat, but also promotion of population expansion into accessible potential habitat and reintroduction of populations into inaccessible potential habitat. Thus, to guide future research and management of the study species, we also classified potential habitat as accessible or inaccessible for each species by assuming habitat was accessible if it was either adjacent to occupied habitat or connected by any type of grassland (Fig. 6). We assumed that study species were able to move through all grassland habitats, even when unsuitable for occupation, but unlikely to move through forest matrix (Knudsen 2003, Camfield et al. 2011, Kaye et al. 2011). More potential habitat is accessible for expansion within the Artillery Impact Area (from 31% for the gopher to 40% for the butterfly and 55% for the lark) than outside the Artillery Impact Area (from 14% for the gopher to 17% for both the butterfly and lark; Fig. 6). Whereas more than one-third of potential habitat remains inaccessible to the butterfly (41%) and gopher (34%), all but 5% of potential habitat is accessible to the lark (Fig. 6).

Corroborating model output

To test if parameterization of HRA models using broadly classified data was ecologically sound, we compared risk predicted for each study species under current conditions to maps of current species distributions. We used HRA model output for each study species under current conditions to calculate the cumulative risk of all stressors to a species for each 30 × 30-m pixel within potential habitat at Joint Base Lewis-McChord. We used a chi-square analysis to test if cumulative risk summed across pixels within verifiably occupied habitat (yellow areas in Fig. 6) differed from that within unoccupied potential habitat (green areas in Fig. 6), given total cumulative risk within all potential habitat (area outlined in black in Fig. 6) under current conditions. We assume risk is negatively related to habitat quality and that a realistic characterization of risk (i.e., parameterization of the HRA model) will result in significantly lower cumulative risk in verifiably occupied habitat than unoccupied potential habitat.

Table 5. Area, total risk, and mean risk of verifiably occupied habitat, unoccupied potential habitat, and all potential habitat calculated for lark, butterfly, and gopher under current conditions at Joint Base Lewis-McChord.

Type of potential habitat	Lark			Butterfly			Gopher		
	Area (ha)	Total risk	Mean risk	Area (ha)	Total risk	Mean risk	Area (ha)	Total risk	Mean risk
Occupied habitat	744	2120	2.85	118	176	1.49	1257	3027	2.41
Unoccupied potential habitat	2520	7802	3.10	5310	22 931	4.32	4568	23 503	5.15
All potential habitat	3264	9922	3.04	5428	23 107	4.26	5825	26 530	4.55

Note: Chi-squared tests comparing total risk between verifiably occupied habitat and unoccupied potential habitat were $\chi^2_1 = 11.55, P < 0.01$ (lark), $\chi^2_1 = 217.31, P < 0.01$ (butterfly), and $\chi^2_1 = 1623.35, P < 0.01$ (gopher); all tests significant at $P < 0.05$.

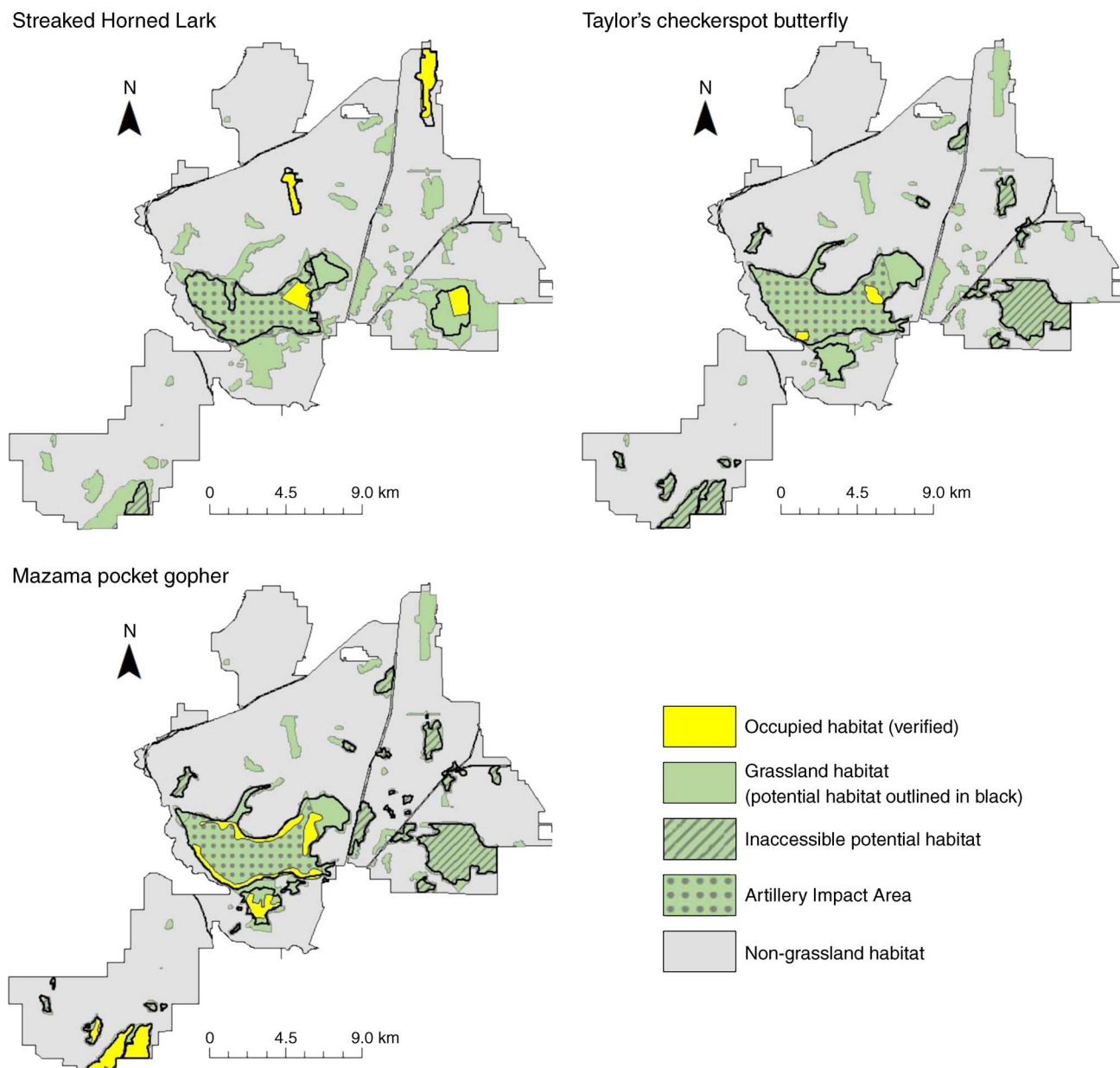


Fig. 6. Verifiably occupied grassland habitat and unoccupied grassland habitat for Streaked Horned Lark (*Eremophila alpestris strigata*), Taylor's checkerspot butterfly (*Euphydryas editha taylori*), and Mazama pocket gopher (*Thomomys mazama*) at Joint Base Lewis-McChord. Unverified occupancy of the study species may occur in the Artillery Impact Area. For each study species, potential habitat is outlined in black and inaccessible potential habitat is designated by hatching.

Results

Mapping and quantifying risk under current conditions

We present written results for all three study species here; results for the Mazama pocket gopher are similar to those of the Taylor's checkerspot butterfly, and we thus relegate figures illustrating them to the Appendix: Figs. A1, A2. Current risk ranges from ~1 to 13 for each species. When risk is averaged in areas of potential habitat classified as occupied, accessible, or inaccessible, either inside or outside the Artillery Impact Area, the

lowest mean risk occurs in both occupied and accessible habitat within the Artillery Impact Area (Figs. 6 and 7; Appendix: Fig. A1), with risk ranging from 1.4 for the Streaked Horned Lark to 1.5 for the butterfly and 1.6 for the gopher. Outside the Artillery Impact Area, occupied habitat currently averages lower levels of risk (from 3.0 for the gopher to 3.3 for the lark) than potential habitat that is unoccupied, but accessible via expansion (Figs. 6 and 7; Appendix: Fig. A1). Of all potential habitat, accessible habitat outside the Artillery Impact Area experiences the greatest mean risk under current conditions (Figs. 6 and 7; Appendix: Fig. A1), with

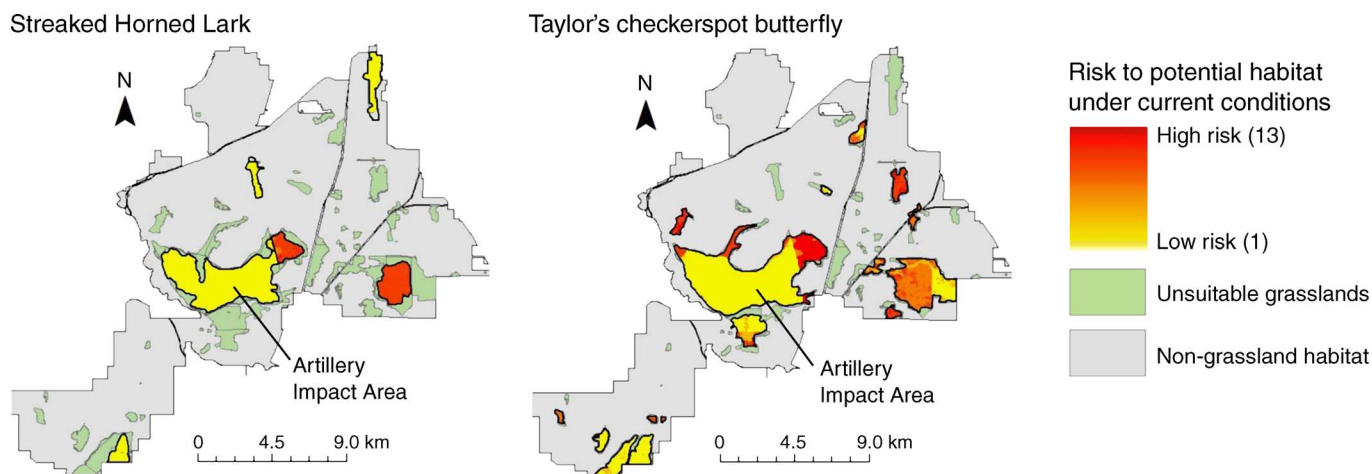


Fig. 7. Risk to lark and butterfly within potential habitat for each species under current conditions at Joint Base Lewis-McChord. Green indicates areas of grassland habitat unsuitable for occupation and areas outlined in black designate potential habitat for each study species. See Appendix: Fig. A1 for risk to gopher.

values varying from 7.5 for the butterfly to 8.0 for the gopher and 8.6 for the lark. The mean risk in currently inaccessible habitat varies more among species than any other type of potential habitat, ranging from 2.4 for the lark to 5.8 for the butterfly and 7.2 for the gopher (Figs. 6 and 7; Appendix: Fig. A1).

Corroborating model output

For all three study species, mean risk in verifiably occupied habitat is lower than in unoccupied potential habitat (Table 5). A model of current conditions for lark predicted risk across potential habitat averages 3.04; mean risk (3.10) in 2520 ha of unoccupied potential habitat (total risk of 7802) is higher, and mean risk (2.85) in 744 ha of occupied habitat (total risk of 2120) is lower ($\chi^2_1 = 11.55$, $P < 0.01$; all analyses significant at $P < 0.05$; Table 5). Risk within potential habitat averages 4.26 for butterfly under current conditions. Whereas the model predicted a similar mean risk (4.32) in 5310 ha of unoccupied potential habitat (total risk of 22 931), mean risk (1.49) in 118 ha of occupied habitat (total risk of 176) is lower ($\chi^2_1 = 217.31$, $P < 0.01$; Table 5). Last, our model of current conditions for gopher predicted a mean risk of 4.55 in potential habitat; mean risk (5.15) in 4568 ha of unoccupied potential habitat (total risk of 23 503) is higher, but mean risk (2.41) in 1257 ha of occupied habitat (total risk of 3027) is lower ($\chi^2_1 = 1623.35$, $P < 0.01$; Table 5).

Mapping, quantifying, and comparing risk under alternative management scenarios

Varying management scenarios had only a moderate effect on risk in potential habitat, with changes in risk occurring primarily outside the Artillery Impact Area (Figs. 6 and 8; Appendix: Fig. A1). We present results for

assessment under current conditions, Scotch broom removal, and additional year-round restrictions here; results under scenarios including additional seasonal restrictions, as well as additional seasonal restrictions combined with Scotch broom removal, were similar to those under the Scotch broom removal scenario and are illustrated in Appendix: Fig. A3.

Average risk decreases slightly when Scotch broom removal is added to current conditions (Fig. 8; Appendix: Fig. A1). Potential habitat most improved by Scotch broom treatment is accessible to the lark via grassland habitat (change in risk, Δ risk = 0.3; Figs. 8 and 9). Under current conditions, 77% (572 ha) of habitat occupied by the lark occurs at a risk value ≤ 2 and 21% (159 ha) occurs between 2 and 8. With Scotch broom removal, the percentage of habitat accessible to the lark with risk values between 2 and 8 (i.e., values with potential to support population persistence, given occurrence in occupied habitat) increases from 48% (274 ha) to 59% (338 ha; Fig. 9). In contrast to the lark, potential habitat most improved by Scotch broom treatment for the butterfly (Δ risk = 0.4) and gopher (Δ risk = 0.4) is not connected to occupied habitat via grasslands and is inaccessible (Figs. 8 and 9; Appendix: Figs. A1, A2). Under current conditions, 99% (117 ha) of habitat occupied by the butterfly and 85% (1070 ha) occupied by the gopher occurs at a risk < 2 ; an additional 11% (183 ha) of habitat occupied by the gopher occurs with risk between 2 and 8. With Scotch broom removal, the percentage of habitat inaccessible to the butterfly at risk levels ≤ 2 increases from 37% (815 ha) to 39% (870 ha; Fig. 9). Additionally, in a scenario with Scotch broom removal, the percentage of habitat inaccessible to the gopher at risk values between 2 and 8 increases from 44% (861 ha) to 55% (1075 ha; Appendix: Fig. A2).

Decrease in average risk is greatest under scenarios with additional year-round restrictions (Fig. 7; Appen-

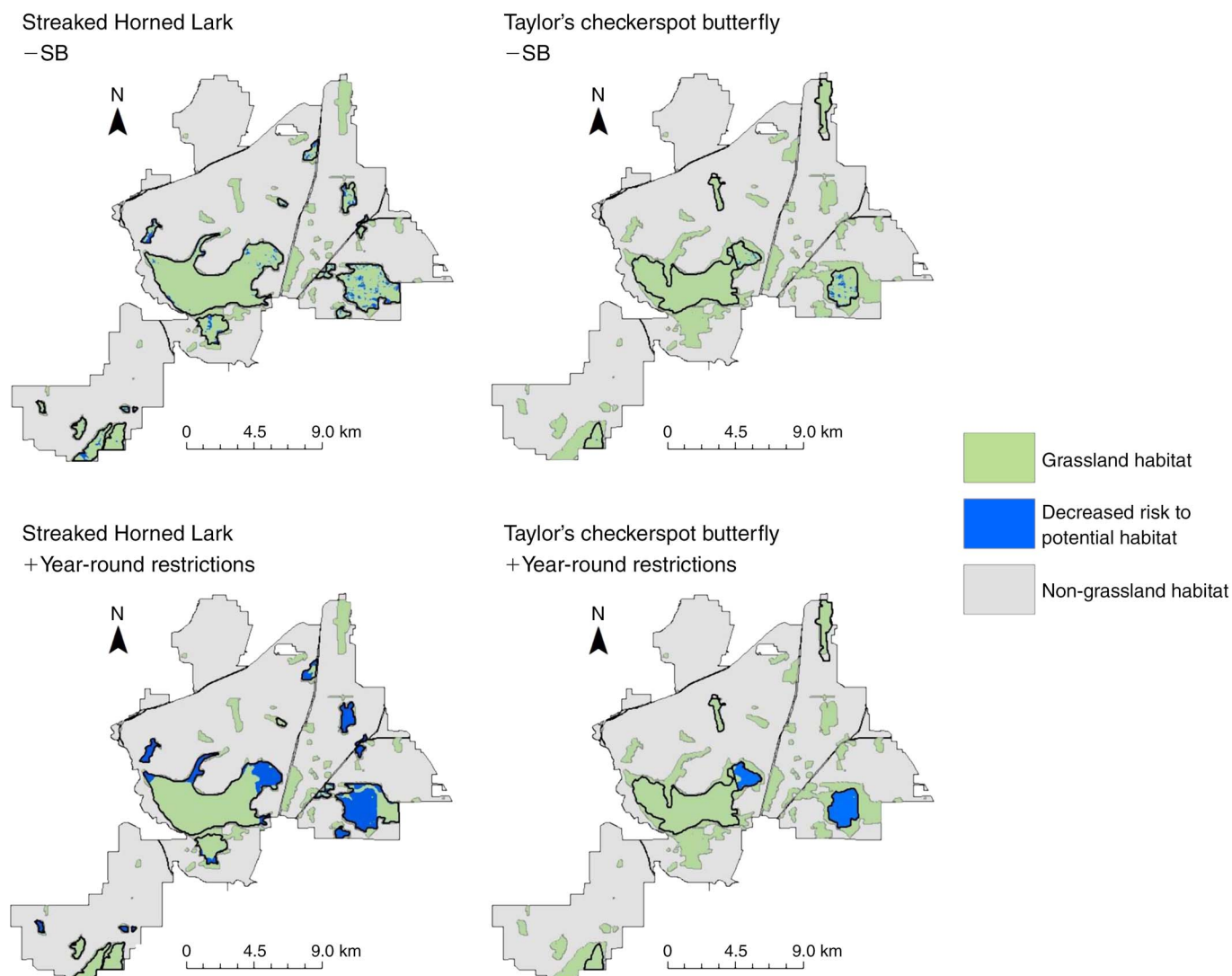


Fig. 8. Change in risk from current conditions to alternative management scenario (100% Scotch broom removal [-SB], additional year-round restrictions) to potential habitat for lark and butterfly at Joint Base Lewis-McChord. Green indicates areas of grassland habitat unsuitable for occupation and areas outlined in black designate potential habitat for each study species. See Appendix: Fig. A1 for change in risk to potential habitat for gopher.

dix: Fig. A2). Areas most improved with additional restrictions are entirely accessible to the lark (Δ risk = 0.8), with improvement even occurring in an area occupied by the species (Δ risk = 0.3; Figs. 7 and 8). With additional year-round restrictions, 21% of occupied habitat (159 ha) and 43% of accessible habitat (245 ha) decreases in risk value from 7 to 6 (Fig. 8). In contrast, much of the area most improved with additional year-round restrictions remains inaccessible to the butterfly (Δ risk = 0.4) and gopher (Δ risk = 0.6; Figs. 7 and 8; Appendix: Figs. A1, A2). Under a scenario with additional year-round restrictions, the percentage of habitat that is inaccessible to the butterfly at risk levels ≤ 2 decreases from 37% (815 ha) to 35% (771 ha), but at risk levels between 2 and 8 increases from 38% (843 ha) to 42% (924 ha; Fig. 8). Similarly, with year-round restrictions, the percentage of habitat that is

inaccessible to the gopher at risk levels ≤ 2 decreases from 17% (326 ha) to 13% (263 ha), but at risk levels between 2 and 8 increases from 44% (861 ha) to 50% (984 ha; Appendix: Fig. A2).

Discussion

Using an approach that combines a spatially explicit risk assessment model with scenario modeling, we were able to quantify and map effects of alternative land-use and management on risk in a terrestrial system. We found alteration of land use and management can potentially reduce risk to population persistence for three rare prairie species. We identified which actions have the greatest potential for reducing risk, where such reductions are likely to occur, and how monitoring and research can be prioritized to guide implementation of

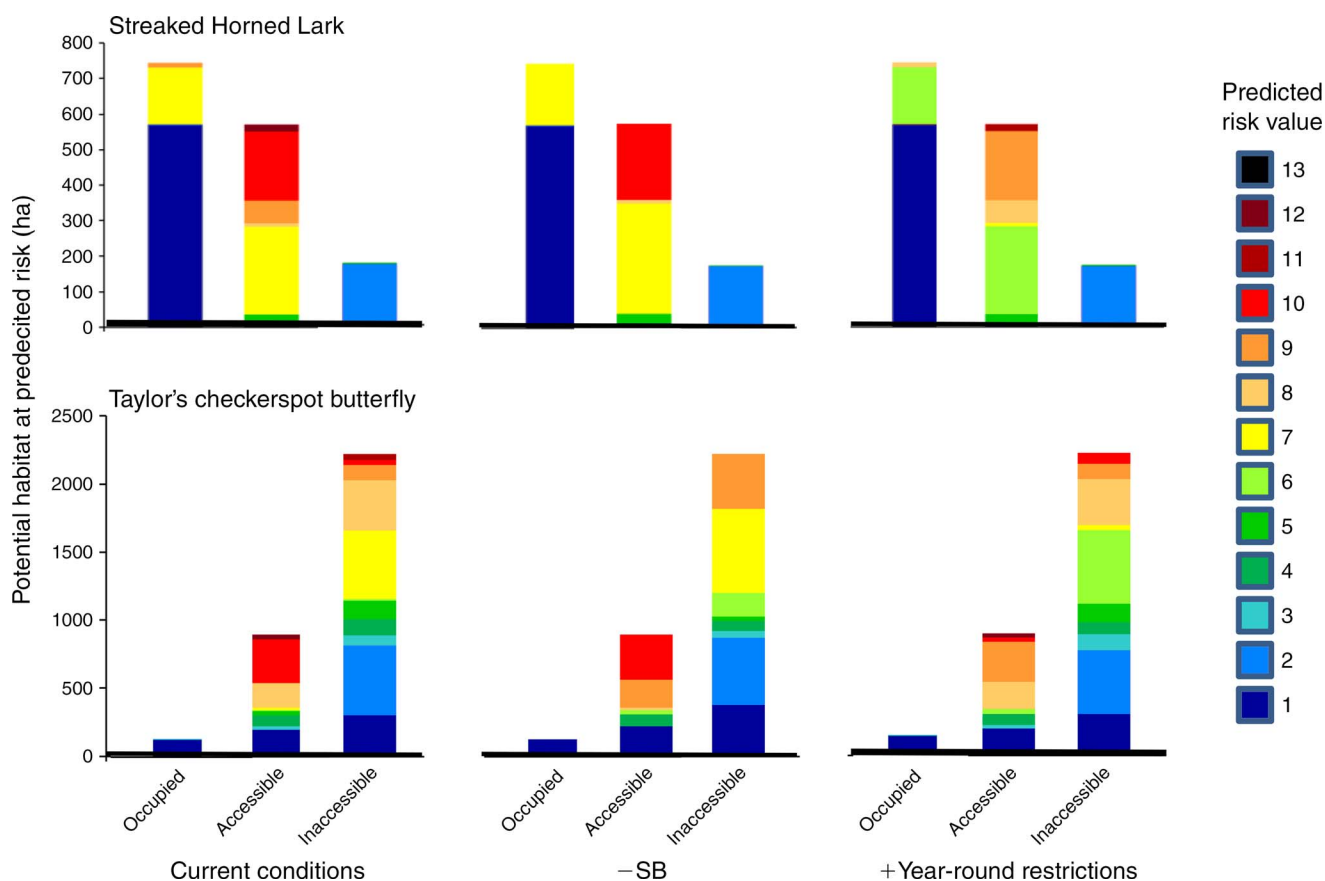


Fig. 9. Potential habitat at predicted risk (ha) for lark and butterfly within areas verified as occupied, areas accessible outside the Artillery Impact Area, and areas inaccessible outside the Artillery Impact Area under three alternative management scenarios at Joint Base Lewis-McChord: (1) current conditions, (2) 100% Scotch broom removal (–SB), and (3) additional year-round restrictions. See Appendix: Fig. A2 for potential habitat (ha) at predicted risk for gopher.

management actions. Managers tasked with ensuring the persistence of these populations now have information about the relative levels of risk predicted in occupied habitat, areas accessible for expansion, and inaccessible habitat suitable for reintroductions. This information, combined with species-specific details resulting from monitoring and research (e.g., risk threshold for persistence, potential for successful reintroduction), as well as economic and social data (e.g., monetary costs of alterations in land use and management, changes in capacity to support military training, public support for alterations) can be used to guide management decisions in an adaptive fashion (Fig. 1). What is more, we were able to attain this information without the time, labor, and cost necessary to conduct field research and without potential harm to the study species. Indeed, where data on the consequences to study species of exposure to stressors were lacking, we were able to develop model inputs from expert opinion. Corroboration of our model output for current conditions with occupancy data for the study species suggests reasonable parameterization of our models, even when rated using broad criteria found in the InVEST user guide (Tallis et al. 2011, Sharp et al. 2014) with inputs

based on expert opinion.

Once models are parameterized to demonstrate a relationship between current risk and species persistence (e.g., species distribution, habitat quality), risk predicted under altered management can be compared among occupied habitat, areas accessible for expansion, and inaccessible habitat suitable for reintroductions to help prioritize areas of future monitoring and research and refine species management plans. In this study, 77% of habitat occupied by Streaked Horned Lark occurs at a risk <2; the remainder occurs at values from 7 to 9, primarily in Training Area 14 where most stressors included in this study are present. Overall, lark populations at Joint Base Lewis-McChord are declining (Camfield et al. 2011). If managers use monitoring or research data to confirm that only habitat occurring at a risk <2 supports the persistence of lark populations (i.e., the lark is declining in high-risk locations such as Training Area 14), they might prioritize efforts to maintain currently occupied habitat, since little habitat at a risk <2 occurs outside these areas under any of the scenarios examined in this study (Fig. 9). Alternatively, if managers have reason to believe that the lark is not declining where it occurs on habitat with risk values

from 7 to 9, they might instead prioritize the establishment of year-round training restrictions. With year-round training restrictions, 99% of potential habitat for the lark occurs at a risk ≤ 9 , more than quadrupling the amount of habitat able to support persistence of the species (Fig. 9). If managers were to choose this management option, however, they would need to determine why lark populations have not already expanded into accessible areas that occur at a risk ≤ 9 so that any issues preventing the success of future expansions or reintroductions could be addressed. Tests of translocation techniques for the lark have already begun and have been met with some success; the feasibility of using audio/visual conspecific cues to attract larks to unoccupied habitat are also being explored (Streaked Horned Lark Annual Working Group 2013).

In contrast to the lark, Taylor's checkerspot butterfly is fairly sensitive to changes in vegetation structure caused by stressors at Joint Base Lewis-McChord (Table 2), in part, because these changes reflect loss of host plants on which the butterfly larvae depend (USFWS 2013a). The species is verified to occur in just two small areas within the Artillery Impact Area where, of the stressors examined in this study, only ordnance training is present. As a result, fully 99% of occupied habitat occurs at a risk < 2 . If managers can use monitoring or research data to confirm that butterfly populations are at equilibrium, they might reason that unoccupied areas of potential habitat with risk < 2 are also likely to support butterfly populations. Because the amount of potential habitat with risk < 2 varies little among management scenarios (Fig. 9), managers might prioritize efforts to maximize butterfly use of these low-risk areas over those to increase the amount of low-risk habitat. Research could be focused to examine why the butterfly is not currently in accessible areas with risk < 2 and if potential exists for reintroductions into inaccessible areas with risk < 2 . Indeed, a number of successful tests of captive breeding and translocation techniques for the butterfly have already been conducted (Grosboll 2004, Linders 2008, Schultz et al. 2011). Studies could also examine the ability of the butterfly to persist in habitat occurring at the higher risk values, particularly values from 5 to 6, which will increase in availability if year-round training restrictions are enforced in potential habitat (Fig. 9).

Managers rarely have the opportunity to focus their efforts entirely on the management of rare species without balancing additional land-use or management concerns. Nowhere is this more apparent than on a military installation. Our analyses indicate that altering land use and management can potentially reduce risk in habitat for the study species. However, such reduction will require drastic measures. Predicted reduction in risk to rare species is greatest in a scenario with year-round training restrictions enforced in all potential habitat (Fig.

8). Scenarios with seasonal training restrictions reduce exposure to off-road vehicles, digging, and camping for limited periods of time in limited areas of potential habitat, but the small decreases in exposure have little impact on risk to study species. Decreasing risk by restricting additional training activities will likely compromise military training and testing objectives and thus be highly unpalatable to base managers. However, because reduced training would likely be limited to Training Areas 6 and 14, where the most prairie habitat with potential for reduced risk occurs (Figs. 3 and 8), it might be possible to achieve significant risk reduction without a great disruption of training. The fact that Training Area 14 is not easily accessed by butterfly or Mazama pocket gopher emphasizes the important role that reintroductions to suitable, but inaccessible habitat may play in the management of these species. Mapping potential risk across the base can help managers choose which, if any, training areas should receive restrictions on use of off-road vehicles, digging, and camping.

The approach demonstrated in this study could be used to inform management of rare species in diverse land-planning processes. For instance, the National Park Service recently drafted an off-road vehicle management plan and environmental impact statement for Glen Canyon National Recreation Area, in Arizona and Utah, USA (National Park Service, U.S. Department of the Interior 2014). The plan evaluates the effects of off-road vehicle use, as well as potential management actions to provide for the recreational use and enjoyment of Glen Canyon while protecting its resources, under five alternative action scenarios (National Park Service, U.S. Department of the Interior 2014). Planners used GIS analyses to summarize the effects of both off-road vehicles and management actions on species at the park. The spatially explicit output provided by our risk assessment model for each scenario would supplement existing analyses by pinpointing specific locations where off-road vehicles, as well as invasive species and military overflights from nearby bases, would present the most risk to species and where management actions are most likely to reduce risk. Such information would be valuable in guiding wildlife management and balancing it with recreation in Glen Canyon.

Planners could also use the proposed approach in less traditional, stakeholder-driven planning processes. For example, the Pacific Northwest Ecosystem Research Consortium recently conducted a landscape-planning project to inform community decisions regarding land and water use in the Willamette River Basin, Oregon, USA (Baker et al. 2004). The group used input from stakeholders to create three alternative future scenarios and evaluated the likely effects of land-use change on water availability, stream condition, and terrestrial wildlife (Baker et al. 2004). Researchers conducted two assessments predicting changes in abundance and

distribution of terrestrial species. The simpler assessment relied on GIS imagery and species–habitat relationships based on expert opinion for 279 terrestrial species (Schumaker et al. 2004). The more complex assessment used an individual-based, spatially explicit population model (PATCH, now HexSim) that required data on area needs, survival, reproduction, and movement; it was applied to 17 terrestrial species (Schumaker et al. 2004). For eight of these species, there was no positive correlation in predictions between the two assessments. Researchers indicated the simpler assessment may have been insufficient for some species and that inclusion of models of medium complexity would have been instructive (Schumaker et al. 2004). Our proposed approach could provide just such a model; similar to the simple assessment, it can use data based on expert opinion, but like the complex assessment, it can also include detailed information on species-specific attributes such as survival, reproduction, and connectivity.

Finally, given the flexibility in data requirements of the proposed approach, it could provide a valuable addition to planning projects for which formal analyses examining potential effects of changed land use and management of terrestrial species are lacking. For example, researchers recently conducted a state-level assessment of climate change impacts intended to facilitate the development of adaptation strategies in the state of New York, USA (ClimAID; Rosenzweig et al. 2011). In the report resulting from this assessment, researchers identified species of conservation concern, potential stressors, and management alternatives to mitigate effects of stressors. Given the availability of this information, it is likely researchers also had access to biologists willing to provide expert opinion, if not detailed data, that could serve as inputs for a risk assessment model. While ClimAID did provide decision makers with information about the state's vulnerability to climate change, the addition of our spatially explicit risk assessment modeling approach could move this project to the next step; decision support for on-the-ground management of species of conservation concern in the state of New York.

Conclusions

A scenario-based approach using the spatially explicit HRA model found in InVEST is applicable to a wide array of issues encountered by wildlife managers in terrestrial systems in which land use and cover are predicted to change. The approach can be implemented quickly because it does not necessarily rely on the accumulation of large sample sizes or experimental outcomes. The approach is also transparent and repeatable, allowing ready uptake into policy-making. It is especially beneficial to wildlife managers because it provides spatially explicit output useful for prioritizing

monitoring and research and guiding management in an adaptive fashion. Finally, the InVEST HRA model is flexible in data requirements and can be used in data-poor environments. Indeed, our approach is well suited to an adaptive management program, in part, because of the ease with which InVEST HRA models can be parameterized, run, corroborated, and updated. Together, these characteristics make our approach ideal for assessing risk to species of conservation concern when time or cost are limiting factors and initial management decisions must be made before experimental results and/or fine-scale data will be available.

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Supplemental Material

Ecological Archives

The Appendix is available online: <http://dx.doi.org/10.1890/14-0009.1.sm>

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