

Full Length Research Paper

Integrating environmental influences on patch occupancy into reserve selection and prioritization for the imperiled Carson Valley silverspot butterfly (*Speyeria nokomis carsonensis*)

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Integrating ecological information into conservation prioritization strategies is needed to facilitate land-use decisions about which habitat areas should be protected for imperiled species. Little effort has been directed toward incorporating variations in environmental determinants of patch occupancy across habitat types to optimize site selections for land acquisitions or habitat management activities, despite that variable other than patch area and isolation may significantly affect occupancy patterns of a species. This study examined how reserve networks differ in terms of sites selected, area reserved, and economic costs when comparing “traditional” systems (where only patch area and isolation affect occupancy) to “habitat-specific” systems that integrate variations in the environmental determinants of patch occupancy across distinct habitat types. Data on habitat variability and determinants of occupancy of an imperiled butterfly, the Carson Valley silverspot (*Speyeria nokomis carsonensis*) were integrated in an optimal reserve design procedure in Marxan. Analyses illustrated that reserve networks differed substantially between the traditional and habitat-specific systems. Cost efficiency (cost per area to protect habitat) was best for riparian habitats under the habitat-specific system, nearly 250% more efficient than the traditional reserve system. This study demonstrated that integrating environmental determinants of patch occupancy into site selection procedures more optimally selects suites of high quality habitat for an imperiled species. Moreover, these results provide land use decision-makers with cost-efficient prioritization strategies for habitat protection of an imperiled butterfly that can improve conservation actions and policies.

Key words: *Speyeria nokomis*, reserve selection, imperiled species, endangered species act, conservation planning, prioritization, cost-area efficiency.

INTRODUCTION

Integrating ecological science into land use and land management pursuant to the United States Endangered Species Act of 1973, as amended (ESA), is a critical challenge for effective conservation of imperiled species in the United States (Clark et al., 2002). This issue has spurred ecological guidelines for land-use planning in recent years (Dale et al., 2000; ELI, 2003) but the

immediacy of demands put on land planners and regulatory agencies forces them to establish conservation priorities whether information to guide reserve design and management of species and their habitats is available or not (Theobald and Hobbs, 2002). There is a widely acknowledged shortfall of pertinent species-specific habitat data for most imperiled species, and that

frequently contributes to misdirecting conservation resources, regulatory actions and mitigation activities (Tear et al., 1993; Scott et al., 1995; Wilcove et al., 1998; Campbell et al., 2002). Given the increasing extent of land transformation (Vitousek et al., 1997; Brown et al., 2005), and the frequency of smaller land areas included in reserve systems (Groom et al., 2006; Chape et al., 2007), conservation decisions require planners to recognize and consider the variability in characteristics and comparative values of landscape areas that are occupied by imperiled species. Unfortunately, knowledge of that sort rarely can be found in listing petitions and recovery plans under the ESA (Wilcove et al., 1998; Campbell et al., 2002; Gerber and Hatch, 2002), greatly impeding effective conservation and prioritization strategies for imperiled species (Goble et al., 2006).

Substantial improvements are needed for prioritizing habitats for imperiled species listed under the ESA or species that may warrant listing under the ESA. Little attention has been directed to this need, at least in part, because descriptions of resource use and habitat attributes are few for imperiled species and areas fitting simplistic habitat definitions are often afforded similar levels of protection (Wilcove et al., 1998; Campbell et al., 2002).

The immediacy of conservation demands typically forces land planners to use only readily available data on imperiled species such as patch area and isolation metrics that can be obtained from a geographic information system for reserve design approaches. While work on species that occur on patchy landscapes or as a metapopulation has demonstrated that habitat quality parameters explain equal or great variation in patch occupancy compared to area and isolation (Moilanen and Hanski, 1998; Bradford et al., 2003; Xu et al., 2006); more recent research has demonstrated that some imperiled species occur within distinct habitat types and that environmental variables differentially influence patch occupancy depending on habitat type (Talley et al., 2007; Sanford et al., 2011). Conservation goals are likely to be compromised if all sites are collectively considered to contain the same habitat features (Sanford et al., 2011). In addition, an optimal solution for a reserve network likely is compromised for imperiled species if such variability in the determinants of patch occupancy is not integrated into the site-selection procedures.

The goal of this study was to examine differences in two reserve design approaches (“traditional” versus “habitat-specific”) in a system where habitat areas occupied by an imperiled species exhibit variability in environmental parameters that affect its occupancy status. The traditional reserve design approach integrates only the influences of patch area and isolation on patch occupancy into site selection procedures, whereas the habitat-specific approach integrates variability in the determinants of patch occupancy among distinct habitat

types. Most studies in which optimization procedures select reserve systems for imperiled species have included demographic models of population viability (Montgomery et al., 1994; Haight and Travis, 2008). Despite benefits to those approaches, imperiled species rarely are studied to the extent that parameterization of demographic models is highly accurate or even possible (Lindenmayer et al., 2000; Ralls et al., 2002). Rather, assessments of imperiled species more frequently include simple presence/absence data, and therefore, there is a substantial need to inform prioritization strategies for imperiled species where occurrence and habitat data are available. Because decision-makers seek to maximize conservation attributes, such as habitat area or habitat quality, and minimize economic costs to protect habitat, this study uses an optimization procedure that prioritizes habitat areas based on their environmental variables that influence patch occupancy, while minimizing economic costs of the reserve network. That approach allows for different quantities of environmental variables and different habitat patches to enhance the range of conservation options available to land use decision-makers.

This study posed three main questions: how do reserve networks differ between traditional and habitat-specific approaches? How are sites prioritized within habitat types and what are the cost efficiencies of those reserve systems? And what suite of sites represents the irreplaceable units within the study system? These questions are addressed using data on the Carson Valley silverspot butterfly (*Speyeria nokomis carsonensis*), an imperiled species previously categorized as a ‘candidate 2’ for listing under Section 4 of the ESA. This butterfly is the subject of past and present conservation attention and inevitably it will be the subject of future conservation action pursuant to the ESA (WildEarth Guardians, 2010), given that its distribution has been greatly reduced and threats from livestock grazing and water diversions remain unabated at the majority of habitat patches (Sanford, 2011).

MATERIALS AND METHODS

Study area and species

The silverspot butterfly occurs in disjunct wet meadow habitats along the western fringe of the Great Basin in California and Nevada (Austin, 1998; Sanford, 2011). This region is part of the Basin and Range Province, creating an elevationally diverse landscape (1460 to 3505 m). The Great Basin is a semi-arid desert with only a very small fraction of land area occurring as isolated wetlands or riparian areas. Over half of the wetlands in the Great Basin have been eliminated due to human land uses since the 1850's (Dahl, 2000), and remaining wetlands are currently more isolated than they were historically and they remain subject to impacts from human uses including livestock grazing, water diversions, recreation and land development (Brussard et al., 1998; Sada and Vinyard, 2002). As a result of those anthropogenic

disturbances, the spatial distribution and total area of occupancy of the silverspot have been reduced (Sanford, 2011). Within the western Great Basin, the silverspot butterfly's habitat consists of three distinct habitat types: 12 agri-exurban sites, 14 isolated springs and 36 riparian meadows (Sanford, 2011). Agri-exurban habitats are wet lowland meadows that are privately owned and occur in or adjacent to agricultural lands. Isolated springs are spring- and seep-fed meadows surrounded by dry uplands that include sagebrush-dominated shrublands (*Artemisia tridentata*) and pinyon juniper woodlands (*Pinus monophylla*). These habitat patches occur on public lands administered both by the U.S. Bureau of Land Management (BLM) and U.S. Forest Service (USFS) that are subject to livestock grazing, water diversions and recreational use. Riparian meadows consist of relatively narrow meadows along riparian corridors and are owned by private and public entities.

Within these habitat patches are generally surrounded by an otherwise unsuitable matrix including agricultural lands, sagebrush-dominated communities and conifer-dominated communities. Within these habitats, seven habitat variables were particularly important in explaining occupancy of the silverspot butterfly: percent cover of the silverspot's larval food plant (*Viola nephrophylla*), cover of nectar resources, vegetation height, litter depth, disturbance, patch area and distance to the nearest occupied patch (Sanford et al, 2011). Across habitat types, average cover of *V. nephrophylla* ranged from 2.98 to 5.11%; cover of nectar plants ranged from 2.98 to 5.98%; vegetation height ranged from 49 to 68 cm; litter depth ranged from 3.5 to 5.4 cm; mean distances to the nearest occupied patch ranged from 304 to 4650 m; patch area ranged from 0.13 to 2.58 ha; and site disturbance did not vary among habitat types but was a highly significant factor in explaining occupancy of the silverspot (Sanford et al, 2011). The relative influences of habitat variables on silverspot occupancy, as indicated by model-averaged coefficients from regression analyses varied from 0.01 to 0.99 depending on habitat type. These observations were integrated into reserve scenario construction and optimization procedures.

Simulated annealing

To compare reserve design outcomes between the traditional and habitat-specific approaches, simulated annealing was used (Kirkpatrick et al., 1983; Ball and Possingham, 2000). Simulated annealing provides for decision support analyses in systematic conservation planning (Margules and Pressey, 2000; Cabeza et al., 2004a; Williams et al., 2004), and it identifies the optimum and minimum set of a large number of sites that contain specific conservation features. The simulated annealing algorithm minimizes an objective function and starts with a completely random reserve system. Trial solutions then are explored iteratively through sequential random changes to the set of planning units, or sites, in the entire system. At each step, the new set of units is compared with the previous set and the best one is accepted (Possingham et al., 2000). As the process continues, the algorithm becomes more selective in terms of what changes lead to the best system of sites.

The simulated annealing algorithm consistently has outperformed simpler iterative or heuristic algorithms (Ball, 2000; Ball and Possingham, 2000).

Reserve scenario construction and site selection

Different reserve scenarios were explored using Marxan 1.8.2 software package (Ball and Possingham, 2000) with the objective of

examining alternative reserve designs to identify a reserve system that minimizes the cost of habitat protection while ensuring that conservation goals for each habitat type were captured. The process occurred in several steps. First, a traditional reserve system was generated where only patch area and isolation influenced patch occupancy and thus reserve design. Secondly, habitat-specific reserve systems were generated by integrating variability of the environmental determinants of patch occupancy by the silverspot butterfly between habitat types (Sanford et al, 2011). These two approaches were used to prioritize habitat areas for land management activities by providing the best suite of habitat variables within individual sites at the lowest economic cost. Five reserve scenarios were generated to prioritize areas for conservation within the traditional and habitat-specific systems (Table 1). These reserve scenarios, or conservation priority levels, were based on analyses of the relative influences of seven environmental variables on patch occupancy. Optimum values of variables were calculated separately for the traditional system and for each habitat type in the habitat-specific system (Table 2).

The following equation was used to calculate optimum values:

$$P_o = \sum w_i V_n \times 100,$$

Where P_o is the optimum value of a habitat variable, $\sum w_i$ is the model-averaged coefficient which provides the total weight that a habitat variable has on patch occupancy of the silverspot butterfly and V_n is the average standardized value of a given habitat variable across patches. Thus, P_o is a weighted value that emphasizes the relative influence of a particular variable on occupancy.

The optima were used to calculate habitat values at 5, 15, 30 and 50% below the optima, corresponding to priority levels 2 to 5 (Table 1). These gradations from optima informed the prioritization scheme for the reserve system, because they represented a suite of conservation features at levels still pertinent for silverspot habitat conservation. Marxan software required multiple input files, three of which warrant description here. First, a planning unit file consisted of a list of planning units (or sites), relational identification numbers, easting and northing universal transverse mercator (UTM) coordinates and economic cost. Estimation of the cost of each planning unit depended on land ownership. For private lands, land values averaged US\$ 151,500 in 2005 dollars across the study region. For sites on public lands, conservation costs were estimated as the cost to construct and maintain fences around sites to prevent degradation from livestock or human use. Here, total cost = (perimeter) (cost of fence construction and maintenance per year). The perimeter of each site was calculated using Xtools extension in ArcView 9.1. Costs of fence construction and maintenance were derived from estimates provided in Meyer and Olsen (2005). Thus, costs for public lands are annual costs, whereas private land costs are actual property values needed for acquisitions or easements.

Secondly, the conservation feature file consisted of various habitat variables depending on the reserve design approach (traditional or habitat-specific). Each habitat variable received a unique and relational identifier and the optimum value for each habitat variable (P_o). A conservation penalty factor also was included to help weight or penalize features if the value was not met within a planning unit. Thirdly, the conservation feature versus planning unit file was a relational file containing planning units and their respective values for each habitat variable. These values for a given habitat variable were mean values across patches (unstandardized V_n). Thus, this third file contained a planning unit identifier, conservation feature identifier and the value of each habitat variable within each planning unit. I ran one million iterations of the simulated annealing algorithm for each reserve scenario under the traditional and habitat-specific systems. The best network of reserves had the lowest value of the objective function in the

Table 1. Summary of data for multiple reserve scenarios in traditional and habitat-specific reserve systems of *Speyeria nokomis carsonensis*. The number of sites available and included in optimization analyses for each reserve scenario is provided, in addition to the number of reserves selected by Marxan. Cost is the total minimized economic cost for reserving the selected network of reserves for each reserve scenario.

Reserve system	Reserve Scenario	Target percentage (%)	No. of sites	No. reserves	Score	Cost
Habitat-specific reserves						
Agri-Exurban	P1	Optimum	12	7	1989281	1113108
	P2	5	5	1	2.97E+08	2014192
	P3	15				
	P4	30				
	P5	50				
Isolated springs	P1	Optimum	14	3	1183	710
	P2	5	11	3	1396	1396
	P3	15	8	3	2043	2043
	P4	30	5	2	6370	1268
	P5	50	3	2	1544	904
Riparian meadows	P1	Optimum	36	14	193971	11594
	P2	5	22	2	658446	8521
	P3	15	20	1	909944	1432
	P4	30				
	P5	50				
Traditional reserves						
All sites	P1	Optimum	62	5	4153	3910
	P2	5	57	5	2988	2946
	P3	15	52	5	1971	1887
	P4	30	47	3	901	901
	P5	50	44	1	784	761

Table 2. Conservation targets expressed as a unit-less optimal value of a given environmental variable (P_o , described in materials and methods) for the traditional and habitat-specific (agri-exurban, spring and riparian habitats) reserve systems across seven environmental variables important for explaining patch occupancy of *S. nokomis carsonensis*.

Environmental Variable	Conservation targets (P_o) per reserve system			
	Traditional	Agri-exurban	Spring	Riparian
Nectar cover	-	0.41	6.18	8.45
Viola cover	-	1.65	1.15	9.36
Vegetation height	-	84.41	30.03	44.60
Litter depth	-	1.76	0.32	0.27
Disturbance index	-	3.69	0.50	2.79
Patch area	40.99	0.19	0.50	23.62
Patch isolation	35.19	2.66	2.78	25.13

reserve design problem (Ball and Possingham, 2000; Possingham et al., 2000). After the optimum set of reserves was selected by

Marxan from the pool of sites, that particular set of planning units was deleted from the input files before running the alternative

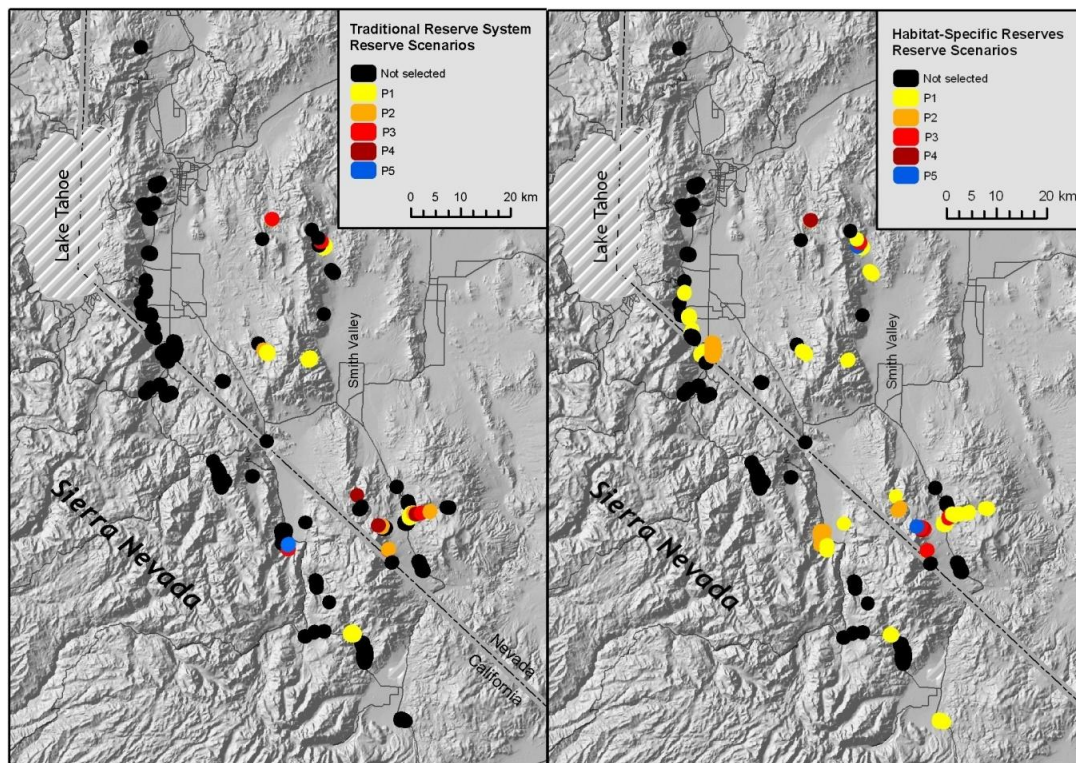


Figure 1. Map of sites selected from one million runs of simulated annealing in Marxan under different reserve scenarios (Table 1) for the traditional and habitat-specific reserve systems of *S. nokomis carsonensis*.

reserve scenarios (P2 to P5; Table 1). I continued this procedure through all scenarios. Because the goal was to prioritize sites according to particular conservation features within planning units, the chance for planning units to be selected again was eliminated for lower priority reserves such that each priority level was a different suite of planning units.

In addition to running simulated annealing algorithms, ad hoc irreplaceability analyses were conducted (Pressey et al., 1996), where irreplaceability was defined as the number of times a planning unit was included in the reserve system out of 1000 MARXAN runs. This concept is similar to Pressey et al. (1994) idea of irreplaceability, where irreplaceability is defined as the likelihood that any of the areas in a region will be needed to achieve an explicit conservation goal. This analysis was used to identify the irreplaceable planning units within the study system for both the traditional and habitat-specific system. Planning units with a high irreplaceability value are the sites that are the most difficult to replace in a reserve system (that is, high quality habitat), and therefore, should be given high priority for inclusion in a specified reserve system. Irreplaceability scores of sites within each reserve system were grouped as selection frequencies as 0, 1 to 99, 100 to 499, 500 to 999 and 1000.

RESULTS

The maps of reserve networks illustrated substantial differences in the sites selected between traditional and

habitat-specific reserve systems (Figure 1). Only three site matches occurred between traditional and habitat-specific reserves in the P1 scenario, and none of the agri-exurban or spring sites matched traditional sites in the P1 reserve scenario. Across all reserve scenarios, the traditional reserve system included a suite of 19 sites with a combined area of 3.78 ha, while the habitat-specific reserve system comprised a suite of 38 sites totaling 45.16 ha (Table 1, Figure 2a). The optimal solution for the traditional reserve system included five sites for a combined area of 1.99 ha, which were a subset of sites selected as the optimal solution for riparian and isolated spring sites. None of the agri-exurban sites were included in the traditional reserve system. In contrast, a total of 24 planning units (11.79 ha) were identified for the optimal habitat-integrated reserve system, seven of which constituted agri-exurban habitats (7.35 ha) (Figure 2a). Together, the P1 reserve network of both isolated springs and riparian sites comprised 17 planning units with a combined area and annualized cost of 4.44 ha and US\$ 12,304, respectively (Figure 2a, b).

The annualized cost for the P1 reserve network for riparian sites was approximately 1.6 times greater than the annualized cost of the P1 reserve system for isolated springs (Figure 2b). The cost of reserve systems was

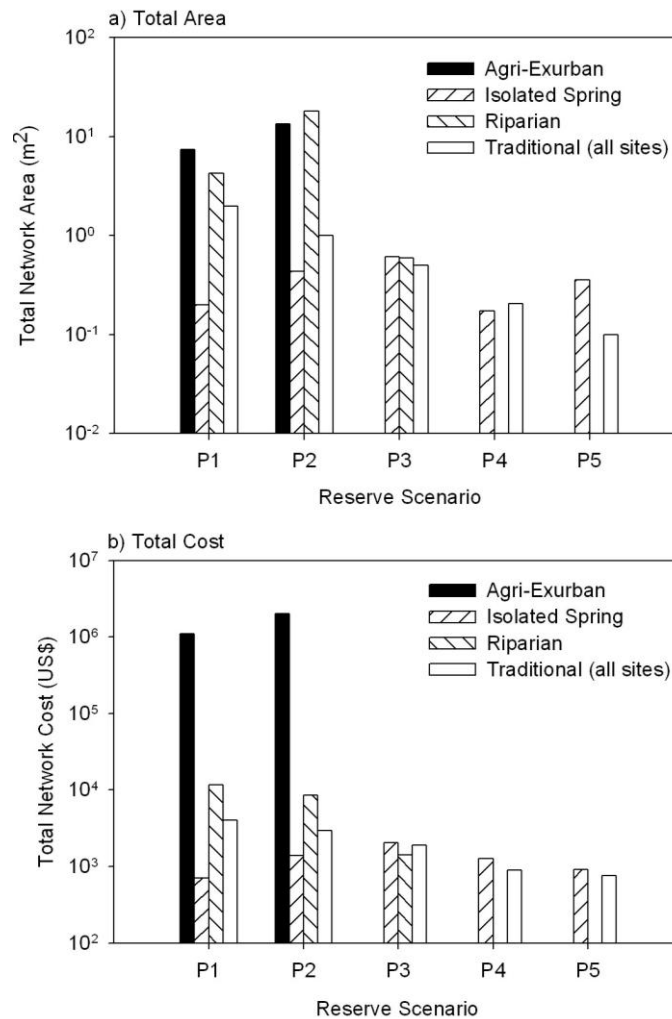


Figure 2. Total area (a) and cost (b) of reserve networks for the traditional reserve system and habitat-specific system (agri-exurban, isolated spring and riparian habitats) under different reserve scenarios.

generally the least for isolated springs (Figure 2b), and accordingly comprised the least amount of area (Figure 2a). These data illustrate large differences in area and cost between the traditional and habitat-specific reserve networks. Cost efficiencies varied between reserve types as evidenced by cost-area ratios. Agri-exurban reserves had a very high cost (Figure 2b) and a high cumulative cost-area ratio compared to isolated spring and riparian reserves (Figure 3), indicating a substantial inefficiency of conserving agri-exurban sites for the silverspot butterfly. Agri-exurban reserves demonstrated cost-area ratios that nearly reached 30 as a result of the high cost of land in the agri-exurban system (Figure 3). Cumulative cost-area ratios for isolated springs were nearly equal to cost-area ratios for the traditional reserve system, especially in

reserve scenarios P3-P5. Riparian reserves were over 250% more efficient in terms of cost per area than either the spring or traditional reserve system, illustrating that more riparian sites can be set as reserves for the lowest cost. Importantly for the riparian reserve system, the cost-area ratio only marginally increased with the accumulation of sites from P1 through P3 (Figure 3). Because the slopes of the cumulative area versus cumulative cost curves were less than one-half (Figure 4), reserve systems that added sites from P1 through P5 scenarios provided more reservation area per cost (Figure 3).

Under the assumption that the high cost of conserving silverspot butterfly habitat on agri-exurban lands would be a significant deterrent for the overall conservation of

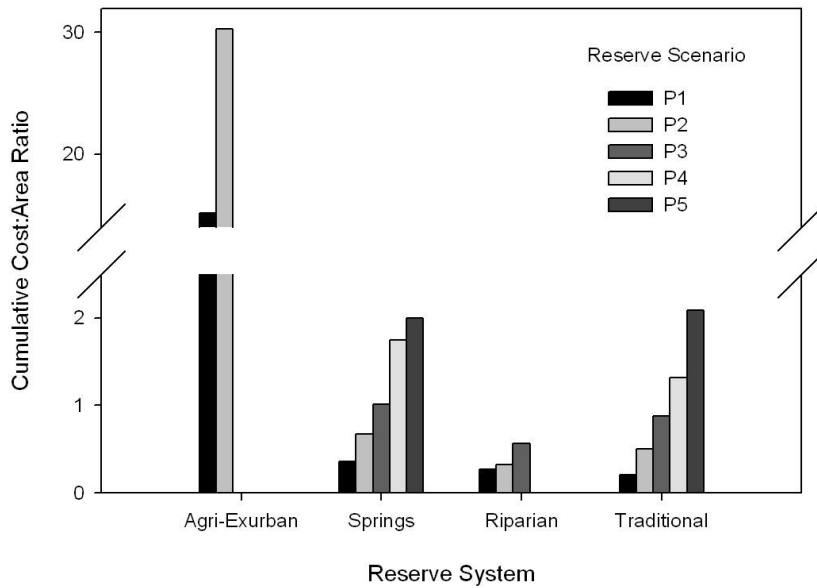


Figure 3. Cumulative cost-area ratio for each reserve system partitioned according to the different reserve scenarios (Table 1).

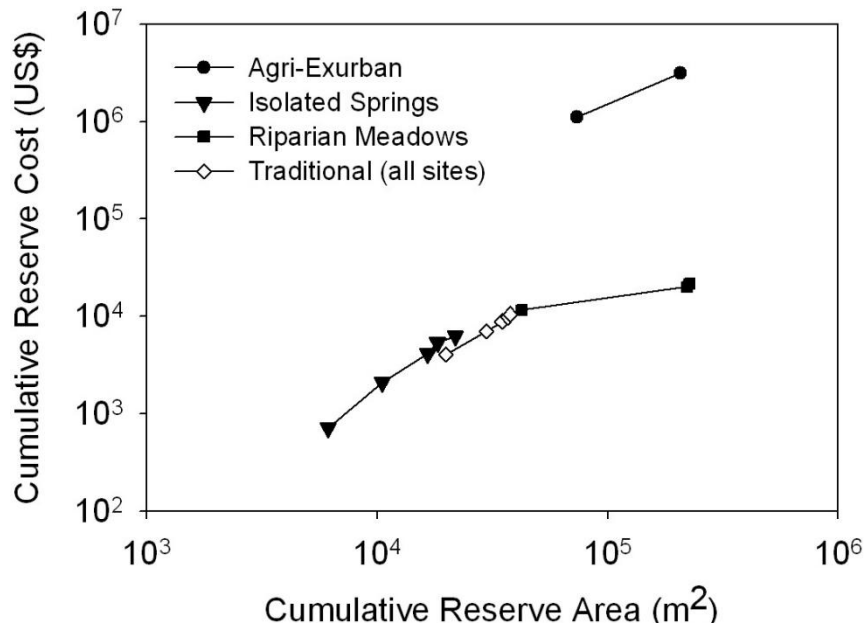


Figure 4. Cumulative cost plotted against cumulative area for each reserve system illustrating how cost of reserves in each system increase with increasing area as sites are added from reserve scenarios P1 through P5.

the species, the extent of habitat loss if those sites were not incorporated into a reserve system was determined. A loss of agri-exurban sites would constitute a loss of eight sites, or subpopulations, and a loss in habitat area

of 20.64 ha. The remaining isolated spring and riparian sites that were selected in the reserve analyses would constitute 24.52 ha of habitat for the silverspot at a total annualized cost of US\$ 27,871. Ad hoc

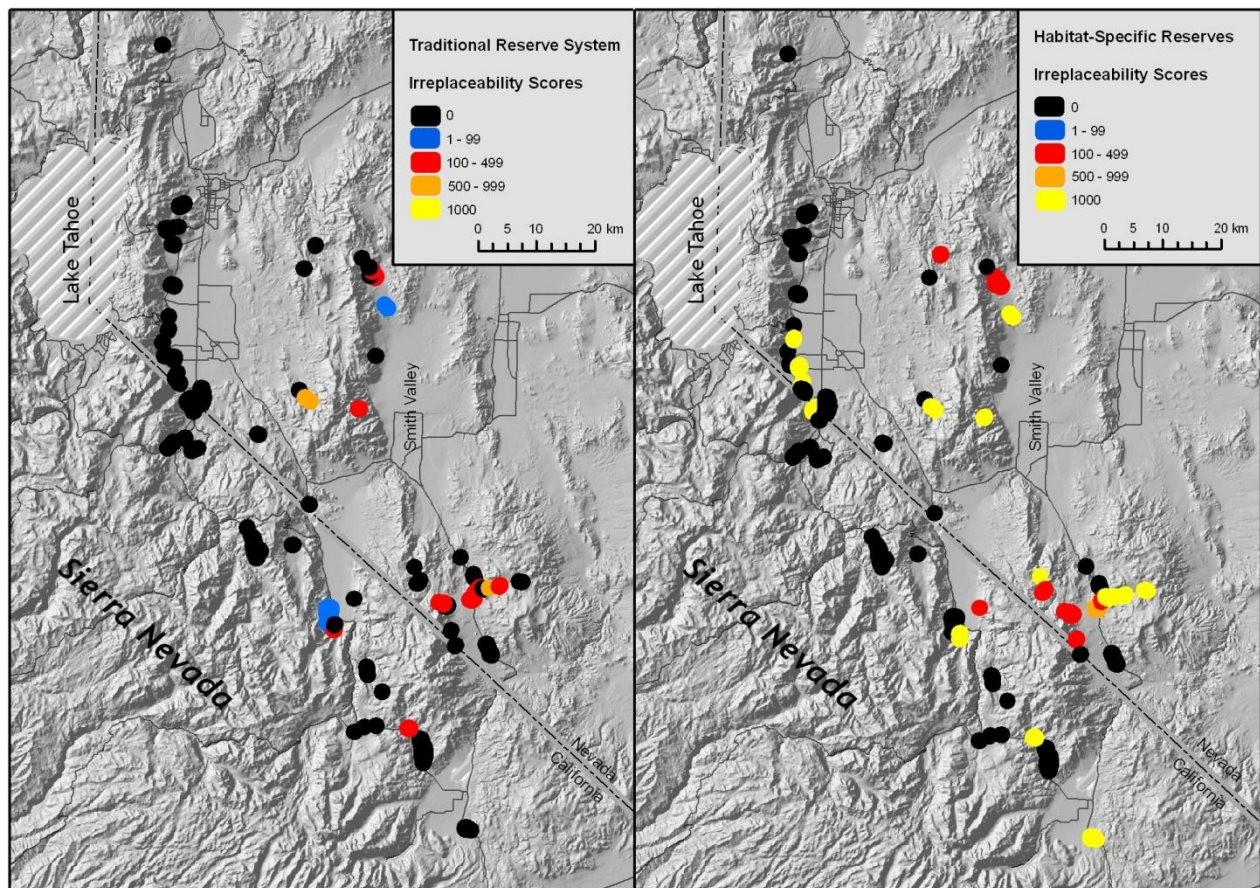


Figure 5. Sites selected for each reserve system from irreplaceability analyses using 1,000 runs in Marxan. Sites are coded by irreplaceability scores, or selection frequencies, where higher scores indicate that a site is highly irreplaceable.

irreplaceability analyses was run on the network scenarios generated from simulated annealing to assess whether there was flexibility of which sites were selected for conservation within reserve systems. For the traditional reserve system, no sites were selected 100% of the time, and three sites that met the specified conservation feature goals were selected about 50% of the time (Figure 5). In contrast, habitat-specific systems had 20 sites that were identified 100% of the time—seven agri-exurban and 13 riparian sites (Figure 5). Irreplaceability analyses for isolated springs indicated that no sites were absolutely irreplaceable and that there is some degree of flexibility in the way spring reserve systems are designed for silverspot conservation. The traditional reserve system had 46 sites that were never selected during the 1000 runs.

The habitat-specific reserve system had 36 sites that were never selected: the agri-exurban system had seven out of 12 sites chosen; isolated springs had 13 of 14 sites selected; and riparian habitats had a total of 16 reserves selected and 19 sites never selected in 1000 runs.

Whereas agri-exurban and riparian sites had very little flexibility in which sites were irreplaceable reserves, isolated springs did exhibit that flexibility.

DISCUSSION

Land use decision-makers often ask what the best sites are to conserve for an imperiled species, while minimizing economic cost. This study addresses that question directly by exploring how key environmental variables among habitat types influenced reserve networks, identifying priority areas for conservation and minimizing reserve cost. Results presented here demonstrated that drastically different reserve networks were identified from reserve selection analyses if variability in the determinants of patch occupancy across habitat types were integrated into site-selection procedures. The traditional reserve approach misrepresented the best sites for the silverspot butterfly, while the habitat-specific approach selected the highest

quality habitats. Because funding for conservation is limited, cost-efficient conservation strategies for imperiled species are important when the expansion of protected habitat is considered on either expensive private lands or multi-use public lands. The habitat-specific approach described in this study for selecting the best quality sites provides key information for focused discussion among decision-makers about conservation actions on public and private lands. One important result of the habitat-specific approach is that it indicated some degree of reserve clustering may be required for silverspot habitats. At least three reasons support the idea that clustered reserves are beneficial in this system.

First, clusters of higher quality habitats occurred throughout the range of the silverspot butterfly and such clustering can be logistically and economically more feasible to conserve. Secondly, dispersal distances for the butterfly are thought to be limited (Britten et al., 1994, 2003). Thirdly, environmental stochasticity can eliminate severely isolated populations over longer time periods (Packer, 1994). These circumstances may preclude reserve networks for the silverspot butterfly to be highly dispersed despite that such reserve dispersion may protect against catastrophic events that rapidly extirpate clustered populations (Diamond and May, 1981). Although clustering reserves can reduce the negative effects of fragmentation (Heijnis et al., 1999; Possingham et al., 2000; Cabeza et al., 2004b) and can be preferable for sociopolitical reasons (Roberts et al., 2003), some species are relatively indifferent to fragmentation (Moilanen, 2005). This system of silverspot butterfly habitats has a naturally high degree of fragmentation (now exacerbated by human land uses) because habitat patches are often largely disjunct.

As one possible way of clustering sites, a metric of patch isolation was included in the site selection process with an associated penalty factor. That approach was more appropriate for this study, rather than using a boundary length modifier, because the boundary modifiers were designed to address systems partitioned as a matrix of adjoining grid cells (Ball and Possingham, 2000; Possingham et al., 2000). Another important result of this work is that it provides a method to improve the efficiency of allocating limited conservation resources for imperiled species, especially given that decision-makers often are concerned with obtaining higher efficiencies for conservation actions. The reserve design analyses demonstrated that cost efficiencies were the best for riparian reserves, outperforming cost-efficiencies of the traditional system by 250%. The increase in number of riparian reserves from P1 to P2 only increased cost efficiency by a small amount and this pattern also was observed for isolated spring habitats. Moreover, adding sites to a reserve network from the isolated spring scenarios P1 to P3 yielded the greatest cost efficiency, whereas a reserve network for riparian habitats would be

most cost-efficient if all sites identified in the reserve scenarios (P1 to P5) were marked for protection. These findings are particularly important because they support the hypothesis that more reserve area can be conserved at lower costs if a habitat-specific approach is used in reserve designing reserves for a species, which simultaneously prioritizes particular reserves within habitat types.

Because conservation funds are limited and substantial land use pressures exist, developing cost-effective reserve networks that possess flexibility in which sites are reserved is an important facet of achieving habitat protection (Pressey et al., 1993; Pressey, 1998; Araújo and Williams, 2000; Margules and Pressey, 2000). Reserve design outputs presented here represent a prioritization strategy for conservation action of habitat areas, whereby reserves identified under the P1 scenario should receive first priority for conservation action, while sites selected under P2 to P5 scenarios would receive lower priority. Identifying the irreplaceable sites within this study system validated these priority levels from their selection frequencies. The high degree of irreplaceability among agri-exurban and riparian reserves indicates an apparent lack of flexibility in choosing sites for reservation. The apparent lack of irreplaceability among spring reserves suggests no spring site was 100% irreplaceable, and thus yielded some degree of flexibility in which sites are selected for a particular reserve network. Highly irreplaceable sites should be targeted for conservation first and this study demonstrated that those sites coincided with the high priority level reserves. Scheduling reserve acquisitions or management activities is often necessary when sufficient funding for the entirety of a conservation goal is unavailable at one time (Pressey and Taffs, 2001). The agri-exurban reserve system provides a case in point. Certainly, the cumulative cost of US\$ 3.1 million for the acquisition of eight, independently-owned reserves has the potential difficulty of negotiating eight independent easements or acquisitions simultaneously, in addition to the potential difficulty of securing sufficient funding resources at one time. However, scheduling easements or acquisitions for reserves over multiple years becomes a more tractable endeavor as it provides opportunities to acquire or appropriate funds through various funding mechanisms and to appropriate those funds for specific conservation actions.

Applying results from this study toward conservation and land management policy and action have direct application to circumventing the need for the silverspot butterfly to be listed under the ESA, improving mitigation effectiveness, and improving land-use planning. If particular habitat areas are not targeted for conservation prior to land development, the development of imperiled species habitats may trigger an ESA listing (16 U.S.C. §1531(4)), Section 7 consultations (16 U.S.C. §1531(7)),

or Section 10 habitat conservation plans (HCPs; 16 U.S.C. §1531(10)(a)). The habitat-specific approach to single-species reserve designs may be an effective way of avoiding inappropriate mitigation costs and/or a way to identify areas most suited for effective and cost-efficient mitigation activities. By using flexible reserve design approaches that account for habitat variability of an imperiled species, land-use planners can protect habitat areas most important for the species while minimizing economic costs and land-use conflicts. For example, acquiring a taken permit for developing a protected site could be mitigated by protecting an equally sized unit of optimal habitat or by protecting many units of suboptimal habitat.

The reserve design analyses presented in this paper highlights that the reserves are non-static and that multiple options for reserve selection exist to maximize the representation of particular conservation features at minimized costs. Considering the potential loss of a habitat area and rerunning the reserve design analysis not only could identify the suite of potential sites to be protected under mitigation requirements, but also facilitate land-use planning negotiations among stakeholders. These conservation challenges and opportunities for the silverspot butterfly are exemplary of a large list of other imperiled species. Collectively, findings from this study provide important insights into future reserve design and conservation planning approaches for imperiled species that occur in patchy landscapes.

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REFERENCES

- Araújo MB, Williams PH (2000). Selecting areas for species persistence using occurrence data. *Biol. Conserv.*, 96: 331-345.
- Austin GT (1998). New subspecies of Nymphalidae (Lepidoptera) from Nevada and California. In: Emmel TE (ed), *Systematic of western North American butterflies*. Mariposa Press, Gainesville, Florida.
- Ball IR (2000). Mathematical applications for conservation ecology: the dynamics of tree hollows and the design of nature reserves. Dissertation. University of Adelaide, South Australia.
- Ball IR, Possingham HP (2000). MARXAN version 1.8.2: Marine Reserve Design Using Spatially Explicit Annealing, a Manual. <http://www.ecology.uq.edu.au/>.
- Bradford DF, Neale AC, Nash MS, Sada DW, Jaeger JR (2003). Habitat occupancy by toads (*Bufo punctatus*) in a naturally fragmented desert landscape. *Ecology*, 84: 81012-81023.
- Britten HB, Brussard PF, Murphy DD, Austin GT (1994). Colony isolation and isozyme variability of the western seep fritillary, *Speyeria nokomis apacheana* (Nymphalidae), in the western Great Basin. *Great Basin Nat.*, 54: 97-105.
- Britten HB, Fleishman E, Austin GT, Murphy DD (2003). Genetically effective and adult population sizes in the Apache silverspot butterfly, *Speyeria nokomis apacheana* (Lepidoptera: Nymphalidae). *West N. Am. Nat.*, 63: 229-235.
- Brown DG, Johnson KM, Loveland TR, Theobald DM (2005). Rural land-use trends in the conterminous United States, 1950-2000. *Ecol. Appl.*, 15: 1851-1863.
- Brussard PF, Charlet DA, Dobkin DS (1998). Great Basin-Mojave Desert Region. In: Mac MJ, Opler PA, Puckett Haecker CE, Doran PD (eds), *Status and trends of the nation's biological resources*. U.S. Department of the Interior, U.S. Geological Survey, Reston, Virginia. pp. 505-542.
- Cabeza M, Moilanen A, Possingham HP (2004a). Metapopulation dynamics and reserve network design. In: Hanski I, Gaggiotti O (eds), *Ecology, genetics and evolution of metapopulations*. Elsevier Academic Press, London, UK. pp. 541-564.
- Cabeza M, Araujo MB, Wilson RJ, Thomas CD, Cowley MJR, Moilanen A (2004b). Combining probabilities of occurrence with spatial reserve design. *J. Appl. Ecol.*, 41: 252-262.
- Campbell SP, Clark JA, Crampton LH, Guerry AD, Hatch LT, Hosseini PR, Lawler JJ, O'Connor RJ (2002). An assessment of monitoring efforts in endangered species recovery plans. *Ecol. Appl.*, 12: 674-681.
- Chape S, Spalding MD, Jenkins MD (eds) (2007). *The world's protected areas: status, values, and prospects in the twenty-first century*. University of California Press, Berkeley, California.
- Clark JA, Hoekstra JM, Dee Boersma P, Kareiva P (2002). Improving U.S. Endangered Species Act recovery plans: key findings and recommendations of the SCB Recovery Plan Project. *Conserv. Biol.*, 16: 1510-1519.
- Dahl TE (2000). Status and trends of wetlands in the conterminous United States 1986-1997. U.S. Department of the Interior, Fish and Wildlife Service, Washington, DC.
- Dale VH, Brown S, Haeuber RA, Hobbs NT, Huntly N, Naiman RJ, Riebsame WE, Turner MG, Valone TJ (2000). Ecological principles and guidelines for managing the use of land: a report from the Ecological Society of America. *Ecol. Appl.*, 10: 639-670.
- Diamond JM, May R (1981). Island biogeography and the design of nature reserves. In: May RM (ed), *Theoretical ecology: principles and applications*, 2nd edn. Blackwell, Boston, Massachusetts. pp. 228-252.
- Environmental Law Institute (ELI) (2003). *Conservation thresholds for land use planners*. Environmental Law Institute. Washington DC.
- Gerber LR, Hatch LT (2002). Are we recovering? An evaluation of recovery criteria under the US Endangered Species Act. *Ecol. Appl.*, 12: 668-673.
- Goble DD, Scott JM, Davis FD (eds) (2006). *The Endangered Species Act at thirty: renewing the conservation promise*. Island Press, Washington, DC.
- Groom MJ, Meffe GK, Carroll CR (2006). *Principles of Conservation Biology*, 3rd edn. Sinauer, Sunderland, Massachusetts.
- Haight RG, Travis LE (2008) Reserve design to maximize species persistence. *Environ. Model Assess.*, 13: 243-253.
- Hejnis CE, Lombard AT, Cowling RM, Desmet PG (1999). Picking up the pieces: a biosphere reserve framework for a fragmented landscape – the coastal lowlands of the Western Cape, South Africa. *Biodivers. Conserv.*, 8: 471-496.
- Kirkpatrick S, Gelatt CD Jr, Vecchi MP (1983). Optimization by simulated annealing. *Science*, 220: 671-680.
- Lindenmayer DB, Lacy RC, Pope ML (2000). Testing a simulation

- model for population viability analysis. *Ecol. Appl.*, 10: 580-597.
- Margules CR, Pressey RL (2000). Systematic conservation planning. *Nature*, 405: 243-253.
- Meyer R, Olsen T (2005). Estimated costs for livestock fencing. *Ag Decision Maker*. B1(75): 1-4.
- Montgomery CA, Brown GM Jr, Adams DM (1994). The marginal cost of species preservation: the Northern Spotted Owl. *J. Environ. Econ. Manage.*, 26: 111-128.
- Moilanen A (2005). Reserve selection using nonlinear species distribution models. *Am. Nat.*, 165: 695-706.
- Moilanen A, Hanski I (1998). Metapopulation dynamics: effects of habitat quality and landscape structure. *Ecol.*, 79: 2503-2515.
- Packer L (1994). The extirpation of the Karner blue butterfly in Ontario. In: Andow DA, Baker RJ, Lane CP (eds), *Karner blue butterfly: a symbol of a vanishing landscape*. Minnesota Agricultural Experiment Station, St. Paul, Minnesota. pp. 143-151.
- Possingham HP, Ball I, Andelman S (2000). Mathematical methods for identifying representative reserve networks. In: Ferson S, Burgman M (eds), *Quantitative methods for conservation biology*. Springer-Verlag, New York. pp. 291-306.
- Pressey RL (1998). Algorithms, politics and timber: an example of the role of science in a public, political negotiation process over new conservation areas in production forests. In: Wills RT, Hobbs RJ (eds), *Ecology for everyone: communicating ecology to scientists, the public and the politicians*. Surrey Beatty & Sons, Chipping Norton, New South Wales, Australia. pp. 73-87.
- Pressey RL, Humphries CJ, Margules CR, Vane-Wright RI, Williams PH (1993). Beyond opportunism: key principles for systematic reserve selection. *Trends Ecol. Evol.*, 8: 124-128.
- Pressey RL, Johnson IR, Wilson PD (1994). Shades of irreplaceability: towards a measure of the contribution of sites to a reservation goal. *Biodiver. Conserv.*, 3: 242-262.
- Pressey RL, Possingham HP, Margules CR (1996). Optimality in reserve selection algorithms: when does it matter and how much? *Biol. Conserv.*, 76: 259-267.
- Pressey RL, Taffs KH (2001). Scheduling conservation action in production landscapes: priority areas in western New South Wales defined by irreplaceability and vulnerability to vegetation loss. *Biol. Conserv.*, 100: 355-376.
- Ralls K, Beisinger S, Cochrane JF (2002). Guidelines for using PVA for endangered species management in "population viability analysis." In: McCullough D, Beisinger S (eds), *University of Chicago Press*, Chicago, Illinois. pp. 521-550.
- Roberts CM, Andelman S, Branch G, Bustamante RH, Castilla JC, Dugan J, Halpern B, Lafferty KD, Leslie H, Lubchenco J, McArdle D, Possingham H, Ruckelshaus M, Warner RR (2003). Ecological criteria for evaluating candidate sites for marine reserves. *Ecol. Appl.*, 13: S199-S214.
- Sada DW, Vinyard GL (2002). Anthropogenic changes in historical biogeography of Great Basin aquatic biota. *Smithson Contrib. Earth Sci.*, 33: 277-293.
- Sanford MP (2011). Improving conservation and management of the imperiled Carson Valley silverspot butterfly *Speyeria nokomis carsonensis* (Lepidoptera: Nymphalidae) based on rapid assessments of distribution, habitat, and threats. *J. Insect Conserv.*, Published online. DOI 10.1007/s10841-010-9371-6, 15: 715-725.
- Sanford MP, Murphy DD, Brussard PF (2011). Distinguishing habitat types and the relative influences of environmental factors on patch occupancy for a butterfly metapopulation. *J. Insect Conserv.*, Published online. DOI: 10.1007/s10841-011-9376-9, 15: 775-785.
- Scott JM, Goble DD, Wiens JA, Wilcove DS, Bean M, Male T (2005). Recovery of imperiled species under the Endangered Species Act: the need for a new approach. *Front Ecol. Environ.*, 3: 383-389.
- Talley TS, Fleishman E, Holyoak M, Murphy DD, Ballard A (2007). Rethinking a rare-species conservation strategy in an urban landscape: The case of the valley elderberry longhorn beetle. *Biol. Conserv.*, 35: 21-32.
- Tear TH, Scott JM, Hayward PH, Griffith B (1993). Status and prospects for success of the Endangered Species Act – a look at recovery plans. *Sci.*, 262: 976-977.
- Theobald DM, Hobbs NT (2002). A framework for evaluating land use planning alternatives: protecting biodiversity on private land. *Conserv Ecol*. 6(1): 5.
- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997). Human domination of Earth's ecosystems. *Sci.*, 277: 494-504.
- Wilcove DS, Rothstein D, Dubow J, Phillips A, Losos E (1998). Quantifying threats to imperiled species in the United States. *Biosci.*, 48: 607-615.
- WildEarth Guardians (2010). Petition to list ten Great Basin butterflies under the U.S. Endangered Species Act. *WildEarth Guardians*. http://www.wildearthguardians.org/Portals/0/legal/listing_petition_gre_at_basin_butterflies.pdf.
- Williams J, ReVelle CS, Levin SA (2004). Using mathematical optimization models to design nature reserves. *Front Ecol. Environ.*, 2: 98-105.
- Xu D, Feng Z, Allen LJS, Swihart RK (2006). Spatially structured metapopulation model patch dynamics. *J. Theor. Biol.*, 239: 469-481.