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A modeling framework for life history-based conservation planning

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ABSTRACT

Reserve site selection models can be enhanced by including habitat conditions that populations need for food, shelter, and reproduction. We present a new population protection function that determines whether minimum areas of land with desired habitat features are present within the desired spatial conditions in the protected sites. Embedding the protection function as a constraint in reserve site selection models provides a way to select sets of sites that satisfy these habitat requirements. We illustrate the mechanics and the flexibility of the protection function by embedding it in two linear-integer programming models for reserve site selection and applying the models to a case study of *Myotis* bat conservation on Lopez Island, United States. The models capture high-resolution, species-specific habitat requirements that are critical for *Myotis* persistence. The models help quantify the increasing marginal costs of protecting *Myotis* habitat and show that optimal site selection strategies are sensitive to the relative importance of habitat requirements.

1. Introduction

Conservation planners make land use and management decisions to ensure the long term viability of species and ecosystems (Margules and Pressey, 2000). One facet of conservation planning is the decision about which parcels of land to purchase or restore given budget limits (Moilanen, 2005). Many types of quantitative tools have been developed to address this reserve site selection problem (see Sarkar et al., 2006 or Moilanen et al., 2009 for reviews). Integer programming formulations typically use number of species represented, number of times species are represented, reserve area, and measures of connectedness and fragmentation as criteria for site selection (e.g., ReVelle et al., 2002; Williams et al., 2004). Most experts agree that these criteria are limited because they do not account for all the factors that affect the long-term viability of populations, including the amount, quality, and spatial arrangement of habitat features that species need to persist (e.g., Church et al., 2000; Sarkar et al., 2006).

To address this limitation, we present a population protection function that can be used to represent habitat requirements in linear-integer formulations of reserve site selection models. The protection function is based on the assumption that every species has specific habitat requirements for food, shelter, and reproduction. Further, these requirements can be expressed using measures of land cover and vegetation structure at the patch and landscape scales. The protection function determines whether minimum areas of land with desired habitat features are present within desired spatial conditions in the protected sites. We demonstrate how the protection function can be embedded as a constraint in two types of reserve site selection models. In both cases, a set of sites that meets all of the habitat requirements for a given species must be contained in the reserve system for that species to be considered adequately protected.

The population protection function is akin to a habitat suitability index (HSI) model, a tool developed in the 1980s to evaluate wildlife habitat (U.S. Fish and Wildlife Service, 1980, 1981). HSI models express habitat quality on a suitability index scaled from zero to one based on functional relationships between species presence and habitat variables. HSI models are widely used in forest planning simulation to evaluate trends in indicators of biodiversity (Marzluff et al., 2002; Larson et al., 2004; Edenius and Mikusiński, 2006; Spies et al., 2007). They are also embedded in timber harvest scheduling models to determine the optimal timing and location of harvest areas while providing desired levels of landscape structure and composition associated with suitable wildlife habitat (Öhman et al., 2011).

A few reserve site selection models include persistence-limiting factors based on habitat quality and location. For example, Church et al. (2000) classify sites by habitat quality and assign weights to protecting species based on the levels of habitat quality that are available in the protected sites. The objective of the model is to maximize the weighted sum of species present. Malcolm and ReVelle (2002) and Williams et al. (2003) develop flyway models

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for migrating birds that identify sets of sites that are within a maximum distance of each other to facilitate migration. Miller et al. (2009) select parcels to restore and protect wetland habitat in agricultural landscapes surrounding core butterfly reserves. Our population protection function provides a general framework for including habitat features and spatial conditions at the individual site and landscape scale in reserve site selection models. This framework is useful at a time when the accumulation of knowledge about the needs and life history of sensitive species has reached unprecedented resolutions due to technological advances in remote sensing, wildlife tracking and statistical analyses (e.g., Barclay and Kurta, 2007; Tomkiewicz et al., 2010; Cagnacci et al., 2010).

A few reserve site selection models directly optimize the likelihood of species presence or persistence as functions of habitat features of the candidate sites. For example, Moilanen (2005) estimates the probability of species presence in each site as a nonlinear function of habitat quality in and around the site. The reserve selection model minimizes the cost of protecting sites subject to a lower bound on the expected number of sites containing each species. Polasky et al. (2008) predict species persistence in a landscape as a nonlinear function of habitat preferences, area requirements, and dispersal abilities in a given land use pattern. They choose land uses to maximize the expected number of species sustained on the landscape subject to economic constraints. While these models contain detailed relationships for the likelihood of species presence or persistence, they are nonlinear-integer formulations that require heuristic algorithms and custom software for solution. Further, the solutions have no guarantee of optimality. In contrast, our population protection function can be embedded in linear-integer programming formulations, for which exact solutions can be found using off-the-shelf commercial software such as ILOG CPLEX (IBM, 2011).

Lastly, we mention that in the facility location literature, problems with compound coverage requirements similar to that of the general species protection function depicted in this paper have been documented. Schilling et al. (1979) considered a fire protection system for the City of Baltimore, United States, where demand nodes were covered only if both primary and certain specialty fire fighting equipment were available. While the logical structure of Schilling et al.'s (1979) model was similar, the model proposed here is more general in that the coverage requirements are not restricted to be binary in nature.

We first present our generalized population protection function and then demonstrate how it can be embedded in two types of reserve site selection models. We illustrate how the model and the generalized protection function work in practice with a case study of protecting habitat for *Myotis* bats on Lopez Island, United States. The models capture high-resolution, species-specific habitat requirements that are critical for species persistence. We show how sensitive the set of optimal reserves might be to the relative importance of various habitat requirements. We conclude by discussing the flexibility and limitations of the proposed approach, and illustrate its compatibility with other spatial models.

2. Methods

2.1. A generalized concept of protection

In the following, we provide a general definition of our concept of protection to motivate the proposed mathematical programming models. The principles of representativeness and persistence advocated by Margules and Pressey (2000) imply that a species may be considered effectively protected only if at least one sustainable population is protected, indicating that a population is the unit of conservation concern. Accordingly, we define a population as a group of conspecific individuals occupying a particular place for a particular time. To distinguish one population from another, we assume that each population retains exclusive use of some resource, defining its particular place as distinct from other populations.

Using terminology defined in Williams et al. (2005), a site refers to a single decision unit that can be selected or not, a reserve is a spatially cohesive (e.g., connected) set of sites selected together, and a reserve system is a set of reserves that makes up the solution to a reserve design problem. Let K_j be the set of distinct survival requirements for population j of a given species, and let k index set K_j. Set K_j may vary between species, but will be the same for each population j of a given species. For simplicity, we refer to K_j as habitat requirements, although it does not need to be restricted in practice since survival requirements other than habitat may include such factors as the availability of prey or the presence of reproductive males and females. Index k appears as a superscript throughout the mathematical notation in this paper to distinguish it from other indices. Lastly, I denotes the set of sites where conservation action may be taken as part of creating a reserve system, and J denotes the set of populations that need and can receive protection. Let i index set I and j index set J. The proposed species specific population protection function, $y_j(\vec{x})$ is a continuous function that determines the amount of protection afforded to population j in the reserve system:

$$y_j(\vec{x}) = \min_{k \in K_j} \left(\frac{1}{m_j^k} \sum_{i \in S_j^k} a_{ij}^k x_i \right) \tag{1}$$

Decision variable x_i is binary: $x_i = 1$ if site i is selected for protection, 0otherwise. Parameters m_j^k and a_{ij}^k, respectively, are the minimum amount of habitat k required by population j, and the amount of habitat k available to population j in location i. We note that this specification assumes that multiple populations (or species) can share commonly accessible resources without any foregone benefits. A discussion about the relaxation of this assumption is presented in the Conclusions. Set S_j^k denotes the resource locations that population j can use to satisfy its habitat requirement k. The summation term is thus the total amount of habitat k available to population j. Dividing by the minimum amount that is required scales the sum so that values below one indicate under-protection, and values above one indicate that requirement k is met. The function $y_j(\vec{x})$, therefore, takes a value greater than one only if all habitat requirements (K_j) are satisfied for population j. The value of the function is strictly less than one if any one of the habitat requirements in K_j is unsatisfied, indicating inadequate protection. In the next section, we show how this population protection function can be embedded in a linear-integer reserve site selection model.

2.2. Model formulation

Mathematical programming is a useful tool to design conservation reserves because of its flexibility to incorporate various conservation goals and because efficient, off-the shelf software is available to formulate and identify optimal solutions. Efficiency in optimization is particularly important when the number of possible conservation actions is high, and the constraints on these actions are complex. Mathematical programs comprise objective functions that represent quantitative goals, such as maximizing conservation benefits or minimizing costs, and inequalities that represent resource limitations or conservation requirements. An example of the latter in our context is the requirement for a population to be considered protected. Multi-objective mathematical programs, including the two models presented below, can identify sets of solutions (i.e., reserves) that represent tradeoffs among the objectives. We embed the population protection function (Eq. (1)) in two dual-objective programs to illustrate the tradeoff analyses that can be performed using our new concept of protection.

The first model, the Generalized Maximal Covering Problem (GMCP) is as follows:

$$\text{Max}\sum_{J} y_j \tag{2}$$

$$\text{Min}\sum_{i} c_i x_i \tag{3}$$

Subject to:

$$y_j \leqslant \frac{1}{m_j^k}\sum_{i\in S_j^k} a_{ij}^k x_i \quad \forall k \in K_j,\ j \in J \tag{4}$$

$$x_i,\ y_j \in \{0,1\} \quad \forall i \in I,\ j \in J \tag{5}$$

where c_i denotes the cost of taking conservation action in site i, y_j is a binary indicator of whether population j is adequately protected in a particular solution and all other parameters are defined as for function (1). Common conservation actions include the outright purchase of a site for conservation, the ecological restoration of a degraded site, and the acquisition of a conservation easement (Salafsky et al., 2008). Our proposed framework can include any or all of these options as long as the associated costs and benefits are known. For a discussion of the costs of alternative conservation actions, see Naidoo et al. (2006). Other facility or species coverage models with budget constraints include Church and Davis (1992) and Ando et al. (1998).

Objective function (2) maximizes the number of protected populations, while objective (3) minimizes the amount spent on protection. Constraint set (4) captures the meaning of the population protection function (1). In Eq. (1), the function $y_j(\vec{x})$ takes a value greater than one only if all habitat requirements (K_j) are satisfied for population j. Because one constraint of form (4) is written for each survival requirement k, the 0–1 indicator variable y_j can equal one only if all the habitat requirements (K_j) are satisfied for population j, and $y_j = 0$ wherever one or more of the habitat requirements are not satisfied. Lastly, constraints (5) are the binary restrictions on the decision variables x_i and the indicator variables y_j. Since one of the objective functions maximizes the sum of y_j's, these variables will take the largest values (0 or 1) allowed by constraints (4).

Fig. 1 illustrates the application of the GMCP to a population (j) of a hypothetical species in a model landscape. Suppose this particular species requires three habitat elements in varying amounts, m_j^k (for k = 1, 2 and 3) to survive. Two of the habitat requirements, water (k = 2), which is represented by light gray polygons in Fig. 1, and forage (k = 3), which is represented by the dark gray polygons, may be shared between populations. Requirement k = 1 on the other hand is unique to each population. This unique element may represent a home site such as a den, a nest or a roost. Assume that this habitat element (black dot on Fig. 1) occurs only on Site 3 and that the other two habitat requirements must also be available within the home range of the species (dashed circle) for the population to survive. In this particular application, sets S_1^k (for k = 1, 2 and 3) represent the sites within the population's home range where habitat element k occurs. Assuming that the amount of habitat that are available for each component in each of the five sites that overlap with the home range each exceed the corresponding minimum requirements m_1^k ($\forall k$), there are two combination of sites, Sites 3 and 4, and Sites 3 and 7, that are minimally sufficient to satisfy the three protection constraints (4) for population 1.

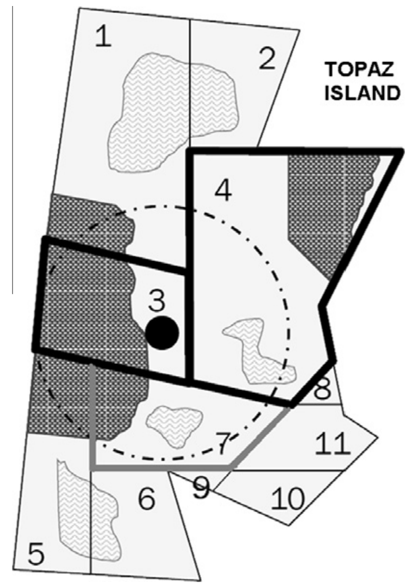

Fig. 1. Schematic illustration of sites and habitat areas for a hypothetical species for application of the General Maximal Covering Problem (GMCP) and the General Maximal Protection Problem (GMPP). Depending on whether Site 4 or Site 7 is the less expensive, the single optimal solution to the dual-objective GMCP either {3,4} or {3,7}. For the GMPP, either Sites 3 and 4, 4 and 7, or the trio of 3, 4, and 7 is optimal depending on their costs and the relative importance of water vs. forage habitat.

Depending on whether Sites 4 or 7 is less expensive, the single optimal solution to the dual-objective program (2)–(5) is either {3,4} or {3,7}.

In application of the GMCP, the scope of the model may be as broad as protecting global biodiversity, or as fine grain as providing a single species with adequate habitat to promote its persistence in a portion of its range. In the special case where (1) each population in set J represent a distinct species, (2) there is only one habitat requirement for each population (i.e., $|K_j| = 1\forall j$), and (3) the minimum habitat requirements and the site-specific habitat availabilities are both unitary (i.e., $m_j^k = 1 \quad \forall j$ and $a_{ij}^k = 1 \forall i,j$), set S_j reduces to a presence-absence vector for each species j in the network, and constraint (4) reduces to

$$y_j \leqslant \sum_{i\in S_j} x_i \quad \forall j \in J \tag{6}$$

Constraint set (6) is the most commonly used definition of protection in the reserve selection literature. Underhill (1994) first used this definition with the objective of minimizing the costs of protection subject to the condition that each species is protected in the system at least once. Church et al. (1996) used the same definition of protection to address the complementary problem of maximizing the number of species in the system subject to a budget on site acquisitions. Williams et al. (2005) refer to these problems, respectively, as the Species Set Covering Problem (SSCP) and the Maximal Covering Species Problem (MCSP). We refer to Model (2)–(5) as the Generalized Maximal Covering Problem, in reference both to the embedded generalized protection function, and to the fact that the model may be used to design reserves for a single species as well as to conserve species diversity.

The second model, the Generalized Maximal Protection Problem (GMPP), adds another level of sophistication to the proposed concept of protection by creating more differentiation in how the model rewards alternative conservation choices. The GMPP allows populations whose protection is already ensured to add value to the reserve system based on the amount by which their habitat requirements are met above the minimum. It also allows planners to distinguish between sufficient sets of sites by more than monetary criteria.

$$\text{Max} \sum_k \sum_{i \in S_j^k} w_j^k a_{ij}^k x_i \quad \forall j \in J \tag{7}$$

$$\text{Min} \sum_i c_i x_i \tag{8}$$

Subject to:

$$y_j \leqslant \frac{1}{m^k} \sum_{i \in S_j^k} a_{ij}^k x_i \quad \forall k \in K_j,\ j \in J \tag{9}$$

$$x_i \leqslant \sum_{j \in P_i} y_j \qquad \forall i \in I \tag{10}$$

$$x_i,\ y_j \in \{0, 1\} \qquad \forall i \in I,\ j \in J \tag{11}$$

where P_i is the set of populations to which site i can contribute protection, and w_j^k is a weighting constant representing the relative importance of each habitat requirement k for population j.

The first objective function of the GMPP (7) maximizes the weighted sum of protection provided by the network for population j for each associated habitat requirement. One function of type (7) is written for each population in need of protection. Objective (8) and constraints (9) and (11) are identical to objective (3) and constraints (4) and (5) in the GMCP. Constraint set (10) is new; it allows x_i to be 1, and thus contribute to the objective function value, if at least one population that has access to site i is protected. It is important to note that constraint (10) allows site i to remain unprotected (i.e., $x_i = 0$) even if the above condition holds if other sites can contribute the same amount of habitat for the protected populations at a lower price. Constraints (10) ensure that the model, in its attempt to maximize area-weighted protection, does not select parcels for acquisition if these parcel are inaccessible for the given population or species.

The weights (w_j^k) in objective (7) can capture several modeling concerns that might arise in practice. For example, suppose that for a given population j, habitat requirement 1 is an order of magnitude more important than habitat requirement 2. The weights $w_j^1 = 10$, $w_j^2 = 1$ tell the model that if one additional piece of land can be purchased (or restored), between equally priced choices of 1 ha of requirement 1 and 9 ha of requirement 2, the 1 ha of requirement 1 should be preferred (10×1 ha > 1×9 ha). Another example where the weights could serve to parameterize the relative importance of different habitat types is the case of prey species with different energy transfer rates and/or abundances that vary by habitat. Lastly, the w_j^k's may be used to indicate the relative importance of covering various species, where importance may be driven by such factors as perceived vulnerabilities.

Fig. 1 illustrates the application of GMPP to the same hypothetical population in the model landscape. The same two sets of sites (3 and 4, 3 and 7) are still minimally sufficient to satisfy the protection constraints for population 1. As in the GMCP, the relative costs of those sites are an important driver of optimality. However, the first objective function of GMPP (7) can distinguish between varying levels and types of protection. The pair of sites that provides the most protection depends on the weights associated with habitat elements 2 and 3. If the pair of Sites 3 and 4 is less expensive and provides more protection, it will be strictly preferred (dominant) to the pair 3 and 7. If Sites 3 and 7 provide more protection, however, the two solutions could each be efficient. Sites 3, 4, and 7 together may constitute a third efficient solution that is both more protective and more expensive than either of the first two solutions.

It is also possible that conservation planners will wish to analyze the tradeoffs between weighted protection and the number of populations/species covered. In this case, a combined, three-objective model that appends the GMCP's Objective (2) to the GMPP can be used to identify parcel selections that are Pareto-optimal with respect to costs, weighted protection and the number of species covered.

In the next section, we illustrate the use of GMCP and GMPP in a case study, and highlight their advantages over current methods. We also demonstrate the benefits of the combined, three-objective model. The case study is suggestive of the benefits of reserve design models that can use the full power of habitat and species information that are available today.

2.3. Case study: Myotis bats on Lopez Island

The 7721 ha Lopez Island is located in the San Juan Archipelago in northwestern Washington State (Fig. 2). It has a small, but growing population of human inhabitants (U.S. Census 2010). The Island is heavily forested with 74.3% of the land area classified as private forest holdings (University of Washington Geographic Information Service, 2007). Conversion of forest lands to real estate development is a serious concern because of the Island's proximity to the Seattle metropolitan area and the availability of waterfront properties and other premium lots for sale (Tóth et al., 2011). In 1992–2001 alone, the latest 10-year period for which data is currently available, private forest conversion occurred at an average annual rate of 4.88% in San Juan County (Bolsinger et al., 1997; Gray et al., 2005).

Lopez Island is also home to seven species of conservation concern, five of which are bats: the Big Brown Bat (*Eptesicus fuscus*) and four smaller *Myotis* species (Washington Department of Fish and Wildlife, 2010). Resident bat populations are particularly vulnerable to habitat loss (Johnson and Gates, 2008; Oprea et al., 2009). One strategy to mitigate the problem is to retain lots that provide bat habitat by outright purchases or by acquiring conservation easements on the lots before they fall victim to development (Tóth et al., 2011). In our study, Lopez Island will serve to demonstrate the use of the proposed protection function, via the GMCP and GMPP models, to design reserves for bats. Without loss of generality, we focus on the four *Myotis* species. The protection of the Big Brown Bat and the two other listed species, the Bald Eagle (*Haliaeetus leucocephalus*) and the Peregrine Falcon (*Falco peregrinus*) would involve the same steps that follow in life history identification, data collection and model specification.

2.3.1. Assumptions – Myotis life history and habitat requirements

The four *Myotis* species on Lopez Island are the California Myotis (*Myotis californicus*), Western Long-Eared Myotis (*Myotis evotis*), Long-Legged Myotis (*Myotis volans*), and Yuma Myotis (*Myotis yumanensis*). Between the four species, life history traits are similar. All are nocturnal, leaving their roosts at night to eat and drink. As all bats must, the four species drink water at least nightly, from open water sources such as ponds, streams or stock tanks. The Myotis bats feed mainly on insects, at times gleaning insects from water or other surfaces. Foraging is done over water sources, around trees and cliffs, in forest or woodland openings, or among shrubs—in places close to cover but without full canopy closure (Zeiner et al., 1988).

During the day, *Myotis* bats roost in places with favorable temperature fluctuations and minimal wind including buildings, mines, caves, or crevices, spaces under bark, and snags (Zeiner et al., 1988). Males and non-reproductive females typically roost separately from reproductive females and young, either singly or in small groups, although the Long-Legged Myotis may be found in large colonies. Multiple species may be found roosting or feeding

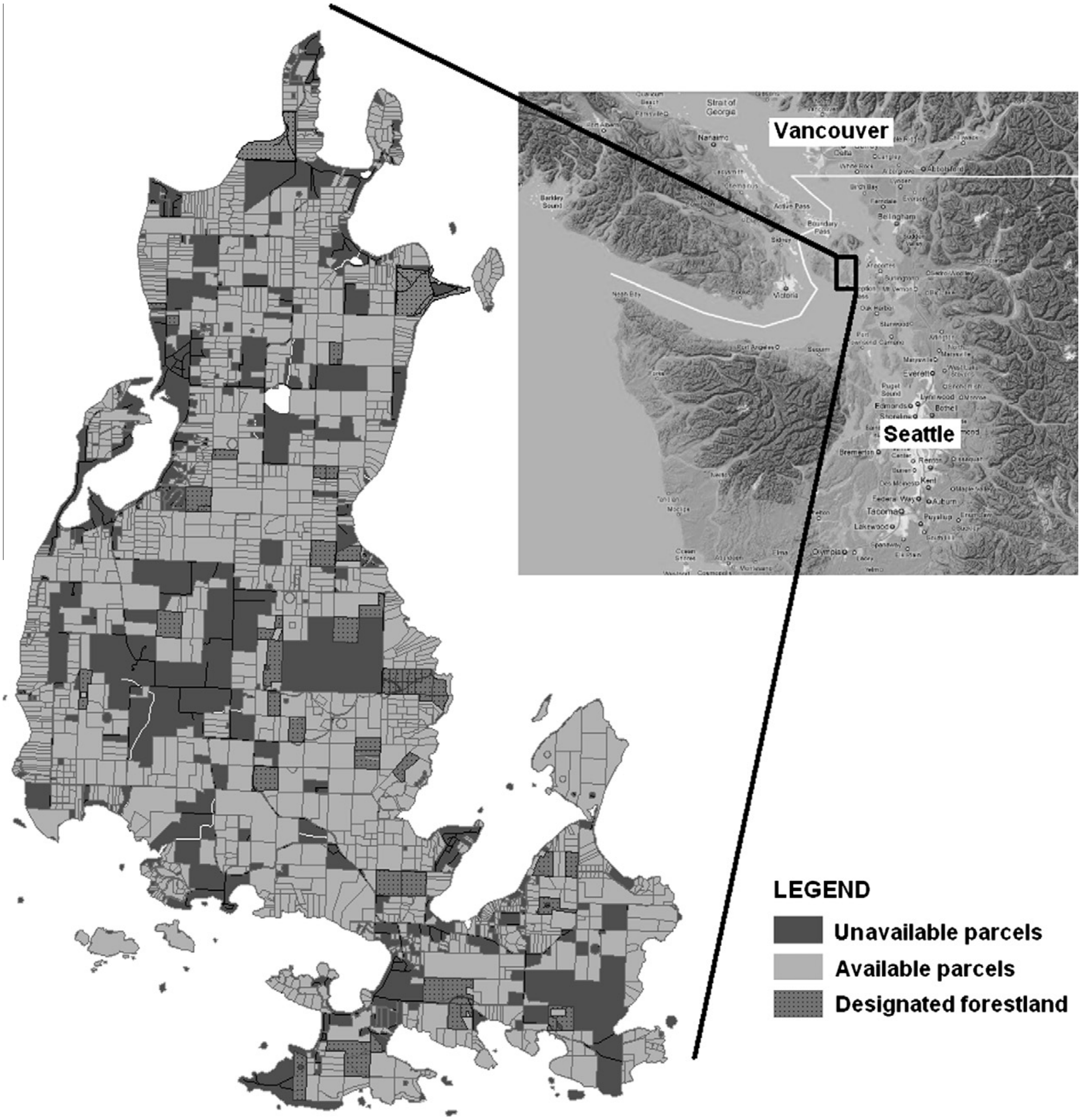

Fig. 2. Lopez Island is situated in the Pacific Northwest United States roughly halfway between Seattle, Washington and Vancouver, Canada. A set of 1395 available land parcels have been identified as potential candidates for the *Myotis* reserve system.

together. Maternity roosts, which are generally found in warmer locations than other roosts, vary in size by species from 12 to 30 mothers and young (Long-Eared Myotis) to several thousand (Yuma Myotis). Bats may make migrations to suitable hibernacula for the winter. Such migrations are necessary where day roosts are frequently disturbed, or lack the temperature and wind regulation necessary for hibernation. The preceding life history accounts are based on capture data from California and were confirmed for the northern end of the species range in British Columbia by Nagorsen and Brigham (1993). Four basic habitat requirements can be identified based on this information: open water, forage habitat, roosts, and hibernacula.

Myotis bats primarily forage along forest edges with partially closed canopies (Grindal and Brigham, 1999). We treat forage areas and water separately since water can also function as forage habitat but forage habitat cannot function as a water source (Thomas and West, 1991). For this reason, we will assume in our models that water is more important for the bats than forage habitat. Since the relative importance of the two requirements is not known with accuracy, we run sensitivity analyses. We assume that *Myotis* bats primarily roost in old houses and barns on Lopez Island and take water from nearby sources. We do not explicitly address the fourth habitat requirement, hibernacula, in the case study because *Myotis* bats can migrate long distances to find appropriate locations.

Finally, a reserve design consideration that can affect species persistence is access to the various habitat elements. As bats can fly between portions of their home range, it is not necessary for their reserves to be structurally connected by shared boundaries. Bats can rely on functionally connected networks (Tischendorf and Fahrig, 2000a,b) that require only spatial proximity among the component reserves. In our case study, spatial proximity will be ensured by requiring that the habitat components can be reached from each roost (c.f. Williams et al., 2005). Beyond this, we do not explicitly address connectivity, functional or structural, of the reserve system by way of additional constraints. Implicitly, we assume that bats may migrate distances greater than the length of the Island to find hibernacula, thus rendering the entire Island functionally connected. While there are arguments for disconnected reserves for bats due to the potential spread of white nose disease from the eastern United States (Frick et al., 2010), these concerns would therefore only become relevant for reserve design problems on a larger scale.

Using these assumptions, we apply the GMCP to maximize the number of protected roosts, and the GMPP to maximize the importance-weighted area of habitat provided in the reserve system. We chose to apply both models in the case study to demonstrate two common conservation scenarios. In some cases, it may be more important to have many roosts with minimally sufficient protection, whereas in other cases protecting fewer roosts with more habitat resources could be more valuable. To analyze the tradeoffs among all three concerns of cost minimization, the maximization of weighted protection, and the maximization of the number of protected roosts, we also solve a combined model that has three objectives: Eqs. (2), (7), and (8) subject to the constraints of the GMPP: In Eqs. (9)–(11). Our analyses demonstrate the utility of the proposed protection function to conservation planners, in terms of identifying robust conservation strategies.

2.3.2. Parcel data

The Washington State Digital Parcel Database (WAGIS, 2007) was used as a primary data source for the models. The database identifies each parcel on the Island (see Fig. 2) that is potentially available for conservation acquisitions. We focused on acquisitions only; conservation easements and ecological restorations were not considered as applicable alternatives in this case study. We also assumed that close to 100 specific parcels were safe from development. These parcels are currently either in conservation, agriculture or recreation ownerships, or are designated forestlands. A "forestland" designation is a beneficial tax status in Washington State for lands exclusively used for forest management. We used the National Land Cover Dataset (U.S. Geological Survey, 2007) to estimate forest areas within each parcel, and selected a total of 1395 parcels (4913.48 ha) that were above 0.5 ha in size and contained at least 0.25 ha of forest cover. We assumed that these parcels were all available for conservation at 2007 market prices that were obtained from San Juan County assessors.

2.3.3. Satellite imagery

ArcGIS World Imagery, a high-resolution (<1 m for the United States) map service provided by Esri (2008), was used to delineate the three habitat elements required by *Myotis* bats. While for Lopez Island this was done manually using the graphical interface of ArcGIS (Esri, 2009), automated pattern-recognition algorithms can be used for larger applications to speed up processing. We identified 44 possible roost sites in old barns spread across the Island. Open freshwater sources and forest edges were delineated within 500 m of each potential roost (Fig. 3). The choice of a 500 m range was based on expert opinion.

2.3.4. Model specifications

For both GMCP and GMPP, we set I to be equal to the set of 1395 parcels identified as per the details in Section 2.3.2. Set J is populated by the 44 potential roost sites or populations. There are three habitat requirements $K = \{1, 2, 3\}$ denoting water, forage, and roosts, respectively. While parameter a_{ij}^1 represents the area of water, a_{ij}^2 represents the area of forage available to roost j in site i. The values of a_{ij}^1 range from 0 to 2.55 ha per roost with a total of 30.38 ha for all roosts, and a_{ij}^2 ranges from 0 to 28.49 ha per roost, with a total of 717.66 ha. Parameter a_{ij}^3 is binary: it represents roost availability to population j in site i. It is 1 if site i contains roost j, 0 otherwise.

In the GMPP, we start with weights of 10 for w_j^1 and 1 for w_j^2 indicating that water is an order of magnitude greater in importance than forage (Thomas and West, 1991). We test the sensitivity of the solutions with respect to the relative importance of these two habitat components by varying w_j^1 between 1 (no difference in importance) and 100 (two orders of magnitude difference). Finally, w_j^3 is set to 0 for each $j \in J$ because no population or roost can be declared protected, as per constraints (9), unless the site that contains the roost is protected. Since $m_j^3 = a_{ij}^3 = 1$ for each $j \in J$ and $i \in S_j^k$, constraint set (9) already guarantees that the importance of protecting roost sites is infinite relative to that of protecting water or forage habitat without including a specific weight for the roost in the objective function. The minimum habitat requirements for water and forage (m_j^1 and m_j^2) were both set to 1 m^2 because Myotis bats are able to drink from very small water surfaces (Christy and West, 1993). To illustrate how the GMCP and GMPP can be combined to investigate the tradeoffs behind importance weighted protection, the number of protected roosts and acquisition costs, we solve model (2), (7)–(11) with $w_j^1 = 10$.

We apply the GMCP, the GMPP, and the combined models to the Lopez Island parcel set to determine the optimal allocation of conservation funds to *Myotis* protection. As the precise amount of funds is unlikely to be known at the beginning of the conservation effort, we analyze the tradeoffs between protection and expenditure for a range of budgets (US$1M–40M) that represent both the "reasonably realistic", the "possible", and everything in between. As an example of conservation effort, the San Juan Preservation Trust has protected over 5600 ha in the San Juan Archipelago since 1979. With a land price of $100,000/ha, this level of protection costs over $15M per year.

We use specialized multi-objective mathematical programming techniques, the ε-Constraining Method (Haimes et al., 1971) for the GMCP and the GMPP, and the Alpha–Delta Method (Tóth and McDill, 2009) for the combined model, to find sets of parcel selections that are on the efficiency frontier with respect to acquisition costs and protection. A set of parcels is on the efficiency frontier if any change in the set does not improve either the acquisition cost or the protection function without compromising the other. The sets of solutions on the efficiency frontier allow conservation planners to weigh the *minimum* costs of protection in a holistic and rigorous manner.

The ε-Constraining Method, which was designed to solve discrete multi-objective programs like the GMCP, starts by optimizing one of the objectives of the program without regard to the other. We first maximize the number of roosts (Step 1). Then, using the maximum number of roosts as a constraint, we minimized the costs to guarantee efficiency (Step 2). This leads to the first solution on the efficiency frontier. In Step 3, we maximize the number of roosts for a cost less than or equal to the cost of the first solution minus a small ε. To ensure that this solution achieves the maximum number of roosts at minimum cost, the ε-Constraining Method "turns around" the problem yet again (Step 4) and minimizes costs subject to the number of roosts that were possible in Step 3. The resulting solution will be the second on the efficiency frontier. To find the entire set, we repeat the four steps until the value of the roost maximizing function becomes zero. The resolution of the efficiency frontier can be controlled by parameter ε: smaller values allow more solutions to be detected at the price of extra computing time. We set ε to US$0.25M to provide sufficient detail for the dual objectives of the GMCP. Alternatives to ε-Constraining that could be used include the Alpha–Delta and the Tschebycheff Methods (Tóth et al., 2006).

For the GMPP, we used a modified version of the ε-Constraining Method to account for the fact that, unlike the GMCP's function (2),

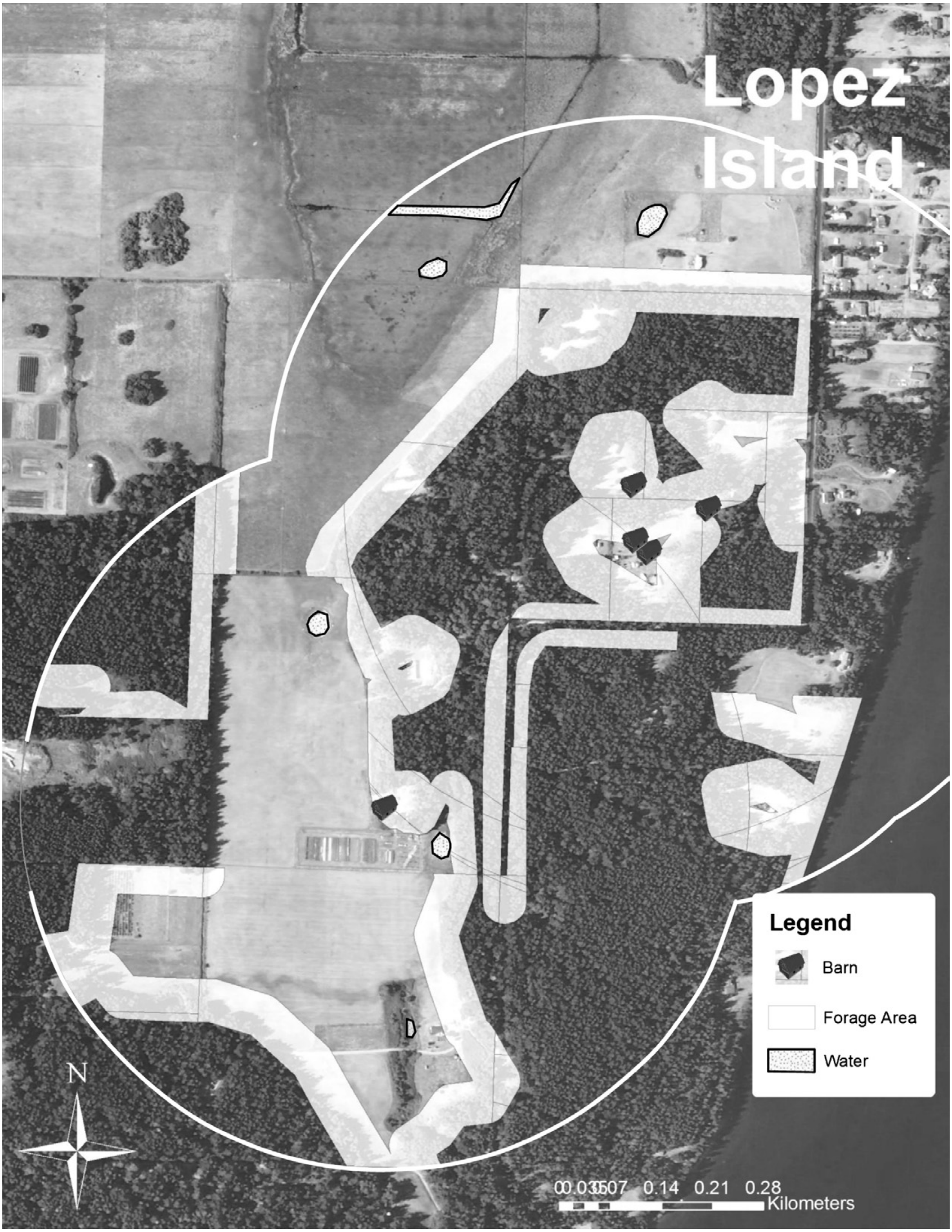

Fig. 3. *Myotis* habitat identification on Lopez Island using satellite imagery. Open water and forage habitat are shown within 500 m of each potential roost site (old barns).

the image of GMPP's function (7) is continuous for all practical purposes. Due to the high number of combinations of sites that can be acquired to contribute hectares of water and/or forage protection, the value of objective function (7) can closely map a continuum only restricted by budget constraints. Since the ε-Constraining Method was specifically designed to solve discrete optimization problems such as the GMCP, we used a slightly different approach for the GMPP and find a subset of solutions on the efficiency frontier in two steps. In the first step, we maximized function (7) for a discrete set of budgets between US$1M and US$40M in US$1M increments. Then, using the maximum protections as constraints, we minimized the acquisition costs for each of the 40 solutions.

We note that there are other ways to solve dual-objective reserve site selection problems in which species or habitat coverage is traded off against total area or cost of selected sites. These methods include the constraint method in which species or habitat coverage is optimized for increasing levels of a budget constraint or the multi-objective weighting method in which a weighted sum of the objective functions is optimized for different values of the weight (e.g., Snyder et al., 2004). We chose the ε-Constraining Method to ensure that solutions with a given maximum level of protection also minimize cost. For problems like ours with discrete objective functions, there may be several solutions that provide the same level of protection with different levels of cost and this concern led us to use ε-Constraining Method, where the solutions that maximize protection are also checked and corrected for cost efficiency.

For the three-objective, combined model, we use Tóth and McDill's (2009) Alpha–Delta Algorithm that is specifically designed to enumerate Pareto-efficient (non-dominated) solutions for three or more objective integer programs. This algorithm assigns an inordinate amount of weight to one of the objectives and negligible weights to the others. Using this "slightly tilted" composite objective function (α accounts for the degree of the tilt), the Alpha–Delta Method systematically explores the objective space via *either-or* logical structures. The slightly tilted objective function ensures that only efficient solutions are selected. The three parameters of the algorithm, α and one δ for each of the two objectives that are assigned negligible weights in the composite objective function, are set to 1°, 10 weighed hectares for the protection function and 0.1 for the number of roosts, respectively. These settings are made to ensure an adequate but not excessively detailed coverage of the tradeoffs among the three objectives (see Fig. 8). For further details on this algorithm, please see Tóth and McDill (2009).

MS Visual Basic was used to populate the proposed GMPP, GMCP, and combined models with the parcel data and IBM ILOG CPLEX Optimization Studio version 12.1 and 12.2 were used to solve them. Execution time was not an issue because a solution to each optimization problem was found in seconds.

3. Results

3.1. GMCP and GMPP model solutions

The GMCP model identifies the parcels that will protect the greatest number of roosts for a range of budgets. Fig. 4 shows the efficiency frontier for the GMCP in terms of the number of protected *Myotis* roosts and acquisitions costs. The ε-Constraining Method found 44 solutions corresponding to the 1–44 roosts that can possibly be protected. The rightmost point on the curve represents the 44-roost solution that is available for US$21.5M. Because we identified only 44 roost sites, investments greater than this amount will not be helpful assuming that minimally sufficient protection guarantees the long-term persistence of the populations. The increasing slope of the efficiency frontier suggests that the marginal cost of protecting an additional *Myotis* roost on Lopez Island increases as the number of protected roosts increases. This finding is in agreement with similar patterns that have been documented in other environmental protection functions (e.g., Kushch et al., 2012).

Fig. 5(left) shows the map of the optimal reserve system under GMCP at US$10M. Thirty roosts can be protected with this budget by purchasing 36 sites (see solid black on Fig. 5). To contrast the two models, we also map a GMPP solution that is optimal for roughly the same US$10M budget. This solution provides 11.4 ha of water and 204.7 ha of forage habitat for only 13 roosts, as opposed to the GMCP's 30, through the purchase of 40 parcels. The tradeoff between the GMCP and the GMPP solution is clear: the former supplies more roosts at minimally sufficient protection, whereas the latter supplies more protection for a lesser number of roosts.

The efficient frontier for GMPP at $w_j^1 = 10$ is shown as a solid black curve on Fig. 6. This curve exhibits a similar, although not as pronounced, pattern of increasing marginal cost of *Myotis* roost protection as the GMCP. It is noteworthy that while the GMCP curve reaches its maximum level of protecting 44 roosts at about US$21.5, the GMPP requires US$140M to protect all 44 roosts. The graph on Fig. 6 only shows the solutions up to US$40M.

3.2. Sensitivity analysis on relative habitat importance

Fig. 6 shows the efficient frontier of GMPP solutions for values of w_j^1 between 1 and 100. Because the value of w_j^1 changes the scale of the objective values, the horizontal axis of the chart measures the total area of protected water and forage habitat instead of importance-weighed area. The solid line corresponds to the original parameterization ($w_j^1 = 10$), with lighter gray indicating the other frontiers.

For values of $w_j^1 < 10$, greater total area is conserved in the optimal solutions. For values of $w_j^1 > 10$, a smaller total area is conserved, since additional area of water increases the value of the reserve system due to its higher relative weight. When w_j^1 is increased substantially, approaching two orders of magnitude greater than w_j^2, there are some low budget levels for which the slope of the frontier is decreasing, meaning that after a relatively large initial investment, the next few protection increases can be made at lower marginal cost. The implication is that the optimal reserve systems and the efficient frontiers are sensitive to the parameterization of w_j^1 – the relative importance of different habitat requirements. Fig. 7 demonstrates that even relatively modest changes in w_j^1 can induce reserve networks that are dramatically different in terms of water and forage habitat. This suggests that having a good handle on the role of various habitat requirements for a given species can be very important to making optimal conservation decisions for at-risk populations.

The preservation of "locally and regionally significant rare plant or animal habitats" is a priority of the San Juan Preservation Trust (http://www.sjpt.org/page.php?content_id=21). In the light of our findings, we recommend that the organization, along with others who have a stake in protecting open space on Lopez Island, invest in determining the relative benefits of the different habitat components that are associated with priority species, including *Myotis* bats.

3.3. Sensitivity analysis on relative habitat importance

Fig. 8 shows the set of non-dominated solutions that were found by the Alpha–Delta Algorithm (Tóth and McDill, 2009) for the three-objective model that combined the objectives of both the GMPP and the GMCP. It is clear that if both the importance weighted protection and the number of protected roosts are to be maximized, the acquisition costs increase exponentially. The tradeoff surface in Fig. 8 allows the conservation planner to analyze the tradeoffs between weighted protection and costs at a given number of desired roosts. For example, if one wishes to preserve 20 roosts, 113.52 weighted hectares of protection can be achieved (3.56 ha of water and 77.95 ha of forage) for US$4.82M, while 248.7 (8.8 ha of water and 160.6 ha of forage) is possible for US$8.09M, and 395.88 (14.16 ha of water and 254.24 ha of forage) is possible for US$13.82M. Fig. 8 shows several additional compromise alternatives that are possible for 20 roosts.

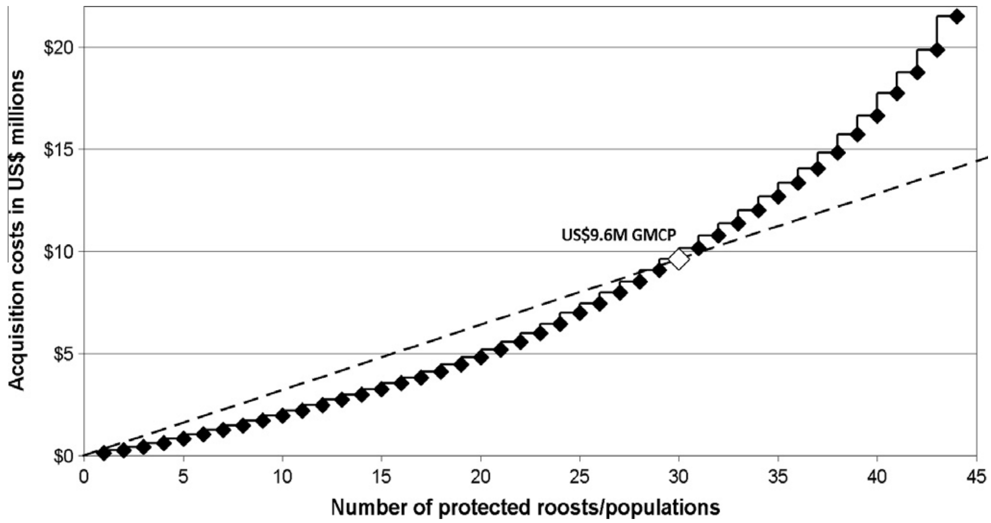

Fig. 4. The efficient frontier for the general maximal covering problem applied to *Myotis* habitat protection on Lopez Island. The US$9.6M solution is mapped out in Fig. 5. The dashed line separates the solutions that are cheaper in terms of average protection cost per roost from those that are more expensive. The slope of the curve illustrates the increasing marginal cost of protecting roost sites on Lopez Island.

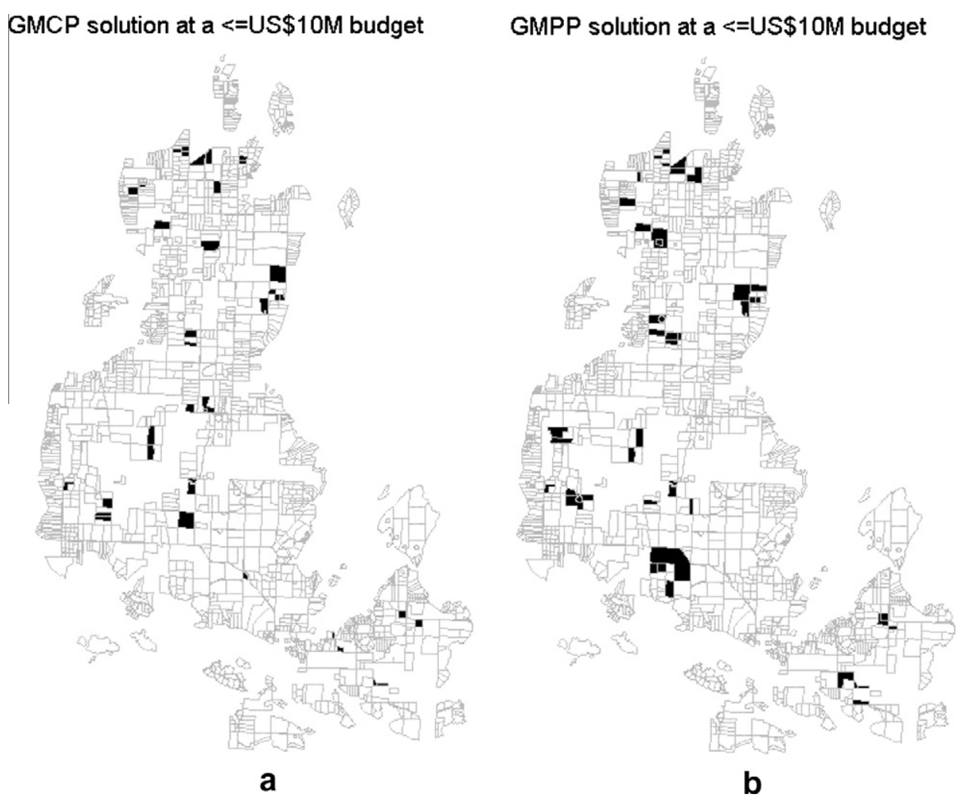

Fig. 5. The map on the left shows parcels in black that form the optimal selection for the general maximal covering problem at a budget of US$9.6. This solution allows the protection of 30 *Myotis* roosts. To protect one more roost, the US$10M budget is insufficient. The map on the right shows the corresponding solution to the general maximal protection problems for a budget of US$9.96M. This solution provides much more protection for only 13 *Myotis* roosts.

4. Conclusions

We introduce a scalable population protection function that can make use of increasingly available high-resolution, species-specific habitat data in reserve selection models. We embed the protection function in two mathematical-programming models which we call the General Maximal Covering Problem and the General Maximal Protection Problem. We illustrate the mechanics and the benefits of the new models in a case study of bat conservation. The models help quantify the increasing marginal costs of protecting *Myotis* habitat and show that optimal site selection strategies are sensitive to the relative importance of habitat requirements. We also show how the two models can be combined to explore the tradeoffs among acquisition costs and both weighted protection and the number of protected roosts.

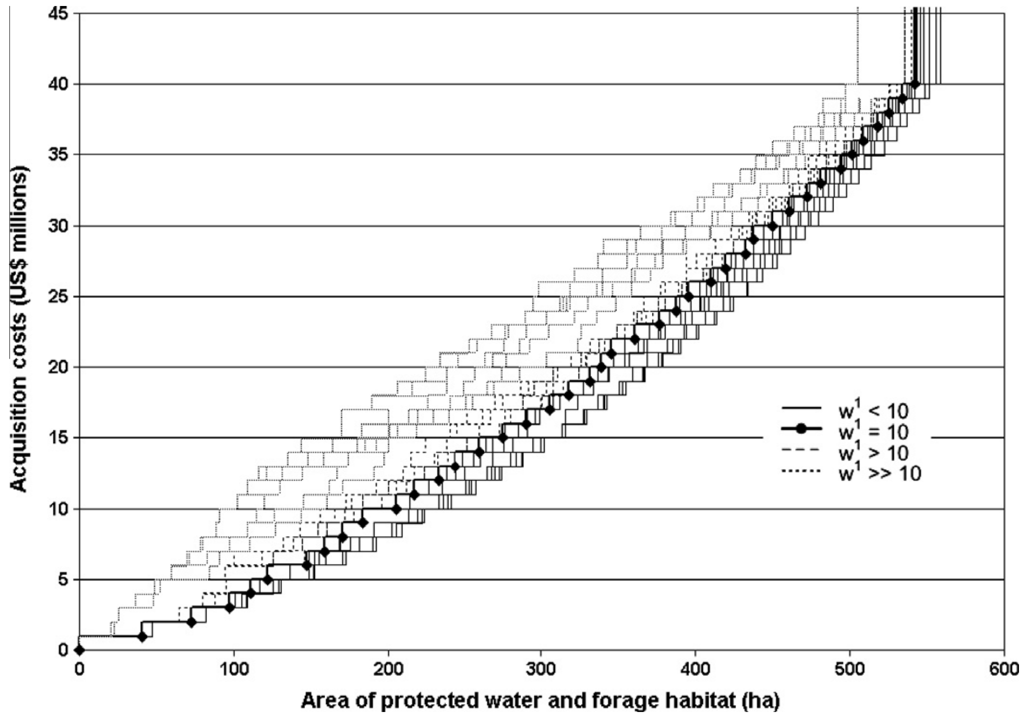

Fig. 6. Sensitivity analysis showing the change in the efficient frontier with changes in the relative importance of water vs. forage habitat for *Myotis* conservation on Lopez Island. Because the relative weights change the scale of the amount of protection, the unit on the horizontal axis is total area of water and forage protected.

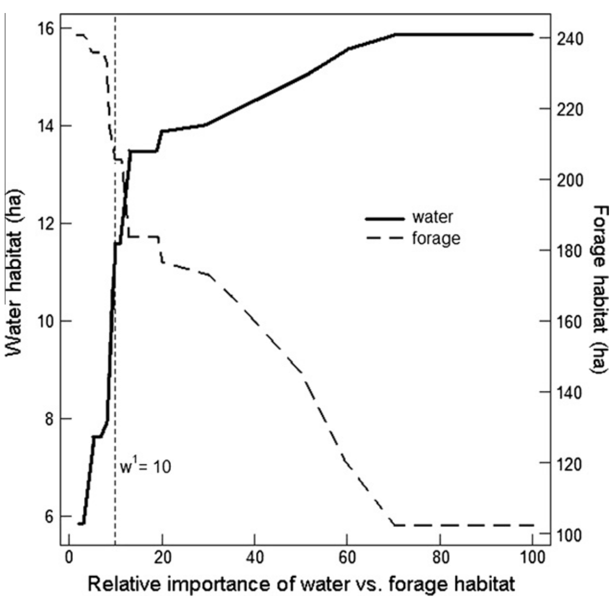

Fig. 7. Hectares of water vs. forage habitat included in optimal solutions of the generalized maximal protection problem at a budget of US$10 million in response to varying w_j^1 from 1 to 100.

We note that the protection function has the flexibility to relax existing habitat requirements or to allow the inclusion of other habitat requirements in reserve site selection models. As an example of the former, bat biologists are discussing whether and to what extent bats exhibit roost fidelity. Some suggest that fidelity is related to permanence of the roost structure, so that bats roost in buildings (e.g. barns) more consistently than they would in tree cavities or under bark (Barclay and Kurta, 2007). By relaxing the assumption that a bat population is associated with only one roost and instead identifying discrete segments of the landscape as supporting distinct populations, the model could easily reflect a different, perhaps more accurate understanding of roost fidelity. The protection function would simply require that a certain number of roost sites are protected within a specified distance, each of which could potentially serve as the actual roost for a given population. As an example of the latter, the logical structure of the protection function allows applications where the objects of conservation have different needs: it can assess such varied requirements as prey density, stream lengths, or even stream lengths categorized by temperature gradients or stream order. It is also fully compatible with existing mathematical programming constructs such as those introduced by Önal and Briers (2006) for habitat connectivity, by Tóth et al. (2009) for habitat contiguity, or by Tóth and McDill (2008) for habitat compactness.

One caveat is that the proposed models do not differentiate between the value of protecting one particular population versus another. Reproduction and survival rates can be different in different sites and allocating resources to protecting *sink* populations might not be the best conservation investment. A potential solution involves assigning different weights to the variables that indicate whether or not a particular population is adequately protected.

Another limitation of the model is related to potential competition among populations or species for certain habitat resources. The US$9.6M GMCP solution on Fig. 4 as an example provides 2.76 ha of water and 52.87 ha of forage habitat for 30 roosts but 33.3 and 53.1% of these areas, respectively, are shared between two or more populations. If competition exists, then the proposed models need to be modified to account for the carrying capacity of each site. If we assume that habitat component k in site i is evenly split among the populations (or species) that have access to the resource, then constraints (4) and (9) could be modified as follows:

$$y_j m_j^k \leqslant \sum_{i \in S_j^k} \frac{a_{ij}^k x_i}{1 + \sum_{l \in P_i \setminus \{j\}} y_l} \quad \forall k \in K_j,\ j \in J \tag{12}$$

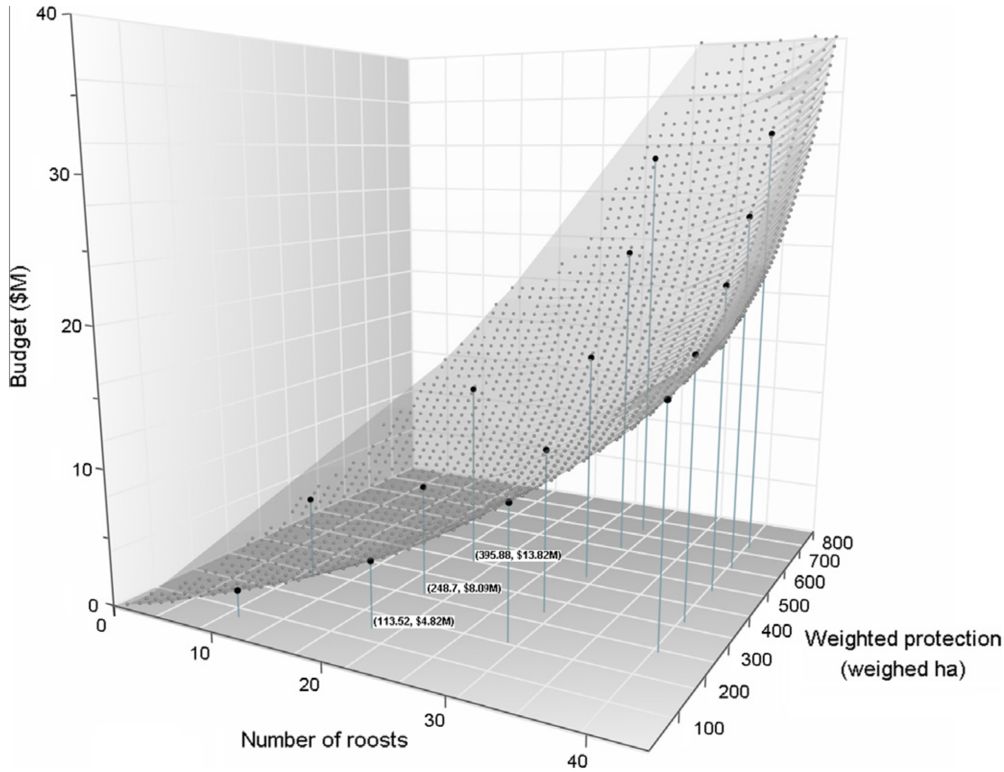

Fig. 8. Three-way tradeoffs among parcel selections that are Pareto-optimal with respect to (1) cost, (2) number of roosts and (3) weighted protection under $w_j^1 = 10$. Three of the solutions that provided 20 roosts were labeled for weighted protection and cost.

In constraint (12), habitat component k that is available for population j from site i (a_{ij}^k) depends (endogenously) on the number of populations that are protected and have access to the resource on site i : $1 + \sum_{l \in P_i \setminus \{j\}} y_l$. As an example, if there is one population with access to site i other than population j, and both site i and the other population are protected, then only half of a_{ij}^k will be available for population j to satisfy m_j^k due to $1 + \sum_{l \in P_i \setminus \{j\}} y_l$ being equal to 2. A critical issue with constraint set (12) is that there does not appear to be an obvious way to linearize the fractional term on the right-hand-side. This would leave the analyst with a nonlinear integer programming problem whose optimization requires specialized software. A much simpler modification of constraints (4) and (9) could assume that commonly accessible resources are available for only one population:

$$y_j m_j^k \leqslant \sum_{i \in S_j^k} a_{ij}^k \left(1 - \sum_{l \in P_i \setminus \{j\}} y_l\right) x_i \quad \forall k \in K_j,\ j \in J \tag{13}$$

Constraints (13) say that the contribution of site i to habitat component k for population j is zero if there is one more population (other than j) with access to site i that has been declared protected. Otherwise, the contribution equals a_{ij}^k. While the right-hand-side of Inequality (13) is nonlinear, the linearization of cross-products between binary variables is trivial (Williams, 1999, p. 164). Whether construct (13) would be appropriate in a particular situation will depend on the species in need of protection. The computational study of the "competition" problem identified above could serve as the subject of future research.

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