

Optimal Selection of a Connected Reserve Network

Hayri Önal

Department of Agricultural and Consumer Economics, University of Illinois at Urbana-Champaign,
Urbana, Illinois 61801, h-onal@uiuc.edu

Robert A. Briers

School of Life Sciences, Napier University, 10 Colinton Road, Edinburgh, EH10 5DT, United Kingdom,
r.briers@napier.ac.uk

Spatial considerations are important in conservation reserve design. A particularly important spatial requirement is the connectivity of selected sites. Direct connections between reserve sites increase the likelihood of species persistence by allowing dispersal and colonization of other areas within the network without species having to leave the reserve. The conventional set-covering and maximal-covering formulations of the reserve selection problem assume that species representation is the only criterion in site selection. This approach usually results in a small but highly fragmented reserve, which may not be desirable. We present a linear integer programming framework incorporating spatial contiguity as an additional site selection criterion. An empirical application to a data set on the occurrence of breeding birds in Berkshire, United Kingdom, demonstrates that site connectivity requires a significantly larger reserve. Incorporation of spatial criteria increases the computational complexity of the problem. To overcome this, we use a two-stage procedure where the original sites are aggregated first and an optimum solution is determined for the aggregate sites. Then, site selection is restricted to original sites included in the aggregate solution and a connected reserve is determined. In this particular application the above procedure generated a significantly more efficient reserve than a heuristic selection.

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1. Introduction

In past decades various biodiversity conservation programs have been introduced to protect species from anthropogenic habitat loss. Among these, conservation reserves, where land is protected from development or modification and managed to maintain or enhance species and habitat diversity, are considered as particularly effective means of species preservation. Motivated by this, selection of an efficient set of reserve sites has been an important problem in the biological conservation literature, especially in the past decade. The problem has been approached using either heuristic methods (e.g., Margules et al. 1988; Vane-Wright et al. 1991; Nicholls and Margules 1993; Pressey et al. 1993, 1996, 1997; Csuti et al. 1997) or formal optimization, specifically linear integer programming (e.g., Church et al. 1996; Ando et al. 1998; Polasky et al. 2001a, 2001b; Rodrigues and Gaston 2002).

In its simplest form, the problem is stated as selecting a minimum number of reserve sites that contain populations of a specified set of species, or maximizing the number of species that can be protected under a conservation budget constraint. Both problems can be formulated as linear integer programs (IP), being special cases of the

prototype set-covering problem and the maximal-covering problem (Toregas and ReVelle 1973, Church and ReVelle 1974, Underhill 1994, Camm et al. 1996, Williams and ReVelle 1997). In this approach, the only site-selection criterion is the “representation” (or “coverage”) of target species, which requires that there is at least one site in the reserve that covers a protected species (i.e., the species is either present or can survive at that site). This presents a deterministic approach to the problem. Haight et al. (2000) and Camm et al. (2002) incorporated uncertainty into the maximal-covering framework.

Most of the empirical IP applications presented to date have been limited largely to the two basic formulations of the reserve selection problem mentioned above. An important shortcoming of these formulations is the negligence of the reserve’s spatial layout. Typically, solutions of both the set-covering and maximal-covering formulations exhibit a highly dispersed and fragmented reserve structure, which restricts the opportunities for dispersal of species between sites and may adversely influence the probability of species persistence (Macdonald and Johnson 2001). Spatial considerations may take a variety of forms, such as compactness, proximity of selected reserve sites,

total boundary size, or connectivity (adjacency) of sites that form the reserve (McDonnell et al. 2002). In the literature, heuristic approaches have been used to incorporate such selection criteria (e.g., Nicholls and Margules 1993, Briers 2002), although this approach is known to yield generally suboptimum solutions, and therefore an inefficient use of economic resources. The degree of inefficiency (suboptimality) can be as much as 10%–15% (Church et al. 1996, Pressey et al. 1996, Rodrigues and Gaston 2002, Önal 2003). The lack of spatial optimization studies in reserve design is partly due to the computational complexity of IP, which may be restrictive when working with a large number of reserve sites. More importantly, it is often argued that spatial considerations would require computationally intractable nonlinear IP formulations (see, for example, Pressey et al. 1996).

In the past decade there has been significant progress in spatial optimization, with special emphasis on land acquisition and habitat design. Several studies have presented linear IP formulations involving various types of spatial criteria and have shown that the modeling complexity argument is not entirely true. For instance, Ruliffson et al. (2003) incorporated distances from selected reserve sites to a metropolitan area while considering the twin objectives of maximizing public access and species representation. Önal and Briers (2002) developed a linear IP model to determine a compact reserve configuration by minimizing the sum of pairwise distances between selected sites. Nalle et al. (2002a, b) modeled this problem as a quadratic IP, and due to the solution difficulty, they used a combination of greedy heuristic search and simulated annealing to solve the problem. Wright et al. (1983) developed a linear IP model where the boundary length of the selected area was minimized. Hof and Joyce (1993) and, more recently, Önal and Briers (2003) presented alternative and more efficient formulations of the same problem. A few studies have addressed the problem of site contiguity/adjacency. Sessions (1992) used a Steiner network approach for selecting a minimal set of land parcels that connect a given set of existing sites. Although exact solution methods exist for the Steiner network problem (Hwang et al. 1992), noting the computational complexity of those methods, Sessions (1992) suggested a heuristic algorithm to be able to solve large-scale problems. However, Williams (1998) presented an exact linear IP formulation of the problem and reported that the solutions of the relaxed linear program were binary. Thus, the problem could be solved easily without performing excessive branch-and-bound iterations. Optimum selection of a core reserve area with an adjacent buffer zone surrounding the core was modeled as a linear IP by Williams and ReVelle (1996, 1998). Hof and Bevers (1998) discuss linear formulations of some other spatial optimization problems where ecosystem objectives are to be incorporated when managing forest resources. Computational experience reported in most of the above studies shows that

moderate-size problems can be solved conveniently using commercial optimization software.

This paper focuses on an important spatial consideration in reserve selection. A conservation reserve is often desired to be “fully connected,” namely, for any pair of sites in the reserve network there must be a chain of adjacent reserve sites that connect the two sites. Increasing rates of anthropogenic habitat destruction and alteration (Hannah et al. 1995) mean that many species populations exist in fragmented patches of habitat, separated by land that is often developed or altered in a way that makes it unsuitable for species to inhabit or disperse through. Suitable habitat may therefore remain uncolonized because species cannot reach it. Creating connected reserve networks is of particular concern when attempting to conserve multiple populations of target species within a reserve, as is likely to be required to ensure long-term species persistence (Rodrigues et al. 2000). By connecting species populations in different sites through a continuous reserve network, the likelihood of interpopulation dispersal, and hence long-term persistence (Hanski 1999, Macdonald and Johnson 2001), is increased.

Note that sites within the network of a protected habitat may not necessarily support populations of all targeted species; rather, they provide a conduit of protected habitat along which species can disperse between patches of suitable habitat scattered throughout the network. Whilst some habitat-specialist species may be unable to disperse through reserve sites that do not contain the correct habitat, many species are able to traverse other terrain in the search for suitable habitat (Dunning et al. 1995, Sutcliffe and Thomas 1996, Bolger et al. 2001). The importance of protected corridors to allow movement between habitat patches has been demonstrated by a number of studies (e.g., Haas 1995, Machtans et al. 1996, Bolger et al. 2001, Kondo and Nakagoshi 2002, Haddad et al. 2003), although the technique is not without its critics (Simberloff et al. 1992). In this paper, we assume that reserved areas are suitable for dispersal of all species and that species are unable to traverse or inhabit areas outside the protected reserve.

The reserve design problem with this criterion can be stated explicitly as follows: Suppose that a target set of species is to be protected in a conservation area that is partitioned into reserve sites, each supporting a known subset of species. Determine a fully connected subset of those sites (if it exists) that includes all the target species. Selection of a reserve with the property described above is a complex optimization problem. The purpose of this paper is to develop a linear IP formulation of the problem and present an empirical application. This paper also compares the performance of the optimization model with a heuristic site-selection algorithm when applied to the same data set.

2. Methodology

Before developing the IP reserve selection model, we first introduce some definitions and theoretical results related to

graph theory. Suppose that a potential conservation reserve area is partitioned into square units, which will be called *cells* (the square-cell assumption is not restrictive; the approach developed here can be applied to other geometric forms, such as triangles, rectangles, polygons, or even irregular forms). A *reserve* is a subset of cells in the partition that collectively provide habitat services to a specified set of species. *Adjacent cells* are defined as cells that have a common edge. Two cells in a reserve are *connected* if they belong to a *continuous chain* of mutually adjacent cells included in the reserve, and the reserve is *connected* if any two cells in it are connected.

We will establish an association between a connected reserve and a connected graph. For this, we first overlay a special graph $G = (V, E)$ on the grid partition, where V is a set of nodes and E is a set of arcs. Each node in V corresponds to a cell in the partition. Two nodes are adjacent if the corresponding cells are adjacent. Although no orientation (flow direction) is actually needed for reserve connectivity, we require that each arc in E is directed, originating from a node and directing into an adjacent node, in which case we say the first node is linked to the second. Thus, a given node may have up to four arcs originating from it and up to four arcs may be directed into it (the number of arcs can be fewer for those nodes corresponding to the cells on the area boundary).

A *reserve network* R is defined as a special subgraph of G , i.e., $R = (\tilde{V}, \tilde{E})$, where $\tilde{V} \subseteq V$ contains mutually adjacent nodes in V and $\tilde{E} \subseteq E$ is a subset of arcs linking the nodes in \tilde{V} . We require that only one arc in \tilde{E} can originate from each node in \tilde{V} , but more than one arc can be directed into a given node. From here on, all nodes and arcs are restricted to those associated with R . A *path* in R is a chain of arcs and nodes where each arc in the chain originates from the node at which the previous arc ends and a node on the path cannot be repeated, i.e., a *cycle* cannot occur. A node is called a *source* if no arc is directed into it, and a *sink node* is defined as a node from which no arc originates. A reserve network is connected if any two nodes in the network can be connected to each other by a path.

The following proposition plays a central role in the model development:

PROPOSITION 1. *If a subgraph $R \subseteq G$ associated with a reserve with n cells has no cycle and contains $n - 1$ directed arcs, then the network (and therefore the reserve) is connected.*

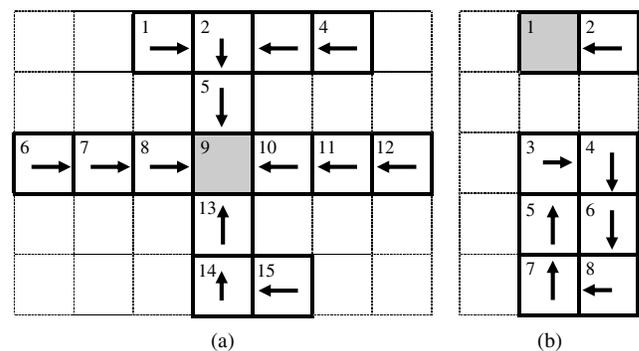
PROOF. See Bazaraa et al. (1990, p. 424).

A reserve network satisfying the conditions in Proposition 1 is called a *tree*. Numerous trees can be constructed from G . Here, we require two additional properties. First, the cells corresponding to the nodes in the tree must cover all the species under consideration. Second, the tree must be minimal in the sense that it consists of a minimum number of nodes. Thus, the problem of designing a connected

reserve can be stated as finding a minimal representative subset of cells on which a tree can be overlaid. We will formulate this problem as a linear IP problem.

The condition between the number of nodes and the number of arcs in the network, both to be determined endogenously, can be formulated easily as a linear equation. The main difficulty of the problem is to ensure that no cycle can occur in the network. For this, we will make use of a *tail-length* function $t: \tilde{V} \rightarrow \mathbb{R}$ satisfying the following properties: (i) $t(v) \geq 0 \forall v \in \tilde{V}$, and (ii) if $\{v_i\}$ is a set of adjacent nodes each linked to v by a directed arc, then $t(v) > \sum_i t(v_i)$. As an example, consider a special network where each node is connected to a set of source nodes through a path and only one arc can originate from a given node. Set $t(v) = 0$ for all source nodes, and for other nodes define $t(v)$ as the number of nodes contained in all paths originating from source nodes and ending at v (or equivalently, the number of arcs included in all such paths). It can be shown that this defines a function t satisfying the above properties. Figure 1a illustrates this special case, where a reserve network including 15 cells is depicted. The network has five source nodes associated with the cells labeled with 1, 4, 6, 12, and 15, while cell 9 corresponds to the sink node (note that by changing the direction of the arcs appropriately, any other node can be made a sink). The tail length of node 2, for instance, is 3 (because three directed arcs link nodes 1, 3, and 4 to this node), while the tail length of node 5 is 4. Figure 1b exhibits a reserve network with eight nodes and seven arcs. Although the relation between the number of nodes and arcs holds as stated in Proposition 1, this network has two disconnected components. The reason for this is the cycle formed by the six arcs in the larger component, which separates those nodes from the rest of

Figure 1. Connected and disconnected reserve configurations.



Notes. Dashed lines depict the boundaries of individual cells in the partition, while the solid lines depict the boundaries of the cells contained in the reserve. (a) depicts a connected reserve network with 15 cells, where the shaded cell (9) corresponds to the sink node. (b) depicts a reserve with two disconnected components and a cycle. The shaded cell (1) corresponds to the sink node for the small component, but that node is not a sink node for the entire reserve network because none of the nodes in the larger component is connected to it as the arcs in that component form a cycle.

the network. The following proposition is instrumental for eliminating the possibility of such cycle formation.

PROPOSITION 2. *If a function t with properties (i) and (ii) stated above can be defined on the set of nodes in a network, then no cycle can occur in the network.*

PROOF. First note that if node u is linked to node v , then we have $t(v) > t(u)$, which follows directly from property (ii). Suppose that a cycle occurs in the network. Consider two nodes u and v included in the cycle and the path originating from u and ending at v (which is part of the cycle). Let $\{u_i\}_{i=1,\dots,k}$ denote the set of nodes on that path, where $u = u_1$ and $u_k = v$. Then, we have $t(v) = t(u_k) > t(u_{k-1}) > \dots > t(u_1) = t(u)$, thus $t(v) > t(u)$. Reversing the argument implies that $t(u) > t(v)$, which is a contradiction. \square

In the model, instead of defining an explicit function t with properties (i) and (ii), for each node $v \in \tilde{V}$ we introduce a nonnegative endogenous variable that represents $t(v)$ and impose property (ii) by means of a linear inequality. We elaborate on this more in the next section.

The reserve network problem described above has some similarities to two prototype network problems, the Steiner network and the minimum spanning-tree problems, studied extensively in the operations research literature. However, there are fundamental differences between the present problem and those two prototype problems. The Steiner network problem begins with a known subset of nodes within a graph and aims to find a minimal tree within the graph that spans (i.e., connects) those nodes (Sessions 1992, Williams 1998). In the present problem, however, we are concerned with the selection of a representative reserve (the given subset of nodes in the Steiner network problem) in the first place, which is done simultaneously with the selection of the connecting cells. Therefore, some cells in the selection are *primary* cells, which collectively cover the target species, while some others may be *auxiliary*, i.e., they are selected just to connect the primary cells. The Steiner network problem is concerned with the selection of the latter group for a given set of primary cells. On the other hand, the minimum spanning-tree problem is defined as finding a network tree $T = (V, \tilde{E})$ from a given graph $G = (V, E)$, where $\tilde{E} \subseteq E$, such that the tree T has minimum total length (Cheriton and Tarjan 1976, Hillier and Lieberman 1986, Williams 2001). Note that the same set of nodes V is involved in both T and G , and the selection is concerned with the minimal subset of arcs, \tilde{E} , that spans V . If we define the distance between any two adjacent cells as zero, the connectivity requirement in the reserve selection problem implies that the total length of an optimal reserve network must be zero. Therefore, the desired network has the minimum-length property. However, the set of nodes that must be spanned is not available a priori. In fact, selection of the minimal representative subset of sites, among a typically much larger set of reserve sites, is the crux of the

problem here. Because of these unique features, there is no prototype formulation presented in the operations research literature that adequately represents the problem at hand. In the following section, we develop a linear IP model for this problem using the results of the propositions stated above.

3. The Model

The following notation is used in the model: i, j denote individual cells, which we will also use to denote nodes in the reserve network (if cell i is selected, node i is included in the reserve network); A_j is the set of cells that are adjacent to cell j ; S is the set of species targeted for preservation; δ_{si} is a parameter, where $\delta_{si} = 1$ if species s is present at cell i , $\delta_{si} = 0$ otherwise; k_s is a user-specified parameter that represents the minimum number of cells in the reserve that must contain species s ; m is an arbitrarily large number that serves as an overestimate of the number of cells in the reserve; X_i is a binary variable, where $X_i = 1$ if cell i is in the reserve, $X_i = 0$ otherwise; Y_{ij} is a binary variable defined for each j and $i \in A_j$, where $Y_{ij} = 1$ if a directed arc originates from node i and ends at node j , otherwise $Y_{ij} = 0$; W_j is a nonnegative variable that represents the tail length of node j ; and Z_{ij} is a nonnegative variable that represents the tail-length contribution of node i when it is linked to an adjacent node j (note that an explicit tail-length function is not specified; rather, it is built in the model as explained below).

The standard set-covering formulation aims to minimize the number of cells in the reserve, while satisfying the species-representation condition. Using the above notation, this problem can be formulated as a linear IP as follows (Church and ReVelle 1974, Underhill 1994, Camm et al. 1996):

$$\text{Minimize } \sum_i X_i \quad (1)$$

$$\text{such that } \sum_i \delta_{si} X_i \geq k_s \quad \text{for all } s \in S. \quad (2)$$

The objective function (1) represents the number of cells in the reserve, while constraint (2) represents the species-coverage requirement, namely, the reserve must include at least k_s sites that include each species s (the standard set-covering formulation assumes that $k_s = 1$).

The formation of arcs in the graph is controlled by the following two constraints:

$$\sum_{i \in A_j} Y_{ij} \leq 4X_j \quad \text{for all } j, \quad (3)$$

$$\sum_{j \in A_i} Y_{ij} \leq X_i \quad \text{for all } i. \quad (4)$$

Constraint (3) states that if cell j is not selected, then no arc can be directed to node j from an adjacent node i ($Y_{ij} = 0$). If cell j is selected, the graph may have up to four arcs (originated from adjacent nodes) directed to node j .

Constraint (4) implies that if cell i is selected, then at most one arc can originate from node i (directed into an adjacent node). If cell i is not selected, no arc is allowed to originate from node i . Note that the constraint is stated as an inequality, rather than a strict equation, to accommodate the requirement that no arc originates from the sink node. However, due to constraint (5) given below, (4) will always be satisfied as a strict equation in the solution for all nodes except the sink node.

The condition relating the number of arcs and the number of nodes, stated in Proposition 1, is represented by the constraint

$$\sum_{i,j} Y_{ij} = \sum_i X_i - 1. \quad (5)$$

Finally, the following two constraints build a tail-length function and eliminate the possibility of cycle formation as stated in Proposition 2:

$$Z_{ij} \geq W_i + 1 - m(1 - Y_{ij}) \quad \text{for all } i, j \text{ with } i \neq j, \quad (6)$$

$$W_j = \sum_i Z_{ij} \quad \text{for all } j. \quad (7)$$

To see how these two constraints work, first consider $Y_{ij} = 0$, i.e., node i is not linked to node j . Because m is an arbitrarily specified large number, for a sufficiently large m , the right-hand side of (6) becomes negative and this constraint is practically equivalent to $Z_{ij} \geq 0$. If $Y_{ij} = 1$ for some i , i.e., node i is linked to node j , then (6) becomes $Z_{ij} \geq W_i + 1$ and constraint (7) implies $W_j = \sum_i Z_{ij} \geq \sum_i \{1 + W_i\} > \sum_i W_i$. This is the required property (ii) for a tail-length function. Therefore, together constraints (6) and (7) perform the cycle-breaking role of a tail-length function according to Proposition 2. In numerical solutions of the model, the solver always assigns the minimum feasible value to Z_{ij} , namely, $Z_{ij} = 0$ when $Y_{ij} = 0$, and $Z_{ij} = W_i + 1$ when $Y_{ij} = 1$. In this case, W_j serves as a node/arc counter, although this is not absolutely required for the applicability of Proposition 2.¹

4. An Empirical Application

To demonstrate the workings of the model and also investigate its computational efficiency with a real-world reserve-selection problem, the model was applied to a data set for the occurrence of breeding bird species in the county of Berkshire, United Kingdom (Standley et al. 1996). Global bird biodiversity has suffered significant losses through habitat change and destruction (Gaston et al. 2003), and the rapid development and urbanization of Berkshire is likely to threaten the status of many bird species (Standley et al. 1996). Movement corridors are very important for bird species (Haas 1995, Machtans et al. 1996, Bolger et al. 2001, Kondo and Nakagoshi 2002, Haddad et al. 2003), and hence it is particularly appropriate to apply the techniques developed here to this data set.

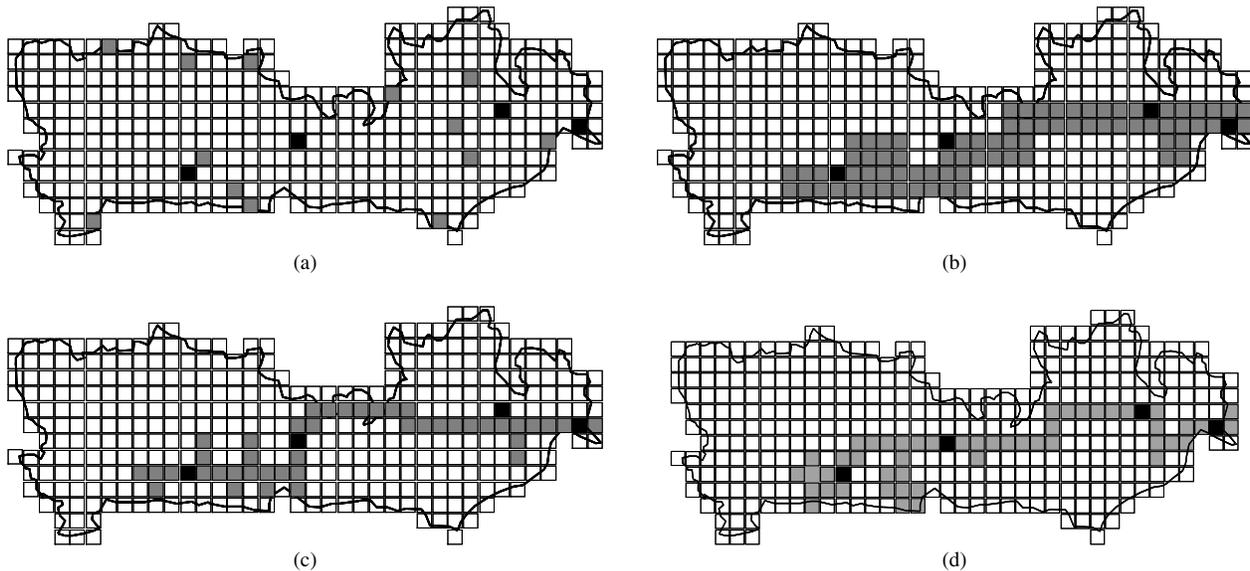
Between 1987 and 1989, a survey of all 391 cells (2×2 km squares) that fall within the administrative boundary of Berkshire was undertaken to record the distribution of breeding bird species. A total of 121 species were recorded as breeding within the county; our analyses are based on the distribution of all species except the feral pigeon/rock dove (*Columba livia* Gmelin), which was excluded due to doubt over the domesticated status of many of the records; the chukar (*Alectoris chukkar* Gray), an introduced species that does not form self-sustaining wild populations; and the stone curlew (*Burhinus oedipnemus* (L.)), a nationally endangered species whose distribution was not mapped in Standley et al. (1996). Thus, altogether, 118 species were included in the analysis. The species-presence data in those cells range from 1 (i.e., the species is present in one cell only) to 391 (the species is present in all cells). Two species were present in one cell only (although the cells were different), while one species was present in two cells only. On the other hand, some species were common and present in most cells (five species were found in all 391 cells; therefore, those species could actually be dropped from the analysis).

In the species representation constraint, i.e., constraint (2), we considered $k_s = \min\{2, n_s\}$ for all s , where n_s denotes the number of cells in which species s is present. This implies that if a species is present in one cell only, then $k_s = 1$ for that species and that cell has to be included in the reserve. For other species, it would generally be preferable to conserve more than one cell, as this would more likely result in long-term persistence of the species. If a species is present in two cells only, then $k_s = 2$ and both cells have to be selected. These cells are called *irreplaceable cells*. For all other species, $k_s = 2$, which means that at least two cells including those species must be included in the reserve.

The optimum reserve configuration without consideration of the spatial selection criterion (connectivity) is shown in Figure 2a. It should be noted that the optimum selection was not unique, which is typical in most empirical applications. In the figure, the county border is shown with the irregular curve, the cells with darker shading indicate the irreplaceable cells (which must be selected in any feasible solution), and the gray-shaded cells indicate other selected cells. As shown in the figure, the optimum reserve configuration included highly dispersed sites scattered throughout the area.

When a small number of reserve sites is involved, the model defined by (1)–(7) can be solved directly to determine an exact optimum connected solution. However, computational difficulties may arise when the number of cells in the partition is large, and it may not be possible to obtain a confirmed optimum solution in a reasonable processing time. The main reasons are the number of binary site-selection variables (X_i) and the number of cycle elimination constraints (6), but most importantly the number of binary Y_{ij} variables, which increase the size of

Figure 2. (a) Map of cells within the administrative boundary of Berkshire, United Kingdom (bold irregular line) selected by the set-covering formulation for $k_s = \min\{2, n_s\}$. Black squares indicate the irreplaceable cells that must be included to satisfy the species-representation constraints, and shaded squares indicate other selected cells in the optimum solution. (b) A fully connected optimum reserve network of aggregated cells, each consisting of four cells. (c) A fully connected reserve network of original cells obtained by restricting the selection to the aggregate solution in Figure 2b. (d) A fully connected reserve network of original cells selected by the heuristic algorithm.



the branch-and-bound tree severely when a large number of cells is involved in the partition. In this application, CPLEX 8.1, incorporated with GAMS (Brooke et al. 1998), was used to solve the model described above. A PC with a Pentium III processor with 500 MHz CPU and 256 MB RAM was used in all runs. It turned out that the model size was large enough to cause computational difficulties for this data set, and even an integer-feasible solution could not be obtained within two hours when all 391 cells were included in the analysis.² Unfortunately, in practice, reserve-selection problems are often larger than this. Therefore, computational complexity may be a limiting factor for practical applications of the model.

The computational difficulty discussed above can be overcome by using different approaches. A cursory review of the irreplaceable sites may indicate where the connected solutions should lie, and therefore the selection may be restricted to that section of the potential reserve area. This may allow elimination of a large number of binary variables, including both Y_{ij} and X_i , and make the model solvable. Another practical approach is to use a two-stage procedure, where in the first stage the reserve sites are aggregated into larger and fewer sites and a connected solution formed by those aggregate sites is determined. In the second stage, the site selection is restricted to only those original sites contained in the aggregate solution (or a sufficiently small area that contains the aggregate solution), while excluding the remaining sites. In a way, the second stage removes unnecessary original sites included in

the aggregate solution (or adds new sites when the second stage considers extra aggregate sites around the first-stage solution) without violating either the connectivity or the species-representation requirements. It is important to note that because the aggregate solution in the first stage is connected, in the second stage one can always find a connected reserve configuration formed by the original sites. It should also be emphasized that the end result of this procedure may or may not be the true optimum solution of the problem because in the second stage the selection is restricted to a subset of sites that may not necessarily include the true optimum solution.

In this application, we used the two-step procedure explained above. In the first stage, four adjacent cells that form a square were considered as one aggregate cell. A new database for species presence was created for those aggregate cells. This procedure generated 152 aggregate cells, but only 115 of those were considered in the model because some aggregate cells were completely outside the county border.³ The resulting aggregate model included 511 discrete variables and was solvable to an exact optimum. The connected aggregate solution is shown in Figure 2b. This solution indicates that 20 aggregate cells would be sufficient to create a connected reserve with the specified species-representation requirements. Therefore, in the second stage, the model could include only 80 cells to determine a connected and representative reserve formed by the original cells. However, we considered several extra aggregate cells surrounding the first-stage solution to increase

the chances for finding the true optimum solution. The best solution found with this approach is the reserve configuration shown in Figure 2c. The minimum number of cells needed to satisfy both the species representation and connectivity requirements was increased from 17 to 45 cells. Most of those additional cells were *auxiliary*, i.e., selected to make the reserve connected, rather than to contribute to species representation. Many species were covered by multiple cells due to the selection of extra cells for connectivity. For instance, while 15 of 118 species were covered by two sites, 67 species were covered by at least 20 sites (the average was 24.4).

The solution shown in Figure 2b is a confirmed optimum solution and was obtained after solving 55,727 branch-and-bound nodes (which took 809 seconds). The second-stage model included 314 discrete variables, and a confirmed optimum could not be obtained after running CPLEX for 25 hours.⁴ Several integer solutions were obtained during the branch-and-bound process. The one shown in Figure 2c, with 45 cells selected, is the best integer solution found after solving nearly 10 million branch-and-bound nodes (the dual bound on the optimal solution reported by CPLEX when it was stopped was 43).⁵

To see how good the above solutions were, and whether improvements in efficiency offset the computational complexity of IP, we determined connected reserve solutions by using a heuristic site-selection algorithm applied to the same data set. In the following section, we describe the heuristic approach and compare the resulting solutions with the IP solution shown in Figure 2c.

5. Heuristic Approach

The heuristic algorithm utilized here is an extension of the greedy algorithm (Church and ReVelle 1974) designed to select a fully connected reserve network while satisfying the species-representation constraint (2). A description of the steps used in site selection is given below:

Step 1. Select all irreplaceable cells. Develop and label blocks of selected cells, where each block includes either an irreplaceable cell or a set of adjacent irreplaceable cells.

Step 2. Find a cell that is adjacent to one of the selected blocks and adds the maximum number of species to the set of previously covered species. If there is a tie between two candidate cells (i.e., more than one cell adds the same number of uncovered species), then select the cell that is closest to another block of selected cells. If a selected cell connects two or more blocks, merge those blocks into a single block.

Step 3. If a previously selected cell becomes redundant (i.e., is no longer required to represent species—due to the addition of subsequent cells—and elimination of that cell does not divide a block into disconnected blocks), eliminate that cell. If no redundant cell is left, go to Step 4.

Step 4. If all species are represented at least k_s times in the reserve, go to Step 5. Otherwise, go to Step 2.

Step 5. If the number of selected blocks is reduced to one, the reserve is fully connected, stop. Otherwise, go to Step 2.

The connected reserve network produced by the above heuristic algorithm is shown in Figure 2d. The number of cells required to achieve a desired reserve network was 53, which is significantly larger than that produced by the IP model (45 cells). Once again, this demonstrates the relative inefficiency of heuristic algorithms compared to IP solutions. Even if the solutions resulting from the two-stage procedure are not true optimum solutions, the empirical results show that one may be better-off using this approach rather than the heuristic approach. Therefore, when computational complexity of the IP model becomes restrictive in large-scale applications, the aggregation procedure presented here may be a viable approach that is preferable to the use of heuristics.

6. Discussion

This paper demonstrates that it is possible to formulate the problem of designing a fully connected reserve network as a linear integer program, whilst maintaining optimal use of conservation resources (in this case, minimizing the number of cells included in the reserve). A fully connected reserve network is likely to require many more cells than the standard set-covering solution, resulting in potentially greater economic cost to develop and maintain the network. However, the economic cost may be outweighed by the greater likelihood of species persisting within the network, as they can freely disperse and colonise other areas within the network. The value of corridors connecting habitat patches in promoting intersite dispersal has been demonstrated for bird and mammal species (Haas 1995, Machtans et al. 1996, Bolger et al. 2001). Wildlife corridors may result in higher species richness of individual sites (Bolger et al. 2001), greater chance of colonization of vacant habitat (Dunning et al. 1995), and wider distribution of species than in fragmented habitats (Kondo and Nakagoshi 2002). There may be, however, potential disadvantages of fully connected reserve networks. An outbreak of disease and/or pest species within the reserve are likely to spread freely throughout the protected area, as there are no barriers to movement, and clustered reserve sites are also at risk from spatially correlated environmental fluctuations (Possingham et al. 2000, Shafer 2001). However, given the influence of dispersal between sites in determining the regional abundance and distribution of many species (Hanski 1999), the potential benefits of having a connected reserve network are likely to outweigh any potential disadvantages.

The IP approach developed here has some drawbacks in terms of computational efficiency. Many real-world applications of reserve selection involve considerable numbers of sites (e.g., Pressey et al. 1996, Csuti et al. 1997, Siitonen et al. 2002). Selection problems of this size may not be solvable without preprocessing the data, such as the aggregation technique presented above, to reduce the number of

sites from which the reserve is to be selected. Whilst this approach may result in suboptimal solutions, the model still produces a fully connected reserve network as required. Moreover, the results presented here suggest that the best solutions found with this approach can still be significantly more efficient (less costly) than the reserve networks produced by heuristic algorithms, reinforcing previous assertions regarding the inefficiency of heuristics. This assertion, however, is based on just one piece of evidence and may not be generalized to all large-scale reserve selection problems involving connectivity. More experimentation with different data sets and different heuristic approaches is needed for this.

The model developed here can be extended easily to cases where a reserve with more than one connected component can be acceptable. As noted earlier, a fully connected reserve network may require selection of a substantial number of reserve sites to connect the sites that are needed for species coverage, rather than directly contributing to species coverage by themselves. Thus, if irreplaceable sites are found at distant segments of a large potential reserve area, then numerous sites would be needed to connect them. This may not be the best possible solution due to unreasonably high economic costs of land acquisition and maintenance. Instead, a viable conservation policy may comprise one connected component at each segment, thus resulting in a patchy reserve with two or more sufficiently large components each being a connected subreserve itself while jointly satisfying the species-coverage requirement. The model can be modified in a straightforward manner to accommodate this type of reserve configuration by partitioning the set of all sites into a few subsets (which may be disjoint or slightly overlapping) and imposing the connectivity requirement to the sites selected in each segment rather than full connectivity of all selected sites. Because the Y_{ij} variables are defined for adjacent cells only, this modification does not result in an increase in the model size, and therefore may not cause additional computational complexity.

The model can also be extended to incorporate land costs in the objective function, in which case the total cost of the selected reserve is to be minimized instead of the reserve size (which assumes that all sites are of equal economic value). This can be important in practice when costs vary significantly across the potential reserve sites, which may have important implications on the optimal reserve design.

Endnotes

1. If desired, this property (i.e., assigning the minimum feasible values) can be enforced by incorporating a penalty term $\sum_{i,j} Z_{ij}$ in the objective function (1).
2. Various run-time simplifications were made to reduce the model size and improve its computational performance. For example: (i) we fixed the site-selection variables (X_i) at 1 for irreplaceable cells; (ii) one of the nodes corresponding to irreplaceable cells was specified as “sink node”

and constraint (4) was stated as a strict equation for all nodes other than the sink node (which means that there must be exactly one arc, instead of less than or equal to one, directed from node i if the cell corresponding to that node is selected); and (iii) constraint (4) was excluded in the model for the sink node.

3. Aggregation can be done in different ways. In this application, we first considered a rectangular cover of the region partitioned into cells. Starting with the northwest corner, the first two rows and columns were aggregated. Then, the next two rows and columns were aggregated, etc., to form aggregate squares of four cells. Some aggregate cells near the county border contained fewer than four cells included in the original partition; therefore, the number of aggregate cells was more than one-fourth of the total number of cells in the data. Producing alternative optima with different aggregation procedures can be worthwhile if the economic cost differences between those selections are significant. Here we provide only one set of results obtained with the aggregation procedure described above.

4. The number of binary variables in the second-stage model was significantly less than the aggregate model (specifically, 314 versus 511), and both models have the same algebraic structure. However, the substantial solution time for the second-stage model shows that besides the model structure and size, the data set used in the model is also an important determinant of computational complexity when using the IP model.

5. Here we assume that the true optimum solutions are in the regions considered for selection in the second stage, which may or may not always be the case. Several additional runs were made with the second-stage model by adding more aggregate cells surrounding the first-stage solution, but a better solution than the ones presented here could not be obtained in either case. Thus, it is likely that the solution shown in Figure 2c is the true optimum solution.

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References

- Ando, A., J. D. Camm, S. Polasky, A. Solow. 1998. Species distribution, land values and efficient conservation. *Science* **279** 2126–2128.
- Bazaraa, M., J. J. Jarvis, H. D. Sherali. 1990. *Linear Programming and Network Flows*. John Wiley and Sons, New York.
- Bolger, D. T., T. A. Scott, J. T. Rotenberry. 2001. Use of corridor-like structures by bird and small mammal species. *Biol. Conservation* **102** 213–224.
- Briers, R. A. 2002. Incorporating connectivity into reserve selection procedures. *Biol. Conservation* **103** 77–83.

- Brooke, A., D. Kendrick, A. Meeraus, R. Raman. 1998. *GAMS—A User's Guide*. GAMS Development Corporation, Washington, DC.
- Camm, J. D., S. K. Norman, S. Polasky, A. Solow. 2002. Nature reserve site selection to maximize expected species covered. *Oper. Res.* **50** 946–955.
- Camm, J. D., S. Polasky, A. Solow, B. Csuti. 1996. A note on optimal algorithms for reserve site selection. *Biol. Conservation* **78** 353–355.
- Cheriton, D., R. E. Tarjan. 1976. Finding minimum spanning trees. *SIAM J. Comput.* **5** 725–742.
- Church, R. L., C. ReVelle. 1974. The maximum covering location problem. *Papers Regional Sci. Association* **32** 101–118.
- Church, R. L., D. M. Stoms, F. W. Davis. 1996. Reserve selection as a maximal covering location problem. *Biol. Conservation* **76** 105–112.
- Csuti, B., S. Polasky, P. H. Williams, R. L. Pressey, J. D. Camm, M. Kershaw, R. Kiestler, B. Downs, R. Hamilton, M. Huso, K. Sahr. 1997. A comparison of reserve selection algorithms using data on terrestrial vertebrates in Oregon. *Biol. Conservation* **80** 83–97.
- Dunning, J. B., R. Borgella, K. Clements, G. K. Meffe. 1995. Patch isolation, corridor effects, and colonization by a resident sparrow in a managed pine woodland. *Conservation Biol.* **9** 542–550.
- Gaston, K. J., T. M. Blackburn, K. Klein Goldewijk. 2003. Habitat conversion and global avian biodiversity loss. *Proc. Roy. Soc. London B* **270** 1293–1300.
- Haas, C. A. 1995. Dispersal and use of corridors by birds in wooded patches on an agricultural landscape. *Conservation Biol.* **9** 845–854.
- Haddad, N. M., D. R. Bowne, A. Cunningham, B. J. Danielson, D. J. Levey, S. Sargent, T. Spira. 2003. Corridor use by diverse taxa. *Ecology* **84** 609–615.
- Haight, R. G., C. S. ReVelle, S. A. Snyder. 2000. An integer optimization approach to a probabilistic reserve site selection problem. *Oper. Res.* **48** 697–708.
- Hannah, L., J. L. Carr, A. Lanerani. 1995. Human disturbance and natural habitat: A biome level analysis of a global data set. *Biodiversity Conservation* **4** 128–155.
- Hanski, I. 1999. *Metapopulation Ecology*. Oxford University Press, Oxford, UK.
- Hillier, F. S., G. J. Lieberman. 1986. *Introduction to Operations Research*. McGraw-Hill Publishing Co., New York.
- Hof, J. G., M. Bevers. 1998. *Spatial Optimization for Managed Ecosystems*. Columbia University Press, New York.
- Hof, J. G., L. A. Joyce. 1993. A mixed integer linear programming approach for spatially optimizing wildlife and timber in managed forest ecosystems. *Forest Sci.* **39** 816–834.
- Hwang, F. K., D. S. Richards, P. Winter. 1992. *The Steiner Tree Problem*. North-Holland, Amsterdam, The Netherlands.
- Kondo, T., N. Nakagoshi. 2002. Effect of forest structure and connectivity on bird distribution in a riparian landscape. *Phytocoenologia* **32** 665–676.
- Macdonald, D. W., D. D. P. Johnson. 2001. Dispersal in theory and practice: Consequences for conservation biology. J. Clobert, E. Danchin, A. A. Dhondt, J. D. Nichols, eds. *Dispersal*. Oxford University Press, Oxford, UK, 358–372.
- Machtans, C. S., M. A. Villard, S. J. Hannon. 1996. Use of riparian buffer strips as movement corridors by forest birds. *Conservation Biol.* **10** 1366–1379.
- Margules, C. R., A. O. Nicholls, R. L. Pressey. 1988. Selecting networks of reserves to maximise biological diversity. *Biol. Conservation* **43** 63–76.
- McDonnell, M. D., H. P. Possingham, I. R. Ball, E. A. Cousins. 2002. Mathematical methods for spatially cohesive reserve design. *Environ. Model. Assessment* **7** 107–114.
- Nalle, D. J., J. L. Arthur, J. Sessions. 2002a. Designing compact and contiguous reserve networks with a hybrid heuristic algorithm. *Forest Sci.* **48** 59–68.
- Nalle, D. J., J. L. Arthur, C. A. Montgomery, J. Sessions. 2002b. Economic and spatial impacts of an existing reserve network on future augmentation. *Environ. Model. Assessment* **7** 99–105.
- Nicholls, A. O., C. R. Margules. 1993. An upgraded reserve selection algorithm. *Biol. Conservation* **64** 165–169.
- Önal, H. 2003. First best, second best, and heuristic solutions in conservation reserve selection. *Biol. Conservation* **115** 55–62.
- Önal, H., R. A. Briers. 2002. Incorporating spatial criteria in optimum reserve selection. *Proc. Roy. Soc. London B* **269** 2437–2441.
- Önal, H., R. A. Briers. 2003. Selection of a minimum boundary reserve network using integer programming. *Proc. Roy. Soc. London B* **270** 1487–1491.
- Polasky, S., J. D. Camm, B. Garber-Yonts. 2001a. Selecting biological reserves cost-effectively: An application to terrestrial vertebrate conservation in Oregon. *Land Econom.* **77** 68–78.
- Polasky, S., B. Csuti, C. A. Vossler, S. M. Meyers. 2001b. A comparison of taxonomic distinctness versus richness as criteria for setting conservation priorities for North American Birds. *Biol. Conservation* **97** 99–105.
- Possingham, H., I. Ball, S. Andelman. 2000. Mathematical methods for identifying representative reserve networks. S. Ferson, M. Burgman, eds. *Quantitative Methods for Conservation Biology*. Springer, New York, 291–306.
- Pressey, R. L., H. P. Possingham, J. R. Day. 1997. Effectiveness of alternative heuristic algorithms for identifying indicative minimum requirements for conservation reserves. *Biol. Conservation* **80** 207–219.
- Pressey, R. L., H. P. Possingham, C. R. Margules. 1996. Optimality in reserve selection algorithms: When does it matter and how much? *Biol. Conservation* **76** 259–267.
- Pressey, R. L., C. J. Humphries, C. R. Margules, R. I. Vane-Wright, P. H. Williams. 1993. Beyond opportunism: Key principles for systematic reserve selection. *Trends Ecology Evolution* **8** 124–128.
- Rodrigues, A. S. L., K. J. Gaston. 2002. Optimisation in reserve selection procedures—Why not? *Biol. Conservation* **107** 123–129.
- Rodrigues, A. S. L., R. D. Gregory, K. J. Gaston. 2000. Robustness of reserve selection procedures under temporal species turnover. *Proc. Roy. Soc. London B* **267** 49–55.
- Ruliffson, A. A., R. G. Haight, P. H. Gobster, F. R. Homans. 2003. Metropolitan natural area protection to maximize public access and species representation. *Environ. Sci. Policy* **6** 291–299.
- Sessions, J. 1992. Solving for habitat connections as a Steiner network problem. *Forest Sci.* **38** 203–207.
- Shafer, C. L. 2001. Inter-reserve distance. *Biol. Conservation* **100** 215–227.
- Siitonen, P., A. Tanskanen, A. Lehtinen. 2002. Method for selection of old-forest reserves. *Conservation Biol.* **16** 1398–1408.
- Simberloff, D., J. A. Farr, J. Cox, D. W. Moehlman. 1992. Movement corridors: Conservation bargains or poor investments. *Conservation Biol.* **6** 493–504.
- Standley, P., N. J. Bucknell, A. Swash, I. D. Collins. 1996. *The Birds of Berkshire*. Berkshire Atlas Group, Reading, UK.
- Sutcliffe, O. T., C. D. Thomas. 1996. Open corridors appear to facilitate dispersal by ringlet butterflies (*Aphantopus hyperantus*) between woodland clearings. *Conservation Biol.* **10** 1359–1365.
- Toregas, C., C. ReVelle. 1973. Binary logic solutions to a class of location problems. *Geographical Anal.* **5** 145–155.
- Underhill, L. G. 1994. Optimal and suboptimal reserve selection algorithms. *Biol. Conservation* **70** 85–87.
- Vane-Wright, R. I., C. J. Humphries, P. H. Williams. 1991. What to protect? Systematics and the agony of choice. *Biol. Conservation* **55** 235–254.
- Williams, J. C. 1998. Delineating protected wildlife corridors with multi-objective programming. *Environ. Model. Assessment* **3** 77–86.

- Williams, J. C. 2001. A linear-zero-one programming model for the minimum spanning tree problem in planar graphs. *Networks* **39** 53–60.
- Williams, J. C., C. S. ReVelle. 1996. A 0-1 programming approach to delineating protected reserves. *Environ. Planning B* **23** 607–622.
- Williams, J. C., C. S. ReVelle. 1997. Applying mathematical programming to reserve selection. *Environ. Model. Assessment* **2** 167–175.
- Williams, J. C., C. S. ReVelle. 1998. Reserve assemblage of critical areas: A zero-one programming approach. *Eur. J. Oper. Res.* **104** 497–509.
- Wright, J., C. ReVelle, J. Cohon. 1983. A multiobjective integer programming model for the land acquisition problem. *Regional Sci. Urban Econom.* **13** 31–53.