Using mathematical optimization models to design nature reserves

Justin C Williams¹, Charles S ReVelle¹, and Simon A Levin²

Designing an optimal nature reserve for the protection of biological diversity has been a long-standing challenge in conservation biology. A fundamental question has always been, which areas of land should be set aside. During the past two decades, quantitative methods from the field of operations research have been applied to the problem of selecting reserve sites. Here, we trace the development of decision models for systematic reserve design, from the iterative methods developed in the 1980s to the sophisticated spatial models being formulated today. Collaborations among ecologists, conservation biologists, and operations researchers have been key to the progress made thus far. We expect that mathematical reserve design models will become more widely used, in response to a growing need to identify effective alternatives for complex conservation problems worldwide.

Front Ecol Environ 2004; 2(2): 98-105

A fundamental challenge in conservation biology involves the development of principles and methods for the design of nature reserves. Difficult theoretical and practical issues arise, and ecologists and conservation biologists have been grappling with these issues at least since Diamond (1975) and others first proposed a set of geometric reserve design guidelines nearly 30 years ago (Figure 1; Kingsland 2002). The planning of a reserve or reserve system, such as a wildlife refuge or national park (Figure 2), depends on the conservation goals for the area in question, and involves identifying parcels or patches of habitat – here called "sites" – to be managed for these purposes.

In recent decades, a variety of decision models and methodologies have been developed to help conservation planners select reserve sites. These methods are intended to identify a reserve system that is "optimal" with respect to a particular conservation goal, while also responding to important socioeconomic considerations. Due to an emphasis on optimality, many of these methods have

In a nutshell:

- The challenge of designing nature reserves can be met in part by the application of mathematical optimization models
- Numerous models for optimal reserve site selection have been formulated by collaborating ecologists, conservation biologists, and operations researchers
- Key remaining issues include broadening the use of these models and integrating dynamic population models within a spatial optimization framework
- Ultimately, the value of reserve design models lies not in prescribing solutions, but in informing and guiding the planning and decision-making process

¹Department of Geography and Environmental Engineering, Johns Hopkins University, Baltimore, MD (jcwjr@jhu.edu); ²Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ employed quantitative approaches from the field of operations research. Through collaborations among ecologists, conservation biologists, and operations researchers, reserve design models have evolved considerably in response to the recognition of new conservation problems worldwide.

Early methods for reserve selection

The first quantitative methods for systematically identifying "good" reserve sites were developed 20 to 25 years ago in Australia. The goal was to preserve biological diversity by protecting all the species, communities, or other conservation features on a given list. These methods, which utilized presence/absence data for species and other features, took two forms. The first used numerical scoring to rank candidate sites in terms of multiple criteria such as species richness, rarity, naturalness, and size (Smith and Theberge 1986). An appropriate subset of reserve sites – usually those with the highest scores - was then recommended (Purdie et al. 1986; Bedward et al. 1991). This approach, however, often required an unreasonably large number of sites to represent all species or other features, because the top-ranked sites frequently contained similar sets of species while missing others; one might need to go far down the ranked list of sites before all species were represented. A proposed remedy was complementarity (Vane-Wright et al. 1991), which held that one should select sites with minimum overlap in the species they contain.

The second approach for site selection dealt directly with the complementarity issue by asking: what is the minimum number of sites, or minimum total area, necessary to represent all species. This also arose from the practical need to justify conservation decisions within a



Figure 1. Reserve design guidelines, after Diamond (1975). (a) A large reserve is better than a small reserve; (b) a single large reserve is better than several small reserves of the same total area; (c) and (d) reserves that are close together are better than reserves that are far apart; (e) reserves that are connected by wildlife corridors are better than unconnected reserves; and (f) a compact (circular) reserve is better than an elongated reserve.

context of competing land uses and other socioeconomic pressures (Finkel 1998). An efficient reserve system – one that removed a minimum of land resources from other uses – would probably attract broad support. A variety of iterative procedures, such as those of Kirkpatrick (1983) and Margules *et al.* (1988), were developed for identifying such a "minimum reserve set". Scoring was used in these methods as well, but site scores were adjusted in each iteration to account for those species represented by sites selected in prior steps. In each step, the site adding the most as-yet unrepresented species would be selected. Sites were selected sequentially under this type of "greedy adding" rule, until all species were represented.

By the mid-1990s, dozens of iterative methods had been developed for variations of the minimum reserve set problem, and had been applied in numerous case studies in Africa, Australia, Europe, and North America (Csuti *et al.* 1997; Pressey *et al.* 1997; Rodrigues and Gaston 2002). Pressey (2002) recounts the historic development of several lines of research into iterative methods, beginning with Kirkpatrick's (1983) pioneering work.

Reserve selection and mathematical programming

The problem of identifying a minimum reserve set was subsequently recognized as the type of problem that can be formulated as an integer program (IP), a well-known class of mathematical optimization model from operations research (Possingham et al. 1993; Underhill 1994). The minimum reserve set problem (known in operations research as the "set covering problem") is shown formulated as an IP model (Panel 1). Such models are termed "integer programs" because "yes" or "no" decisions in this case, whether to select a site or not - are represented by 1 and 0. Solutions to IPs can be found using commercially available linear programming software that can be run on personal computers. Integer programming had actually been applied to reserve selection several years earlier with the "integer goal program" model of Cocks and Baird (1989), but it was the minimum reserve set IP that firmly established the link between reserve selection and operations research.

The minimum reserve set IP was seen as an improvement over iterative methods because exact mathematical optima can be found for the IP. In contrast, the iterative methods cannot guarantee optimal solutions. Given the same species presence/absence data, the IP

Panel 1. An integer program formulation for the minimum reserve set problem

The objective (1) is to minimize the total number of sites selected for the reserve system. The species representation constraints (2) ensure that, for each species, at least one site is selected which contains the species in question. The number of times each species is represented can be increased by changing the right-hand side of the equation. Statement (3) is a binary integer requirement for the decision variables.

minimize:
$$\sum_{j \ge J} x_j$$
 (1)

 $i \in M$

 $\sum xj \ge 1$ for all $i \in I(2)$

 $x_i = 0 \text{ or } I \text{ for all } j \in J$

subject to:

where:

- i, I are the index and set of species, respectively
- j, J are the index and set of candidate sites
- M_i is the set of candidate sites j that contain species i
- x_j is a zero-one decision variable: 1 if site j is selected for the reserve system, and 0 if site j is not selected

(3)

will find a true minimum reserve set, but the iterative methods might find a larger-than-minimum set (Possingham et al. 1993; Underhill 1994). This advantage of IP over iterative methods was tempered by instances in which very large problems involving hundreds of species and thousands of sites took days to solve using IP, but were solved (at least approximately) in minutes by iterative methods (Pressey et al. 1996). This dichotomy in the methods – the guarantee of optimality vs faster solution times - prompted a debate over whether IP or iterative methods ought to be used. Recently, Rodrigues and Gaston (2002) and Onal (2003) have argued in favor of IP. They demonstrated that state-of-the-art IP solvers run on modern desktop computers consistently outperform iterative methods for at least some versions of the minimum reserve set problem, in terms of both computing time and nearness to optimality.

Once the minimum reserve set problem had been formulated as an IP, several other related problems were quickly articulated (ReVelle *et al.* 2002). The first was the "maximal covering problem" for reserves, in which the total area of the reserve is fixed, and the objective is to maximize the number of species that can be represented (Camm *et al.* 1996; Church *et al.* 1996). Mathematical programming models were also formulated for problems in which the presence or absence of a species in a site is not known with certainty, but can be expressed probabilistically. These models involve maximizing the expected number of species represented (Polasky *et al.* 2000) or maximizing the number of species represented with a particular level of reliability (Haight *et al.* 2000), given a fixed total reserve area.

Other variations of the minimum reserve set problem more accurately address the economic aspects of preserving land. In regions with varying per-unit land costs, minimizing total cost, or keeping costs within a budget, may make more sense than minimizing or limiting total area (Ando *et al.* 1998).

Spatial attributes and optimal reserve design

Efficient reserve systems such as the minimum reserve set are of interest because conservation resources are often severely limited. However, efficient reserves have a major drawback: they may be spatially unsuitable for the species and other features they are intended to protect. Depending on how the species and the other features are distributed in the landscape, optimal solutions to the minimum reserve set problem may be collections of scattered sites that lack spatial coherence (Figure 3a). The IP models and iterative methods for the minimum reserve set problem and its variations give no consideration to the spatial attributes that are thought to be important for reserves. Such attributes include reserve size and shape, the number of reserves created (as opposed to the number of sites selected), and the proximity and connectivity of



Figure 2. Joshua Tree National Park, California.

reserves to each other (Figure 1). These attributes were originally discussed by Diamond (1975) and others, and while the pros and cons of Diamond's particular guidelines have been vigorously debated (Margules *et al.* 1982), the attributes themselves are inherent aspects of any reserve design problem.

The spatial properties of a reserve system are important because they affect habitat quality and ecosystem processes, such as the ability of individuals to migrate and to colonize new areas, and ultimately influence whether or not species survive within the reserve. It is the long-term persistence of species and other components of biological diversity, not their representation in the short term, that is the real goal of reserves. Thus, although fragmented systems typical of the minimum reserve set problem may efficiently represent species at the outset, they may not promote the long-term survival of those same species. This is especially true when the size of individual sites is small relative to habitat needs. For large mammals, long-term persistence is unlikely in small, scattered reserves that, over time, become "islands" within an inhospitable matrix of urbanization and large-scale agriculture.

Short of preserving everything, there are no easy answers for designing spatially coherent reserve systems to protect large numbers of plant and animal

JC Williams et al.



coherence while still representing all species. All species can be represented in a reserve system of 20 widely scattered sites. This is the minimum number of sites needed to represent all species. (b) The model of Williams and ReVelle (1998) promotes the formation of a compact and connected reserve, with additional area required for the buffer zone. (c) The model of Nalle et al. (2002) promotes the formation of a clustered reserve system with many adjacent sites. (d) The model of Onal and Briers (2002) also promotes the formation of a tightly clustered reserve system, although site adjacencies may be less prevalent than in (c). (e) The model of McDonnell et al. (2002) promotes the formation of a relatively small number of compact reserves that may be more widely dispersed than in (c) or (d).

species. In the same way, there is no one-size-fits-all reserve design model. Any conservation plan must begin by identifying those components of biodiversity that are most valued, and those with the greatest need for protection. This in turn should suggest, on a caseby-case basis, the particular characteristics needed for spatial coherence, such as the extent to which individual sites ought to be aggregated into large, connected reserves. These spatial characteristics can then, in principle, be optimized by an appropriate reserve design model.

additional sites are needed to improve spatial

In the past several years, new reserve design models have been developed for this purpose. These models have as a predecessor the Conservation Options and Decisions Analysis method (CODA) (Bedward *et al.* 1992), an iterative procedure for improving the spatial coherence of the minimum reserve set. Four IP models that have followed CODA are summarized below. Each seeks to represent all species or other conservation features, but each also delineates a reserve system with improved shape and connectivity – one that is less fragmented than the minimum reserve set. These models exemplify a larger trend towards spatial optimization in reserve design (Williams *et al.* in press).

Model 1 (Williams and ReVelle 1998)

This model simultaneously identifies a reserve core that contains all species and delineates a buffer zone that surrounds the core. The objective is to minimize the cost of the entire reserve (core plus buffer sites). The core/buffer relationship also promotes connectivity and compactness in the reserve (Figure 3b).

Model 2 (Nalle et al. 2002)

This model generates a more highly connected and tightly clustered reserve system (Figure 3c) than would be expected of the minimum reserve set. Clustering is achieved by minimizing the sum of distances between all pairs of selected sites, and connectivity is promoted by maximizing the number of adjacent pairs of sites selected. The model was applied to a mountainous coastal region in California and Oregon.

Model 3 (Onal and Briers 2002)

This model also creates a tightly clustered reserve system using two objectives: minimizing the sum of distances between all pairs of selected sites, and minimizing the diameter of the reserve system. In an application, pond sites were identified in Oxfordshire, UK for the protection of invertebrate species. The resulting reserve systems (Figure 3d) tended to have a lower spatial dispersion than the minimum reserve set.

Model 4 (McDonnell et al. 2002)

This model identifies a reserve system (Figure 3e) that is more compact than the minimum reserve set. Compactness is achieved by minimizing the total perimeter length, which operates in tandem with an objective of minimizing total area. The model was applied in a case study to the Northern Territory, Australia.

The ability to achieve better spatial coherence in reserves through spatial modeling is an important step forward relative to methods of site selection in which spatial criteria are absent. However, designing reserves that both represent species and satisfy spatial criteria such as connectivity and compactness is, in fact, largely a surrogate for finding the particular configuration that best protects biological diversity in the long term. The extent to which spatial surrogates actually promote long-term species persistence is currently unknown, due to the long time scales involved and to the difficulty of performing controlled studies. Ideally, however, reserve design models would select sites based not on surrogates, but on the underlying reasons why spatial attributes are important.

Population models and optimal reserve design

Ecological regions are systems of sites or patches with interacting populations that "re-seed" one another over space and time. Decisions regarding the fate of one site will affect populations in other, nearby sites. For example, if site A has a high biodiversity value, but neighboring sites B and C are removed as sources, the value of A will be diminished. Multiplied over a large landscape with thousands of sites and hundreds of species, these interactions and interdependencies become enormously complex. Spatial surrogates may not adequately capture such complexities.

Characterizing complex dynamics is the purpose of spatially explicit population models (SEPMs), whose history in ecology may be summarized in terms of three principal directions. First are the diffusion approaches pioneered by Skellam's (1951) landmark paper, and later chronicled in Okubo (1980). A modern survey of diffusion models can be found in Okubo and Levin (2001). Second, the metapopulation approach so relevant to conservation biology began with the work of Levins (1969, 1970), and Levin (1974, 1976a, 1976b) provides a bridge between the metapopulation and diffusion approaches. Third, individual-based approaches (DeAngelis and Gross 1992; Pacala *et al.* 1996) have attained prominence in recent years due to the increased capability for high-speed computation (Levin *et al.* 1997). As a class of models, SEPMs have also become recognized as descriptive and predictive tools for land management and conservation (Dunning *et al.* 1995; Kareiva and Wennergren 1995). A current key challenge in reserve design modeling is to incorporate the dynamic and interdependent aspects of ecological regions, as captured by SEPMs, within an optimization framework.

Initial forays using this sort of modeling approach have already begun along at least two lines. The first involves embedding population dynamics within spatially and temporally explicit optimization models for site selection. Models of this type have been developed for maximizing the future population sizes of one or two target species, such as black-footed ferrets (Bevers et al. 1997), prairie dogs (Hof et al. 2002), and hawks and voles (Rothley 2002). A compelling aspect of these models is that site selection is driven not by spatial surrogates, but by the dynamic dispersal of animals among sites, so that the configuration of the reserve system results from population growth rates and patterns of inter-site migration. Although these models optimize for only one or two species, application to multiple species seems possible either by explicitly modeling the dynamics of many species or, perhaps more practicably, by modeling a small number of "umbrella" species.

The second approach is to submit preconfigured reserve designs to a SEPM, which would, through simulations, evaluate each design in terms of how it affects the populations of target species over time. One could ask which reserve design maximizes species richness at equilibrium or at a time t in the future. This type of approach has already been used to predict the persistence of a single species within a small number of alternative habitat configurations (Adler and Nuernberger 1994; Day and Possingham 1995). However, the real potential of this method lies in evaluating a large number of alternative reserve systems for many species. This problem has received little attention so far, although a recent paper by Chave et al. (2002), which modeled the impacts of alternative patterns of forest fragmentation on plant biodiversity, suggests a direction for this line of research.

The merging of SEPMs and optimization models for reserve site selection presents researchers with severe computational challenges. The first is problem size. Population models are typically applied to landscapes partitioned into 10000 or more sites or cells – often one or two orders of magnitude more. Reserve design IPs, in contrast, tend to reach a computational limit on desktop computers at 10000 or fewer sites due to a combinatorial "explosion" (*n* sites implies 2^n possible yes/no outcomes). Thus, finding exact optimal solutions for landscape scales typical of SEPM simulations may be virtually impossible. Iterative methods in the form of sophisticated "meta-

heuristics" (eg Osman and Kelly 1996) offer the most promise for finding at least approximate solutions to such large problems.

A second challenge is non-linearity. Temporal relationships between and within populations may be expressible only through non-linear mathematics. Unfortunately, non-linearities preclude the use of linear programmingbased methods typically used to solve IPs. Iterative methods, for which non-linearities pose much less of a barrier, may also be the best way to tackle non-linear problems.

The role of optimization models in reserve design

Margules and Pressey (2000) and Pressey and Cowling (2001) have included reserve selection and design models within a multi-stage process for systematic conservation planning. While these authors identify an appropriate role for optimization models (their term is "algorithms"), this role deserves further articulation.

Optimization models are primarily tools for decision support. Their purpose is not to prescribe a course of action, but rather to provide guidance, information, and insight to planning and decision making. To this end, optimization models as analytical tools offer several benefits to reserve planning in addition to finding an "optimal solution". First, the model provides a concise, explicit formulation of the problem. The modeled problem can typically be stated in terms of several algebraic equalities or inequalities. The minimum reserve set IP, for example, has just three lines of mathematics (Panel 1). The model may not perfectly mirror reality, but it is transparent and therefore open to criticism and possible improvement. Although the model's mathematics may be inaccessible to non-specialists, its purpose and function can usually be explained in plain language – and it is the responsibility of the modeler to do this.

Second, optimization models are highly general, in that they can be transferred from one setting to another and from one dataset to another, as indicated above by the many regional case studies for the minimum reserve set model. In addition, results are replicable; different users employing the same model and the same data will obtain the same results.

However, results that take the form of a single optimal solution are unlikely to be satisfactory in conservation planning. Flexibility is needed – being able to compare at least several reasonable alternatives. This is the third benefit of optimization models: the ability to generate a variety of alternate optimal or near-optimal solutions in addition to the optimum. Furthermore, by generating alternatives that address competing objectives (eg maximizing species richness versus minimizing cost), appropriate trade-offs between environmental and socioeconomic concerns can be identified.

The generation and evaluation of alternative reserve systems can usually be done in real time on today's computers. Similarly, geographic information systems enable the rapid visualization of alternatives. These features rapid generation, evaluation, and visualization – describe a broad class of computer tools known collectively as decision and planning support systems (DPSSs). A large number of DPSSs have been developed in recent years, and are used by government agencies and other organizations to help resolve complex environmental planning problems. Not all DPSSs employ optimization methods, although some do. One DPSS that has been developed for reserve design is SITES (Andelman et al. 1999), a software package which has a GIS interface and uses a sophisticated iterative method (greedy adding and "simulated annealing") to select an approximate optimal set of reserve sites. The site selection model inside SITES is similar to the model of McDonnell et al. (2002) described above, which seeks to minimize the total area of the reserve system and minimize total perimeter length.

In SITES, like other DPSSs, the user interacts with a "friendly" interface, while the mechanics of the model occur behind the scenes. As a result, DPSSs are often viewed as "black boxes" that accept user input in at one end and, via some hidden algorithm, produce optimized solutions - in our case reserve designs - out at the other end. While it is useful to have decision and planning support tools that are both sophisticated and convenient for non-specialists, it is also important to make the black boxes more transparent. The main point here is that reserve design models and reserve design DPSSs like SITES are two different things. Two DPSSs may purport to do the same thing, but if their underlying methods for site selection are different, the results they get will also be different. For example, two DPSSs may each claim to produce highly connected reserve systems, but one might generate a system that looks like Figure 3c, while the other produces a system like Figure 3e. It is therefore important for the user to be aware of differences in the underlying models.

Optimization models, then, may either be used as standalone tools or embedded within a DPSS. But either way, to what extent do environmental planners and land managers actually use such models to design reserves? Prendergast et al. (1999) explored this question and found that, by the late 1990s, reserve selection and design models were not yet in widespread use. This was evidently due to several factors: lags in technology transfer; a perception that the models require exceptionally high quality data; and differences in expertise and worldviews between practitioners and modelers (Prendergast et al. 1999; Pressey and Cowling 2001).. However, recent anecdotal evidence suggests that site selection models are becoming more accessible. At an October 2003 reserve design conference attended by one of the authors (Williams), several independent groups of practitioners each reported on the use of SITES to help formulate reserve plans.

Our prognosis is that models for reserve selection and design will be much more widely used in the future. This is based on two foreseeable trends. First, the growing tension between an expanding human population and the need to conserve and protect biological resources will require highly targeted and optimized approaches to conservation decisions. As new conservation problems are recognized worldwide, reserve design models will be used more frequently. Second, the number of people working on and with reserve design models has grown considerably in recent years, as evidenced by the rapid increase in the number of publications on this topic. Reserve design modeling has become a major focus of collaboration among researchers in conservation biology, ecology, operations research, and other disciplines. Having now reached a "critical mass", reserve design models are becoming increasingly visible to practitioners. These models are now being taught in undergraduate and graduate courses, suggesting that the next generation of conservation professionals will have them as an integral part of their toolkits.

Acknowledgements

We thank Sharon Kingsland for helpful comments on an earlier draft of this article. Our research was supported by a grant from the David and Lucille Packard Foundation's Interdisciplinary Science Program.

References

- Adler FR and Nuernberger B. 1994. Persistence in patchy irregular landscapes. *Theor Popul Biol* **45**: 41–75.
- Andelman S, Ball I, Davis F, and Stoms D. 1999. SITES 1.0: an analytical toolbox for designing ecoregional conservation portfolios . www.biogeog.ucsb.edu. Viewed XX.
- Ando A, Camm J, Polasky S, and Solow A. 1998. Species distributions, land values, and efficient conservation. Science 279: 2126–28.
- Bedward M, Pressey RL, and Nicholls AO. 1991. Scores and score classes for evaluation criteria: a comparison based on the cost of reserving all natural features. *Biol Conserv* **56**: 281–94.
- Bedward M, Pressey RL, and Keith DA. 1992. A new approach for selecting fully representative reserve networks: addressing efficiency, reserve design and land suitability with an iterative analysis. *Biol Conserv* 62: 115–25.
- Bevers M, Hof J, Uresk DW, and Schenbeck GL. 1997. Spatial optimization of prairie dog colonies for black-footed ferret recovery. *Oper Res* **45**: 495–507.
- Camm JD, Polasky S, Solow A, and Csuti B. 1996. A note on optimal algorithms for reserve site selection. *Biol Conserv* 78: 353–55.
- Chave J, Wiegand K, and Levin S. 2002. Spatial and biological aspects of reserve design. *Environ Model Assess* 7: 115–22.
- Church RL, Stoms DM, and Davis FW. 1996. Reserve selection as a maximal covering location problem. *Biol Conserv* **76**: 105–12.
- Cocks KD and Baird IA. 1989. Using mathematical programming to address the multiple reserve selection problem: an example from the Eyre Peninsula, South Australia. *Biol Conserv* **49**: 113–30.
- Csuti B, Polasky S, Williams PH, et al. 1997. A comparison of reserve selection algorithms using data on terrestrial vertebrates in Oregon. Biol Conserv 80: 83–97.
- Day JR and Possingham HP. 1995. A stochastic metapopulation model with variability in patch size and position. *Theor Popul Biol* 48: 333–60.

DeAngelis DS and Gross LJ. 1992. Individual-based models and

approaches in ecology: populations, communities and ecosystems. New York: Chapman & Hall.

- Diamond JM. 1975. The island dilemma: lessons of modern biogeographic studies for the design of nature reserves. *Biol Conserv* 7: 129–46.
- Dunning JB, Stewart DJ, Danielson BJ, *et al.* 1995. Spatially explicit population models: current forms and future uses. *Ecol Appl* **5**: 3–11.
- Finkel E. 1998. Software helps Australia manage forest debate. Science 281: 1789–91.
- Haight R, ReVelle C, and Snyder S. 2000. An integer optimization approach to a probabilistic reserve site selection problem. *Oper Res* **48**: 697–708.
- Heywood VH. 1994. The measurement of biodiversity and the politics of implementation. In: Forey PL, Humphries CJ, and Vane-Wright RI (Eds). Systematics and conservation evaluation. New York: Oxford University Press. p 15–22.
- Hof J, Bevers M, Uresk DW, and Schenbeck GL. 2002. Optimizing habitat location for black-tailed prairie dogs in southwestern South Dakota. *Ecol Model* **147**: 11–21.
- Kareiva P and Wennergren U. 1995. Connecting landscape patterns to ecosystem and population processes. *Nature* **373**: 299–302.
- Kingsland SE. 2002. Creating a science of nature reserve design: perspectives from history. *Environ Model Assess* 7: 61–69.
- Kirkpatrick JB. 1983. An iterative method for establishing priorities for the selection of nature reserves: an example from Tasmania. *Biol Conserv* 25: 127–34.
- Levin SA. 1974. Dispersion and population interactions. *Am Nat* 108: 207–28.
- Levin SA. 1976a. Population dynamic models in heterogeneous environments. Ann Rev Ecol Syst 7: 287–311.
- Levin SA. 1976b. Spatial patterning and the structure of ecological communities. In: Levin SA (Ed). Lectures on mathematics in the life sciences, Vol 8: some mathematical questions in biology VII. Providence, RI: American Mathematical Society. p 1–36.
- Levin SA, Grenfell B, Hastings A, and Perelson AS. 1997. Mathematical and computational challenges in population biology and ecosystems science. *Science* **275**: 334–42.
- Levins R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull Entomol Soc Amer* **15**: 237–40.
- Levins R. 1970. Extinction. In: Gesternhaber M (Ed). Some mathematical problems in biology. Providence, RI: American Mathematical Society. p 77–107.
- Margules CR and Pressey RL. 2000. Systematic conservation planning. *Nature* **405**: 243–53.
- Margules CR, Higgs AJ, and Rafe RW. 1982. Modern biogeographic theory: are there any lessons for nature reserve design? *Biol Conserv* 24: 115–28.
- Margules CR, Nicholls AO, and Pressey RL. 1988. Selecting networks of reserves to maximize biological diversity. *Biol Conserv* 43: 63–76.
- McDonnell M, Possingham H, Ball I, and Cousins E. 2002. Mathematical methods for spatially cohesive reserve design. *Environ Model Assess* 7: 107–14.
- Nalle DJ, Arthur JL, and Sessions J. 2002. Designing compact and contiguous reserve networks with a hybrid heuristic algorithm. *Forest Sci* **48**: 59–68.
- Okubo A. 1980. Diffusion and ecological problems: mathematical models. Heidelberg, Germany: Springer-Verlag.
- Okubo A and Levin SA. 2001. Diffusion and ecological problems: modern perspectives, 2nd ed. New York, NY: Springer.
- Onal H. 2003. First-best, second-best, and heuristic solutions in conservation reserve site selection. *Biol Conserv* 115: 55–62.
- Onal H and Briers RA. 2002. Incorporating spatial criteria in optimum reserve network selection. *Proc Roy Soc Lond B Bio* **269**: 2437–41.
- Osman IH and Kelly JP. 1996. Meta-heuristics: theory and applica-

tions. Boston, MA: Kluwer Academic Publishers.

- Pacala SW, Canham CD, Saponara J, *et al.* 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecol Monogr* **66**: 1–43.
- Polasky S, Camm J, Solow A, *et al.* 2000. Choosing reserve networks with incomplete species information. *Biol Conserv* 94: 1–10.
- Possingham H, Day J, Goldfinch M, and Salzborn F. 1993. The mathematics of designing a network of protected areas for conservation. In: Sutton D, Cousins E, and Pierce C (Eds). Decision sciences, tools for today. Proceedings of the 12th Australian Operations Research Conference. Adelaide, Australia: Australian Society for Operations Research. p 536–45.
- Prendergast JR, Quinn RM, and Lawton JH. 1999. The gap between theory and practice in selecting nature reserves. *Cons Biol* 13: 484–92.
- Pressey RL. 2002. The first reserve selection algorithm a retrospective on Jamie Kirkpatrick's 1983 paper. *Prog Phys Geogr* 26: 434–41.
- Pressey RL and Cowling RM. 2001. Reserve selection algorithms and the real world. Cons Biol 15: 275–77.
- Pressey RL, Possingham HP, and Margules CR. 1996. Optimality in reserve selection algorithms: when does it matter and how much? *Biol Conserv* **76**: 259–67.
- Pressey RL, Possingham HP, and Day JR. 1997. Effectiveness of alternative heuristic algorithms for identifying indicative minimum

- requirements for conservation reserves. *Biol Conserv* 80: 207–19. Purdie RW, Blick R, and Bolton MP. 1986. Selection of a conservation reserve network in the Mulga biogeographic region of
- southwestern Queensland, Australia. *Biol Conserv* **38**: 369–84. ReVelle CS, Williams JC, and Boland JJ. 2002. Counterpart mod-
- els in facility location science and reserve selection science. Environ Model Assess 7: 71–80. Rodrigues ASL and Gaston KI. 2002. Optimization in reserve
- selection procedures why not? *Biol Conserv* **107**: 123–29.
- Rothley KD. 2002. Dynamically-based criteria for the identification of optimal bioreserve networks. *Environ Model Assess* 7: 123–28.
- Skellam JG. 1951. Random dispersal in theoretical populations. Biometrika 38: 196–218.
- Smith PGR and Theberge JB. 1986. A review of criteria for evaluating natural areas. *Environ Manage* **10**: 715–34.
- Underhill L. 1994. Optimal and suboptimal reserve selection algorithms. *Biol Conserv* **35**: 85–87.
- Vane-Wright RI, Humphries CJ, and Williams PH. 1991. What to protect? Systematics and the agony of choice. *Biol Conserv* 55: 235–54.
- Williams JC and ReVelle CS. 1998. Reserve assemblage of critical areas: a zero-one programming approach. Eur J Oper Res 104: 497–509.
- Williams JC, ReVelle CS, and Levin SA. Spatial attributes and reserve design models: a review. *Environ Model Assess*. In press.

© The Ecological Society of America