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Short communcation

# Optimisation in reserve selection procedures—why not?

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**Abstract**

Linear programming techniques provide an appropriate tool for solving reserve selection problems. Although this has long been known, most published analyses persist in the use of intuitive heuristics, which cannot guarantee the optimality of the solutions found. Here, we dispute two of the most common justifications for the use of intuitive heuristics, namely that optimisation techniques are too slow and cannot solve the most realistic selection problems. By presenting an overview of processing times obtained when solving a diversity of reserve selection problems, we demonstrate that most of those published could almost certainly be solved very quickly by standard optimisation software using current widely available computing technology. Even for those problems that take longer to solve, solutions with low levels of sub-optimality can be obtained quite quickly, presenting a better alternative to intuitive heuristics. 

*Keywords:* Complementarity; Conservation priorities; Linear programming; Heuristics

> During World War II, British military leaders asked scientists to analyze several military problems: the development of radar and the management of convoy, bombing, antisubmarine and mining operations. The application of mathematics and the scientific method to military operations was called operations research. Today, the term operations research (or, often, management science) means a scientific approach to decision making, which seeks to determine how best to design and operate a system, usually under conditions requiring the allocation of scarce resources (Winston, 1994, p. 1)

Methods for the selection of priority areas for conservation based on the complementarity principle (Vane-Wright et al., 1991) have been receiving extensive interest in conservation literature (e.g. Pressey et al., 1993; Dobson et al., 1997; Ando et al., 1998; Howard et al., 1998; Margules and Pressey, 2000). These methods have been proposed in response to the acknowledgement that resources available for conservation purposes are scarce and should therefore be employed in efficient ways that maximise the diversity of biological features benefited (Pressey and Nicholls, 1989; Pressey et al., 1993; Scott et al., 1993).

The first papers on this subject (e.g. Kirkpatrick, 1983; Margules et al., 1988; Pressey and Nicholls, 1989; Bedward et al., 1992; Nicholls and Margules, 1993; Pressey et al., 1993) stressed the efficiency of these methods in relation to previously more popular scoring procedures. Efficiency (sensu Pressey and Nicholls, 1989) has been defined as being inversely related to the cost needed to acquire a reserve network which achieves a given conservation target (such as representing all species at least a given number of times), and has been widely considered to be an important attribute of a good reserve selection procedure (e.g. Bedward et al., 1992; Rebelo and Siegfried, 1992; Saetersdal et al., 1993; Lombard et al., 1995; Kershaw et al., 1994; Castro Parga et al., 1996; Willis et al., 1996; Ando et al., 1998; Freitag et al., 1998; Hacker et al., 1998; Nantel et al., 1998).

Those first papers also presented the basic heuristic algorithms which (in their original or modified form) subsequently became popular in the conservation literature. However, it was observed early on that reserve selection problems can be solved optimally (i.e. with

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maximum efficiency) by application of a standard operations research technique, namely integer linear programming (e.g. Cocks and Baird, 1989; Underhill, 1994; Church et al., 1996). The use of intuitive heuristics that cannot guarantee the optimality of the solutions found has therefore been criticised (Underhill, 1994). In response to these criticisms, two subsequent papers (Pressey et al., 1996, 1997) defended the importance of heuristics in 'real-world conservation planning', with three main arguments:

1. That 'good' heuristics provide results which are only slightly sub-optimal;
2. That optimisation methods may not be able to provide solutions to more realistic problems. Pressey et al. (1996, 1997) reported being unable to obtain an optimal solution for the problem of finding the minimum set of sites (or the minimum area) representing at least 5% of the area of each of 248 land types (distributed across 1885 pastoral holdings): using standard optimisation packages, the problem ran for weeks without finding solutions.
3. That optimisation methods may be too slow and therefore inadequate for interactive practical conservation planning (where managers and

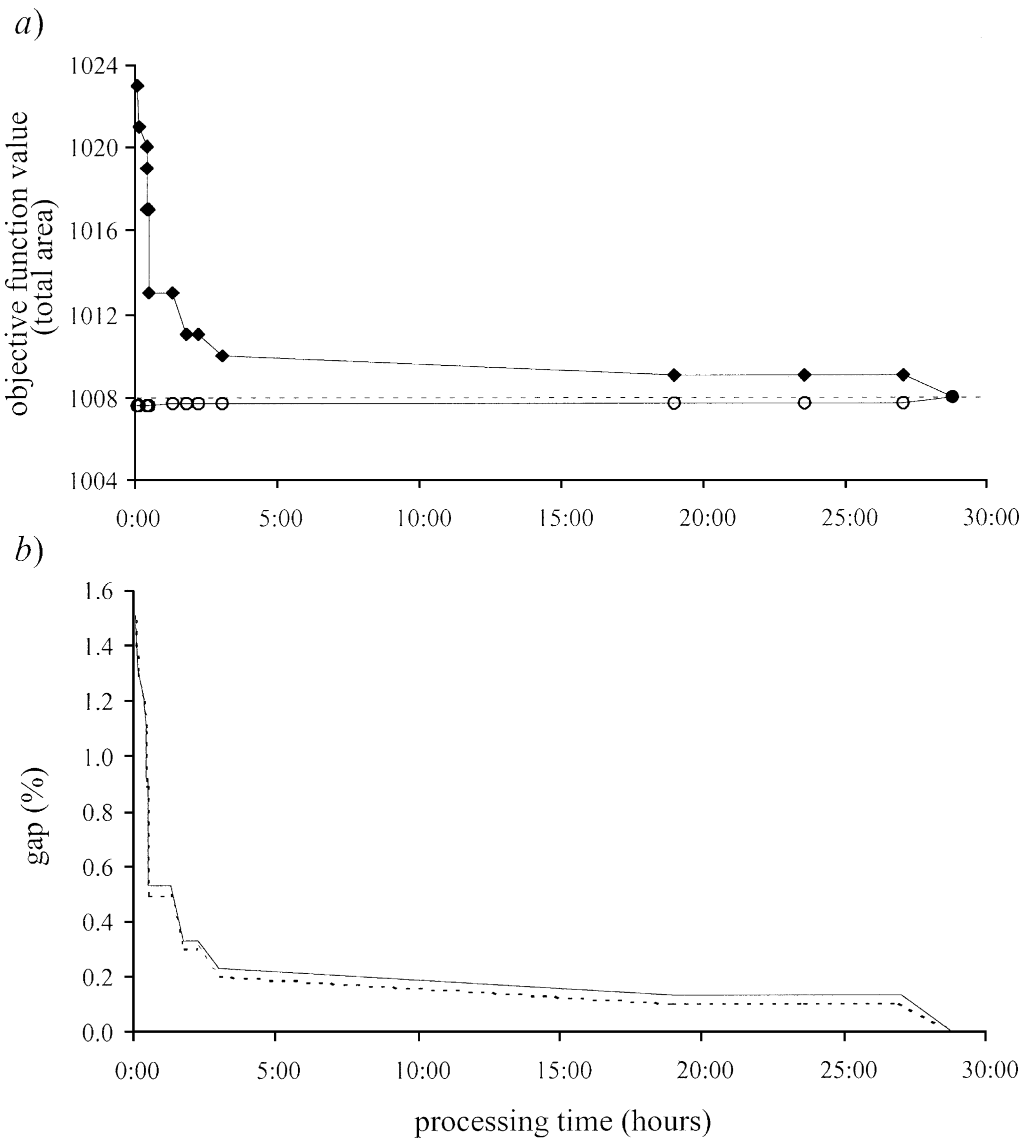


Fig. 1. Values provided by C-Plex (ILOG, 1999) during processing of problem 4 in Table 2. (a) Trend in the values of the objective function (total area) for the best solution found (dark diamonds) and for the best lower bound obtained (open circles). The horizontal broken line indicates the position of the true optimal solution (only known at the end of processing, when the best integer and the best lower bound coincide). (b) Trend in the values of the known gap (solid line) and the true gap (broken line). The known gap is given by the difference between the values of the best solution and the best lower bound in relation to the value of the best solution, and this is an upper bound of the true gap (calculated in relation to the true optimal instead of the best known solution), providing an over-estimate of the degree of sub-optimality of each solution found.

Table 1
Summary of examples of published studies which used complementarity-based methods for the selection of networks of priority areas for conservation

| Reference | Data | No. features | No. sites | Problem |
|---|---|---|---|---|
| 1. Rebelo and Siegfried, 1992 | Plants, South Africa | 332 | 550 | Find a set with minimum number of sites representing all species at least 1×, 2×, 3×, 4×, 5× and 10× |
| 2. Saetersdal et al., 1993[a] | Plants and birds, Norway | 321, 47 | 60 | Find a set with minimum number of sites representing all species at least once |
| 3. Kershaw et al., 1994 | Antelopes, Africa | 99 | 249 | Find a set with minimum number of sites representing all species at least once |
| 4. Margules et al., 1994 | Plants, UK | 50 | 77 | Find a set with minimum number of sites representing all species at least 1×, 2×, 3×, 4×, and 5× |
| 5. Lombard et al., 1995 | Snakes, South Africa | 122 | ~1900 | Find a set with minimum number of sites representing all species at least 1×, 2×, 3×, 4×, and 5× |
| 6. Turpie, 1995 | Birds, South Africa | 88 | 42 | Find a set with minimum number of sites representing all species at least once |
| 7. Castro Parga et al., 1996 | Plants, Iberian Peninsula | 801, 2133 | 5184, 259 | Find a set with minimum number of sites representing all species at least once |
| 8. Church et al., 1996[a] | Vertebrates, USA | 333 | 280 | Find a set which maximises the number of species that can be represented within a given number of sites |
| 9. Williams et al., 1996a | Plants, Neotropics | 729 | 1751 | Find a set which maximises the number of species that can be represented within a given number of sites |
| 10. Williams et al., 1996b | Birds, UK | 218 | 2827 | Find a set with minimum number of sites representing all species at least once |
| 11. Willis et al., 1996[a] | Plants, South Africa | 110 | 53 | Find a set with minimum number of sites representing all species at least 1×, 2×, 3×, 4×, and 5× |
| 12. Dobson et al., 1997 | Endangered species, USA | 924, 503, 107, 84, 72, 58, 57, 43 | 2858 | Find a set with minimum number of sites representing all species at least once |
| 13. Lombard et al., 1997 | Vegetation types and plant species, South Africa | 97 species + 11 veg. types | 193 | Find a set with minimum number of sites representing all plant species and a target percentage of area of each vegetation type |
| 14. Muriuki et al., 1997 | Birds, Kenya | 970 | 210 | Find a set with minimum number of sites representing all species at least once |
| 15. Pressey et al., 1997[a] | Land systems, Australia | 248 | 1885 | Find a set with minimum number of sites representing all land systems at least once |
| 16. Pressey et al., 1997[a] | Land systems, Australia | 248 | 1885 | Find a set with minimum area which represents all land systems at least once |
| 17. Pressey et al., 1997 | Land systems, Australia | 248 | 1885 | Find a set with minimum number of sites which represents each land system by at least 5% of its regional extent |
| 18. Pressey et al., 1997 | Land systems, Australia | 248 | 1885 | Find set with minimum area which represents each land system by at least 5% of its regional extent |
| 19. Stokland, 1997 | Birds and insects, Norway | 32, 309 | 40, 17 | Find a set which maximises the number of species that can be represented within a given number of sites |
| 20. Ando et al., 1998[a] | Endangered taxa, USA | 911 | 2851 | Find a set which maximises the number of taxa that can be represented in a given number of sites or in at set with a given acquisition cost |
| 21. Fjeldså and Rahbek, 1998 | Birds, South America | ~1700 | 913, 118, 226, 456, 540 | Find a set with minimum number of sites representing all species at least 3× |
| 22. Freitag and van Jaarsveld, 1998 | Mammals, South Africa | 192 | 474 | Find a set with minimum number of sites representing all species at least once |
| 23. Hacker et al., 1998 | Primates, Africa and Madagascar | 205 | 1825 | Find a set with minimum number of sites representing all species at least once |

(*Table continued on next page*)

Table 1 (*continued*)

| Reference | Data | No. features | No. sites | Problem |
|---|---|---|---|---|
| 24. Howard et al., 1998 | Plants and animals, Uganda | 2452 (and subsets of variable size) | 50 | Find a set which maximises the number of species that can be represented within a given number of sites |
| 25. Nantel et al., 1998 | Plants, Canada | 244 | 456 | Find a set with minimum number of sites representing all species at least once |
| 26. Pressey and Logan, 1998[a] | Land systems, Australia | 248 | 1885, 5278, 247 | Find a set with minimum area such that each land system is represented in a given percentage of area target |
| 27. Lombard et al., 1999 | Plants, South Africa | 851, 771 | 197, 188 | Find a set with minimum number of sites representing all species at least once |
| 28. Virolainen et al., 1999 | Plants, Finland | 32 | 25 | Find a set with minimum number of sites representing all species at least once |
| 29. Araújo and Williams, 2000 | Trees, Europe | 174 | 4419 | Find a set which maximises the number of species that can be represented within a given number of sites |
| 30. Reyers et al., 2000 | Plants and animals, South Africa | 1588, 574, 328, 214, 427 | 215 | Find a set with minimum number of sites representing all species at least once |
| 31. Williams et al., 2000 | Plants and vertebrates, Europe | 2435 | 3143 | Find a set which maximises the number of species that can be represented within a given number of sites |
| 32. Polasky et al., 2001 | Birds, USA | 167 | 1223 | Find a set which maximises the number of genera that can be represented within a given number of sites |

[a] Refers to studies that used optimisation procedures (sometimes alongside heuristines); others only used heuristic approaches.

> politicians may be waiting to see the results). Pressey et al. (1996, 1997) reported long processing times (days or, in a more recent version of the software, 10 h) for the problem of finding the minimum number of sites needed to represent each of 248 land types on 1885 pastoral holdings.

The large majority of subsequent papers about complementarity-based methods for reserve selection have persisted in the use of intuitive heuristics, often justifying their application by quoting the three arguments presented by Pressey et al. (1996, 1997): that the results are expected to be similar (e.g. Howard et al., 1998; Williams et al., 1996a, b; Williams, 1998); that optimisation methods are unable to solve some more realistic problems (e.g. Lombard et al., 1997; Pressey and Logan, 1998; Williams, 1998; Polasky et al., 2001); and/or that optimal solutions would take too long to obtain (e.g. Erasmus et al., 1999; Lombard et al., 1997; Williams et al., 1996a, b; Williams, 1998).

In a previous paper (Rodrigues et al., 2000), we have argued that intuitive heuristics cannot offer guarantees of providing good solutions to reserve selection problems. Here, we focus on rebutting the other two arguments, concerning the tractability and speed of problem resolution using optimisation methods. We argue that, given the capability of currently existing software and computers, these are no longer a real obstacle to the use of optimisation procedures for most of the reserve selection problems being published in the literature.

Table 1 presents a list of published studies which used complementarity-based methods for the selection of sets of priority sites. This provides an overview of the size (number of biodiversity features, such as species, and number of selection units) and type of problems most frequently addressed in the literature. Table 2 presents the processing times we have recorded for reserve selection problems of sizes and types that embrace this variation. All problems were tractable and could be solved exactly using the C-PLEX software (ILOG, 1999) on a Pentium II processor with 128.0 MB RAM. Most problems, even some of the larger ones, took just a few seconds to solve. It is likely that this would also be the case with the majority of problems addressed in the literature (Table 1). Indeed, Ando et al. (1998), working with a large data set (see problem 20 in Table 1) did not report any difficulty in obtaining optimal solutions and Church et al. (1996), working with a medium-sized problem (number 8 in Table 1), reported an average processing time of 2.9 s (9 s maximum).

Two of the largest problems we explored did take significant time to solve (problems 3 and 4 in Table 2, which took 26 and 29 h, respectively). However, in both cases, the optimisation software found relatively good solutions to the problems after just a few minutes. During processing, C-PLEX continuously calculates lower bounds to the solutions to minimisation problems (Fig. 1a), i.e. values that are known to be below or equal to the true, unknown, optimal value (in maximisation problems, upper bounds are calculated). Using these

Table 2
Processing times needed to solve a diversity of linear integer problems using the C-PLEX software (ILOG, 1999) on a Pentium II processor with 128 MB RAM

| References | Data | No. species | No. sites | Problem | Processing time |
|---|---|---|---|---|---|
| 1. Harrison et al., 1997 | Birds, Southern Africa | 852 | 3885 | Find a set with minimum number of sites representing each species at least once | 4.71 s |
| 2. Harrison et al., 1997 | Birds, Southern Africa | 852 | 3885 | Find a set with minimum number of sites representing each species at least five times | 1.58 s |
| 3. Harrison et al., 1997 | Birds, Southern Africa | 852 | 3885 | Find a set which maximises the number of species that can be represented within 10 sites | 92,911 s (∼26 h) |
| 4. Harrison et al., 1997 | Birds, Southern Africa | 852 | 3885 | Find a set with minimum area such that each species is represented within at least 5% of its range (variation in the size of the selection units was simulated by attributing to each cell an area obtained as a random integer number between 1 and 10) | 103,404 s (∼29 h) |
| 5. Harrison et al., 1997; Gaston et al., 2001 | Birds, South Africa and Lesotho | 651 | 1858 | Find a set with minimum number of sites representing each species at least once | 1.79 s |
| 6. Harrison et al., 1997 | Birds, South Africa and Lesotho | 651 | 1858 | Find a set which maximises the number of species that can be represented within 20 sites | 18.08 s |
| 7. Balmford et al., 2000; Mace and Balmford, 2000 | Mammals, World | 4228 | 111 | Find a set with minimum number of sites representing each species at least once | 0.11 s |
| 8. Balmford et al., 2000; Mace and Balmford, 2000 | Mammals, World | 4228 | 111 | Find a set which maximises the number of species that can be represented at a cost of 50% of the minimum needed to represent all species | 90.13 s |
| 9. Murray et al., 1998 | Birds, Scotland | 138 | 1756 | Find a set with minimum number of sites representing each species at least once | 1.80 s |
| 10. Murray et al., 1998 | Birds, Scotland | 138 | 1756 | Find a set which maximises the number of species that can be represented within 4 sites | 3.34 s |
| 11. Sawford, 1987 | Butterflies, UK | 45 | 496 | Find a set with minimum number of sites representing each species at least once | 0.06 s |
| 12. Sawford, 1987 | Butterflies, UK | 45 | 496 | Find a set which maximises the number of species that can be represented within 4 sites | 151.25 s |

lower bounds, C-PLEX obtains an estimate of the sub-optimality of the best solution found at any given time; this is defined as the gap, which is given by the difference between the lower bound and the best solution found in relation to the value of the best solution (Fig. 1b). Even when the total processing times (needed to find the true optimal solution) are very long, optimisation software may find good solutions quite fast. In problem 3, a solution reported to have a gap of $\leqslant$7.42% was found after just 7 min, while after 21 min the level of sub-optimality was known to be $\leqslant$4.90%. Twenty-five out of the 26 h of processing time were consumed in improving a solution with a known sub-optimality $\leqslant$4%. In problem 4, the gap after 6 min processing was $\leqslant$1.50%, which had dropped to $\leqslant$0.92% after 26 min (Fig. 1). Twenty-seven out of 29 h of processing time were spent finding solutions with a gap $\leqslant$0.33%.

These levels of sub-optimality are better than the average figures reported for intuitive heuristics (Table 1 in Rodrigues et al., 2000). Therefore, optimisation software may also be used to obtain good solutions (even if not optimal) for more complex problems in a reasonable processing time. The main advantage of the solutions obtained in this way is that an estimate of the level of sub-optimality is known, and there is always an option to extend the processing time in order to improve the result. Solutions obtained by intuitive heuristics have a substantial risk of being grossly sub-optimal, and having previously obtained a good result with a given heuristic cannot guarantee its efficiency for all data sets (Rodrigues et al., 2000).

Problem 4 differs from the others in Table 2 by having non-integer values in the restriction inequalities (corresponding to the values of the percentage of the range of each species located within each site). The number of decimal places chosen makes a significant difference to processing time. The results referred to earlier and in Table 2 (∼29 h processing time) were obtained for four decimal places (i.e. the minimum unit was 0.0001%). Setting the number of decimal places to eight (i.e. up to 0.00000001%) the problem takes about 7 days to solve—but a solution with $\leqslant$3.13% gap is found after 1 h, and after 20 h the solution has $\leqslant$0.16% gap. Nevertheless, this difference in processing time (as well as the evolution of computers and software) may also help to explain why, for example, Pressey et al. (1997) failed to find an optimal solution to an equivalent problem (problem 18 in Table 1) despite working with a smaller data set.

There are certainly situations where reserve selection problems cannot be solved by the straightforward application of linear programming. This is, of course, particularly true of non-linear problems (e.g. Polasky et al., 2000; Williams and Araújo, 2000). It is also possible that extremely large problems may exceed the computational capacity of currently existing software and computers (although these are continuously improving). But to date we have not encountered such problems, and for the large majority of the problems found in the literature (Table 1) there is really no good reason why optimisation approaches cannot be used.

On the other hand, there are several good reasons why optimisation should be used. Not only are the solutions found expected to be more efficient, there is also great flexibility in the type of data and concerns that can be integrated in linear integer problems, while retaining the accountability of the decision process (Rodrigues et al., 2000).

The use of optimisation techniques implemented by software such as C-PLEX does not require expert programming skills. Actually, it requires less programming than needed to solve most 'intuitive' heuristics when applied to moderate-sized data sets, because the solving procedure itself is comprised of existing routines (such as branch-and-bound) already incorporated in the software. The fundamental step is being able to convert the selection problem in hand into a linear programming one, which can be done for most selection problems with only basic knowledge of operations research theory (e.g. Winston, 1994). Rodrigues et al. (2000) explain in detail how problems such as the ones in Table 1 can be represented as integer linear problems.

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## References

Ando, A., Camm, J., Polasky, S., Solow, A., 1998. Species distributions, land values, and efficient conservation. Science 279, 2126–2128.

Araújo, M.B., Williams, P.H., 2000. Selecting areas for species persistence using occurrence data. Biological Conservation 96, 331–345.

Balmford, A., Gaston, K.J., Rodrigues, A.S.L., James, A., 2000. Integrating costs of conservation into international priority setting. Conservation Biology 14, 597–605.

Bedward, M., Pressey, R.L., Keith, D.A., 1992. A new approach for selecting fully representative reserve networks: addressing efficiency, reserve designs and land suitability with an iterative analysis. Biological Conservation 62, 115–125.

Castro Parga, I., Moreno-Saiz, J.C., Humphries, C.J., Williams, P.H., 1996. Strengthening the Natural and National Park system of Iberia to conserve vascular plants. Botanical Journal of the Linnean Society 121, 189–206.

Church, R.L., Stoms, D.M., Davis, F.W., 1996. Reserve selection as a maximal covering location problem. Biological Conservation 76, 105–112.

Cocks, K.D., Baird, I.A., 1989. Using mathematical programming to address the multiple reserve selection problem: an example from the Eyre Peninsula, South Australia. Biological Conservation 49, 113–130.

Dobson, A.P., Rodriguez, J.P., Roberts, W.M., Wilcove, D.S., 1997. Geographic distribution of endangered species in the United States. Science 275, 550–553.

Erasmus, B.F.N., Freitag, S., Gaston, K.J., Erasmus, B.H., van Jaarsveld, A.S., 1999. Scale and conservation in the real world. Proceedings of the Royal Society of London B 266, 315–319.

Fjeldså, J., Rahbek, C., 1998. Continent-wide conservation priorities and diversification processes. In: Mace, G.M., Balmford, A., Ginsberg, J.R. (Eds.), Conservation in a Changing World. Cambridge University Press, Cambridge, pp. 139–160.

Freitag, S., Nicholls, A.O., van Jaarsveld, A.S., 1998. Dealing with established reserve networks and incomplete distribution data sets in conservation planning. South African Journal of Science 94, 79–86.

Freitag, S., van Jaarsveld, A.S., 1998. Sensitivity of selection procedures for priority conservation areas to survey extent, survey intensity and taxonomic knowledge. Proceedings of the Royal Society of London B 265, 1475–1482.

Gaston, K.J., Rodrigues, A.S.L., van Rensburg, B.J., Koleff, P., Chown, S.L., 2001. Complementary representation and ecological transition. Ecology Letters 4–10.

Hacker, J.E., Cowlishaw, G., Williams, P.H., 1998. Patterns of African primate diversity and their evaluation for the selection of conservation areas. Biological Conservation 84, 251–262.

Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V., Brown, C.J. (Eds.), 1997. The atlas of southern African birds. BirdLife South Africa, Johannesburg.

Howard, P.C., Viskanic, P., Davenport, T.R.B., Kigenyi, F.W., Baltzer, M., Dickinson, C.J., Lwanga, J.S., Matthews, R.A., Balmford, A., 1998. Complementarity and the use of indicator groups for reserve selection in Uganda. Nature 394, 472–475.

ILOG, 1999. CPLEX 6.5. ILOG. Gentilly, France.

Kershaw, M., Williams, P.H., Mace, G.M., 1994. Conservation of afrotropical antelopes: consequences and efficiency of using different site selection methods and diversity criteria. Biodiversity and Conservation 3, 354–372.

Kirkpatrick, J.B., 1983. An iterative method for establishing priorities for the selection of nature reserves: an example from Tasmania. Biological Conservation 25, 127–134.

Lombard, A.T., Cowling, R.M., Pressey, R.L., Mustart, P.J., 1997. Reserve selection in a species-rich and fragmented landscape on the Agulhas Plain, South Africa. Conservation Biology 11, 1101–1116.

Lombard, A.T., Hilton-Taylor, C., Rebelo, A.G., Pressey, R.L., Cowling, R.M., 1999. Reserve selection in the Succulent Karoo, South Africa: coping with high compositional turnover. Plant Ecology 142, 35–55.

Lombard, A.T., Nicholls, A.O., August, P.V., 1995. Where should nature reserves be located in South Africa: a snake's perspective. Conservation Biology 9, 363–372.

Mace, G.M., Balmford, A., 2000. Patterns and processes in contemporary mammalian extinction. In: Entwistle, A., Dunstone, N. (Eds.), Priorities for the Conservation of Mammalian Diversity—has the Panda had its Day? Cambridge University Press, Cambridge, pp. 27–52.

Margules, C.R., Nicholls, A.O., Pressey, R.L., 1988. Selecting networks of reserves to maximise biological diversity. Biological Conservation 43, 63–76.

Margules, C.R., Nicholls, A.O., Usher, M.B., 1994. Apparent species turnover, probability of extinction and the selection of nature reserves: a case study of the Ingleborough Limestone Pavements. Conservation Biology 8, 398–409.

Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. Nature 405, 243–253.

Muriuki, J.N., De Klerk, H.M., Williams, P.H., Bennun, L.A., Crowe, T.M., Berge, E.V., 1997. Using patterns of distribution and diversity of Kenyan birds to select and prioritize areas for conservation. Biodiversity and Conservation 6, 191–210.

Murray, R.D., Holling, M., Dott, H.E.M., Vandome, P., 1998. The Breeding Birds of South-East Scotland—a Tetrad Altas 1988–1994. The Scottish Ornithologists Club, Edinburgh, UK.

Nantel, P., Bouchard, A., Brouillet, L., Hay, S., 1998. Selection of areas for protecting rare plants with integration of land use conflicts: a case study for the west coast of Newfoundland, Canada. Biological Conservation 84, 223–243.

Nicholls, A.O., Margules, C.R., 1993. An upgraded reserve selection algorithm. Biological Conservation 64, 165–169.

Polasky, S., Camm, J.D., Solow, A.R., Csuti, B., White, D., Ding, R., 2000. Choosing reserve networks with incomplete species information. Biological Conservation 94, 1–10.

Polasky, S., Csuti, B., Vossler, C.A., Meyers, S.M., 2001. A comparison of taxonomic distinctness versus richness as criteria for setting conservation priorities for North American birds. Biological Conservation 97, 99–105.

Pressey, R.L., Humphries, C.J., Margules, C.R., Vane-Wright, D., Williams, P., 1993. Beyond opportunism—key principles for systematic reserve selection. Trends in Ecology and Evolution 8, 124–128.

Pressey, R.L., Logan, V.S., 1998. Size of selection units for future reserves and its influence on actual vs targeted representation of features: a case study in western New South Wales. Biological Conservation 85, 305–319.

Pressey, R.L., Nicholls, A.O., 1989. Efficiency in conservation evaluation—scoring versus iterative approaches. Biological Conservation 50, 199–218.

Pressey, R.L., Possingham, H.P., Margules, C.R., 1996. Optimality in reserve selection algorithms: when does it matter and how much? Biological Conservation 76, 259–267.

Pressey, R.L., Possingham, H.P., Day, J.R., 1997. Effectiveness of alternative heuristic algorithms for identifying indicative minimum requirements for conservation reserves. Biological Conservation 80, 207–219.

Rebelo, A., Siegfried, W.R., 1992. Where should nature reserves be located in the Cape Floristic Region, South Africa? Models for the spatial configuration of a reserve network aimed at maximizing the protection of floral diversity. Conservation Biology 6, 243–252.

Reyers, B., van Jaarsveld, A.S., Krüger, M., 2000. Complementarity as a biodiversity indicator strategy. Proceedings of the Royal Society of London B 267, 505–513.

Rodrigues, A.S., Orestes Cerdeira, J., Gaston, K.J., 2000. Flexibility, efficiency, and accountability: adapting reserve selection algorithms to more complex conservation problems. Ecography 23, 565–574.

Saetersdal, M., Line, J.M., Birks, H.B., 1993. How to maximize biological diversity in nature reserve selection: vascular plants and breeding birds in deciduous woodlands, Western Norway. Biological Conservation 66, 131–138.

Sawford, B., 1987. The Butterflies of Hertfordshire. Castlemead Publications, Ware, UK.

Scott, J.M., Davis, F., Csuti, B., Noss, R.F., Butterfield, B., Groves, C., Anderson, H., Caicco, H., D'Erchia, F., Edwards, T.C., Ulliman, J., Wright, R.G., 1993. Gap analysis: a geographic approach to protection of biological diversity. Wildlife Monographs 123, 1–41.

Stokland, J.N., 1997. Representativeness and efficiency of bird and insect conservation in Norwegian boreal forest reserves. Conservation Biology 11, 101–111.

Turpie, J.K., 1995. Prioritizing South African estuaries for conservation: a practical example using waterbirds. Biological Conservation 74, 175–185.

Underhill, L.G., 1994. Optimal and suboptimal reserve selection algorithms. Biological Conservation 70, 85–87.

Vane-Wright, R.I., Humphries, C.J., Williams, P.H., 1991. What to protect?—Systematics and the agony of choice. Biological Conservation 55, 235–254.

Virolainen, K.M., Virola, T., Suhonen, J., Kuitunen, M., Lammi, A., Siikamäki, P., 1999. Selecting networks of nature reserves: methods do affect the long-term outcome. Proceedings of the Royal Society of London B 266, 1141–1146.

Williams, P.H., 1998. Key sites for conservation: area-selection methods for biodiversity. In: Mace, G.M., Balmford, A., Ginsberg, J.R. (Eds.), Conservation in a Changing World. Cambridge University Press, Cambridge, pp. 211–249.

Williams, P.H., Araüjo, M.B., 2000. Using probability of persistence to identify important areas for biodiversity conservation. Proceedings of the Royal Society of London B 267, 1959–1966.

Williams, P.H., Gibbons, D., Margules, C., Rebelo, A., Humphries, C., Pressey, R., 1996a. A comparison of richness hotspots, rarity hotspots, and complementary areas for conserving diversity of British birds. Conservation Biology 10, 155–174.

Williams, P.H., Prance, G.T., Humphries, C.J., Edwards, K.S., 1996b. Promise and problems of applying quantitative complementary areas for representing the diversity of some Neotropical plants (families *Dichapetalaceae*, *Lecythidaceae*, *Caryocaraceae*, *Chrysobalanaceae* and *Proteaceae*). Biological Journal of the Linnean Society 58, 125–143.

Williams, P., Humphries, C., Araújo, M., Lampinen, R., Hagemeijer, W., Gasc, J.-P., Mitchell-Jones, T., 2000. Endemism and important areas for representing European biodiversity: a preliminary exploration of atlas data for plants and terrestrial vertebrates. Belgian Journal of Entomology 2, 21–46.

Willis, C.K., Lombard, A.T., Cowling, R.M., Heydenrych, B.J., Burgers, C.J., 1996. Reserve systems for limestone endemic flora of the Cape lowland fynbos: iterative vs. linear programming. Biological Conservation 77, 53–62.

Winston, W.L., 1994. Operations research—applications and algorithms, third ed. Duxbury Press, Belmont, CA.