*Research Report*

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# Dispersal-based indices and mapping of landscape connectivity

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## Abstract

Connectivity is often recommended as a coarse-filter indicator of landscape-level biodiversity, but useable measures of the concept for management applications are poorly developed. We describe a dispersal-based algorithm to index and map connectivity, modified from Richards *et al.* (2002). Users define hypothetical species with simple habitat and dispersal suitability models, home range sizes, and potential dispersal scales. Dispersal is simulated from suitable home ranges, with habitat-based declines in survivorship imposed with distance travelled. Indices include suitable home ranges, suitable home ranges encountered by dispersers, and a combined index of amount and connectivity of suitable habitat. Dispersal success and dispersers passing through each cell are mapped to help guide detailed landscape planning. We illustrate the connectivity algorithm with landscape scenarios simulated on a landscape in the North Thompson drainage of southern British Columbia. Compared to the simulated fire regime, clearcutting led to moderate declines in suitable home ranges and connectivity, clearcutting with Old-Growth Management Areas (OGMAs) produced a slight recovery by year 100, while partial cutting increased suitable habitat and dispersal. OGMAs and partial cuts better maintained some corridors. The connectivity algorithm, in conjunction with other indicators, is a useful tool for comparing planning scenarios, indexing progress over time, and guiding more detailed landscape planning.

**KEYWORDS:** *biodiversity indicators, dispersal, landscape connectivity, landscape planning.*

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## Introduction

Connectivity underlies several ecological functions that are concerns for landscape-level conservation (Turner 1989; Kareiva and Wennergren 1995). Metapopulation theory proposes that populations exist in discrete patches, with overall dynamics determined by dispersers connecting sub-populations (Hanski 1999; Heinz *et al.* 2006). More realistic spatial models recognize a gradient of source and sink habitats, with the population in sink habitats maintained by dispersers from the source areas (Pulliam 1988). The ability of offspring to find available habitat suitable for reproduction is critical to population stability (Pulliam and Danielson 1991), and genetic exchange within a population needs to be maintained to prevent inbreeding and reduced genetic diversity (Keller and Weller 2002). At a finer scale, individual animals move between different resources daily and seasonally. Connectivity is therefore a concern of conservation biologists, forest managers, environmental groups, and the general public. As a result, it is frequently included as a landscape-level indicator for assessing conservation of biodiversity (Noss 1990; Lindenmayer *et al.* 2000; Forest Stewardship Council 2003; Hickey and Innes 2005).

The practical difficulty with connectivity as a general indicator is that there is no clear way to measure it. Landscape planners and public reviewers typically assess connectivity informally, by simply looking at maps. This intuitive approach has limitations, including the following:

- It requires a "black-and-white" view, focussing on one type of forest (typically old stands) and has difficulty incorporating gradients of stand age, disturbance severity, etc., as well as patchy habitats and modest breaks in habitat contiguity.
- It tends to consider only one scale, approximately that of a human walking across the landscape.
- The approach is not quantitative, limiting the ability to compare alternative landscape plans objectively, or to demonstrate progress in improving connectivity over time.

At the other end of the spectrum, quantitative landscape ecologists have developed a variety of landscape metrics, some of them relating to connectivity (McGarigal and Marks 1995; Riitters *et al.* 1995; Brooks 2003). Many of these metrics have been criticized as having little relevance to actual biological features, such as species abundance or occurrence (Schumaker 1996; Lindenmayer *et al.* 2002; Winfree *et al.* 2005). It is also often unclear what these metrics mean, and what a change in their value would indicate.

*The ability of offspring to find available habitat suitable for reproduction is critical to population stability, and genetic exchange within a population needs to be maintained to prevent inbreeding and reduced genetic diversity.*

A basic problem with measuring connectivity as a general landscape indicator is that connectivity is inherently species-specific (Goodwin 2003; Belisle 2005). Most fundamental is the question of what constitutes the "habitat" that is being connected. This clearly differs among species. Species also differ in their abilities to disperse across different types of habitat, in the scale of their home ranges, and in the distance they can disperse (D'Eon *et al.* 2002; Richards *et al.* 2002; Brooks 2003). A meaningful index of connectivity needs to take these species-specific aspects into account. At the same time, it is impossible to evaluate each species individually. Even monitoring programs that include a representative range of individual species require coarser-filter general indicators (Lindenmayer *et al.* 2000).

Richards *et al.* (2002) developed a solution to this conflict between species-specificity and the need for a set of general indices by modelling dispersal of "hypothetical species." Hypothetical species are defined by simple models of habitat requirements (based on stand age classes in Richards *et al.* 2002) and dispersal habitat. Each hypothetical species is assessed using a set of home range sizes and potential dispersal distances that cover a range relevant to the landscape being assessed. Incorporating these species-specific aspects of connectivity ensures that the resulting assessment of connectivity has a meaningful biological interpretation. The intent is not to model real species, but to provide general indices of connectivity that are relevant to real species. Because the procedure is a spatial model, its output also includes maps that can be directly useful to landscape planners by indicating source or sink areas and "corridors" or dispersal barriers.

In this paper, we describe an approach to indexing and mapping connectivity based on the work of Richards *et al.* (2002), but with several modifications that make the approach more suitable for use in operational landscape planning and projection modelling in British Columbia. Improvements include the following:

1. Removal of the stochastic aspects of the model used by Richards *et al.* (2002), particularly individual mortality and the distinction between occupied and vacant suitable home ranges. This makes the algorithm deterministic, eliminating the need for time-consuming computer iterations. This simplification, in turn, allows evaluation of more scenarios, or the use of a greater number of hypothetical species.
2. Dispersal steps that can differ in scale from the home range size. This allows dispersal to be more selective of smaller suitable areas, such as narrow corridors or reserve patches smaller than a home range, which are often used in operational landscapes to improve connectivity.
3. An algorithm for directional dispersal that allows a disperser flexibility to follow meandering habitat, such as riparian areas.
4. Additional summary and mapped variables that help evaluate and compare landscape scenarios.

Our emphasis in this paper is on describing our approach to assessing connectivity, and demonstrating its application with four scenarios for an operational landscape in British Columbia. The scenarios are used here to illustrate the connectivity algorithm. We do not focus on assessing the value of the specific scenarios, because they were only four of over 20 scenarios evaluated as part of a larger planning exercise assessing multiple values in a planning context that has changed repeatedly in the past few years.

## Methods

### Overview of Algorithm and Pilot Study

The overall approach to evaluating and mapping connectivity takes a habitat map of the area derived from either current conditions or projections created by a forest simulation model, grids it into hexagonal home ranges of user-defined sizes, calculates the habitat suitability of each home range from habitat suitability index (HSI) models for hypothetical "species," and identifies all suitable home ranges (HSI above a user-defined threshold). For each suitable home range, a disperser is then sent in each of the six directions on the hexagonal array using an algorithm that allows movement through the best habitats with directional constraints. At each dispersal step, the disperser experiences a mortality rate that is dependent on the dispersal suitability of the habitat being traversed. Dispersal continues until the disperser has less than 5% survivorship. Suitable home ranges encountered during dispersal are counted, weighted by the disperser's survivorship when the suitable home range was encountered. The algorithm tracks the survivorship-weighted number of suitable home ranges ("dispersal success") from each suitable home range, the average dispersal success across all suitable home ranges, and the total survivorship of dispersers passing through each dispersal polygon. Details for each step are provided below.

As a pilot study, we analyzed connectivity in four projected scenarios for a 109 000-ha landscape in the North Thompson watershed of southern British Columbia (Figure 1):

1. Clearcutting using cutblocks ranging from 5–30 ha, with standard operational rules limiting adjacency of recently harvested blocks.
2. Clearcutting with Old-Growth Management Areas (OGMAs) set aside as reserves, following landscape planning guidelines recently used in British Columbia to ensure representation or recruitment of old forest (Province of British Columbia 1999). OGMAs were designated to represent different ecosystem types, using areas already constrained

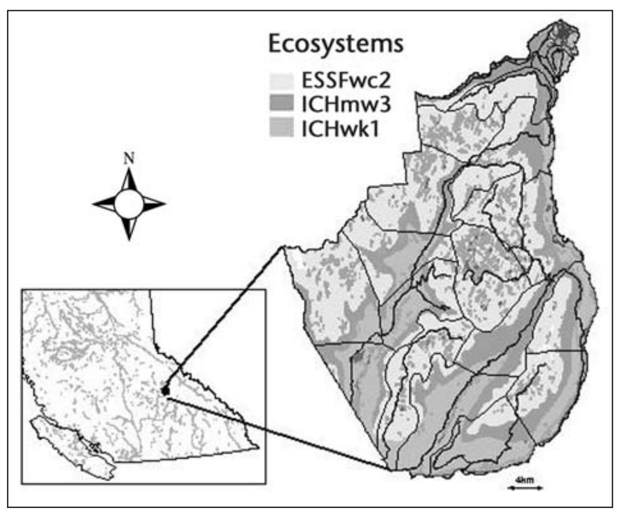



**FIGURE 1.** The 109 000-ha landscape in the North Thompson drainage of southern British Columbia. Ecosystem types include high-elevation Engelmann Spruce–Subalpine Fir (ESSF) and two variants of lower-elevation Interior Cedar Hemlock (ICH). Scattered small grey patches are unproductive or non-forested areas. Thick lines are main roads; thinner lines are operational units used in the simulation modelling.

from harvesting where possible. OGMAS therefore make the most incremental contribution to old forest in ecosystems with less area that is otherwise constrained.

3. Uneven-aged management with 20% volume removal on a 20-year re-entry cycle, a system used operationally in drier areas of the British Columbia Interior.
4. A fire regime with return intervals and range of fire sizes similar to a typical natural regime for the area, with no harvesting.

The three harvest scenarios removed the same volume of timber each year. Projections started from current conditions, which include young seral stands resulting from clearcutting in the last 30 years and natural disturbances. The landscape includes two major forest types, which affect harvest and natural disturbances. The simple habitat suitability models used in the case study did not differ between the forest types. The study area also included naturally non-forested land and water, which do affect habitat and dispersal quality. Again, we chose these scenarios to illustrate our approach to assessing connectivity, not to evaluate those specific scenarios (which may not even be currently relevant under rapidly changing contexts for planning).

Landscape projections were made using the Tool for Exploratory Landscape Scenario Analyses (TELSA) (Klenner *et al.* 1997; Kurz *et al.* 2000). The TELSA model delineates stands and schedules their harvest based on age, timber type, and development of road networks, in a way that reasonably mimics operational development plans. Modelled fires follow natural recurrence and size distributions, but not necessarily all the spatial complexities of real fires. All landscape projection models have limitations, including a lack of other disturbance types in these runs, and, more fundamentally, an inability to predict how changing social values in the future will modify actual development plans. The scenarios are therefore intended to show some of the predictable long-term consequences of current management choices, and for the current study, simply to provide a basis for illustrating the application of the connectivity algorithm. Landscapes were analyzed for indices of connectivity at year 0 (current conditions) and years 25, 50, 75, and 100 in the four projections.

## Algorithm Steps[1]

### *Step 1. Simple HSI-type Model*

We define habitat suitability index (HSI) models for hypothetical species. An HSI model is a simple set of equations or look-up tables that convert habitat characteristics into a suitability score ranging from 0 to 1. The simple HSI approach does not try to capture a real species' complex habitat needs, but instead is used as a necessary component of indexing connectivity for a general group of species. In our case study, we used two species defined by their relationship to stand age and disturbance type for clearcuts and fires, or to number of harvest entries for partial cuts (Table 1). Species A is associated with older forest, while species B is also forest-dwelling but more tolerant of younger stands. The specific values used in Table 1 were chosen simply to produce smooth transitions in habitat suitability from unsuitable young stands to fully suitable old (species A) or mature (species B) stands. Suitability of partially cut stands decreased evenly as subsequent entries reduced habitat structures, with species B being more tolerant of the reduced structure in partially cut stands after a full cycle of harvest entries.

### *Step 2. Dispersal Cost Model*

Dispersal has a mortality cost, which depends on the underlying habitat. Each hypothetical species defined by an HSI model also has an associated model of dispersal costs in different habitats. Models for habitat suitability and dispersal cost can differ, as in, for example, a species associated with old forest that can disperse readily through a wide range of stand ages. The simple models of dispersal cost for the two hypothetical species in our case study reflect a moderately broader tolerance of habitats for dispersal than for habitat suitability (Table 1). Completely unsuitable habitats, such as non-forest or water, allow some dispersal, but at a very high mortality cost.

### *Step 3. Home Range Sizes*

The sizes of home ranges affect the scale at which connectivity is assessed for a given species. For our case study examples, we used a set of three home range scales: 5, 30, and 100 ha. These were meant to encompass a reasonable range of scales for indexing connectivity in this large landscape. Smaller home ranges would require modelling habitat structures within individual cutblocks, which is excessively detailed for this broad

[1] A user-friendly version of the algorithm is available for download at *www.forestbiodiversityinbc.ca/downloads.asp*

**TABLE 1.** Scores used for example hypothetical species for habitat suitability (dispersal suitability in parentheses), by stand age for clearcuts and burns and by number of harvest entries for partial cuts. Scores range from 0 for completely unsuitable to 1 for ideal.

| **Species A: Old-forest associate** | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Forest type | Year 1 | Year 21 | Year 41 | Year 61 | Year 81 | Year 101 | Year 141 | Year >250 |
| Clearcut | 0 (0.2) | 0 (0.3) | 0 (0.5) | 0 (0.7) | 0.2 (0.8) | 0.6 (0.9) | 0.9 (1) | 1 (1) |
| Burn | 0.3 (0.7) | 0.2 (0.6) | 0.1 (0.55) | 0.1 (0.73) | 0.28 (0.82) | 0.64 (0.91) | 0.91 (1) | 1 (1) |
| | Entry 1 | Entry 2 | Entry 3 | Entry 4 | Entry 5+ | | | |
| 20% partial cut | 0.82 (0.91) | 0.64 (0.82) | 0.46 (0.73) | 0.28 (0.64) | 0.1 (0.5) | | | |
| Non-forest land | 0 (0.2) | | | | | | | |
| Water | 0 (0.1) | | | | | | | |
| **Species B: Forest generalist** | | | | | | | | |
| Forest type | Year 1 | Year 21 | Year 41 | Year 61 | Year 81 | Year 101 | Year 141 | Year >250 |
| Clearcut | 0 (0.3) | 0.1 (0.5) | 0.3 (0.8) | 0.5 (1) | 0.7 (1) | 0.9 (1) | 1 (1) | 1 (1) |
| Burn | 0.5 (0.7) | 0.47 (0.75) | 0.51 (0.86) | 0.65 (1) | 0.79 (1) | 0.93 (1) | 1 (1) | 1 (1) |
| | Entry 1 | Entry 2 | Entry 3 | Entry 4 | Entry 5+ | | | |
| 20% partial cut | 0.9 (0.95) | 0.8 (0.9) | 0.7 (0.85) | 0.6 (0.8) | 0.5 (0.75) | | | |
| Non-forest land | 0 (0.3) | | | | | | | |
| Water | 0 (0.1) | | | | | | | |

landscape analysis. Home ranges of greater than 100 ha are not suitable for evaluating typical landscape units, because there would be few home ranges in the landscape, and many of the longer dispersers would frequently encounter the map edge. (The procedure at the map edge is explained below). Output maps from TELSA used 30m × 30m raster cells, providing 56 rasters for the smallest home ranges. A minimum of 50 rasters per home range is recommended for spatial habitat models (Schulz and Joyce 1992).

### *Step 4. Scale of Dispersal*

In addition to home range size, a range of maximum potential dispersal distances are used for each species. Following Richards *et al.* (2002), these are defined as the distance at which a disperser's survivorship declines to 5% in ideal dispersing habitat. The distances are expressed relative to the home range size. We used potential dispersal distances of 3, 10, and 30 home ranges in our examples. There are therefore nine spatial scales being analyzed for each species (three home range sizes multiplied by three potential dispersal distances).

In our algorithm, dispersers move in discrete steps, from one dispersal unit to an adjacent one. Survivorship costs are calculated based on the dispersal suitability of habitat in each dispersal unit. Dispersal units can differ in size from home ranges. Smaller dispersal steps allow dispersers to follow narrow corridors, such as riparian reserves, which can be important operationally for maintaining connectivity. In the case study, we used dispersal units one-ninth the area of home ranges. Each dispersal step, therefore, covered one third of a home range diameter.

Limits on dispersal distance imply that there is always a cost for dispersal, even in ideal habitat; survivorship is always less than 1 for each dispersal step. The maximum survivorship per dispersal step, $S_{MAX}$, is:

$$S_{MAX} = \exp\left(\frac{\log_e(0.05)\sqrt{DU}}{n\sqrt{HR}}\right)$$

where DU = area of dispersal unit, HR = area of home range, and n = maximum potential dispersal distance (in home ranges).

With dispersal units one-ninth the area of home ranges, a maximum potential dispersal distance of 10 home ranges corresponds to 30 dispersal steps, and implies a maximum survivorship of 0.905 for each dispersal step in ideal habitat. The survivorship is decreased for habitats that provide less than ideal dispersal, so that the total dispersal distance is reduced proportional to the dispersal suitability. For example, a dispersal unit with average dispersal suitability of 0.5 in this example would have a survivorship of 0.819, allowing 15 dispersal steps compared to 30 in ideal habitat.

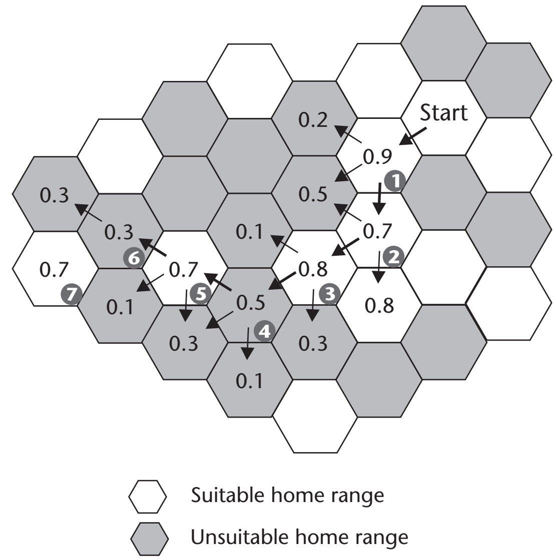
These four steps generate a range of hypothetical species, defined by habitat suitability and dispersal models, to evaluate connectivity across scales that are defined by home range sizes and maximum dispersal distances. The steps below are for simulations of an individual hypothetical species, home range size, and dispersal distance on a particular map representing the spatial pattern of habitats at a particular time. This procedure is deterministic—it does not rely on probabilistic survival or death of individual dispersers—and therefore needs to be done only once per map and combination of species, home range, and dispersal.

***Step 5. Mapping Home Ranges***

The map is covered with hexagonal home ranges and dispersal units, which can differ in size from one another. Hexagons are used because they have equal distances between adjacent centres in all directions. The habitat suitability index for each home range is calculated as the average of the habitat suitabilities for the underlying rasters. The dispersal survivorship for each dispersal unit is similarly calculated as the average survivorship for the underlying rasters. A user-defined cut-off value for the HSI is used to declare whether a home range is suitable or not. In the examples, we used an HSI cutoff of 0.6. This threshold was chosen to provide a moderate amount of suitable habitat at the various scales. A much lower threshold would have made most of the area suitable, obviating the need to examine connectivity; a much higher threshold would have made the species' habitat so rare that the species could not feasibly have existed in the landscape.

***Step 6. Calculating Dispersal-success-weighted Number of Suitable Home Ranges***

For each suitable home range, we calculate the survivorship-weighted number of suitable home ranges encountered by dispersers heading in each of the six hexagonal directions, using the following dispersal rules (Figure 2):




| Step | Survivorship | Survivorship-weighed HR's |
|---|---|---|
| 1 | 0.9 | 0.9 |
| 2 | 0.63 | 1.53 |
| 3 | 0.504 | 2.034 |
| 4 | 0.252 | 2.034 |
| 5 | 0.176 | 2.210 |
| 6 | 0.053 | 2.210 |
| 7 | < 0.05 | |

FIGURE 2. Illustration of a dispersal path using the algorithm for flexible directional dispersal (left), and calculation of survival-weighted number of home ranges encountered along this single dispersal path (right). For simplicity, this example uses a dispersal unit equal to one home range; in the case study, dispersal units were one-ninth the area of the home ranges.

- For each direction, dispersal is limited to the hexagonal dispersal unit in that direction or one of the dispersal units on either side of it.
- The best quality unit for dispersal (highest survivorship) is chosen.
- If the unit in the dispersal direction and a side one are of equal value, the unit in the dispersal direction is chosen (Step 3 in Figure 2).
- If the two dispersal units on the sides are equal and better than the dispersal unit in the dispersal direction, one or the other side units is chosen randomly (Step 6 in Figure 2).

- For the next dispersal step, the straight-ahead direction does not change. For example, if the initial direction was north, but the (approximately) northeast unit was chosen, the straight-ahead direction is still north next time, with the northeast and northwest dispersal units as the other two options.

These rules produce directional dispersal that is flexible enough to follow the best route available at each step. Although real animals may disperse in circuitous routes, retrace their steps, or indeed not disperse at all, the flexible directional dispersal in this algorithm is suitable as an index landscape connectivity without all these ecological complexities.

During dispersal, the survivorship of the disperser is reduced by the mortality cost of the dispersal unit it entered. There is no stochastic event to decide if the disperser has died. Instead, its survivorship is reduced until it drops below 5%, when dispersal in that direction is complete. An equivalent interpretation is that an infinite number of dispersers are sent out from each suitable home range, with the surviving proportion calculated at each step until only 5% are left.

Each suitable home range encountered during dispersal is counted, but weighted by the survivorship of the disperser when it encountered that home range. We call this value the "survivorship-weighted number of suitable home ranges." For example, if the disperser encountered three suitable home ranges, when its survivorship was at 0.9, 0.4, and 0.2, it would have encountered 1.5 survivorship-weighted suitable home ranges in that direction. Equivalently, this measure is the average number of suitable home ranges encountered by each member of an infinitely large cohort of dispersers.

If a disperser encounters a map edge, survivorship-weighted home ranges are extrapolated to a complete dispersal if the survivorship at the edge was less than 50%. If the survivorship at the edge was higher than 50%, the disperser has not dispersed far enough for a reliable extrapolation of dispersal success, and that dispersal direction is not used for that home range or included in the analyses.

This dispersal procedure is repeated for each of the six hexagonal directions, and an average survivorship-weighted number of suitable home ranges is calculated for that suitable home range. The whole procedure is then repeated for all other suitable home ranges on the map.

#### *Step 7. Standardize Dispersal-success-weighted Home Ranges*

The absolute number of survivorship-weighted suitable home ranges encountered during dispersal clearly increases with the maximum potential dispersal distance. To allow equal comparisons of connectivity at the different sampling scales, values are standardized by dividing by the value expected in the ideal situation of completely suitable habitat. The expected value for survivorship-weighted number of suitable home ranges in this ideal world is $S_{MAX} + S_{MAX}^2 + S_{MAX}^3 + \ldots S_{MAX}^n$, where $S_{MAX}$ is defined above, and n is the maximum number of dispersal steps until less than 5% survivorship. A standardized dispersal success of 70%, for example, means that the species encountered 70% of the survivorship-weighted suitable home ranges that it would have encountered in an ideal world of completely suitable habitat.

#### *Step 8. Summarize Results*

The above procedure generates several summary statistics:

1. The percentage of suitable raster cells (30m × 30m in our example). This value is independent of home range size or dispersal ability. It simply provides a standard against which to compare the percentage of suitable home ranges, and is an indication of the rarity of suitable habitat for that hypothetical species.
2. The percentage of suitable home ranges. Comparing this summary statistic to number 1, above, indicates the degree of fragmentation of suitable habitat at the within-home-range scale.
3. The average survivorship-weighted number of suitable home ranges, standardized to a percentage of the ideal value, which we call "dispersal success."
4. Dispersal-adjusted suitable home ranges (DASHR), the result of multiplying statistics 2 and 3 (and dividing by 100 to retain the percentage scale). DASHR is a composite value indexing the percentage of suitable habitat at the home range scale (2), prorated by the degree to which dispersal between suitable home ranges is impeded (3). Summary variables 2 and 3 indicate amount of habitat and its connectivity separately, but forest harvesting typically produces both habitat loss (for old forest species) and reduced connectivity simultaneously. It makes sense operationally to index both effects together with DASHR when evaluating landscape alternatives or changes through time. DASHR can be interpreted as a combined index

of the amount of habitat available to an individual and the likelihood that the individual's dispersing offspring will also encounter suitable habitat.

Maps are also produced that show the survivorship-weighted number of suitable home ranges encountered for dispersers from each suitable home range on the map. The survivorship-weighted number of dispersers through each dispersal unit is also plotted, by summing the survivorships of each disperser who passed through a dispersal unit (similar to the dispersal activity maps of Richards *et al.* [2002], but weighted by survivorship). Areas that have high numbers of dispersers passing through may differ from suitable home ranges with high dispersal success, because dispersal can occur in corridors too narrow to support suitable home ranges (for example, along riparian reserves), and dispersal can occur in areas that are not suitable habitat. High rates of dispersal through an area can also occur when other dispersal options are constrained by poor dispersal habitat in the area. These maps can be plotted separately for each combination of hypothetical species, home range, and dispersal scale, or they can be summed across scales and (or) species. Difference maps between two time periods for a given scenario, or between two scenarios, can also be plotted to highlight changes or differences in dispersal success or dispersal activity.

## Results

### Fire Scenario Recovery to "Natural" Levels

Under the fire scenario, the proportion of suitable home ranges, dispersal success, and their combination, DASHR, increased over time as currently young stands became suitable more quickly than young stands were created by fire (Figure 3). For the more generalist species B, the increase levelled off by year 75, while for species A, associated with older forest, the increase was levelling off by year 100. This suggests that by year 100, these indices of habitat amount and connectivity had approached equilibrium levels under this natural disturbance scenario. For both species and all home range sizes, these levels at year 100 in the fire scenario were well below the maximum possible levels that would be created by "ideal" conditions of 100% old-growth forest, because the seral stage distribution under this natural disturbance scenario and naturally non-forested areas reduce the number of suitable home ranges and dispersal success for these hypothetical species.

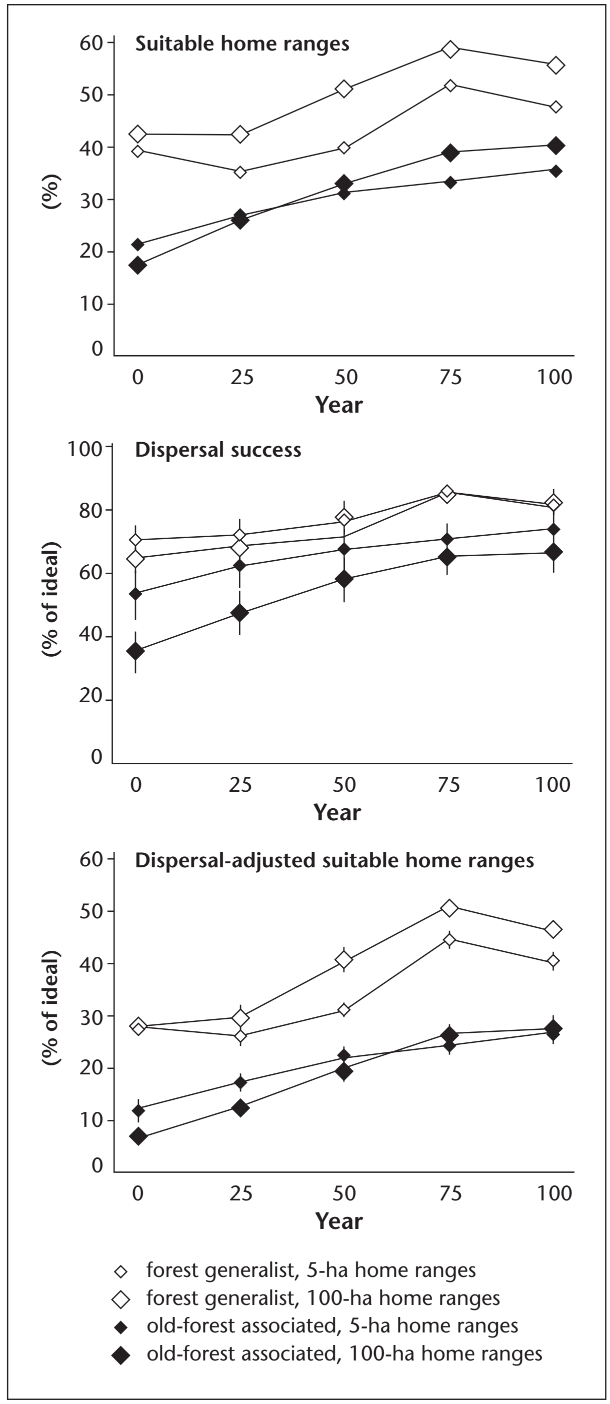



FIGURE 3. Projected trends under the historic fire scenario in suitable home ranges, dispersal success, and dispersal-adjusted suitable home ranges (DASHR). Error bars show the range for potential dispersal distances of three to 30 home ranges (some of these bars are small and hidden by the symbols).

## Habitat Suitability

For the specialist species A, suitable 100-ha home ranges at year 0 were 43.2% of natural levels (based on the fire scenario at year 100), compared to 60.1% of natural for 5-ha home ranges, showing greater aggregation of suitable habitat at the smaller scale. For the more generalist species B, the percentages of natural levels of suitable 5-ha and 100-ha home ranges were higher and more similar (76.2% for 100-ha and 82.6% for 5-ha) (see Figure 4, top). In the scenario of clearcuts without OGMAs, suitable home ranges of all sizes for both species declined slightly over time, with a small improvement at year 100 as currently young cutblocks became suitable (Figure 4, top). The scenario of clearcuts with OGMAs produced slightly fewer suitable home ranges for both species in years 25 and 50, followed by a greater increase in years 75 and 100, as OGMAs reserved to recruit old forest became more suitable. The partial cuts showed a rapid increase in suitability for species A, as existing young forest aged and new partial cuts were still suitable after one harvest entry. Suitable home ranges then leveled off as the reduction in suitability from subsequent partial cutting balanced the increased suitability from aging of currently young stands.

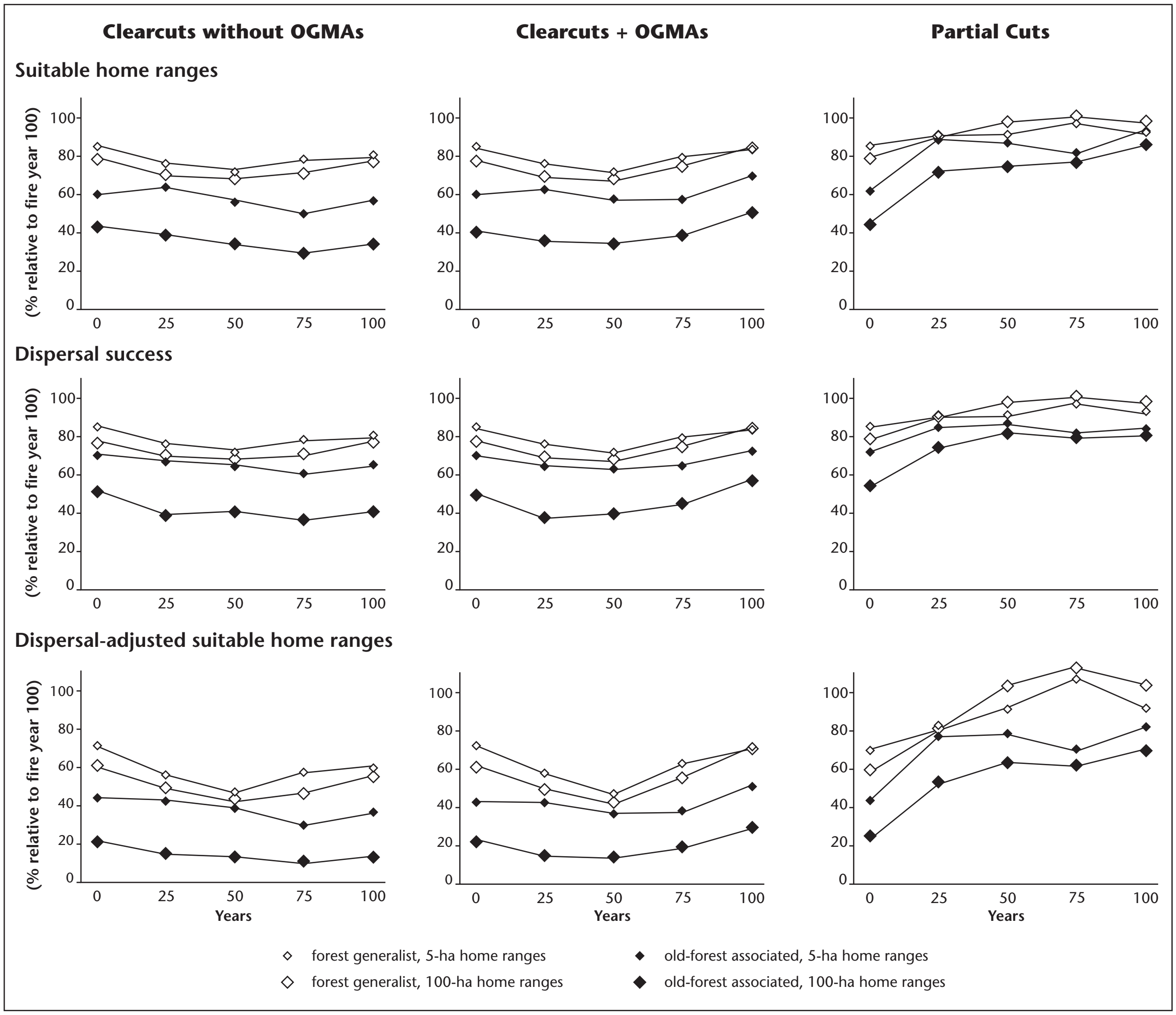



FIGURE 4. Projected trends under three management scenarios for suitable home ranges, dispersal success, and DASHR for hypothetical species. Error bars show the range for potential dispersal distances of three to 30 home ranges. All values are expressed as a percentage of the value for the fire scenario at year 100 (= "natural").

## Dispersal Success

Dispersal success at year 0 ranged from about half of natural conditions (for species A with 100-ha home ranges) to 85% of natural (for species B with 5-ha home ranges) (Figure 4, middle row). Potential dispersal distance had a large effect on the absolute value of dispersal success, but the effect was similar in all scenarios, including fire at year 100. As a result, potential dispersal distance had little effect on results expressed as a percentage of dispersal success under natural conditions.

Dispersal success declined moderately by year 25 under the scenario of clearcuts without OGMAs, and remained at this lower level for species A, with a slight recovery in year 100 for species B. Under the scenario of clearcuts with OGMAs, dispersal success recovered to year 0 levels by year 100. With both clearcutting scenarios, dispersal success for species A was much lower with 100-ha home ranges than 5-ha home ranges. In the partial-cutting scenario, dispersal success for species A leveled off near 80% of natural levels at year 50, while the more tolerant species B showed dispersal success near natural levels by year 50.

## Dispersal-adjusted Suitable Home Ranges

Combining the proportion of suitable home ranges and dispersal success, dispersal-adjusted suitable home ranges (DASHR) emphasized the above trends, with particularly low levels relative to natural for species A with a 100-ha home range, and relatively high levels for species B with 5-ha home ranges (Figure 4, bottom). DASHR levels declined further for species A under the scenario of clearcut without OGMAs, and declined then recovered partially for species B. With OGMAs, DASHR levels recovered to slightly above current levels by year 100, after a more pronounced low period from years 25 to 50. Under partial cutting, DASHR scores improved markedly in the first 50 years, particularly for the larger home ranges.

## Connectivity Maps

Maps of dispersal success from suitable home ranges clearly show differences in the amount and distribution of suitable home ranges (for examples for species A at year 0 and year 25, see Figure 5). Low dispersal success from isolated small patches of suitable habitat is evident in the maps (darker grey in Figure 5), which also show subtler effects of reduced dispersal success around edges of larger patches, particularly where these are convoluted shapes (e.g., peninsulas). The creation of more small patches with poorer dispersal in the clearcut scenarios was also apparent, with some reduction in this fragmentation in the scenario with OGMAs. However, this is accompanied in the latter scenario by greater fragmentation in some areas away from the OGMAs. The partial cut and fire scenarios differ from the clearcut scenarios in creating larger, more connected areas of suitable habitat with high dispersal success. The pattern in partial cuts reflects the greater tolerance of partial cuts assumed for this hypothetical species.

Maps of the number of dispersers passing through each area of the landscape indicate potential "corridors," as well as areas with minimal roles in dispersal (Figure 6). The example landscape currently shows a well-defined travel corridor running northeast-southwest following the north Thompson River valley in the southeastern part of the landscape, and a network of areas with enhanced dispersal activity in the north. The scenario of clearcutting without OGMAs reduces the southeastern corridor, while the OGMAs help to maintain at least the central part of this corridor. Partial cutting maintains dispersal in this valley over a broader area. All three harvest scenarios reduce the network of potential corridors in the northern part of the landscape. Fires remain the largest effect, with large fires creating

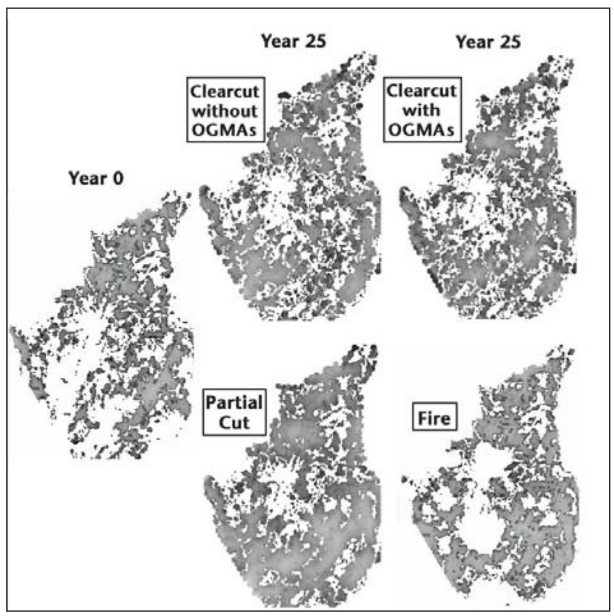



**FIGURE 5.** Dispersal success from suitable home ranges for hypothetical species A at year 0 and at year 25 under the four scenarios. Grey scale indicates success, from dark grey = 0% to light grey =100% of ideal. Blank areas are unsuitable home ranges.

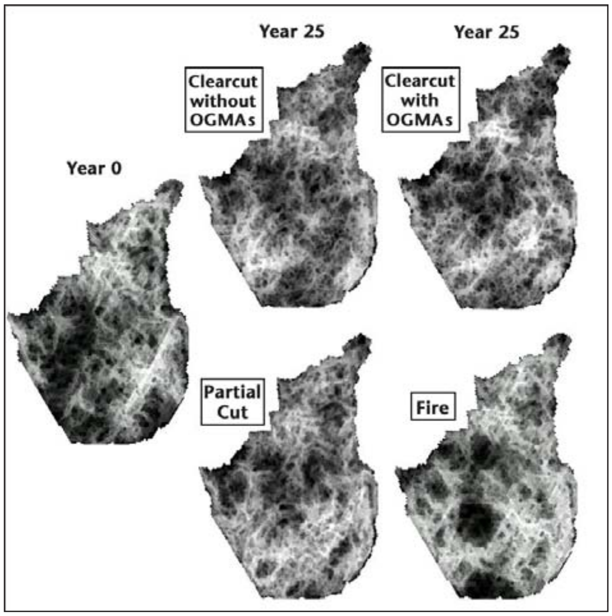



**FIGURE 6.** Dispersal activity for hypothetical species A at year 0 and at year 25 in the four scenarios. Grey scale indicates suitability, from black = 0 dispersers passing through the cell, to white = maximum number.

prominent areas with little dispersal activity for this hypothetical species. Aging of existing stands allows more dispersal activity in some areas that currently have lower activity, such as the south-central part of the landscape.

## Discussion

The dispersal-based connectivity algorithm presented here is a tool to provide one set of coarse-filter indicators for landscape-level biodiversity, as well as detailed maps of dispersal sources or sinks and corridors or dispersal barriers for landscape planning. The coarse-filter indicator values–percentage of suitable home ranges, dispersal success and DASHR–should be used in conjunction with other basic coarse-filter indicators, such as age class distribution, representation of ecosystem types, edge amounts, roads and roadlessness, and stand-level variables such as habitat structures and diversity (Noss 1990; Lindenmayer *et al.* 2000; Kremsater *et al.* 2003). Most of these indicators have better-documented relevance to a range of species than does connectivity. The coarse-filter indicators should also be accompanied by field monitoring of a range of species, as direct fine-filter indicators of success at conserving biodiversity and as part of a research program designed to test the relationship between coarse-filter indicators and biota. The connectivity indices are a useful compromise between species-specificity and abstract generality for assessing biodiversity in this context of monitoring a broader set of coarse- and fine-filter indicators.

An implicit assumption is that a landscape with a higher connectivity index for a particular hypothetical species and scale of home range and dispersal implies that real species with similar characteristics would show greater persistence or higher abundances in that landscape. It is unlikely that this assumption can ever be tested rigorously. Experimental tests with adequately replicated and controlled landscapes are virtually impossible to establish, maintain, and monitor over the necessary long time scales. Simplified experimental landscapes would be of questionable relevance to operational landscapes in any case. Comparisons of existing landscapes are likely to be confounded by many other differences, such as harvest levels, forest types, and natural disturbance histories. Detailed computer modelling of individual species could help confirm that a species' autecology does not greatly affect the assumed relationship between connectivity and population persistence or abundance, but that would be merely a comparison of the consequence of different modelling assumptions, not a direct test. Despite this lack of direct testability, connectivity indices can still be used to assess alternative landscape scenarios and progress in improving conditions over time, and the maps can be used to help detailed planning decisions. Ultimately, though, the untested assumption of the relevance of these indices requires direct monitoring and projection modelling of at least some actual species.

The results produced by this dispersal-based connectivity algorithm clearly depend on the models of habitat and dispersal suitability used to define the hypothetical species. In the case studies, for example, both species were associated with old-forest and benefited from the structural retention in partial cuts. The partial cut scenario therefore had more suitable home ranges and better dispersal success than the two clearcut scenarios. This dependence of connectivity on the definition of suitable habitat is one of the inherent species-specific aspects of connectivity. The practical implication is that assessments of connectivity as general indices of biodiversity should use several hypothetical species with different habitat and dispersal models, rather than just two, as in our example. The issue then becomes how to handle the numerous values produced for each scenario: too many indices eventually become as uninformative as too few. One option would be to use a weighted average across the different species, with weights based on the approximate number of real species that each hypothetical species is believed to represent. The difficulty would be a lack of empirical data to classify most real species. An alternative is to focus on the hypothetical species that show the lowest dispersal success or DASHR values, and modify landscape plans or choose alternatives that minimize the impact on these most sensitive species.

An important aspect of interpreting our results was the explicit comparison to a "natural disturbance" scenario. The calculation that standardizes the survivorship-weighted number of home ranges to a percentage of an ideal value accounts for the simple fact that longer dispersers are expected to encounter more suitable home ranges than shorter ones. However, the ideal of a perfectly suitable landscape will never occur for any species. Without a natural benchmark scenario to compare to, there is no value-scale for interpreting results from other scenarios. For example, if scenario A has a dispersal success of 10% of ideal for a particular species, and scenario B has 15%, scenario B is clearly better, but we do not know how much better. If the dispersal success expected under natural conditions is 20%, B is substantially better than A, but if the natural level is 90%, both A and B are poor options.

The natural scenario also helps reveal whether the hypothetical species are reasonable. If dispersal success or the proportion of suitable home ranges in the natural scenario is very low for a species, it is unlikely to represent any real species; any such real species would not have existed in that landscape naturally (although this situation may be reasonable for evaluating introduced species, where we might be trying to reduce connectivity back to low natural levels). A natural scenario further aids interpretation by showing how long the effects of past harvesting are expected to last (Wallin *et al.* 1994). In the fire scenario in the case study, rough equilibrium levels of connectivity took 75 years to re-develop for the generalist species and 100 years for the old-forest associate. Although a "natural disturbance regime" is difficult to define both conceptually and empirically, a scenario with a reasonable natural disturbance regime is an important component for interpreting results from management scenarios.

Overall connectivity indices help evaluate alternative scenarios and progress through time, but the map output from this algorithm can also guide finer-scale location of harvesting. Planning goals would be to minimize disruptions to areas with high dispersal success, and areas that have high levels of dispersal activity (in the context, of course, of meeting many other management goals, including those for other indicators of biodiversity). However, the idea of "corridors", where dispersal activity is notably high (Beier and Noss 1998), should be used with some caution. In particular, high-use corridors can be created simply by harvesting in adjacent areas so that dispersers have no choice other than to use the corridor. This creates corridors, but does not improve overall connectivity. Preserving existing corridors is a positive goal, but creating new corridors is more ambiguous. Overall dispersal success or DASHR values should be used to check that a new corridor is actually making a positive contribution, rather than just indicating greater adjacent constraints on dispersers.

The case study compared simple scenarios in which one type of harvesting was used across the landscape. More detailed planning to maintain connectivity within landscapes should consider the location and proportions of a mix of management options, including large and small cutblocks and areas of partial cutting. The dispersal algorithm allows evaluations of the effectiveness of these more complex scenarios over time, which would be very difficult to assess by a simple intuitive look at maps.

The focus in the case study examples was on older forest connectivity, because that is a common, familiar concern. The same approach can also be used to assess connectivity for early-seral species, including assessing introduced or competitive generalist species where the management goal is to reduce connectivity. An example in the case study area is trying to limit early seral connectivity for deer and moose, which are thought to have negative indirect effects on mountain caribou. The approach is also adaptable to non-forests such as grasslands or wetlands, wherever meaningful, definable habitat characteristics can be mapped and projected under different scenarios.

## Management Applications

The connectivity indices produced by the DASHR algorithm are intended as one landscape-level indicator of biodiversity. They should be used as part of a broader monitoring program that includes more fundamental measures, such as ecosystem representation, seral stage distributions, and edge versus interior area. Direct monitoring of a representative range of species is required to test that these indicators are meeting their ultimate goal of maintaining species.

Connectivity monitoring fits into landscape planning processes at two points:

***1. Comparisons of Overall Approaches to Managing Landscapes***

This was illustrated by the simple comparisons of partial cutting and clearcutting with and without OGMAS in our case studies. Other comparisons would include the use of designated landscape corridors (for example, forest ecosystem networks [FENS]) versus similar reserve areas allocated at a finer spatial scales (e.g., within variable retention cutblocks), strategies to aggregate harvesting compared to widely dispersed cutblocks, or different approaches to salvaging natural disturbances.

Connectivity could also be assessed to compare different ways of allocating reserves that have other primary purposes. For example, OGMAS are meant to represent different ecosystem types in older-forest reserves, but different placements of OGMAS may contribute more or less to maintaining landscape connectivity. Different locations for wildlife habitat areas can also contribute more or less to connectivity while meeting their primary goal of providing habitat.

An important part of this assessment is projecting the long-term consequences of the currently available options. This would ideally include examining how much flexibility the options allow if there are unexpected natural disturbances in the future.

This broad-scale assessment of connectivity would be done as part of the initial strategic planning for landscape units, and renewed periodically as conditions and values change.

***2. Finer-scale Planning of Harvest Blocks***

At a finer scale, maps of areas that provide high dispersal success and areas that are important for dispersal can help guide the placement and timing of individual cutblocks. We did not explore this detailed planning in our case studies, but a few areas stood out as potentially important for maintaining this finer-scale connectivity. These areas could be the focus for careful planning to ensure that suitable dispersal habitat is provided through time. This could involve either spatial modelling to provide corridors through time, or the use of alternative silvicultural systems that allow easier animal movement.

In some landscapes, preventing the spread of introduced early-seral species may also be important. In these situations, avoiding creating dispersal corridors for these species may be a goal for detailed planning.

The connectivity maps would be consulted as part of developing local operational plans, such as forest development plans.

More generally, using a formal approach to indexing connectivity—rather than just an intuitive assessment of maps—should help establish connectivity as a standard quantitative measure of landscape conditions, like age structure or amount of edge. Specific algorithms for measuring connectivity also help to define what is meant by the otherwise vague concept of "connectivity."

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# Test Your Knowledge . . .

*Dispersal-based indices and mapping of landscape connectivity*

**How well can you recall some of the main messages in the preceding Research Report? Test your knowledge by answering the following questions. Answers are at the bottom of the page.**

1) The index of connectivity presented here is based on:
   A) Genetic flow between populations
   B) Dispersal success
   C) Visual assessment of maps

2) Connectivity measures are:
   A) Important tools for managing species at risk
   B) A good overall index of biodiversity
   C) One part of a larger set of landscape indices

3) The program to calculate and map Dispersal-Adjusted Suitable Home Ranges is:
   A) DASHR
   B) DANCR
   C) Rudolph

*ANSWERS*

1. B 2. C 3. A