

Cost distance modelling of landscape connectivity and gap-crossing ability using radio-tracking data

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Summary

1. Landscape connectivity, the ability of species to move between different elements of a landscape, has been evaluated mainly by expert opinion, proxy data or homing experiments, all of which have major limitations. Cost distance modelling can overcome these limitations, but the resistance values of different landscape elements are difficult to estimate.

2. Here, we present a novel method combining step selection functions with cost distance modelling to assess functional landscape connectivity. Instead of relying on movement metrics, the method uses a case-control design to assess whether the chosen steps differ from a random sample of alternatives of similar lengths. Alternative models of landscape connectivity and dispersal behaviour are represented as maps of resistance values, and compared using an information-theoretic approach to select those hypotheses that maximize the discrepancy between chosen steps and random alternatives.

3. We applied this method to daily locations recorded along the dispersal paths of 38 juvenile North Island robins *Petroica longipes* in a fragmented pastoral landscape in New Zealand. We compared models with different resistance values for four recognized vegetation types in the landscape and assessed gap-crossing behaviour by changing the resistance value of pasture as a function of distance to the closest woody vegetation.

4. Model comparison showed that juvenile robins move in decreasing order of preference through native forest, plantations and shrubland, and showed a marked reluctance for flying over pasture. Under the best model, the largest gap crossed was 110 m.

5. *Synthesis and applications.* In combination with data on the total cost distances travelled by dispersers, cost distance models of landscape connectivity can be used to predict distributions of dispersal distances in any landscape with similar vegetation types. They can therefore predict responses of species to landscape management or predict spatial dynamics of populations following reintroduction. Our method is potentially applicable to any dispersal data, even with a relatively small number of locations recorded in complex landscapes, meaning models can be fitted to data that cannot be analysed using previous method. Tools are freely available for download to allow researchers and wildlife managers to apply our methods to their own data.

Key-words: choice analysis, conditional logit model, connectivity, cost distance, dispersal, gap crossing, GIS, least-cost path, *Petroica longipes*, resistance

Introduction

Many studies have shown that dispersal can be critical to the distribution and persistence of species in fragmented landscapes (Hanski & Simberloff 1997; Ims & Yoccoz 1997; Wiens 2001). It is now well established that individual movements

between habitat patches are often dependent on the features of the matrix (Ricketts 2001), and the term landscape connectivity is used to indicate 'the degree to which the landscape facilitates or impedes movement among resource patches' (Taylor *et al.* 1993). Connectivity has often been defined based on the spatial structure of a landscape, that is, 'structural connectivity'. However, our perception of landscape structure might be quite different from that of the species of interest; hence, structural connectivity might be of little use in explaining how the

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landscape influences species movements, that is, 'functional connectivity' (Brooks 2003). For instance, the conservation or establishment of corridors is often recommended for mitigating the negative effects of habitat fragmentation (Beier & Noss 1998). However, the effect of corridors on connectivity is usually assessed subjectively rather than based on data on species movements (Beier, Majka & Spencer 2008).

Recent developments such as state-space modelling allow the identification of the factors driving animal movements, even when the data are measured inaccurately or when organisms switch between multiple behavioural states (Patterson *et al.* 2008; review in Schick *et al.* 2008). However, these methods rely on movement metrics, usually step length and/or turning angle, to assess the effect of landscape features on movements. Such methods require many steps (each pair of consecutive recorded dispersal locations) for each individual; so, they cannot be used if locations cannot be recorded frequently. Moreover, movement metrics do not necessarily indicate the ease of movement in a specific environment, as short steps with large turning angles might result from an exploratory behaviour in a suitable habitat, or alternatively from the inability to find a route out of an inhospitable environment.

Alternatively, many studies have tried to characterize landscape connectivity using cost distance modelling (Beier *et al.* 2008), by representing more biologically relevant movements that take into account the interaction between landscape and movements. Cost distance modelling estimates the difficulty of moving between two locations by assigning each pixel of a rasterized map with a resistance value, also called cost or friction (Adriaensen *et al.* 2003). This value denotes the difficulty for an organism or its reluctance to cross the map cell, and it is generally determined based on the substrate type it represents. The cost distance of a destination from a source is the accumulated cost of travelling the easiest path between the two locations, and can be calculated in most geographical information system (GIS) packages. Cost distance is often a more realistic measure than Euclidean distance as it takes into account the landscape configuration and structure from a species' point of view, and can readily replace Euclidean distances in patch isolation metrics already used (e.g. Moilanen & Nieminen 2002; Castellón & Sieving 2006b; Yamanaka *et al.* 2009). However, to be acceptable, any model of landscape connectivity should be corroborated by actual dispersal data. Individuals' movements should correspond to the hypothetical resistance values assigned to the various landscape elements, that is, be more frequent through cells of low resistance and rare through those of high resistance. In other words, cost distance can only represent connectivity if it is correlated with the probability of individual movements.

Unfortunately, resistance values are often decided based on expert judgement (Beier *et al.* 2008), based on proxy data such as the time spent in different habitat types by dispersing animals (e.g. Graham 2001) or by assuming that dispersal habitat is similar to breeding or foraging habitat (Chetkiewicz, Cassady St. Clair & Boyce 2006; e.g. LaRue & Nielsen 2008). Proper estimation of the resistance to movements of landscape elements is difficult and generally requires extensive data (Ims

& Yoccoz 1997) based on capture–recapture (Lebreton *et al.* 2003; Mennechez, Schtickzelle & Baguette 2003; Schtickzelle *et al.* 2005), or on the direct observation of movements across specific barriers (Sieving, Willson & Santo 1996; Grubb & Doherty 1999).

Another problem with cost distance modelling is that it has ignored the spatial organization of costs along a particular path. For example, some forest birds and mammals seem to use stepping stones such as isolated trees when crossing clearings but do not cross large gaps (Brooker, Brooker & Cale 1999; Bakker & Van Vuren 2004). Without considering gap-crossing ability, the accumulated cost of a path with many small gaps is assumed to be equal to the cost of crossing a single large gap of the same total distance. However, quantifying gap-crossing ability is difficult. Several authors have attempted to quantify the gap-crossing ability of species using translocations and homing experiments (Pither & Taylor 1998; Bêlisle & Cassady St. Clair 2001; Boscolo *et al.* 2008), or playback experiments (Desrochers & Hannon 1997; Bêlisle & Desrochers 2002; Desrochers, Bêlisle & Bourque 2002; Tremblay & Cassady St. Clair 2009). However, these animals may not behave in the same way in these situations as they do when dispersing, and the experiments typically use adults although most natural dispersal may be undertaken by juveniles (Sinsch 1992; Paradis *et al.* 1998; Vos & Chardon 1998).

In this article, we present a novel approach combining cost distance modelling and step selection functions that makes it possible to test objectively for the influence of landscape features on animal movements and estimate the associated resistance values using dispersal data. We show that cost distance modelling can also be extended to consider species dispersal behaviour such as gap-crossing ability, which can be quantified using our approach. Our method aims to answer the following question. Given the fact that an individual moved a certain distance, what factors, if any, led this individual to choose the observed destination compared with other available alternatives of similar distance? By not modelling distance directly, our approach does not necessitate a rigorous design for recording dispersal locations and can be applied to any dispersal data. If the starting and final locations are known, the distribution of total cost distances achieved by dispersers can be readily combined with cost distance modelling to make predictions. The results may be extrapolated to other landscapes and be used directly for management recommendations. We apply the method to radio-tracking data of dispersing juveniles of North Island robins *Petroica longipes* (Fleming 1950), a small passerine endemic to New Zealand, inhabiting forest patches created by land conversion to pasture in the central North Island.

Materials and methods

MODEL SPECIES AND STUDY AREA

The North Island robin *P. longipes* is a small (30 g) passerine endemic to New Zealand. It is found predominantly in mature native broad-leaf-podocarp forests and feeds mainly on invertebrates from the leaf litter. It is very territorial and non-migratory, and its detectability is

particularly high owing to its inquisitiveness and strong response to territorial lure calls. After fledging, juveniles are fed by their parents for up to five subsequent weeks (Armstrong *et al.* 2000) and then undergo a dispersal phase until they successfully establish a territory or die. Juvenile dispersal is therefore responsible for most of inter-patch movements and colonization events (Richard 2007). North Island robins have declined greatly in range since human colonization (Bell 1986), although they can still be locally abundant (Robertson *et al.* 2007).

The study took place in an area of about 15 000 ha in the central North Island of New Zealand between the township of Benneydale (175°22'E, 38°32'S) and Pureora Forest Park. The landscape (Fig. 1) is mainly composed of privately owned pastoral land used for cattle and sheep farming, with remnants of native broadleaf-podocarp forest and some areas of scrubland and exotic pine *Pinus radiata* plantations.

RADIO-TRACKING OF DISPERSING JUVENILES

In 13 of the native forest patches of the landscape (Fig. 1), 71 different breeding pairs of adult robins were monitored intensively over three breeding seasons (29 in 2002–2003, 36 in 2003–2004 and 34 in 2004–2005). Juveniles from the successful nests were caught 4–5 weeks after fledging. A total of 53 juveniles (18 in 2002–2003, 18 in 2003–2004 and 17 in 2004–2005), were fitted with a 1.05-g BD-2 transmitter (Holohil Systems Ltd., Ontario, Canada), attached using a Rappole harness around the legs (Rappole & Tipton 1991). We selected juveniles to maximize the number of forest patches they originated from and also to minimize the use of siblings (there were only two pairs of siblings in the data set).

As a result of the short lifetime of the transmitters (maximum 6 weeks), the tracking period was too short to follow all the radio-tracked juveniles until they settled. We therefore doubled the tracking period in 2003–2004 and 2004–2005 by recapturing and retagging each juvenile before the first transmitter was due to fail. Juveniles were visually checked every 2 days while still in the natal territory, then every day after they left. At each check, the position of the bird was recorded with a Garmin® handheld global positioning system (GPS; Olathe, KS, USA), with an accuracy of less than 10 m.

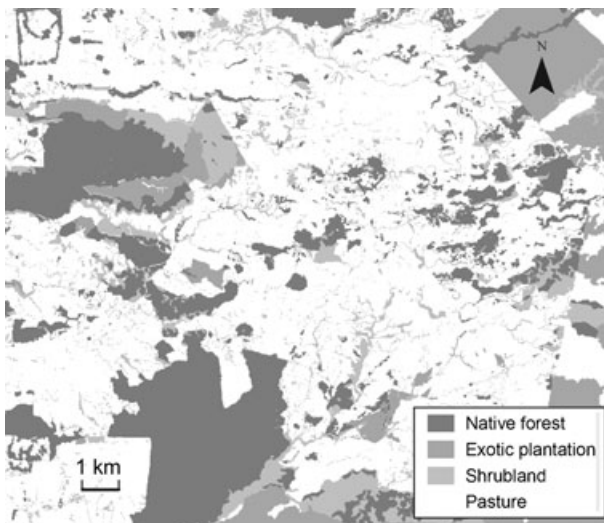


Fig. 1. Digitized map of vegetation cover of the 15 000 ha area used for obtaining data on dispersal movements of juvenile North Island robins.

We used data for all juveniles that moved > 150 m, even if they were found dead or if their signal was lost, as the sampling units were the daily dispersal steps and not the final settlement locations.

COST DISTANCE MODELLING AND ANALYSIS

Base GIS

The GPS locations of the radio-tagged juveniles were transferred into a GIS that included the vegetation cover of the study area. Vegetation was classified as mature native broadleaf/podocarp forest, exotic pine plantation, pasture and shrubland, which was mainly composed of manuka *Leptospermum scoparium*, kanuka *Kunzea ericoides* and young totara *Podocarpus totara*. The vegetation cover map had a cell resolution of 15 m and was manually digitized from recent aerial photographs (5-m resolution) and satellite images using Imagine 8.3.1 (ERDAS, Atlanta, GA, USA) to ensure adequate representation of all the vegetation features of the landscape, including individual trees in pasture. The accuracy of the map and the vegetation classification was assessed in the field during the 3 years of study and modifications were made where necessary.

Cost maps

Alternative models for landscape connectivity had different cost maps consisting of the resistance values assigned to the four recognized vegetation types. The first four models had resistance values of 1 for native forest and 10 for pasture, but different resistance values for exotic plantation and shrubland, respectively, assigning them with values 1 and 1 (no difference in resistance to movements between the three woody vegetation types), 2 and 2, 2 and 3 and 3 and 2 (Table 1; Models 1–4). The resistance values of the three types of woody vegetation in the best of these models were then used for all subsequent models. We created two other cost maps with values of 5 and 20 for pasture (Models 5 and 6) to assess the validity of the value we assigned to pasture for Models 1–4.

We created several cost maps (Fig. 2), where the resistance of pasture cells changed as a function of the distance to the nearest woody vegetation to assess the gap-crossing limitation of robins. Five cost maps (Models 7–11) were created where this function increased linearly with distance (with intercept α and slope β ; Fig. 2), and five cost maps (Models 12–16) where resistance followed a Gompertz function (eqn 1). The Gompertz function was chosen as it seemed a plausible function to model robins' perception of pasture, with a slope first increasing with distance then decreasing before reaching zero for cells very far from any edge of woody vegetation (Fig. 2). The cost of crossing 1 m of pasture was given by:

$$\text{cost} = \frac{K}{15} \cdot \exp\left(\ln\left(\frac{x_0}{K}\right) \cdot \exp(-\alpha \cdot d)\right), \quad \text{eqn 1}$$

where d is the distance in metres to the closest edge of woody vegetation, α is the overall slope of the function and K and x_0 are two scaling parameters that were fixed to 1455 and 15, respectively. These values were chosen so that the first cell of pasture encountered from an edge of woody vegetation was assigned a value of 4, and the maximum resistance value was 100 (Fig. 2).

Cost distances

We used a case-control design similar to Fortin *et al.* (2005) and Coulon *et al.* (2008) to characterize the chosen step in comparison with 10 possible alternatives of similar Euclidean distance (or fewer

Table 1. Comparison of 15 conditional logit models fitted to radio-tracking data for dispersal of juvenile North Island robins, sorted by Akaike information criterion (AIC) value. The coefficient β of cost distance, AIC, Δ AIC (difference in AIC from the best model) and weight (AICw) values of the models are indicated. Linear_x and Gompertz_x denote the models in which resistance of pasture increased, respectively, linearly or following a Gompertz function with distance to the closest edge of woody vegetation, with values of x increasing with the slope of the function (see Fig. 2)

Model #	Resistance values				β	AIC	Δ AIC	AICw
	Native forest	Pines	Shrubland	Pasture				
10	1	2	3	Linear ₄	-2.76	690.88	0.00	0.20
9	1	2	3	Linear ₃	-2.84	691.24	0.36	0.17
11	1	2	3	Linear ₅	-2.61	691.36	0.48	0.16
8	1	2	3	Linear ₂	-3.02	691.87	0.99	0.12
14	1	2	3	Gompertz ₃	-3.15	692.25	1.37	0.10
15	1	2	3	Gompertz ₄	-2.98	692.73	1.85	0.08
13	1	2	3	Gompertz ₂	-3.34	692.91	2.02	0.07
7	1	2	3	Linear ₁	-3.33	693.86	2.98	0.05
3	1	2	3	10	-2.79	695.21	4.33	0.02
12	1	2	3	Gompertz ₁	-3.62	695.32	4.44	0.02
6	1	2	3	20	-2.15	698.18	7.30	0.01
5	1	2	3	5	-3.66	699.54	8.66	0.00
2	1	2	2	10	-2.86	702.65	11.77	0.00
4	1	3	2	10	-2.82	705.56	14.68	0.00
1	1	1	1	10	-2.64	721.20	30.32	0.00

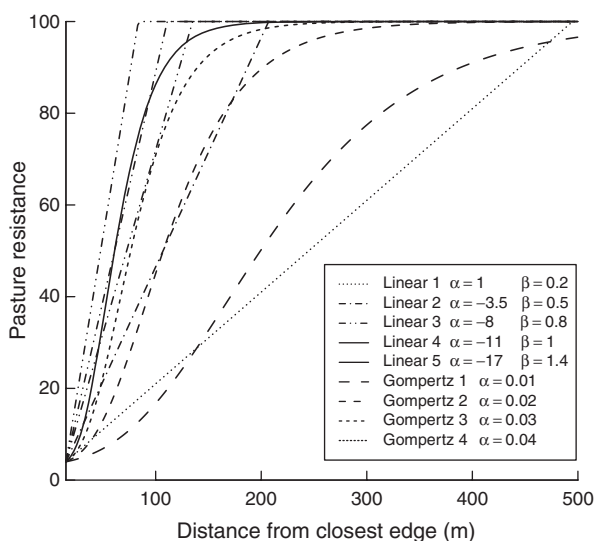


Fig. 2. Costs of crossing 1 m of pasture in relation to the distance from the closest edge of woody vegetation under different dispersal models (see Models 7–15 in Table 1).

when the number of available alternatives was insufficient; Fig. 3). If the movement behaviour of the studied organism is driven by landscape characteristics, one can find the factors and their associated coefficients that maximize the connectivity of the chosen destination in comparison with the alternatives. The random alternatives were created using the free extension of Hawth's Analysis tools for ArcGIS (<http://www.spatial ecology.com/htools>) and constrained to occur in distinct woody vegetation features, to satisfy the model assumption of independence of irrelevant alternatives (see next), and because we never recorded robins in pasture. They were also constrained to be at the same distance from the start point as the observed destination, but with a 200-m tolerance to be able to select a sufficient number of

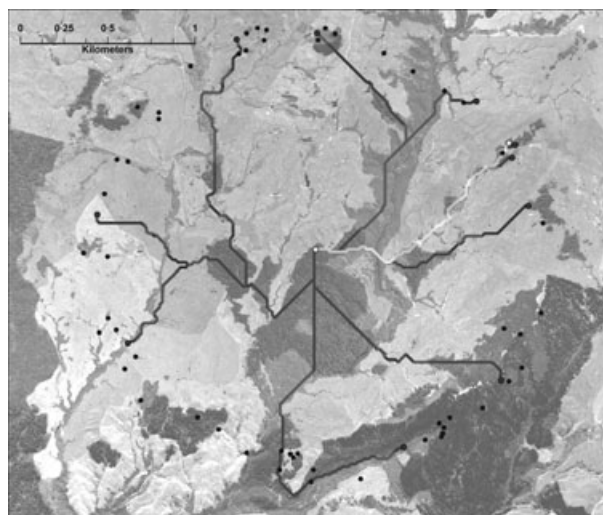


Fig. 3. Example of an observed dispersal step (in white) taken by a juvenile North Island robin matched to 10 randomly sampled alternatives (in dark grey). The black dots represent the set of potential alternatives from which the selected ones were sampled, constrained to have a Euclidean distance within 200 m of that of the observed step. The lines represent the least-cost paths calculated from the cost map of Model 3 (see Table 1).

random alternatives while keeping them similar in distance to the observed destination.

Because the observed dispersal steps were of different lengths, each cost distance was standardized by dividing its value by the Euclidean distance in metres between the start and end point for the steps to be equally weighted. Consequently, the quantity of interest here was not the distance achieved by an individual between two locations, but the mean resistance value per metre, or in other words the mean connectivity of each map pixel along the least-cost path between two locations given the assigned resistance values.

The software ArcGIS 9.2 (ESRI, Redlands, CA, USA) was used to calculate the cost distances for each cost map previously described, using the function CostDistance, and for the selection of random alternatives, automated by a script we wrote in Python for ArcGIS freely available at: http://www.massey.ac.nz/~yrichard/Dispersal_choice_analysis.

Choice analysis

We used conditional logit models (McFadden 1974), sometimes called multinomial logit models (e.g. Cooper & Millsbaugh 1999; but see Hoffman & Duncan 1988), to test whether the preference of dispersers for the observed destinations relative to their matched random alternatives followed a given cost map. To find the cost map that maximized the connectivity of the chosen steps relative to the available alternatives, we compared the models based on their associated AIC (Akaike information criterion) values (Burnham & Anderson 2002). This comparison was made possible because the random alternatives were constrained to be identical among models.

Conditional logit models reflect the fact that an individual chooses the alternative that provides the highest utility (U), and the probability of choosing the alternative i relative to the other alternatives (j) is therefore:

$$p_i = \Pr(U_i > U_j, \forall j \neq i).$$

By expressing utility as a linear model composed of an observed component and an error, this probability can be expressed as:

$$p_i = \Pr(\beta \cdot \text{SCD}_i + e_i > \beta \cdot \text{SCD}_j + e_j, \forall j \neq i),$$

with SCD being the standardized cost distance, β its associated coefficient and e the error. By assuming the independence of irrelevant alternatives (i.e. that the ratio in utility between two alternatives does not change with the addition of another) and that the errors follow a Type-I (Gumbel) extreme value distribution, the choice probability takes the form:

$$p_i = \frac{\exp(\beta \cdot \text{SCD}_i)}{\sum_{i=1}^n \exp(\beta \cdot \text{SCD}_i)}.$$

The part $\exp(\beta \cdot \text{SCD}_i)$ of the equation is often called the step selection function (Boyce *et al.* 2002; Manly *et al.* 2002; Fortin *et al.* 2005) and indicates the acceptability of choice i of cost SCD_i , irrespective of the alternatives. We fitted each model using the function *logit* from the *survival* package in R (R Development Core Team 2008), with the binary-dependent variable being whether the alternative was chosen or not.

Each set of choices was considered to be independent as our data did not show any indication of heterogeneity among individuals or changes in behaviour over individuals' dispersal periods. We checked for the former by adding the individual as a clustering variable in the models (this did not change the results), and checked for the latter by examining cost distances as a function of number of days the individual started dispersing.

A significantly negative β indicates a preference for locations with lower cost distance in comparison with the random alternatives.

Gap-crossing ability

We estimated the maximum gap a juvenile robin can cross by calculating the least-cost paths between each pair of consecutive recorded dispersal points, using the cost maps of the best models. These models

were defined by having $\Delta\text{AIC} < 2$, a common criterion above which models are considered to be significantly inferior (Burnham & Anderson 2002). The maximum distance crossed over pasture by each least-cost path was calculated, giving the maximum gap a juvenile robin is likely to have crossed. Least-cost paths were calculated using the function CostPath in ArcGIS.

Results

Of the 53 radio-tagged juveniles, 38 were relocated out of their natal territories at least once. Of the other 15, two were killed by predators before dispersing, two were never found after capture and ten did not disperse during the lifetime of the transmitters but were not found 3 months after capture within 150 m of their natal territory. Only one juvenile settled next to its natal territory, in the centre of a well-connected 316-ha forest patch. A total of 220 daily dispersal steps were recorded (median length of 389 m; maximum 3762 m), with 1–21 steps recorded per juvenile (median 4.5). Each of the 220 observed steps was matched between 1 and 10 alternative steps (median 10, mean 7.9).

The negative coefficients associated with cost distance were highly significant for all models considered ($P < 10^{-10}$). The worst was Model 1, in which the resistance was identical for the three types of woody vegetation, whereas all other models assumed that dispersal was less likely in pine plantation and shrubland. This indicates that native forest was the least resistant habitat to juvenile robins' movements. The best of Models 2–4, in which the relative resistance of native forest and pasture were held fixed, indicated that juvenile robins disperse more readily through pine plantation than through shrubland. Of the models where pasture resistance increased with distance to the closest edge of woody vegetation (7–15), all but one (12) clearly performed better than those where pasture resistance was spatially invariant. This shows that the spatial arrangement of dispersal barriers is important for robins' dispersal, that is, crossing a gap of length x is less likely than crossing x gaps of 1 length unit.

Using the cost map of the best model (10), the median length of the largest gaps crossed by each juvenile during their dispersal (Fig. 4) was 15 m, indicating that most juveniles moved across the pasture only for very short distances. The largest gap crossed under this model was 109 m, and was consistent among all models with $\Delta\text{AIC} < 2$ (109 m for Models 8–11 and 102 m for Models 14 and 15).

As indicated by Fig. 5, the best model provides a good fit to the data as the distribution of ranks of alternatives randomly chosen from the model matches the observations well. Moreover, the underlying cost map explains well the dispersal choices of dispersers, as the majority of the chosen destinations had a much lower cost distance than random alternatives.

Discussion

Our results show that it is possible to compare models of functional landscape connectivity even from relatively small collections of recorded dispersal locations that cannot be

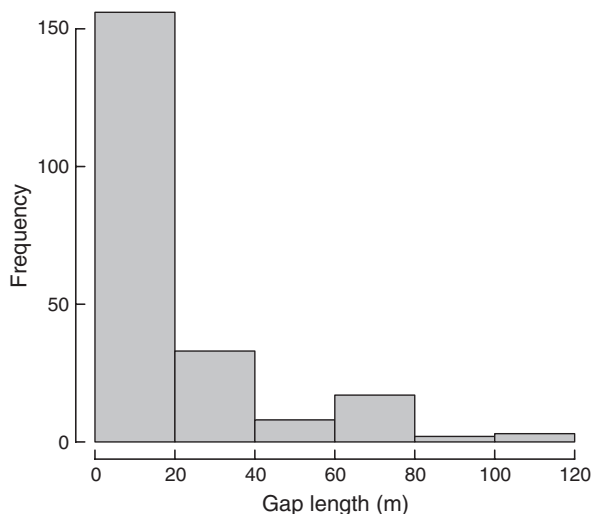


Fig. 4. Distribution of the maximum pasture gap crossed by juvenile North Island robins during their dispersal, where paths taken between recorded locations are assumed to be the least-cost paths calculated from the best model (Table 1).

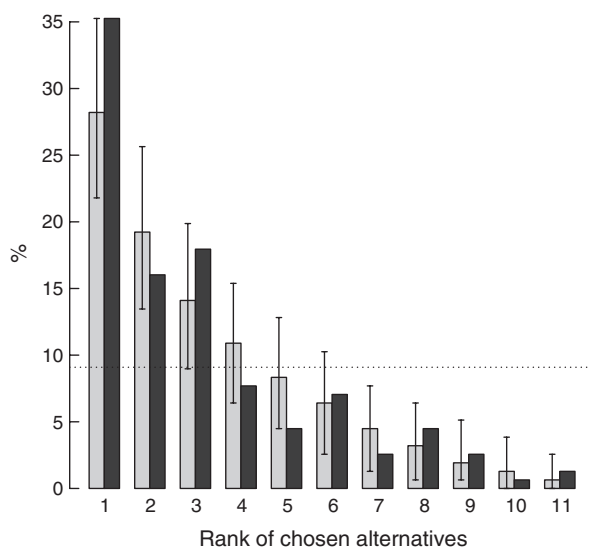


Fig. 5. Distribution of the ranks of observed chosen destinations in terms of cost distance in relation to sampled alternatives (black bars), and median ranks of destinations randomly chosen based on the best supported model (grey bars). Cases where there were fewer than 10 sampled alternatives (17% of observations) are excluded for ease of comparison. Medians are from 5000 simulated sets of choices, and error bars show the 2.5 and 97.5 percentiles. The dashed line indicates the expected distribution if movements were independent of the cost map.

analysed using alternative approaches such as state-space modelling. In many studies, some data on animal movements are often collected and much knowledge can be potentially gained from them, essential for sound management recommendations.

By combining step selection functions and cost distance modelling, the resistance values assigned to various landscape elements can be estimated objectively instead of relying on

expert opinion (Beier *et al.* 2008). It may also be more appropriate than defining the values based on proxy data such as the relative time spent in each habitat type (e.g. Graham 2001), and less costly or more feasible than using genetic markers (e.g. Stevens *et al.* 2006).

Unfortunately, the time required to calculate cost distances currently prevent the estimation of the resistance values by iteration, meaning that only a limited number of possible values and functions can be compared. Indeed, a single cost distance can take several minutes to calculate, and considering multiple hypotheses based on several hundred dispersal steps, each matched to several random alternatives might require several months. Improved communication between statistical and GIS packages (e.g. R and GRASS) along with the continuous increase in computing power will probably overcome this problem in the near future. However, several studies showed that cost distance modelling is very robust to uncertainty in the resistance values, as soon as their rank is correct (e.g. among vegetation types; Beier, Majka & Newell 2009). It might be therefore more beneficial to test for the effect of more factors instead of trying to get more accurate estimates.

Our analysis of the juvenile dispersal of North Island robins clearly showed that robins' movements are determined by both the physiognomy (i.e. the spatial arrangement of elements; Dunning, Danielson & Pulliam 1992) and composition of the landscape. We quantified the resistance of the four main vegetation types present in the study area and found that movements occurred by decreasing order of preference in native forest, pine plantations and shrubland, but movements were impeded by large stretches of pasture between blocks of woody vegetation. Indeed, under the best model none of the studied individuals crossed gaps in woody vegetation larger than 110 m, suggesting that such gaps act as absolute barriers to robin dispersal consistent with Flack's (1979) guess of 100–200 m for South Island robins.

The cost map that best explains observed dispersal steps can then be easily used for the management of landscapes and species. If the start and end points of the dispersal of a number of individuals are known, the multiplication of the cost distance map calculated from a given location by the probability density function fit to the distribution of total cost distances provides a powerful simulation of dispersal from this location. The addition of cost distance maps from multiple locations can reveal the linkages between them and therefore provides a powerful tool to aid corridor design and conservation (e.g. see the corridor function in ArcGIS at: http://webhelp.esri.com/arcgisdesktop/9.2/index.cfm?TopicName=Least_cost_path_and_least_cost_corridor). Similarly, this approach can easily estimate the effect of landscape modifications on a species' movements, which can be used to guide landscape and species management. Being GIS-based, the results can be visually represented, making the information accessible to a range of stakeholders.

The approach aims to identify the mechanisms linking dispersal behaviour to landscape characteristics, and it should be possible to extrapolate the results to other landscapes. The method is also very flexible as most hypotheses about the

factors affecting dispersal may actually be represented as cost maps that can be combined. They can also be applied to different species. One could represent the preference of some species to move through wide corridors instead of narrow ones by making the resistance value of cells a function of corridor width. The avoidance of buildings, roads and valley bottoms by a species, such as roe deer *Capreolus capreolus* (Coulon *et al.* 2008) may be represented by a cost map where the resistance value of each cell would be a function of the distances to these features.

In addition to the analysis of the effect of landscape characteristics on dispersal behaviour, one could also include in the conditional logit model some characteristics of the dispersing individuals such as sex, size, age or sibling status to analyse or control for variations in dispersal behaviour among individuals (Maddala 1983; Hoffman & Duncan 1988; Greene 1991).

Our analysis also illustrates that cost distance modelling can integrate realistic behavioural rules rather than assigning fixed resistance values to cells based only on substrate type. Making the cost of crossing pasture dependent on the distance to the closest woody vegetation significantly improved the fit of the models, indicating that movements are not decided just based on the total distance of each vegetation type that needs to be crossed. Indeed, a path crossing a single gap over x cells of pasture was found to be less likely than one crossing x times a one-cell gap. Ignoring species' gap-crossing abilities may lead to underestimates of connectivity (Castellón & Sieving 2006a) and we therefore recommend that landscape and dispersal ecologists consider it in their studies.

Although the dispersers generally chose destinations with lower-cost distances than random alternatives based on the cost map of the best model (Fig. 5), this was not always the case. However, the situation where all chosen destinations have a lower cost distance than any of their matched random alternatives is unrealistic because this would suggest that the cost map is perfect (i.e. it includes all the elements of the landscape having an effect on dispersal), but also that individuals' dispersal is exactly dictated by the landscape and that individuals have perfect knowledge of their environment. Nonetheless, the explanatory power of our most supported cost map indicates that our methodology was robust to violation of these assumptions. In particular, assuming the individuals' perfect knowledge of the landscape may not be unrealistic in our study, as our observations of the birds suggest that daily steps often involved small exploratory movements that would have given them considerable information about the feasibility of different paths.

The choice of 10 random alternatives per dispersal step is slightly *ad hoc*, and there will be some Monte Carlo error introduced through the random choice. However, the 10 alternatives apply to most of 220 different dispersal steps, meaning the overall sampling effect is likely to be minimal, and re-running the analysis always gave very similar results. Although we did not look at the effect of changing the number of random alternatives, 10 seemed a logical number because increasing this number would lead to a more unbalanced sampling, with many dispersal steps having too few alternative vegetation fea-

tures of similar distance from the starting point. Examination of our landscape also suggests that increasing the number of random alternatives would be unlikely to change the rank of the observed destination among the sets of alternatives. However, the best sampling strategy will depend on the particular landscape, and it would be useful to formally analyse the effects of sampling if the method is to be widely applied.

The role of linkages in the landscape in species persistence has been controversial and heavily debated (Lindenmayer & Fischer 2007), as have the relative effects of habitat loss vs. fragmentation (Fahrig 2002). The controversy may partially reflect the difficulty of studying dispersal, with oversimplification of the dispersal process potentially confounding results in some cases. Modern approaches can overcome many difficulties, and we hope our approach will further enhance the ability of researchers and managers to fit realistic models to a range of data sets, and therefore improve our ability to manage species and landscapes.

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