

Improving inferences about functional connectivity from animal translocation experiments

Matthew G. Betts · Kevin J. Gutzwiller ·
Matthew J. Smith · W. Douglas Robinson ·
Adam S. Hadley

Received: 2 August 2014 / Accepted: 12 January 2015 / Published online: 29 January 2015
© Springer Science+Business Media Dordrecht 2015

Abstract

Context Functional connectivity reflects the ease with which an organism can access different locations within its environment. Because functional connectivity can significantly influence dispersal, habitat selection, and ultimately the viability of populations, it is central to understanding and predicting biological responses to anthropogenic disturbance. Currently, no consensus exists on how to measure functional connectivity.

Objectives and methods Species-centered approaches such as translocation experiments have recently been advocated because they enable strong inferences about functional connectivity. The use of these types of experiments is increasing rapidly, but to date there has been no synthesis of the wide range of methods

available to minimize possible study design problems. Here, we review the recent literature on translocation experiments and highlight potential confounds that may lead to inappropriate conclusions from translocation studies.

Results We report several approaches that can limit the degree to which these confounds affect inferences. We briefly describe paired and repeated-measures designs that use mixed models to address lack of spatial and temporal independence as means for coping with confounds.

Conclusions Such approaches to the design and analyses of translocation experiments should facilitate high-quality measurements of landscape functional connectivity. We encourage investigators to continue functional connectivity research that capitalizes on the advantages of translocations while applying rigorous study designs.

M. G. Betts (✉) · A. S. Hadley
Department of Forest Ecosystems and Society, Oregon
State University, Corvallis, OR 97331, USA
e-mail: matthew.betts@oregonstate.edu

K. J. Gutzwiller
Department of Biology, Baylor University, Waco,
TX 76798, USA

M. J. Smith
Cape Breton Highlands National Park, Ingonish,
NS B0C 1L0, Canada

W. D. Robinson
Department of Fisheries and Wildlife, Oregon State
University, Corvallis 97331, USA

Keywords Animal movement · Dispersal ·
Fragmentation · Functional connectivity · Matrix ·
Structural connectivity

Introduction

Functional connectivity reflects the ease with which an organism can access different locations within its environment by virtue of its mobility, dispersal capacity, and the suitability of landscape elements

(Taylor et al. 1993). In contrast, structural connectivity reflects the physical linkages (e.g., corridors, hedgerows) among locations. Functional connectivity differs from structural connectivity (With and Crist 1995) in that it considers not only the physical configuration of landscape elements, but also animal internal states and motivation as influences on movement across landscapes. Thus, factors such as predator avoidance (Doherty and Grubb 2002; Wilkinson et al. 2013), food availability (Turcotte and Desrochers 2003), perceptual range (Fletcher et al. 2013), and movement capacity (Bélisle et al. 2001) can all affect the functional but not structural connectivity of landscapes. For this reason, functional connectivity is necessarily species- and context-dependent. Understanding functional connectivity is of great importance in landscape ecology and conservation planning because it can strongly influence dispersal, habitat selection, and ultimately the spatial distribution, genetic structure, and viability of populations (Hanski 1998; Baguette and Van Dyck 2007).

There has been a lack of consensus about how to measure connectivity generally (Kindlmann and Burel 2008; Prugh 2009), and this is particularly true of functional connectivity (Bélisle 2005). Taylor et al. (1993) proposed that functional connectivity should be measured for a given individual using “the probability of movement between all points or resource patches in a landscape.” However, the degree of movement in a given landscape can be a poor measure of functional connectivity because the *motivation* to move among patches is unknown in most instances (Bélisle 2005). For example, individuals may show low probability of movement across some cover types (e.g., clearcuts) because resources within their current habitat patch are sufficient to enhance fitness, thereby reducing the *necessity* for movement. But if resources decline in a habitat patch, individuals may be both physically capable and motivated to move across clearcuts to acquire the necessary resources (Smith et al. 2013).

To address the complication of animal motivation, researchers have proposed translocations. Individuals are captured and translocated across landscapes representing gradients in landscape structures (e.g., fragmentation, matrix quality, etc.) to test whether functional connectivity varies in relation to these attributes. Time to home, probability of homing, or probability of gap-crossing are often used as indirect measures of functional connectivity (Brown et al.

2009; Gobeil and Villard 2002; Kennedy and Marra 2010). Because territorial breeding animals have high motivation to return to capture locations, it is argued that translocation experiments standardize motivation and thereby avoid uncertainties about motivation that are inherent in non-experimental studies of routine movements of animals (Magrath et al. 2012; Wilkinson et al. 2013). The experimental aspect of translocation studies can also be logistically efficient; with relatively small sample sizes and low time investments, researchers are able to confront animals with a variety of conditions that might take substantial time to observe under non-experimental conditions (Hadley and Betts 2009). Translocations also offer opportunities for researchers to conduct experiments in landscape ecology—a discipline in which experiments are typically challenging to conduct due to logistical constraints associated with large spatial extents (Eycott et al. 2012).

Experimental translocations are becoming increasingly prevalent in landscape ecology, and they have been used to study functional connectivity for a wide variety of species including mammals (Bowman and Fahrig 2002; McDonald and St. Clair 2004; Smith et al. 2011; Bridgman et al. 2012; Lawes et al. 2013; Smith et al. 2013), temperate and tropical birds (Ibarra-Macias et al. 2011; Kennedy et al. 2011; Bridgman et al. 2012), reptiles (Butler et al. 2005; Brown et al. 2009), amphibians (Huste et al. 2006; Nowakowski et al. 2013), fish (Turgeon et al. 2010), and insects (Conradt et al. 2000; Haynes and Cronin 2006; Fletcher et al. 2013). Using this technique, researchers have assessed the importance of matrix type in facilitating animal movement (Aben et al. 2012; Castellon and Sieving 2006; Kennedy and Marra 2010; Tremblay and St. Clair 2011), reluctance to move through open areas (Desrochers et al. 2011; Smith et al. 2013), the utility of stepping stones to increase connectivity (Boscolo et al. 2008; Gillies and St. Clair 2010), selection of forest fragments while travelling (Hadley and Betts 2009; Gilles et al. 2011; Ibarra-Macias et al. 2011), and landscape isotropy (Bélisle and St. Clair 2001). Empirical data from translocation studies may be particularly useful in parameterizing movement components of individual-based population models (e.g., Schumaker et al. 2014; Severns et al. 2013), which are increasingly used to inform policy decisions (Mawdsley et al. 2009). Translocation data also will enable researchers

to generate more realistic predictions and proper validations of predictions (Aben et al. 2014; St-Louis et al. 2014) from modeling approaches about functional connectivity (e.g., Etherington and Holland 2013; Harju et al. 2013; Santos et al. 2013; Koen et al. 2014).

Three developments are likely to lead to a substantial increase in the number of translocation experiments conducted in the future. First, recent advances in animal tracking technology (Bridge et al. 2011) enable researchers to follow movement paths of translocated individuals as they return home. Second, there is a growing realization that functional connectivity metrics are superior to structural connectivity metrics for predicting population and genetic parameters (Cushman and Lewis 2010; Mimet et al. 2013). Third, the matrix is important in determining species' response to habitat fragmentation (Franklin and Lindenmayer 2009), and its resistance needs to be quantified on a species-specific basis (Betts et al. 2014).

Although translocation experiments offer a powerful approach to measure functional connectivity, several problems with this approach may bias inferences. Existing studies have used a variety of methods to address potential biases, but these methods need to be synthesized so that researchers can more easily access information about various potential biases and systematically address them. Our objective in this *Perspective* article is to stimulate critical thought about possible biases of translocation experiments. Here, we review potential confounds that might lead to inappropriate conclusions from translocation studies, consider recent efforts to overcome these limitations, and suggest possible study designs to improve inferences.

Capture-site quality

The most common response variables measured in translocation studies are the time it takes for an animal to return to the location of capture or 'capture-site', and whether or not an animal returns. The assumptions are that (1) slow return times or no return are both indicators of low functional connectivity, and (2) all translocated animals have the same motivation to return to original capture locations (Bélisle 2005). It is well-known, however, that breeding-site quality is not equivalent across landscapes (Rodenhouse et al. 2003)

and that site quality often can be strongly confounded with the degree of habitat loss and fragmentation (Robinson et al. 1995). Presumably, an individual transported from a high-quality territory that has high potential for breeding success would have stronger motivation to return than would an individual transported from a low-quality territory. Thus, animals from high-quality unfragmented sites could show faster return times or higher propensities to home due only to differences in motivation, irrespective of functional connectivity. In this situation, one cause (motivation due to capture-site quality) for homing speed or probability could be mistaken for another (functional connectivity).

Three approaches could be applied to reduce or eliminate this problem. The most rigorous involves implementing a research design that removes the confounding effect of capture-site quality on motivation. First, if the structure of existing landscapes permits, paired animals from a single patch could be confronted with different treatments. For example, animals captured at the same site near the edge of a contiguous forest could be randomly assigned to two translocation treatments occurring in different directions: toward expected poor-quality matrix, or toward expected high-quality matrix (i.e., a paired design). Alternatively, if individuals of a focal species are difficult to capture, or sufficiently rare that finding multiple animals in the same location is challenging, the same individual could be subjected to both treatments at different points in time (i.e., a repeated-measures design). The strength of this latter approach is that it controls for inter-individual variation that might exist in the first design; its weaknesses are that applying two treatments to the same individual could cause a downward bias in movement rate and animal care regulations may impose a strict limit on the number of times a given individual can be submitted to a stressful experiment. This former effect could be tested for and controlled statistically post hoc by including time since previous treatment as a covariate. Both of these research design solutions require statistical methods that account for the lack of independence between individuals captured in the same patch (e.g., a mixed model with a random effect for patch [for the paired design] or between the two translocations of the same individual [for the repeated-measures design]).

A second approach to deal with the issue of capture-site quality, first used by Bélisle and St. Clair (2001),

involves translocating a subset of individuals that are known to occupy territories with a quality above some known threshold. For instance, individuals known to have paired or bred successfully (Bélisle and St. Clair 2001) or that at least engaged in territorial defense (Gobeil and Villard 2002; Villard and Haché 2012) could be selected.

A third and less-rigorous approach for dealing with problems due to confounding with capture-site quality involves including quantitative estimates of territory quality as covariates in statistical models. For example, habitat characteristics at capture sites of returning and non-returning individuals could be compared (Gobeil and Villard 2002). If it is known a priori that small patches differ from large patches in reproductive success or survival (i.e., some small patches are of lower quality), the effects of these size differences could also be controlled statistically. However, such demographic data are logistically challenging to collect and therefore extremely rare. Even if population-wide estimates exist, these might not correspond to individual demographic rates in specific locations of the landscape. In addition, it is difficult to know which variables should be measured to characterize habitat quality, and unmeasured variables that influence habitat quality at the capture site may be confounded with the landscape features of interest.

Physiological condition of individuals

Through several mechanisms, landscape fragmentation could influence the physiological condition of individuals (Janin et al. 2011; Ellis et al. 2012). For instance, if patch area is reduced to a size smaller than home range size, resource availability will be reduced. In such situations, body condition could decrease directly as a function of resource limitation, or individuals may attempt patch supplementation (use of multiple patches to secure necessary resources; Dunning et al. 1992), which might impose additional stresses from movement through potentially risky matrix (Bonte et al. 2011). This situation raises the possibility that estimates of low functional connectivity in fragmented or poor-matrix landscapes could be due to reduced initial physiological condition rather than to resistance of the landscape itself. This problem could become particularly acute if the stress imposed by the translocation (discussed below) interacts with

initial poor condition of the animal. The statistical solutions to this confound are the same as for instances in which varying quality of capture location is a concern. Specifically, researchers could implement a paired, or a repeated-measures design whereby single individuals are subjected to multiple treatments. Alternatively, researchers could statistically control for animal condition by using covariates in analyses (Villard and Haché 2012).

Release-site quality

Return time and likelihood of an animal returning after translocation also could be influenced by the quality of the habitat into which an animal is released. If the release site is low quality or risky, an individual is likely to be highly motivated to move. Alternatively, if it is high quality, the release site may already be occupied, which could motivate immediate departure due to conflicts with current territorial holders. If a patch is unoccupied and high quality, a translocated individual could simply settle in that patch, thereby leading a researcher to conclude that the intervening landscape is highly unconnected when the lack of movement might have had nothing to do with functional connectivity. In a rare study that monitored fine-scale movements of animals following release, individuals that did not return home were observed settling in unoccupied habitat (Gillies and St. Clair 2008). Although randomly or haphazardly choosing release sites can reduce bias in some contexts (Bélisle et al. 2001), if confounding between release-site quality and the treatment of interest (e.g., fragmentation, matrix quality) is strong, even randomly chosen sites in fragmented landscapes will tend to have lower breeding-site quality, resulting in biases in observed movement behavior.

One solution to this problem is to standardize the quality of release sites. Previous studies have accomplished this in two ways. First, several studies have selected release points where the habitats were as similar as possible in their vegetation composition and spatial configuration of patches (Gobeil and Villard 2002; Kennedy and Marra 2010). Second, investigators have released animals into areas that are known to be inhospitable, such as over water for terrestrial birds (Moore et al. 2008), or into agricultural fields for insects that associate with native plants (Conradt et al.

2000). In the first approach, one can measure habitat conditions to be used as covariates in analyses, under the condition that local habitat quality is not highly confounded with the landscape feature of interest. Strictly speaking, the limitation of the first approach is that the range of inference is limited to the individuals experiencing the specific release-site condition (i.e., individuals under high [or low] motivation to return). Researchers applying the second approach need to realize that release into highly novel contexts (e.g., open water for a forest bird) could result in reactive and unrepresentative behaviors that are based on limited amounts of information about the surrounding landscape. To improve inferences and test the effects of release-site quality, individuals could be grouped into classes that identify them as originating from high or low release-site quality.

Quality of intervening habitat between capture and release sites

Related to the issue of release-site quality is the potential confound caused by site occupancy in the intervening area between capture and release sites. If the intervening landscape exhibits high occupancy by the species in question (as is likely if the species associates with high habitat contiguity and animals are translocated across contiguous habitat), individuals might return to the capture site with greater speed because they are being despotically prevented from tarrying along the way (Rogers 1986). In contrast, individuals of the same species that are translocated across low-quality habitat or highly fragmented landscapes may be afforded the opportunity to return slowly due to the absence of intraspecific competition. This problem is especially important to consider because occupancy is highly likely to be confounded with key variables of interest in such experiments (e.g., matrix composition, fragmentation) (Rizkalla and Swihart 2007). This effect would cause researchers to conclude that functional connectivity is directly influenced by these landscape conditions, when the result might not relate to functional connectivity per se but rather to territorial interactions.

Although this problem may be particularly challenging, there is at least one potential solution; because tracking the detailed movements of many animals is possible with radio-telemetry or global

positioning systems (GPS), it is possible to follow animals and record intraspecific interactions through direct observation, or by inferring them from intersecting path directories to determine whether territorial interactions are an issue (Wilson et al. 2007). If this appears to be the case, a covariate such as the number of interactions observed could be included in multiple regressions to control for this effect statistically. In this vein, Bakker and Van Vuren (2004) accounted for the number of alarm calls of territorial red squirrels (*Tamiasciurus hudsonicus*) when assessing the gap-crossing ability of translocated red squirrels. Of course, interspecific competition could exert the same bias on translocation studies. The magnitude of competition effects is likely to vary greatly among studies, so researchers should determine the degree to which it may bias their specific results.

Release-site familiarity

Another potential confound is the experience of the translocated individual in the release patch. Animals that have previously visited the release patch will presumably home faster and more successfully than individuals that are unfamiliar with the area (Heidinger et al. 2009). The probability of an animal being familiar with a release patch decreases with an increase in distance from the capture site. Homing times are known to increase with distance translocated (Bovet 1984; Desrochers et al. 2011). But it is possible that homing times could be biased low in low-cover landscapes if there is an overall higher probability of previous experience in the surrounding habitat patches. For example, due to patch supplementation, a species may be familiar with surrounding resource patches and as a result return home following a previously travelled route. In contrast, an individual in a larger resource patch may be unfamiliar with nearby patches and take longer to home when translocated the same distance across the same landscape.

At least three approaches are available for dealing with potential familiarity bias. One would be to track an individual's movements, before translocation, to determine its typical area of occupation and whether surrounding habitat patches are visited during normal foraging or breeding activities (Smith et al. 2013). Of course, this will be challenging for individuals that are long-lived and not site-faithful (such information

would be required over multiple years). A second approach would be to translocate animals to areas far removed from their home ranges so that no experience exists with patches in the landscape being traversed until individuals reach the boundary of their home ranges (Castellon and Sieving 2006; Rizkalla and Swihart 2007). Such an experiment might be more likely to approximate the situation during natal dispersal when individuals are naïve to the landscape. A third approach would be to translocate animals only short distances from their home range, which would help to ensure that all individuals will be equally familiar with the release location. This latter approach has been applied in many gap-crossing experiments (Bélisle et al. 2001; Duggan et al. 2012; Smith et al. 2013), but use of short distances may prevent adequate assessment of functional connectivity at *landscape* extents. At a minimum, and with the potential for familiarity bias in mind, authors should justify the translocation distances they use.

Does translocation reflect natural movement and dispersal behavior?

One of the most important assumptions of translocation experiments is that the behavior of animals during movement (hence inferences about functional connectivity) reflects that of individuals under non-experimental (natural or typical) conditions. Most of the translocation studies we reviewed were cautious about inferring results from translocations to dispersal behavior (e.g., Bélisle and St. Clair 2001), even though in some instances the results of such experiments have been successful in predicting species' occupancy at the landscape scale (Desrochers et al. 1999; Jonsen and Taylor 2000). But homing data from translocations may not reflect normal movement for several reasons. First, as noted above, the stress associated with the capture and transport process itself may reduce an individual's vigor (Heidinger et al. 2009). Unless this reduction in vigor interacts with the landscape variable of interest, no between-treatment bias in functional connectivity would be expected; however, overall movement speeds or actual return frequencies could be biased low. To measure the degree of this bias, one could conduct a sham treatment in which individuals are subjected to the

same procedures as are translocated individuals (i.e., capture, transport, etc.) but are returned to their home range. Behavior (e.g., movement and foraging rates) could be compared before and after this treatment in relation to non-manipulated controls (in a before--after-control-impact [BACI]-style design). To our knowledge, only one study of translocation-induced stress has been conducted to date (Volpe et al. 2014).

Of greater concern is that motivation to return to an existing breeding location, where a substantial reproductive investment has already taken place, may constitute higher motivation than might typically exist either during typical foraging movements, or during natal or breeding dispersal. For this reason, some have pointed out that translocation experiments represent an upper bound on the functional connectivity of a landscape (Hadley and Betts 2009; Gillies et al. 2011). However, there are also arguments for the opposite: that dispersers are likely to have *greater* motivation to move than translocated individuals (Rizkalla and Swihart 2007) due to competition avoidance.

Further, observations of the types of vegetation used during return to capture locations could be substantially different during translocation experiments than during dispersal or daily movements. For instance, Rivera et al. (1998) found that during dispersal juvenile wood thrush (*Hylocichla mustelina*) used early successional scrub, a forest type differing substantially from the mature woodland favored by adult breeders.

Studies comparing the habitat selection behavior and movement speeds of animals during translocations to those of non-manipulated animals during routine movements are needed. These comparisons should be fairly straightforward to implement. The priority should be to investigate whether habitat selection during translocations differs from that during natural conditions. Key questions include whether translocated animals are more likely to cross gaps in forest cover, utilize inhospitable matrix, and take direct or more circuitous routes than are non-translocated animals. For instance, Volpe et al. (2014) found that both habitat selection and movement behavior (i.e., propensity to cross gaps) of green hermit hummingbirds (*Phaethornis guy*) were similar between translocation experiments and routine movements.

It will, however, be challenging to test whether translocations reflect functional connectivity of

landscapes for dispersers. Translocation studies tend to rely on adult breeders as experimental subjects precisely because they are highly motivated to return to initial capture (breeding) locations (Bélisle et al. 2001). Translocating juveniles during dispersal would be unlikely to elicit homing behavior. Nevertheless, it would be useful to determine if habitat selection, movement rates, and functional connectivity are comparable between translocated adults and dispersers.

Conclusions

Given the many logistical challenges and confounds that we describe above, researchers may be discouraged from using translocations as a means to determine functional connectivity. However, translocation studies offer a number of benefits for estimating functional connectivity over simply observing routine movements of individuals. Being cognizant of the potential limitations of translocation experiments will tend to strengthen inferences from this tool. The alternatives—making informed guesses about connectivity, or using human-defined landscape structures as proxies for functional connectivity—come at the cost of ignoring key elements of behavioral ecology. Thus, we encourage investigators to develop functional connectivity research that capitalizes on the advantages of translocations, but to apply rigorous study designs that preclude or minimize potential biases.

Acknowledgments This research was supported by funding from NSF-DEB-1457837 to MGB and ASH, and NSF-DEB-1050954 to MGB and WDR. KJG thanks Baylor University for financial support. We are grateful to M. Bélisle and three anonymous reviewers for advice about the manuscript.

References

Aben J, Adriaensen F, Thijs KW, Pellikka P, Siljander M, Lens L, Matthysen E (2012) Effects of matrix composition and configuration on forest bird movements in a fragmented Afrotropical biodiversity hot spot. *Anim Conserv* 15:658–668

Aben J, Strubbe D, Adriaensen F, Palmer SC, Travis JM, Lens L, Matthysen E (2014) Simple individual-based models effectively represent Afrotropical forest bird movement in complex landscapes. *J Appl Ecol* 51:693–702

Baguette M, Van Dyck H (2007) Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. *Landsc Ecol* 22:1117–1129

Bakker VJ, Van Vuren DH (2004) Gap-crossing decisions by the red squirrel, a forest-dependent small mammal. *Conserv Biol* 18:689–697

Bélisle M (2005) Measuring landscape connectivity: the challenge of behavioral landscape ecology. *Ecology* 86:1988–1995

Bélisle M, Desrochers A, Fortin MJ (2001) Influence of forest cover on the movements of forest birds: a homing experiment. *Ecology* 82:1893–1904

Betts MG, Fahrig L, Hadley AS, Halstead KE, Bowman J, Robinson WD, Wiens JA, Lindenmayer DB (2014) A species-centered approach for uncovering generalities in organism responses to habitat loss and fragmentation. *Ecography* 37:517–527

Bonte D, Van Dyck H, Bullock JM, Coulon A, Delgado M, Gibbs M, Travis JM (2011) Costs of dispersal. *Biol Rev Camb Philos Soc* 87:290–312

Boscolo D, Candia-Gallardo C, Awade M, Metzger JP (2008) Importance of interhabitat gaps and stepping-stones for lesser woodcreepers (*Xiphorhynchus fuscus*) in the Atlantic forest, Brazil. *Biotropica* 40:273–276

Bovet J (1984) Strategies of homing behavior in the red squirrel, *Tamiasciurus hudsonicus*. *Behav Ecol Sociobiol* 16:81–88

Bowman J, Fahrig L (2002) Gap crossing by chipmunks: an experimental test of landscape connectivity. *Can J Zool* 80:1556–1561

Bridge ES, Thorup K, Bowlin MS, Chilson PB, Diehl PH, Fléron RW, Wikelski M, philip H (2011) Technology on the move: recent and forthcoming innovations for tracking migratory birds. *Bioscience* 61:689–698

Bridgman LJ, Benitez VV, Graña Grilli M, Mufato N, Acosta D, Guichón ML (2012) Short perceptual range and yet successful invasion of a fragmented landscape: the case of the red-bellied tree squirrel (*Callosciurus erythraeus*) in Argentina. *Landsc Ecol* 27:633–640

Brown JR, Bishop CA, Brooks RJ (2009) Effectiveness of short-distance translocation and its effects on western rattlesnakes. *J Wildl Manag* 73:419–425

Butler H, Malone B, Clemann N (2005) The effects of translocation on the spatial ecology of tiger snakes (*Notechis scutatus*) in a suburban landscape. *Wildl Res* 32:165–171

Bélisle M, St. Clair C (2001) Cumulative effects of barriers on the movements of forest birds. *Conserv Ecol* 5:9

Castellon TD, Sieving KE (2006) An experimental test of matrix permeability and corridor use by an endemic understory bird. *Conserv Biol* 20:135–145

Conradt L, Bodsworth EJ, Roper TJ, Thomas CD (2000) Non-random dispersal in the butterfly *Maniola jurtina*: implications for metapopulation models. *Proc R Soc B-Biol Sci* 267:1505–1510

Cushman SA, Lewis JS (2010) Movement behavior explains genetic differentiation in American black bears. *Landsc Ecol* 25:1613–1625

Desrochers A, Bélisle M, Morand-Ferron J, Bourque J (2011) Integrating GIS and homing experiments to study avian movement costs. *Landsc Ecol* 26:47–58

Desrochers A, Hannon S, Bélisle M, St Clair CC (1999) Movement of songbirds in fragmented forests: can we “scale up” from behaviour to explain occupancy patterns in the landscape? *Int Ornitholog Congr* 22:2447–2464

- Doherty PF, Grubb TC (2002) Survivorship of permanent-resident birds in a fragmented forested landscape. *Ecology* 83:844–857
- Duggan JM, Heske EJ, Schooley RL (2012) Gap-crossing decisions by adult Franklin's ground squirrels in agricultural landscapes. *J Mammal* 93:1231–1239
- Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological processes that affect populations in complex landscape. *Oikos* 65:169–175
- Ellis RD, McWhorter TJ, Maron M (2012) Integrating landscape ecology and conservation physiology. *Landsc Ecol* 27:1–12
- Etherington TR, Holland EP (2013) Least-cost path length versus accumulated-cost as connectivity measures. *Landsc Ecol* 28:1223–1229
- Eycott AE, Stewart GB, Buyung-Ali LM, Bowler DE, Watts K, Pullin AS (2012) A meta-analysis on the impact of different matrix structures on species movement rates. *Landsc Ecol* 27:1263–1278
- Fletcher RJ, Maxwell CW, Andrews JE, Helmeý-Hartman WL (2013) Signal detection theory clarifies the concept of perceptual range and its relevance to landscape connectivity. *Landsc Ecol* 28:57–67
- Franklin JF, Lindenmayer DB (2009) Importance of matrix habitats in maintaining biological diversity. *Proc Natl Acad Sci USA* 106:349–350
- Gillies CS, Beyer HL, St. Clair CC (2011) Fine-scale movement decisions of tropical forest birds in a fragmented landscape. *Ecol Appl* 21:944–954
- Gillies CS, St. Clair CC (2008) Riparian corridors enhance movement of a forest specialist bird in fragmented tropical forest. *Proc Natl Acad Sci USA* 105:19774–19779
- Gillies CS, St. Clair CC (2010) Functional responses in habitat selection by tropical birds moving through fragmented forest. *J Appl Ecol* 47:182–190
- Gobeil JF, Villard MA (2002) Permeability of three boreal forest landscape types to bird movements as determined from experimental translocations. *Oikos* 98:447–458
- Hadley AS, Betts MG (2009) Tropical deforestation alters hummingbird movement patterns. *Biology. Lett.* 5:207–210
- Hanski I (1998) Metapopulation dynamics. *Nature* 396:41–49
- Harju SM, Olson CV, Dzialak MR, Mudd JP, Winstead JB (2013) A flexible approach for assessing functional landscape connectivity, with application to greater sage-grouse (*Centrocercus urophasianus*). *Plos One* 8:e82271
- Haynes KJ, Cronin JT (2006) Interpatch movement and edge effects: the role of behavioral responses to the landscape matrix. *Oikos* 113:43–54
- Heidinger IMM, Poethke HJ, Bonte D, Hein S (2009) The effect of translocation on movement behaviour—A test of the assumptions of behavioural studies. *Behav Process* 82:12–17
- Huste A, Clobert J, Miaud C (2006) The movements and breeding site fidelity of the natterjack toad (*Bufo calamita*) in an urban park near Paris (France) with management recommendations. *Amphib-Reptil* 27:561–568
- Ibarra-Macias A, Robinson WD, Gaines MS (2011) Experimental evaluation of bird movements in a fragmented neotropical landscape. *Biol Conserv* 144:703–712
- Janin A, Lena JP, Joly P (2011) Beyond occurrence: body condition and stress hormone as integrative indicators of habitat availability and fragmentation in the common toad. *Biol Conserv* 144:1008–1016
- Jonsen I, Taylor PD (2000) Calopteryx damselfly dispersions arising from multiscale responses to landscape structure. *Conserv Ecol* 4:[online] URL: <http://www.consecol.org/vol4/iss2/art4/>
- Kennedy CM, Campbell Grant EH, Neel MC, Fagan WF, Marra PP (2011) Landscape matrix mediates occupancy dynamics of Neotropical avian insectivores. *Ecol Appl* 21:1837–1850
- Kennedy CM, Marra PP (2010) Matrix mediates avian movements in tropical forested landscapes: inference from experimental translocations. *Biol Conserv* 143:2136–2145
- Kindlmann P, Burel F (2008) Connectivity measures: a review. *Landsc Ecol* 23:879–890
- Koen EL, Bowman J, Sadowski C, Walpole AA (2014) Landscape connectivity for wildlife: development and validation of multispecies linkage maps. *Methods Ecol Evol* 5:626–633
- Lawes TJ, Anthony RG, Robinson WD, Forbes JT, Lorton GA (2013) Movements and settlement site selection of pygmy rabbits after experimental translocation. *J Wildl Manag* 77:1170–1181
- Magrach A, Larrinaga AR, Santamaria L (2012) Effects of matrix characteristics and interpatch distance on functional connectivity in fragmented temperate rainforests. *Conserv Biol* 26:238–247
- Mawdsley JR, O'Malley R, Ojima DS (2009) A review of climate-change adaptation strategies for wildlife management and biodiversity conservation. *Conserv Biol* 23:1080–1089
- McDonald WR, St. Clair CC (2004) The effects of artificial and natural barriers on the movement of small mammals in Banff National Park, Canada. *Oikos* 105
- Mimet A, Houet T, Julliard R, Simon L (2013) Assessing functional connectivity: a landscape approach for handling multiple ecological requirements. *Methods Ecol Evol* 4:453–463
- Moore RP, Robinson WD, Lovette IJ, Robinson TR (2008) Experimental evidence for extreme dispersal limitation in tropical forest birds. *Ecol Lett* 11:960–968
- Nowakowski AJ, Otero Jiménez B, Allen M, Diaz-Escobar M, Donnelly MA (2013) Landscape resistance to movement of the poison frog, *Oophaga pumilio*, in the lowlands of northeastern Costa Rica. *Anim Conserv* 16:188–197
- Prugh, LR (2009) An evaluation of patch connectivity measures. *Ecol Appl* 19:1300–1310
- Rivera JHV, Rappole JH, McShea WJ, Haas CA (1998) Wood thrush postfledging movements and habitat use in northern Virginia. *Condor* 100:69–78
- Rizkalla CE, Swihart RK (2007) Explaining movement decisions of forest rodents in fragmented landscapes. *Biol Conserv* 140:339–348
- Robinson SK, Thompson FR, Donovan TM, Whitehead DR, Faaborg J (1995) Regional forest fragmentation and the nesting success of migratory birds. *Science* 267:1987–1990
- Rodenhouse NL, Sillett TS, Doran PJ, Holmes RT (2003) Multiple density-dependence mechanisms regulate a

- migratory bird population during the breeding season. *Proc R Soc Lond Ser B* 270:2105–2110
- Rogers LL (1986) Effects of translocation distance on frequency of return by adult black bears. *Wildl Soc Bull* 14:76–80
- Santos SM, Lourenco R, Mira A, Beja P (2013) Relative effects of road risk, habitat suitability, and connectivity on wildlife roadkills: the case of tawny Owls (*Strix aluco*). *Plos One* 8:e79967
- Schumaker NH, Brookes A, Dunk JR, Dunk JR, Woodbridge B, Heinrichs JA, Lawler JJ, Carroll C, LaPlante D (2014) Mapping sources, sinks, and connectivity using a simulation model of northern spotted owls. *Landsc Ecol* 29:579–592
- Severns PM, McIntire EJB, Schultz CB (2013) Evaluating functional connectivity with matrix behavior uncertainty for an endangered butterfly. *Landsc Ecol* 28:559–569
- Smith MJ, Betts MG, Forbes GJ, Kehler DG, Bourgeois MC, Flemming SP (2011) Independent effects of connectivity predict homing success by northern flying squirrel in a forest mosaic. *Landsc Ecol* 26:707–721
- Smith MJ, Forbes GJ, Betts MG (2013) Landscape configuration influences gap-crossing decisions of northern flying squirrel (*Glaucomys sabrinus*). *Biol Conserv* 168:176–183
- St-Louis V, Forester JD, Pelletier D, Bélisle M, Desrochers A, Wulder MA, Cardille JA et al (2014) Circuit theory emphasizes the importance of edge-crossing decisions in dispersal-scale movements of a forest passerine. *Landsc Ecol* 29:831–841
- Taylor PD, Fahrig L, Henein K, Merriam G (1993) Connectivity is a vital element of landscape structure. *Oikos* 68:571–573
- Tremblay MA, St Clair CC (2011) Permeability of a heterogeneous urban landscape to the movements of forest songbirds. *J Appl Ecol* 48:679–688
- Turcotte Y, Desrochers A (2003) Landscape-dependent response to predation risk by forest birds. *Oikos* 100:614–618
- Turgeon K, Robillard A, Gregoire J, Duclos V, Kramer DL (2010) Functional connectivity from a reef fish perspective: behavioral tactics for moving in a fragmented landscape. *Ecology* 91:3332–3342
- Villard M-A, Haché S (2012) Conifer plantations consistently act as barriers to movement in a deciduous forest songbird: a translocation experiment. *Biol Conserv* 155:33–37
- Volpe N, Hadley AS, Robinson WD, Betts MG (2014) Functional connectivity experiments reflect routine movement behavior of a tropical hummingbird species. *Ecol Appl* 24:2122–2131
- Wilkinson EB, Branch LC, Miller DL (2013) Functional habitat connectivity for beach mice depends on perceived predation risk. *Landsc Ecol* 28:547–558
- Wilson RF, Marsh H, Winter J (2007) Importance of canopy connectivity for home range and movements of the rain-forest arboreal ringtail possum (*Hemibelideus lemuroides*). *Wildl Res* 34:177–184
- With KA, Crist TO (1995) Critical thresholds in species responses to landscape structure. *Ecology* 76:2446–2459