

Experimental translocations: pitfalls and alternatives for quantifying animal movement in fragmented landscapes

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ABSTRACT: As anthropogenic change continues to fragment terrestrial habitats, conservation biologists are increasingly concerned with how wild animals move through fragmented landscapes. Experimental translocations have recently gained popularity as a technique to determine landscape permeability by wild animals in fragmented landscapes. In experimental translocations, researchers capture individuals — usually adults — and release them elsewhere in order to determine whether they are able to cross the landscape and return to their original location. We argue that most experimental translocations have two inherent confounding factors — age of the individual and homing ability — and that the narrow spatiotemporal scale of the technique may give it limited ability to address the most important conservation and management questions in fragmented landscapes. We discuss three alternative techniques (telemetry, capture-mark-recapture, and landscape genetics), and recommend that experimental translocations only be undertaken if: 1) they avoid confounding factors; 2) they are validated by other techniques; and 3) no other options are available for obtaining the data. We stress that researchers that do proceed with experimental translocations must acknowledge that they are using an indirect proxy to quantify natural animal movement.

KEY-WORDS: Capture-Mark-Recapture, connectivity, dispersal, landscape genetics, telemetry, translocation experiment.

INTRODUCTION

As anthropogenic change continues to fragment terrestrial habitats, conservation biologists are increasingly concerned with understanding the dynamics of movement (and dispersal) from one habitat patch to another, as these processes are fundamental to source-sink and metapopulation dynamics (Brawn & Robinson 1996), gene flow, genetic structure (Bates *et al.* 2004), and species' persistence in isolated patches (Ferraz *et al.* 2007). Recently, experimental translocations have gained popularity as a means to develop indices of habitat permeability (Boscolo *et al.* 2008; Huste *et al.* 2006; Ibarra-Macias *et al.* 2011; Knowlton & Graham 2010; Villard & Haché 2012). In experimental translocations (also referred to as translocation experiments), researchers capture individuals — usually adults — and release them elsewhere in order to determine whether they are able to cross the landscape and return to their original location. Results are then interpreted as a measure of the likelihood that natural population processes would include the reverse movement (i.e. dispersal), based on the rationale that dispersal events are rare and difficult

to detect directly. Manipulative field experiments can provide powerful contexts for controlling environmental variation, but in the case of experimental translocations, researchers can introduce confounding factors (e.g., age effects, homing ability) that may bias results or make them difficult to interpret. Here we argue that to provide a meaningful index of animal movement, particularly dispersal, in fragmented systems, researchers undertaking experimental translocations must take great care to reduce confounding factors and to validate results with other techniques. We suggest three alternatives to experimental translocations, and discuss how these alternatives can be useful to validate or replace experimental translocations.

CONFOUNDING FACTORS

Age of translocated individuals

Experimental translocations frequently use territorial animals because those individuals are invested in a particular area, and are thus motivated to return to the area after translocation; thus “successful” returns are relatively

easy for technicians to detect (e.g., Wilson *et al.* 2007, Hadley and Betts 2009). Most experimental translocations of this type mimic patterns of adult dispersal (dispersal: directed movement from one territory in search of another; Greenwood and Harvey 1982), as they attempt to quantify an animal's ability to move from one territory to another. The overwhelming majority of dispersal events, however, are undertaken by juveniles (Greenwood & Harvey 1982), so although dispersing adults certainly can contribute to gene flow, their contribution is likely small relative to that of dispersing juveniles. Understanding juvenile dispersal is particularly important in fragmented landscapes where habitat quality is variable, as they may represent pioneers who cross non-habitat matrix and occupy marginal habitats (Johnson 2011; Rohwer 2004) thus contributing disproportionately to metapopulation dynamics compared to adults. Dispersing juveniles generally venture out from their natal home ranges in search of other areas with suitable resources but without intraspecific competitors; unlike translocated adult territory holders, they have no motivation to return to a specific location. Juvenile animals are fundamentally different from adults in their physiological state and level of experience on the landscape (Yoder *et al.* 2004), so attempting to mimic dispersal using territorial adults may produce an inaccurate picture of dispersal patterns (Knowlton & Graham 2010). The inexperience of juveniles makes them vulnerable to predators (Yoder *et al.* 2004), which again suggests that their decisions on how to move about the landscape will be fundamentally different from those of older conspecifics. We know of no experimental translocation that validates the assumption that territorial adults and dispersing juveniles move similarly across fragmented landscapes — a step that we believe is critical if data are to be meaningfully applied to conservation or management.

Homing ability

Experimentally translocated animals are generally tested on their ability to return to or toward their territories, which introduces the confounding factor of homing. When animals are captured for translocation, they are generally placed in an opaque receptacle and blindly transported to a new location for release. An animal attempting to return to its territory should take one of three approaches: (1) prior knowledge of the landscape; (2) internal homing capacity; or (3) undirected movement. Thus, experimental translocations do not control for homing ability of individuals or species — individuals could easily fail to return because they lost their way, died, or simply settled elsewhere, rather than because they encountered barriers to movement. For

example, Kennedy and Marra (2010) acknowledge that the faster return times of translocated wintering migrant American Redstarts (*Setophaga ruticilla*) relative to resident Jamaican Todies (*Todus todus*) could have been because of the redstarts' ability to traverse the matrix, or because their previous experience or homing ability allowed them to better navigate the landscape.

ALTERNATIVE TECHNIQUES

While acknowledging that no technique for studying animal movement is without considerable assumptions, biases, and costs, we present three alternatives that can provide useful data to supplement or replace data provided by translocation experiments.

Telemetry on dispersing individuals

Telemetry is the most direct way to study how individuals move about the landscape. Based on home range size, frequency of movement, or compositional analyses of habitat use (Aebischer *et al.* 1993), researchers can draw conclusions about the suitability of certain landscape types, the permeability of barriers, and the porosity of the matrix. For an assessment of dispersal across variable landscape features, researchers can track juveniles during dispersal. The obvious advantage here is that naturally dispersing animals will reveal their own habitat choices, compared to translocated animals that are instead revealing their response to translocation to a location chosen by the investigator. Indeed, telemetry studies of dispersal can be insightful with a reasonable sample size, but this may be challenging if the focal species is rare, suffers high juvenile mortality, or is too small to support a tracking device. To limit the effects of transmitters on juvenile mortality, tracking devices should generally be <5%, or ideally <3% of body weight for small birds (pers. obs.). Real-world constraints may make it difficult to use telemetry on naturally moving animals to address questions regarding movement decisions, but under the right conditions, it can provide powerful insights (e.g., Riecken and Raths 1996; Yoder *et al.* 2004; Tarwater and Brawn 2010). Transmitters (e.g., radio, global positioning system [GPS], global system for mobile communications [GSM]) can be costly, but technology is evolving rapidly such that smaller, longer-lasting, precise and powerful transmitters are ever more affordable. The benefits of telemetry on juvenile animals must be carefully weighed against the disadvantages, which include the cost of transmitters and the challenge in matching the spatiotemporal scale of data collection to the scale of the research question.

Capture-mark-recapture (CMR) studies

CMR studies have been used for decades to determine how animals move about in fragmented landscapes. For example, researchers have applied state-space CMR models to dozens of different systems (Spendelov *et al.* 1995; Skvarla *et al.* 2004; Royle *et al.* 2013). CMR studies assume that individuals are identifiable, either by marking (e.g., band), or by some distinctive feature (e.g., DNA, unique spot pattern). Other spatially-explicit models consider the locations of “traps” (including nets and camera traps), and are flexible with regards to survey design (Royle *et al.* 2010). These models can be extended to determine how the distribution of habitat on the landscape affects movement among capture locations (Wang *et al.* 2011). With CMR models, biologists can gain a real understanding of both individual movements and population distribution across fragmented landscapes (frequently with the bonus estimation of survival and density) — often with no more effort than experimental translocations. Granted, many long-distance dispersers are never recaptured, but established statistical techniques can account detectability (e.g., Royle *et al.* 2011). Disadvantages to CMR include the lack of spatial resolution on movement paths, the potential computational complexity of statistical models (but see White and Burnham 1999), and the considerable number of recaptures required for models to run. Further, recapture rates may be quite low and vary enormously by organism. To plan for sample size issues, researchers can run simulations to determine the number of recaptures necessary for the desired level of statistical power.

Landscape genetics

Landscape genetics is an essential component of fragmentation research because it can estimate the consequences of dispersal (or the lack thereof) within fragmented landscapes as expressed in the form of gene flow (Manel *et al.* 2003; Storfer *et al.* 2007; Holderegger and Wagner 2008). Once time-consuming and costly, landscape genetics techniques are increasingly inexpensive and straightforward. Primers and reagents are becoming less expensive, genetics labs are more common, and DNA is easier to collect and preserve. Further, the time-consuming task of developing a genetic library (e.g., microsatellites, single nucleotide polymorphisms [SNPs]) has become easier with next-generation sequencing, which can identify hundreds of potentially polymorphic loci that can then be used in analyses of genetic structure (Lerner & Fleischer 2010). In fragmented landscapes, genetic drift, mutation, selection, and dispersal can lead to measurable genetic structure among populations. Researchers can then use measures

of genetic differentiation (e.g., F_{st} , R_{st}) to estimate gene flow (e.g., Woltmann *et al.* 2012) and migration rate among habitat patches (Beerli & Felsenstein 2001). As in CMR studies, researchers can overlay landscape variables to determine how the landscape affects gene flow in fragmented systems (e.g., Pavlacky *et al.* 2009). Using landscape genetics, researchers can track movement of genetic information among populations on the timescale of generations, which reflects dynamic landscape patterns over time.

We believe the important research question is whether fragmented landscapes have sufficient gene flow among populations, thus although translocation experiments may provide interesting insights on individual movement across the matrix (Moore *et al.* 2008), they represent only a small part of the spatiotemporal dynamics of animal movement. Granted, landscapes appropriate for genetics studies can be challenging to locate on the ground, and the technique has its limitations (Storfer *et al.* 2010); however, if researchers take care to find landscape replicates appropriate to address their questions (Beier & Gregory 2012), a well-designed landscape genetics study can address many of the important questions sought by translocation studies (e.g., can species X cross barrier Y?), yet with populations rather than individuals, and without the confounding factors of animal age and homing ability. Species with small, isolated populations and fast generation times are most likely to show genetic structure (Allendorf & Luikart 2007), with minimum divergence times of about 10–20 generations — depending on the effective population size (Slatkin 1993; Waples 2007; Wright 1943). Again, before investing in field work, researchers can run simulations to calculate the number of individuals necessary for the desired level of power (Ryman & Palm 2006). Although the advantages to landscape genetics are many, disadvantages include the cost of lab work, the effort required for capture, and the relatively poor resolution of genetic techniques on small spatiotemporal scales.

EXAMPLES OF MEANINGFUL TRANSLOCATION EXPERIMENTS

When carefully validated with other techniques, translocation experiments may provide useful information for managers — particularly when alternative techniques cannot provide answers at the scale appropriate of the research question. Moore *et al.* (2008) performed an experiment in which they captured birds at Barro Colorado Island in Panama, rowed them out into Lake Gatun, and released them at different distances from

the shore to determine how far they could fly in a single flight. Moore *et al.*'s (2008) study cleverly demonstrated how far birds can fly across water — a critical issue in their island system. Importantly, the fundamental test they performed had nothing to do with interpreting movements back to a territory; rather, the birds were simply trying to return to any dry land. Although Moore *et al.*'s (2008) study addressed an important issue, it remains unclear whether the results provide “evidence for extreme dispersal limitation” in landscapes fragmented by matrices other than water.

In the face of rapid habitat fragmentation, conservation biologists have recently employed large-scale models of how populations move and disperse through variable landscapes to inform conservation planning (Knowlton & Graham 2010; Castellon and Sieving 2007). Those models can be informed (parameterized) using small-scale studies of individuals, including those using occupancy and experimental translocations. In one such example, Castellon and Sieving (2007) elegantly combined data from several of their previous small-scale studies (Castellón & Sieving 2006a 2006b) to parameterize a population viability analysis and landscape movement model designed to evaluate how increases in connectivity among isolated habitat patches would support increases in number of breeding birds called Chucaco Tapaculos (*Scelorchilus rubecula*). Here the authors were appropriately cautious when applying the data from a translocation experiment (Castellón & Sieving 2006a), using them only in the absence of other data to confirm that: 1) tapaculos used wooded corridors; and 2) inter-patch distance was on the scale of typical tapaculo movement. They did not use their data on boundary permeability or return times through different matrix types by translocated adults, which would be a riskier assumption; rather, data on patch size and matrix composition were applied to the model via studies of patch occupancy — a measure of animal presence (MacKenzie *et al.* 2006). In this case, experimental translocations certainly provided an improvement over an uninformed model. On the other hand, the assumption remains that territorial adults returning towards their territories used corridors similarly to dispersing juveniles. To validate this tapaculo population viability analysis and landscape movement model, researchers could employ a well-designed, replicated natural experiment of tapaculo genetic structure across different matrices.

In another well designed example of a translocation experiment, Stevens *et al.* (2006a) captured Natterjack toadlets (*Epidalea* [formerly *Bufo*] *calamita*) and transferred them to a Y-shaped device in which the toadlets could select from two different habitats, i.e. the two branches of the Y. The authors avoided confounding factors of age and homing because: 1) toadlets are the dispersing stage of the species; and, 2) toadlets were not

trying to return to territories. Further, the researchers carefully designed this translocation experiment to assess boundary permeability. Ultimately, Stevens *et al.* (2006b) used the translocation data along with data on dispersal rates obtained from a microsatellite landscape genetics study to test the hypothesis that differences in boundary permeability among habitat types affected dispersal of the species — it did. Here researchers had a specific piece of data in mind that would be difficult to obtain without experimental translocations, performed the experiment with little cost, and integrated results with those obtained from genetics and lab experiments — a combined approach considered advantageous when studying dispersal (Nathan *et al.* 2003; Nathan 2001)

CONCLUSIONS

Given the potential for confounding factors (e.g., individual age, homing ability) in experimental translocations, they should be used with great caution, especially in the absence of results from telemetry, CMR, or landscape genetics (e.g., Lowe *et al.* 2008). Ecosystems are being fragmented at a frightening rate (e.g., Numata, *et al.* 2011) and climate change will force distribution shifts across these altered landscapes (Wright *et al.* 2009). Conservation planning efforts designed to increase connectivity will maximize biodiversity conservation if the studies that inform them are as close to real conditions as possible and at the appropriate spatiotemporal scale for the question. We believe that the critical question in fragmented landscapes is not: “could this translocated adult potentially cross barrier X?”; rather, it is: “does barrier X significantly reduce population processes or gene flow?” Therefore, we caution that translocation experiments may not be applicable to the appropriate conservation questions unless they are part of research aimed at a larger spatiotemporal scale. When the information gained from experimental translocations cannot be obtained elsewhere, researchers must control for confounding effects and use experimental translocations in conjunction with other techniques, such as validating findings from experimental translocations with species-specific studies of naturally moving individuals (Volpe *et al.* 2014). Finally, researchers that do proceed with experimental translocations must acknowledge that they are using an indirect proxy to quantify natural animal movement. Given the great need for us to understand how animals move and disperse through heterogeneous landscapes in this critical period for biodiversity conservation (Barnosky *et al.* 2012; Lawrence & Wright 2009; Van Dyck & Baguette 2005; Wright *et al.* 2009) researchers should apply resources to contemporary techniques that most directly and realistically quantify animal movement

at the appropriate spatiotemporal scale, undertaking experimental translocations cautiously, and only in the absence of other solutions.

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