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## Meta-Analytic Review of Corridor Effectiveness : Una Revisión Meta-analítica de la Efectividad de los Corredores

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# A Meta-Analytic Review of Corridor Effectiveness

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Abstract: Using corridors for conservation is increasing despite a lack of consensus on their efficacy. Specifically, whether corridors increase movement of plants and animals between habitat fragments has been addressed on a case-by-case basis with mixed results. Because of the growing number of well-designed experiments that have addressed this question, we conducted a meta-analysis to determine whether corridors increase movement; whether corridor effectiveness differs among taxa; how recent changes in experimental design bave influenced findings; and whether corridor effectiveness differs between manipulative and natural experiments. To conduct our meta-analysis, we analyzed 78 experiments from 35 studies using a conservative bierarchical Bayesian model that accounts for hierarchical and sampling dependence. We found a highly significant result that corridors increase movement between habitat patches by approximately 50% compared to patches that are not connected with corridors. We found that corridors were more important for the movement of invertebrates, nonavian vertebrates, and plants than they were for birds. Recent methodological advances in corridor experiments, such as controlling for the area added by corridors, did not influence whether corridors increased movement, whereas controlling for the distance between source and connected or unconnected recipient patches decreased movement through corridors. After controlling for taxa differences and whether studies controlled for distance in experimental design, we found that natural corridors (those existing in landscapes prior to the study) showed more movement than manipulated corridors (those created and maintained for the study). Our results suggest that existing corridors increase species movement in fragmented landscapes and that efforts spent on maintaining and creating corridors are worthwhile.

Keywords: connectivity, corridors, habitat fragmentation, immigration, meta-analysis

Una Revisión Meta-analítica de la Efectividad de los Corredores

**Resumen:** La utilización de corredores para la conservación está incrementando no obstante la falta de consenso sobre su eficacia. Específicamente, sí los corredores incrementan el movimiento de plantas y animales entre fragmentos de bábitat ha sido abordado caso por caso, con resultados mixtos. Debido al creciente número de experimentos bien diseñados para abordar esta pregunta, realizamos un meta-análisis para determinar sí los corredores incrementan el movimiento; sí la efectividad de los corredores difiere entre taxa; cómo ban influido en los resultados los recientes cambios en el diseño experimental; y sí la efectividad del corredor difiere entre experimentos manipuladores y naturales. Para realizar el meta-análisis, analizamos 78 experimentos de 35 estudios mediante un modelo Bayesiano jerárquico conservador que considera la dependencia jerárquica y de muestreo. Obtuvimos un resultado altamente significativo en el que los corredores incrementan el movimiento entre fragmentos en casi 50% en comparación con fragmentos que no están conectados, vertebrados excepto aves y plantas que para las aves. Los avances metodológicos recientes en los experimentos de corredores, como controlar el área agregada por los corredores, no influyó en el incremento de movimiento por los corredores, mientras que el movimiento por los corredores disminuyó al controlar la distancia entre la fuente y los fragmentos recipientes conectados o no conectados. Después

§Address correspondence to: K. H. Beard, email karen.beard@usu.edu Paper submitted July 15, 2009; revised manuscript accepted October 14, 2009. de controlar las diferencias entre taxa y sí los estudios controlaban la distancia en el diseño experimental, encontramos que los corredores naturales (aquellos que existen en paisajes antes del estudio) mostraron más movimiento que los corredores manipulados (aquellos que fueron creados y mantenidos para el estudio). Nuestros resultados sugieren que los corredores existentes incrementan el movimiento de especies en paisajes fragmentados y que los esfuerzos para mantener y crear corredores valen la pena.

Palabras Clave: conectividad, corredores, fragmentación del hábitat, inmigración, meta-análisis

#### Introduction

Habitat fragmentation, a frequent consequence of habitat loss, is a primary threat to populations and species (Hanski 1998; Wilcove et al. 1998) because isolated subpopulations are expected to experience reduced population viability and ultimately greater risk of extinction (Hilty et al. 2006). Colonization and gene flow between habitat patches, however, can mitigate these effects (MacArthur & Wilson 1967; Brown & Kodrick-Brown 1977). Thus, movement across the landscape is critical for population and species survival (Haddad et al. 2003). Furthermore, the ability to disperse from one habitat to another is becoming increasingly important given expected range shifts with climate change (McLaughlin et al. 2002).

Land managers have few methods for increasing immigration between habitat patches. A favored option is to create landscape corridors because it has the potential to increase migration rates of many species. Nevertheless, there has been much debate about whether or not organisms actually use corridors (Beier & Noss 1998; Haddad 2008). In a review of corridor studies, Beier and Noss (1998) found that few studies that tested whether corridors increased movement adequately addressed the topic; most of the studies they examined lacked replication, had improper controls, or used inappropriate study organisms. Thus, land managers have in the past implemented corridors without scientific consensus on their utility or guidance on their design (Hess & Fischer 2001; Bennett et al. 2006).

Only over the last 10 years have studies adequately addressed the efficacy of corridors and overcome design flaws described by Beier and Noss (1998). Therefore, until recently, the ability to determine corridor effectiveness has been limited. Although many of the more recent studies conclude that corridors are effective (e.g., Castellón & Sieving 2006; Damschen et al. 2006; Baker 2007), some studies have not (e.g., Collinge 2000; Hoyle & Gilbert 2004; Rantalainen et al. 2005). In addition, although the results from an individual study may be convincing, each study only addresses the issue on a case-by-case basis, often with a limited number of species and replicates and in one ecosystem. Thus, any single study does not address the primary question about corridors that needs answering: Do corridors increase movement between habitat patches for a diverse set of organisms across a wide range of ecosystems?

Meta-analysis is an effective way to synthesize corridor research because it combines data collected through a variety of methods, across a range of scales, and with a diverse set of species. Additionally, a meta-analysis can be used to address important unanswered questions in corridor research, such as which attributes of corridor design make them most effective (Haddad 2008). We used meta-analysis to address some unresolved questions about corridors: Do corridors increase movement? Does corridor effectiveness differ among taxa? How have recent changes in the design of corridor studies influenced conclusions about corridor effectiveness? Is the effectiveness of corridors restricted to manipulative experiments (i.e., experiments in which researchers created and maintained isolated patches and corridors) or are corridors similarly effective in real-world landscapes?

#### Methods

We searched for studies that examined the relationship between corridors and movement by conducting keyword searches in Web of Science (ISI) and the Wildlife and Fisheries Worldwide electronic bibliographic databases. We used different combinations of the keywords *corridor*, *movement*, *effectiveness*, *connectivity*, and *habitat connectivity*. We also searched the Digital Dissertations database for unpublished theses and dissertations. We found additional studies through cited references and contacted authors when data were not readily available in manuscripts.

We found a total of 130 laboratory and field studies dating from 1985 to 2008, but we only used studies with replicated corridor and control treatments. We defined a corridor as a narrow, linear (or near-linear) piece of habitat that connects two larger patches of habitat that are surrounded by a nonhabitat matrix (Beier & Noss 1998). We defined controls as two unconnected patches of similar habitat surrounded by a nonhabitat matrix. We excluded studies that used the matrix itself as the control treatment rather than unconnected habitat patches. We used both direct and indirect measures of movement as response variables (see Supporting Information). Direct measures included measurement of the proportion of individuals that moved, movement rate of individuals (e.g., Collinge 2000; Brinkerhoff 2002), and number of seeds moved (e.g., Haddad et al. 2003). Indirect measures

included measurement of species abundance and richness (e.g., Mabry et al. 2003; Rantalainen et al. 2004), which could result if corridors facilitate dispersal in otherwise isolated patches via the rescue effect (Hanski 1999).

We used the following additional decision criteria. If the study was conducted over multiple years, we used the last year of data to control for the nonindependence of temporal data (Gurevitch & Hedges 2001). When they were part of the study design, we used "winged" or "broken corridor" as opposed to "rectangle" patch as controls (e.g., Hoyle & Gilbert 2004; Levey et al. 2005). Winged and broken corridors added area to control patches and controlled for potential drift-fence effects of corridors, whereas rectangular patches only added area to control patches. If data from an experiment were presented in multiple studies, we used the study that provided the clearest analysis of movement through corridor and control treatments (e.g., Gonzalez et al. 1998; Aars & Ims 1999). If studies measured movement in corridors of different widths or lengths, we used the treatment with the narrowest or longest corridor because we thought these were more representative of real-world corridors and would be more likely to be used as a conduit for movement rather than as increased habitat (Soulé & Gilpin 1991; Andreassen et al. 1996). We excluded studies that were based solely on models (e.g., Falcy & Estades 2007) or in which species did not move of their own volition (e.g., Perault & Lomolino 2000; Forbes & Chase 2002; Falcy & Estades 2007).

We identified five research questions to address with the meta-analysis, each based on some covariate of interest in the data. We determined if there were differences in movement across corridors for each of the following covariates: animals (invertebrates, birds, nonavian vertebrates) and plants; experiments that did and did not control for area; experiments that did and did not control for distance between source and recipient patches; manipulative (i.e., patches and corridors were created and maintained for the experiment) and natural experiments (i.e., prior to the experiment, the corridor existed on the landscape, which may have been modified by humans but not for the purposes of the experiment); and experiments conducted at one study site, the Savannah River Site, South Carolina (U.S.A.), where 40% of the experiments were conducted, compared to all other study sites. Data classifications (e.g., organism type, control for area) were derived directly from manuscripts.

To determine whether movement differed between corridor and control treatments among these covariates, we used a meta-analysis model with random effects (REMA) and a hierarchical Bayes linear model (HBLM) (Stevens & Taylor 2009), which controls for both sampling dependence and hierarchical dependence. Sampling dependence occurs in multiple-treatment studies (Gleser & Olkin 1994), where one control group is compared with more than one experimental group. Hierarchical dependence occurs when many experiments are performed as a part of a single study (e.g., the response of many species is reported for the same experimental units [Stevens & Taylor 2009]). Accounting for dependence in a meta-analysis model (such as our HBLM) reduces the effective sample size and decreases the weight of dependent and extreme estimates of effect size, which leads to more conservative results. Results from the REMA and HBLM analyses were similar (similar significant differences were found with both models); therefore, we only report the results of the HBLM. Statistical methods for both models are available (Kulmatiski et al. 2008; Stevens & Taylor 2009) and were implemented in R (R Development Core Team 2008) with the metahdep package (Stevens & Nicholas 2009). Finally, we used a multiple regression approach with backward elimination to compare the results of models with one covariate to the results of a model with multiple covariates. The model started with all covariates, and the covariates with the largest p-value were iteratively dropped until all remaining *p* values were < 0.10.

To conduct the analyses, for each experiment *i*, we used the mean  $(X_e, X_c)$  and standard deviation  $(S_e, S_c)$  of the response variable and the number of replicates  $(N_e, N_c)$  for both the corridor and control treatments to calculate the unbiased estimate of effect size, *d* (Cooper & Hedges 1994; Gurevitch & Hedges 2001):

$$d_i = J_i \frac{X_e - X_c}{S_p},\tag{1}$$

where  $S_p$  is the pooled standard deviation of the experiment;

$$S_p = \sqrt{\frac{(N_e - 1)S_e^2 + (N_c - 1)S_c^2}{N_e + N_c - 2}},$$
 (2)

where  $J_i$  is the unbiasing constant for the effect size d for each experiment;

$$J_i = 1 - \frac{3}{4(\mathrm{df}_i) - 1},\tag{3}$$

where  $df_i$  is the error degrees of freedom for each experiment; and

$$\mathrm{df}_i = N_e + N_c - 2. \tag{4}$$

Thus, the effect size d is the difference in SD units between the means of experimental and control groups. The variance of  $d_i$  was calculated as

$$V_i = \frac{J_i^2 \cdot \mathrm{df}_i}{\mathrm{df}_i - 2} \cdot \left(\frac{1}{N_e} + \frac{1}{N_c}\right) + \left(\frac{J_i^2 \cdot \mathrm{df}_i}{\mathrm{df}_i - 2} - 1\right) \cdot d_i^2.$$
(5)

Experiments with  $N_e = N_c = 2$  (i.e., df = 2) caused numerical problems (dividing by zero) in the calculation of V. Dividing by zero occurred in five experiments: two in one study (Andreassen et al. 1998) and three in another

(Haddad et al. 2003). So these experiments were pooled by study in an analysis of variance model and resulted in df = 4 for each study, which we used to calculate  $V_i$ . Combining experiments introduced sampling dependence for these studies, but was controlled for statistically by the HBLM model. The combined response variables were arbitrary because only df and the mean square for error were needed for analysis. Finally, we omitted two experiments from the data set: one with  $N_e = N_c = 2$ , which could not be combined with another experiment from the same study (Coffman et al. 2001), and one that reported  $S_e = S_c = 0$  (Darcy & Eggleston 2005), which resulted in an undefined d.

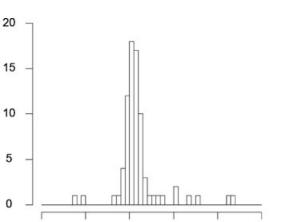
In our study d > 0 indicates corridors increased movement between patches, whereas d < 0 indicates corridors did not increase movement. We used the conventional interpretation of the magnitude of the effect size (Cohen 1988). To ease interpretation of d, we plotted the relationship between d and the proportional change in movement rate  $(X_e - X_c) / |X_c|$  for each experiment. We conducted a Kolmogorov-Smirnov test to determine whether effect sizes were normally distributed. We determined potential effects of publication bias through visual observation of a funnel plot and a normal quantile plot of the standardized estimates of d (Wang & Bushman 1998).

#### Results

The final data set consisted of 78 experiments from 35 studies from 16 ecological journals, theses, and dissertations between 1988 and 2008 (Supporting Information). They included experiments involving amphibians (1 species), birds (7), fishes (2), invertebrates (29), mammals (22), and plants (17). Effect sizes were distributed normally (p = 0.74). A funnel plot showed possible, but very weak, evidence of publication bias, whereas the normal-quantile plot supported the conclusion that no bias existed.

Three of the 35 studies had sampling dependence (Andreassen et al. 1998; Baur 1991; Haddad et al. 2003). Overall, 17 of the 35 studies had mild hierarchical dependence (two to three species), but only four of those had data for over four species (Baur 1991; Tewksbury et al. 2002; Haddad et al. 2003; Rantalainen et al. 2004; Darcy & Eggleston 2005).

Overall, 60 experiments showed positive effect sizes, which suggests corridors increased movement between habitat patches, and 18 experiments showed negative effect sizes (Fig. 1). Across all studies, the mean effect size was positive, of medium strength, and highly significant (d = 0.48 [SE 0.10], p = 0.0001), meaning there was a positive effect of corridors on movement. Statistically, d = 0.48 means that, on average, corridors increased



Number of experiments

-10

-5

Effect size estimate (d)

5

10

15

Figure 1. Number of corridor experiments by effect size. Positive effect sizes suggest species dispersed more to babitat patches connected by corridors than to unconnected patches (n = 78 experiments).

0

movement between habitat patches by approximately 0.5 SD compared with controls. When we compared *d* with the proportional change in movement rate, d = 0.48 represented an approximately 50% increase in movement between habitat patches connected by a corridor relative to movement between unconnected habitat patches (Fig. 2).

Plant movement was higher than animal movement in the single covariate models (p = 0.037). When we divided the animal category into bird, invertebrate, and nonavian vertebrates, we found no difference in movement through corridors among taxa in the single covariate

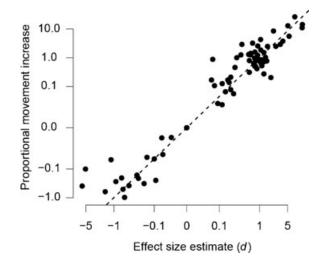


Figure 2. Relationship between effect size (d) and the proportional movement increase  $(X_e - X_c) / |X_c|$ ) for each corridor experiment. To aid visualization, both axes are log scale. The dashed line indicates equality.

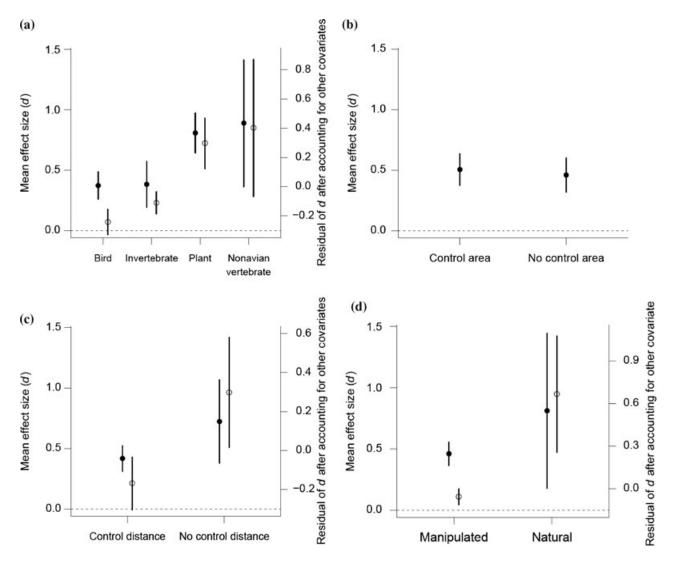


Figure 3. Mean effect size (solid circles) and residual effect size estimates after accounting for other covariates (open circles) (SE 1) (a) for birds (n = 7), invertebrates (n = 29), plants (n = 17), and nonavian vertebrates (n = 25); (b) between studies controlling (n = 28) and not controlling for area (n = 50); (c) between studies controlling (n = 44) and not controlling for distance (n = 34); and (d) between manipulated (n = 66) and natural experiments (n = 12).

model (with bird as the reference level vs. invertebrates, nonavian vertebrates, and plants; p = 0.977, 0.861, and 0.136, respectively; Fig. 3a). Nevertheless, after accounting for the other covariates in the multiple-regression analysis, there was a difference among these taxa. Specifically, after controlling for distance-control and natural differences, there was no difference in the amount of movement through corridors for invertebrates, nonavian vertebrates, and plants, but all three taxa showed more movement through corridors than birds (p = 0.003, 0.006, 0.001, respectively; Fig. 3a). We used birds as the reference level in both models because we had differences only when birds were the reference level in the backward elimination model.

In the single covariate models, experimental design had no effect on movement through corridors, specifically between experiments that controlled for area and those that did not (p = 0.645; Fig. 3b) and between experiments that used the same distance between source and recipient patches (whether connected or not) and those that did not (p = 0.415; Fig. 3c). Nevertheless, after controlling for taxa and natural and manipulated differences in the multiple-regression analysis, experiments that controlled for distance showed significantly less movement than experiments that did not (p = 0.022; Fig. 3c).

Movement through manipulated (created) and natural corridors did not differ in the single covariate model (p = 0.680; Fig. 3d). Nevertheless, after controlling for

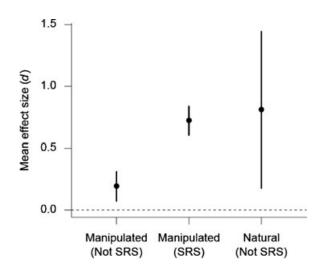


Figure 4. Mean effect size (SE 1) for manipulative experiments not conducted at the Savannab River Site (SRS) (n = 35), manipulative experiments conducted at the Savannab River Site (n = 31), and natural experiments (n = 12).

taxon and distance-control differences in the multipleregression analysis, which reduced the large variation in this covariate, natural experiments showed more movement through corridors than experiments with created corridors (p = 0.005; Fig. 3d).

Movement through corridors in studies conducted at the Savannah River Site was greater than movement through corridors in studies conducted elsewhere (p = 0.011). This finding was not significant in the multiple-regression analysis after controlling for taxon, distance-control, and manipulative and natural differences (p = 0.575). It is likely that this result was not significant in the multiple-regression analysis because the other covariates removed some of the predictive ability of the Savannah River Site (i.e., there were no plant studies conducted outside Savannah River and all experiments at Savannah River were considered manipulative).

When we compared studies conducted at the Savannah River Site, manipulative studies conducted elsewhere, and all natural experiments, we found there was more movement through corridors in studies at the Savannah River Site than in manipulated studies conducted elsewhere (p = 0.004; Fig. 4), although was no difference between manipulative (conducted at Savannah River or elsewhere) and natural studies (p = 0.124; Fig. 4).

#### Discussion

#### **Taxa Differences**

The meta-analytic approach we used here is highly conservative compared with other meta-analytical ap-

proaches (Kulmatiski et al. 2008), and we found that movement was greater between habitat patches connected by a corridor than between isolated habitat patches. The meta-analysis revealed that corridors have a medium effect (as defined in Cohen 1988) on movement between patches across scales, organisms, and ecosystems. In what is probably more relevant from an ecological perspective, there was approximately 50% more movement between habitat patches connected by a corridor than between isolated habitat patches. Although the effect size was not unusually strong compared with other meta-analyses (Kulmatiski et al. 2008), it supported the majority (77%) of single experiments that showed corridors are generally effective in increasing movement.

Almost one-quarter of the experiments (23%) showed that corridors were less effective than the nonhabitat matrix in facilitating movement between habitat patches. Of the 18 experiments that showed corridors were less effective, 10 were conducted with insects, five with nonavian vertebrates, two with birds, and one with a plant. There are several potential explanations for this result. For example, organisms may use matrix habitat rather than corridor habitat if matrix habitat has been misclassified as nonhabitat for a study organism; the scale of the experiment might be inappropriate for the study organism to perceive corridor and matrix habitats; and organisms may not respond to corridors perceived as equal or of only slightly greater quality habitat than the surrounding matrix, considering the greater availability of matrix habitat. That almost a quarter of the studies showed organisms used matrix habitat rather than corridors to move between habitat patches furthers the idea that although corridors may be used by many species, they are unlikely to be used by all species, and whether corridors are relevant for land managers may depend on the species of interest (Haddad & Tewksbury 2006).

Land managers and conservationists need general guidelines on which species are most likely to benefit from corridors (Hudgens & Haddad 2003; Damschen et al. 2008; Haddad 2008). Because species use landscapes differently (Manning et al. 2004), corridor effectiveness likely depends on life history (Gillies & St. Clair 2008). We investigated the most extreme positive and negative effect sizes from single experiments in our review, but it provided little insight into which species may use corridors. For example, we found that land snails may not use corridors (Baur 1991), but we also found that mice, which disperse more readily, respond both very positively (Lanoue 1988) and very negatively to corridors (Orrock & Danielson 2005). Thus, we attempted to determine how species use corridors differently by addressing the question on a taxon basis to determine whether we could generalize corridor use more broadly.

Most corridors are created for terrestrial vertebrates, including birds (Harris & Scheck 1991), although our data suggest that invertebrates and plants also benefit from corridors (Haddad et al. 2003). We found that corridors were likely to work equally well for all taxa, except for birds, which were less likely to move through corridors than nonavian vertebrates, invertebrates, and plants (although this finding was based on a small number of bird studies; n = 7). This result is ecologically intuitive because birds may be able to fly over sections of matrix habitat that may restrict movement of many species. In addition, it may be more difficult to appropriately scale experiments for birds, which often travel relatively easily over large distances. It is important to note that birds did have an overall positive effect size  $(0.382 \pm 0.191)$ that was different from zero (p = 0.049), which suggests birds do use corridors more than matrix habitat to traverse between habitat patches. Thus our results support implementation of corridors to increase bird movement (Harris & Scheck 1991).

We found some evidence that plants were more likely to move through corridors than animals, although this result is difficult to interpret. First, this analysis is confounded by the fact that all plant studies were conducted at one research site and thus in one ecosystem type, the Savannah River Site. Second, movement of plants through corridors is complicated by its connection to movement of animals, with seed dispersal and pollination greatly aided by avian and nonavian vertebrates and insect vectors (Tewksbury et al. 2002). For example, a long-term study at the Savannah River Site shows that corridors increase plant colonization, whether assisted by nonavian vertebrates, wind, or unknown vectors (Damschen et al. 2008), but that plant movement predictions are currently more accurate for animal vectors than wind vectors. Further investigation into the effects of corridors on plant movement in other ecosystems and a more complete understanding of the relationship between dispersal mechanisms and connectivity is needed before findings can be generalized.

#### Methodology

In addition to an increase in connectivity, corridors increase habitat area, which likely increases population size and species diversity through species-area relationships. Recently researchers have tried to control for this by adding winged patches (recipient patches with habitat extensions on opposite sides that are each the same width and half the length of the corridors), broken corridors (source and recipient patches with a corridor between them, which have a break so that the corridors do not actually connect the patches), and rectangular patches (recipient patches that have the area of the corridor added to them) to their experimental design (e.g., see Hoyle & Gilbert 2004; Levey et al. 2005). Because patches with larger areas should have more individuals and therefore more species (Arrhenius 1921; MacArthur & Wilson 1967), we expected studies that did not account for area differences between corridor and control treatments would show greater effects of corridors on movement than studies that did account for these differences. We did not find this, which suggests that area added to habitat patches by corridors does not explain corridor effectiveness (Tewksbury et al. 2002). Furthermore, this result suggests that the area effect is not detectable. Thus, results from studies investigating corridor effectiveness, which have not controlled for area, are not likely an artifact of poor study design.

Similarly, many early studies on corridors did not use control (unconnected) patches and connected patches at the same distance from a source patch (e.g., Haas 1995). More recent studies have controlled for distance in their experimental designs (e.g., Darcy & Eggleston 2005; Orrock & Damschen 2005; Rantalainen et al. 2005). After controlling for taxa levels and manipulative and natural differences, experiments that controlled for distance showed less movement between connected patches than between unconnected patches than experiments that did not control for distance. This suggests that in studies not controlling for distance, connected patches may have been closer than unconnected patches. The only way for future studies to address this issue is to control this variable better.

Because of the limited number of studies (n = 3) that explored how differences in corridor length or width affected movement, we were unable to analyze these data separately to determine optimal corridor size. This is unfortunate because, up to this point, those studying corridor effectiveness have been unable to provide land managers and conservationists with the attributes of corridor design that will make them effective conduits for movement. Haddad (2008) suggests that determining the optimal width of corridors may be the aspect of corridor quality most urgently needed by land managers.

A large percentage of experiments (40%) were conducted at the Savannah River research site. Manipulative experiments at Savannah River had more movement through corridors than manipulative experiments conducted elsewhere. Our results suggest that the positive effects of corridors on movement at the Savannah River Site may be a function of the manipulative experiments being conducted at an appropriate scale for organisms, rather than as a result of controlling for area or distance. The use of appropriate scale has been a criticism of past corridor experiments and can affect results (Beier & Noss 1998). The type of habitat and matrix is also likely to affect results (Prugh et al. 2008). The Savannah River landscape is mature loblolly (Pinus taeda) and longleaf (Pinus palustris) pine forest, and the experiments were conducted in cleared areas and the surrounding forest served as the matrix. If more corridor research is not conducted in other ecosystems, it limits our ability to infer

how these processes might operate in other systems (Haddad & Tewksbury 2006).

#### **Real-World Applications**

We found that, after controlling for taxa and distancecontrol differences, in natural experiments (defined previously) organisms showed greater use of corridors than in manipulative experiments. This result is interesting because manipulative experiments are often perceived to increase or perhaps even "force an effect" (Carpenter 1996; Schindler 1998; Pace 2001) and suggests that natural corridors are perhaps more likely to be used than experimental manipulations suggest. Because the strength of corridor effectiveness was different between natural and manipulative experiments, land managers and conservationists would benefit from more large-scale landscape studies on corridors as opposed to studies of model experimental systems. In addition, the results suggest it may be better to protect natural landscape features that function as corridors rather than attempting to create corridors.

#### Conclusions

Our results show that corridors promote movement and dispersal between habitat patches. Although most of the studies included in our meta-analysis were conducted over the short term, typically one season, the fact that we found corridors generally increased migration between habitat patches by 50% is important. Even minimal migration (i.e., one individual per generation) between habitat patches can mitigate loss of genetic diversity (Mills & Allendorf 1996). We did not investigate whether movement through the corridors or matrix was sufficient to maintain population viability of isolated populations. Few of the studies we examined measured whether corridors increased population size or species diversity (n = 12). Long-term studies are required to determine whether increased migration due to corridors actually reduces population extinction.

#### Acknowledgments

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#### **Supporting Information**

Raw data and calculated effect sizes from studies used in the meta-analysis are available as part of the online article (Appendix S1). The authors are responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

#### **Literature Cited**

- Aars, J., and R. A. Ims. 1999. The effect of habitat corridors on rates of transfer and interbreeding between vole demes. Ecology 80:1648-1655.
- Andreassen, H. P., S. Halle, and R. A. Ims. 1996. Optimal width of corridors for root voles: not too narrow and not too wide. Journal of Applied Ecology 33:63-70.
- Andreassen, H. P., K. Hertzberg, and R. A. Ims. 1998. Space-use responses to habitat fragmentation and connectivity in the root vole *Microtus oeconomus*. Ecology **79:1**223–1235.
- Arrhenius, O. 1921. Species and area. Journal of Ecology 9:95-99.
- Baker, L. 2007. Effect of corridors on the movement behavior of the jumping spider *Phidippus princeps* (Araneae, Salticidae). Canadian Journal of Zoology 85:802–808.
- Baur, A. 1991. Effects of competitive interactions and habitat structure on life history traits and dispersal in land snails. PhD thesis. Uppsala University, Uppsala, Sweden.
- Beier, P., and R. F. Noss. 1998. Do habitat corridors provide connectivity? Conservation Biology 12:1241–1252.
- Bennett, A. F., K. R. Crooks, and M. Sanjayan. 2006. The future of connectivity conservation. Pages 676-694 in K. R. Crooks and M. Sanjayan, editors. Connectivity conservation. Cambridge University Press, Cambridge, United Kindgom.
- Brinkerhoff, R. J. 2002. Responses of prey to the presence of predators in a fragmented landscape with corridors. MS thesis. North Carolina State University, Raleigh, North Carolina.
- Brown, J. H., and A. Kodrick-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58:445-449.
- Carpenter, S. R. 1996. Microcosms have limited relevance for community and ecosystem ecology. Ecology 77:677-680.
- Castellón, T. D., and K. E. Sieving. 2006. An experimental test of matrix permeability and corridor use by an endemic understory bird. Conservation Biology 20:135–145.
- Coffman, C. J., J. D. Nichols, and K. H. Pollock. 2001. Population dynamics of *Microtus pennsylvanicus* in corridor-linked patches. Oikos 93:3-21.
- Cohen, J. 1988. Statistical power analysis for the behavioral sciences. Academic Press, New York.
- Collinge, S. K. 2000. Effects of grassland fragmentation on insect species loss, colonization and movement patterns. Ecology 81:2211–2226.
- Cooper, H., and L. V. Hedges, editors. 1994. The handbook of research synthesis. Russell Sage Foundation, New York.
- Damschen, E. I., L. A. Brudviga, N. M. Haddad, D. J. Levey, J. L. Orrock, and J. J. Tewksbury. 2008. The movement ecology and dynamics of plant communities in fragmented landscapes. Proceedings of the National Academy of Sciences of the United States of America 105:19078-19083.
- Damschen, E. I., N. M. Haddad, J. L. Orrock, J. J. Tewksbury, and D. J. Levey. 2006. Corridors increase plant species richness at large scales. Science 313:1284–1286.
- Darcy, M. C., and D. B. Eggleston. 2005. Do habitat corridors influence animal dispersal and colonization in estuarine systems? Landscape Ecology 20:841–855.
- Falcy, M. R., and C. F. Estades. 2007. Effectiveness of corridors relative to enlargement of habitat patches. Conservation Biology 21:1341–1346.
- Forbes, A. E., and J. M. Chase. 2002. The role of habitat connectivity and landscape geometry in experimental zooplankton metacommunities. Oikos 96:433-440.
- Gillies, C. S., and C. C. St. Clair. 2008. Riparian corridors enhance movement of a forest specialist bird in fragmented tropical forest.

Proceedings of the National Academy of Sciences of the United States of America **105:**19774–19779.

- Gleser, L. J., and L. Olkin. 1994. Stochastically dependent effect sizes. Pages 339-355 in H. Cooper and L. V. Hedges, editors. The handbook of research synthesis. Russell Sage Foundation, New York.
- Gonzalez, A., J. H. Lawton, F. S. Gilbert, T. M. Blackburn, and I. Evans-Freke. 1998. Metapopulation dynamics abundance and distribution in microecosystem. Science 281:2045–2047.
- Gurevitch, J., and L. V. Hedges. 2001. Meta analysis: combining the results of independent experiments. Ecology 80:1142-1149.
- Haas, C. A. 1995. Dispersal and use of corridors by birds in wooded patches on an agricultural landscape. Conservation Biology 9:845-854.
- Haddad, N. M. 2008. Finding the corridor more traveled. Proceedings of the National Academy of Sciences of the United States of America 105:19569-19570.
- Haddad, N. M., D. R. Bowne, A. Cunningham, B. J. Danielson, D. J. Levey, S. Sargent, and T. Spira. 2003. Corridor use by diverse taxa. Ecology 84:609-615.
- Haddad, N. M., and J. J. Tewksbury. 2006. Impacts of corridors on populations and communities. Pages 390–415 in K. R. Crooks and M. A. Sanjayan, editors. Connectivity conservation. Cambridge University Press, Cambridge, United Kingdom.
- Hanski, I. K. 1998. Metapopulation dynamics. Nature 396:41-49.
- Hanski, I., 1999. Metapopulation Ecology. Oxford University Press, Oxford, United Kingdom.
- Harris, L. D., and J. Scheck. 1991. From implications to applications: the dispersal corridor principal applied to the conservation of biological diversity. Pages 189–220 in D. A. Saunders and R. J. Hobbs, editors. Nature conservation 2: the role of corridors. Surrey Beaty and Sons, Chipping Norton, New South Wales.
- Hess, G. R., and R. A. Fischer. 2001. Communicating clearly about conservation corridors. Landscape and Urban Planning 55:195– 208.
- Hilty, J. A., W. Z. Lidicker Jr, and A. M. Merenlender. 2006. Corridor ecology. The science and practice of linking landscapes for biodiversity conservation. Island Press, Washington.
- Hoyle, M., and F. Gilbert. 2004. Species richness of moss landscapes unaffected by short-term fragmentation. Oikos 105:359– 367.
- Hudgens, B., and N. Haddad. 2003. Predicting which species will benefit from corridors in fragmented landscapes from population growth models. The American Naturalist 161:808–820.
- Kulmatiski, A., K. H. Beard, J. R. Stevens, and S. M. Cobbold. 2008. Plant-soil feedbacks: a meta-analytical review. Ecology Letters 11:980–992.
- Lanoue, A. 1988. Use of corridors and scale of movement in farmland by *Peromyscus leucopus*. MS thesis. Carleton University, Ottawa, Ontario.
- Levey, D. J., B. M. Bolker, J. J. Tewksbury, S. Sargent, and N. M. Haddad. 2005. Effects of landscape corridors on seed dispersal by birds. Science 309:146-148.
- MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

Mabry, K. E., E. A. Dreelin, and G. W. Barrett. 2003. Influence of land-

scape elements on population densities and habitat use of three small-mammal species. Journal of Mammalogy 84:20-25.

- Manning, A. D., D. B. Lindenmayer, and H. A. Nix. 2004. Continua and umwelt: Novel perspectives on viewing landscapes. Oikos 104:621-628.
- McLaughlin, J. F., J. J. Hellmann, C. L. Boggs, and P. R. Ehrlich. 2002. Climate change hastens population extinctions. Proceedings of the National Academy of Sciences 99:6070–6074.
- Mills, L. S., and F. W. Allendorf. 1996. The one-migrant-per-generation rule in conservation and management. Conservation Biology 10:1509–1518.
- Orrock, J. L., and E. I. Damschen. 2005. Corridors cause differential seed predation. Ecological Applications 15:793-798.
- Orrock, J. L., and B. J. Danielson. 2005. Patch shape, connectivity, and foraging by oldfield mice (*Peromyscus polionotus*). Journal of Mammalogy 86:569-575.
- Pace, M. L., editor. 2001. Getting it right and wrong: extrapolations across experimental scales. Columbia University Press, New York.
- Perault, D. R., and M. V. Lomolino. 2000. Corridors and mammal community structure across a fragmented, old-growth forest landscape. Ecological Monographs 70:401–422.
- Prugh, L. R., K. E. Hodges, A. R. E. Sinclair, and J. S. Brashares. 2008. Effect of habitat area and isolation on fragmented animal populations. Proceedings of the National Academy of Sciences of the United States of America 105:20770-20775.
- R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Rantalainen, M.-L., H. Fritze, J. Haimi, T. Pennanen, and H. Setälä. 2005. Species richness and food web structure of soil decomposer community as affected by the size of habitat fragment and habitat corridors. Global Change Biology 11:1614-1627.
- Rantalainen, M.-L., J. Haimi, and H. Setälä. 2004. Testing the usefulness of habitat corridors in mitigating the negative effects of fragmentation: the soil faunal community as a model system. Applied Soil Ecology 25:267–274.
- Schindler, D. W. 1998. Replication versus realism: the need for ecosystem-scale experiments. Ecosystems 1:323-334.
- Soulé, M. E., and M. E. Gilpin. 1991. The theory of wildlife corridor capability. Beatty and Sons, Surrey, United Kingdom.
- Stevens, J. R., and G. Nicholas. 2009. Metahdep: meta-analysis of hierarchically dependent gene expression studies. Bioinformatics 25:2619–2620.
- Stevens, J. R., and A. M. Taylor. 2009. Hierarchical dependence in metaanalysis. Journal of Educational and Behavioral Statistics 34:46-73.
- Tewksbury, J. J., D. J. Levey, N. M. Haddad, S. Sargent, J. L. Orrock, A. Weldon, B. J. Danielson, J. Brinkerhoff, E. I. Damschen, and P. Townsend. 2002. Corridors affect plants, animals, and their interactions in fragmented landscapes. Proceedings of the National Academy of Sciences of the United States of America 99:12923–12926.
- Wang, M. C., and B. J. Bushman. 1998. Using the normal quantile plot to explore meta-analytic data sets. Psychological Methods 3:46–54.
- Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. Bio-Science 48:607-615.

