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Abstract	<p>Habitat connectivity plays a central role in wildlife population viability by increasing the available population size, maintaining gene flow among diverse metapopulations, and facilitating regular migration, dispersal, and recolonization. This chapter documents an agent-based simulation model that can improve our understanding of species migration routes between habitat patches. It is based on the Pathway Analysis Through Habitat (PATH) algorithm, first developed for use on a supercomputer by Hargrove, Hoffman, and Efroymson (2004). Using NetLogo (<a href="http://ccl.northwestern.edu/netlogo/">http://ccl.northwestern.edu/netlogo/</a>), the authors of this chapter created a simplified implementation of PATH that operates on a standard desktop computer. PATH identifies and highlights areas in a landscape that contribute to the natural connections among populations; identifies the metapopulation structure; and indicates the relative strength of connections holding a metapopulation together.</p> <p>A major benefit of this NetLogo implementation of PATH is that it does not require a supercomputer to operate. The model encapsulates essential species migration activities and costs into the bare fundamentals—a binary habitat indicator, a movement parameter, a randomness parameter, an energy-accounting function, and a mortality probability. Simulation results can provide valuable insights to support decisions that promote habitat connectivity for purposes of improved wildlife management.</p>
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# Chapter 12 1

## An Implementation of the Pathway 2

### Analysis Through Habitat (PATH) 3

### Algorithm Using NetLogo 4

William W. Hargrove and James D. Westervelt 5

## 12.1 Background 6

When developing plans to protect populations of species at risk, we tend focus on 7  
 protecting and preserving habitat where the species naturally occurs. Ecologists 8  
 employ historic sightings of individuals, habitat suitability index (HSI) models, and 9  
 the expert advice of local naturalists familiar with the environments desired and 10  
 required. In many cases, the optimal habitats are fragmented to the extent that a 11  
 species at risk could be extirpated from any single area by storms, drought, disease, 12  
 or other local insult. Alternately, over time, a small population could become so 13  
 inbred that it is increasingly susceptible to disturbances that increase the probability 14  
 of local extirpation. However, if nearby populations can reach the isolated popula- 15  
 tion across the fragmented space, then the isolated population becomes part of a 16  
 larger metapopulation. The strength of habitat connections, therefore, can be critical 17  
 to ensure the viability of at-risk populations over time. Habitat connectivity plays 18  
 this important role by increasing the effective population size, maintaining gene 19  
 flow, and facilitating regular migration, dispersal, and recolonization. Each of these 20  
 processes helps ensure the long-term persistence of a population. A connected land- 21  
 scape is preferable to a fragmented one (Beier and Noss 1998; Bennett 1999). 22  
 Natural landscapes are generally more connected than landscapes altered or manip- 23  
 ulated by humans, so establishing or maintaining corridors is a viable strategy to 24  
 sustain the natural connectivity (Noss 1987). 25

[AU1]

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26 *Metapopulation* is the term for a collection of discrete local breeding populations  
27 that occupy distinct habitat patches but are connected by migration (Hanski and  
28 Gilpin 1997). Population viability analysis (PVA), a method for forecasting the  
29 probability that a metapopulation will persist over time, has been automated by  
30 numeric modeling applications such as RAMAS (Applied Biomathematics 2003).  
31 A key input to a PVA is the probability of migration among all individual popula-  
32 tions of the metapopulation. Understanding the viability of an at-risk population or  
33 metapopulation depends to a significant extent on identifying the migration routes  
34 that connect the discrete constituent populations. Also, without this understanding,  
35 land managers may not have enough information to protect important migration  
36 paths. That deficiency, in turn, may lead to the loss of more-isolated populations an  
37 increased threat to the survival of the greater metapopulation.

38 In order to help improve our understanding of species migration routes among  
39 separated populations, Hargrove, Hoffman, and Efroymson (2004) developed the [AU2]  
40 Pathway Analysis Through Habitat (PATH) computer simulation model. Originally  
41 developed for implementation on a supercomputer, the purpose of PATH is to help  
42 a decision-maker to reliably predict where potential dispersal corridors are likely to  
43 exist in real-world landscape maps. This information makes it possible to project  
44 which habitats will support population growth (sources) and which will tend to lose  
45 population (sinks). The PATH algorithm works by launching *walkers* (i.e., virtual  
46 animals) from each habitat patch to simulate the journey of individuals through land  
47 cover types in the intervening matrix until arriving at a different habitat patch or  
48 dying. Each walker is given a set of user-specified habitat preferences that direct its  
49 walking behavior to resemble the animal of interest. As originally implemented,  
50 PATH was designed for a massively parallel computing environment in order to  
51 analyze the activity of very large numbers of random walkers in large landscapes  
52 with many habitat patches. PATH produces three outputs: (1) a map of the most  
53 heavily traveled potential migration pathways between patches, (2) a square transfer  
54 matrix that quantifies the flow of animals successfully dispersing from each patch to  
55 every other patch, and (3) a set of importance values that quantifies, for every habi-  
56 tat patch in the map, the contribution of that patch to successful animal movement  
57 across the landscape. The transfer matrix is square and not triangular since the rate  
58 of animal movement is likely to be asymmetrical between any two habitat patches.  
59 That is, the rate of successful migration from patch 1 to patch 2 will likely not equal  
60 the successful migration from 2 to 1.

61 One problem with the original implementation of PATH is the inherent barrier to  
62 its use: the application is designed to perform massive simulations that require a  
63 supercomputer to run them in a reasonable amount of time. This project was con-  
64 ceived as a way to make migration pathway analysis more accessible to users of  
65 desktop computers by implementing the core PATH algorithm in the NetLogo simu-  
66 lation modeling environment (Wilensky 1999).

**12.2 Objective** 67

The objective of this modeling project was to develop a computationally efficient PATH-based tool for desktop computers that can identify important species migration corridors between habitats based on expert information about inter-habitat patch lethality, the energy cost to cross, and the energy available to animals to move outside of core habitat. 68  
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**12.3 Model Description** 73**12.3.1 Purpose** 74

This implementation of PATH is intended to illuminate the essential mechanisms that help to identify animal migration corridors.<sup>1</sup> A premise of the design was to avoid including any data or processes not directly illuminating the successful migration of species between two or more separated habitat patches. This model converts expert knowledge about habitat patch locations, traversal cost, and probability of mortality through the interstitial landscape into information about the relative connectivity of all pairs of habitat patches and the impact of interstitial lands on successful migrations. In future versions, certain additional aspects of “realism,” such as seasonal effects and time steps, could be added in instances where model results might be improved. As you read further you will note that, unlike the other models in this book, this model does not use time steps. 75  
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**12.3.2 State Variables and Scales** 86

The scale and extent of the area are determined by the user, with the practical limit depending on the processing power of the user’s computer. The demonstration data set used in this model supports a simulation space encompassing over 1,000 by 1,000 cells (i.e., one million cells), and the model can execute more than 2,500 migration attempt/s. The primary state variable that changes over simulation time is the number of successful migrations supported by each patch in the simulation space. 87  
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<sup>1</sup>An operational copy of this model is available through <http://extras.springer.com>.

### 93 **12.3.3 Process Overview and Scheduling**

94 The model is initialized by reading data from a set of three location-specific maps  
95 that characterize (1) the location of habitat patches, (2) the energy cost to cross the  
96 space between patches, and (3) the lethality associated with migrating through  
97 non-habitat. During initialization, first the habitat map loads, then the model  
98 aggregates, outlines, and numbers all contiguous habitat patches (i.e., "habitats").  
99 A user's chosen number of travelers is initialized. The simulation runs in discrete  
100 steps, but these steps do not represent time because time has no bearing on an indi-  
101 vidual's energy level, the energy cost of migrating, or patch lethality. At each step  
102 in the simulation, walkers are randomly distributed along the edges of a habitat  
103 based on area size. Walkers are faced away from the habitat interior and started on  
104 a walk that is partially directed with an adjustable level of randomness. The amount  
105 of energy consumed during one step is based on the data provided by the energy cost  
106 input map, and travelers randomly die according to the patch-specific probability of  
107 mortality read from the patch lethality input map. As a traveler moves through the  
108 interstitial space between habitats, it remembers its course. If the traveler succeeds  
109 in arriving alive at a habitat patch different from where it started, it communicates  
110 to every patch along the successful path that the patch supported a successful cross-  
111 ing. Each patch then updates a habitat-to-habitat crossing array that tracks the  
112 number of successful crossings among all patch combinations.

### 113 **12.3.4 Design Concepts**

#### 114 **12.3.4.1 Emergence**

115 PATH reveals the value of every patch in supporting habitat-to-habitat migration  
116 through the emergent behavior of the walkers, as an increasing number of them suc-  
117 cessfully complete migrations and the most favorable paths become more evident.

#### 118 **12.3.4.2 Stochasticity**

119 Walkers begin their attempted migrations by facing away, randomly, from the inte-  
120 rior of their beginning habitats, and then proceed to move through the space separa-  
121 ting habitat patches. The travel direction of walkers may be set to be fully random,  
122 partially random, or fully deterministic depending on the value selected for a user-  
123 set variable. The movement of a walker at each simulation step may be characterized  
124 as a "wiggle," turning to the left between 0 and  $X$  angular degrees (where  $X$  is a user-  
125 selected value); then turning to the right between 0 and  $X$  degrees. If the user sets  $X$   
126 to 0, then the travel path is straight; if the angle is set to 360, then every step is fully  
127 random. The user will assign a value to  $X$  based on what is known of the subject spe-  
128 cies' tendency to maintain a direction; movement tendencies vary among species.

**12.3.4.3 Observation** 129

In this version of the model, walkers observe nothing about their surroundings because that information is largely extraneous to path selection on a collective level. However, this model could be modified for experimentation purposes to support species-specific observation and evaluation of travel-direction options by individual walkers.

**12.3.4.4 Time** 135

This model deals with time in a manner very different from any other model in this book, which all include an idea of time passing as the model executes. In this PATH model, each step involves releasing a new batch of walkers, which expend energy and risk death as they move. One may imagine that time passes as they move, but their “time” is not associated with any other walker’s “time” in any model step. Regardless of the number of ticks, the total set of walkers active during the simulation can be assumed to begin their walking at the same time. Also, the state of the landscape never changes as it often does in other models, which leaves the landscape essentially timeless.

**12.3.5 Initialization** 145

Patches are initialized with data read from the habitat-location, energy-cost, and patch-lethality maps. Habitat quality is represented by a binary variable, either 0 for non-habitat or 1 for habitat. The walkers’ energy store is set by the user before migration attempts begin, and the amount of energy lost to walkers as they cross patches is accounted for by data from the model’s energy-cost map. Finally, the probability of mortality while crossing a patch is represented by a value ranging from 0 to 100 as determined by the model’s lethality map. Also during initialization, as briefly noted above, patches are clumped together to form contiguous habitats, and each habitat is given a unique identification number.

**12.3.6 Input** 155

Input is provided by the three raster maps described above. The habitat-location, energy-cost, and patch-lethality maps are prepared within a raster-based geographic information system (GIS) and provided to the model as Esri ASCII grid files. PATH requires maps that are location- and species-specific. The habitat map could be produced using the results of a HSI study. It also might be based on a regression analysis that correlates known habitat and non-habitat patches with factors in other

162 GIS maps such as slope, land cover, soil type, land use, canopy cover, and elevation.  
163 In any case, the end product must be a map of habitat for the target species—places  
164 where the species can establish a home range and survive. The lethality map repre-  
165 sents the probability (0–100%) that an individual will die while crossing any patch.  
166 A patch lethality value is based on exposure to predators, the probability of being  
167 caught in an inescapable situation, and the species' ability to deal with the land  
168 cover. GIS data involved in developing this information might include land cover,  
169 land use, slope, and aspect. The energy-cost map is similar to the lethality map, but  
170 instead of encountering immediate death in specific patches, the walker loses energy  
171 based on the energy-cost value for the patch being crossed. For example, crossing  
172 through dense woods, a swamp, or a pond may require more energy than crossing  
173 an open short-grass field. Energy cost, of course, varies with the species. Like the  
174 lethality map, the energy-cost map will likely be based on an ecologist's analysis of  
175 land cover, slope, and aspect data.

### 176 12.3.7 Submodels

177 Our NetLogo implementation of PATH sets aside all ecosystem and species func-  
178 tions that are not essential to the modeling of animal migration path formation. It is  
179 a very simple model that operates on data provided by three raster maps as initial-  
180 ized with species-specific values set by the user for a small number of variables.

181 The concept of time is not essential to understanding the establishment of migra-  
182 tion paths, so each NetLogo tick (i.e., step) occurs independently of time, and rep-  
183 represents only one discrete action that involves walkers attempting to migrate from a  
184 home habitat to another habitat. At each NetLogo tick, a user-chosen number of  
185 travelers make a crossing attempt. That number is not critical, but the number of  
186 total attempts is. The number of travelers leaving each habitat is proportional to the  
187 size of the habitat, based on the assumption that larger habitats have larger popula-  
188 tions and therefore will send forth more emigrants. Walkers depart home habitats  
189 from a random edge location.

190 As the simulation proceeds, successful migration paths are traced onto the output  
191 map in black, and each path becomes denser as more individuals use the same path.  
192 These paths accrete into increasingly stable shaded areas that reveal the corridors  
193 between habitats that are most successfully used in migration. The darkest traces  
194 within these grayscale areas indicate the most successfully used corridors.

## 195 12.4 Simulation Experiments

196 We used this PATH application to identify the corridors within Fort Benning, GA,  
197 that might be used by gopher tortoises (*Gopherus polyphemus*) migrating among  
198 tortoise habitat fragments. This animal, an at-risk species that has been nominated



Fig. 12.1 The study area after being initialized

for Federal Threatened status, is carefully managed on Fort Benning. The three 199  
GIS maps required for the model were derived from National Land Cover Data 200  
(NLCD) maps. Areas with land cover suitable for tortoises were selected, and 201  
contiguous areas greater than 18 ha were identified as habitat. Each of the NLCD 202  
land cover types was then associated with a transit-energy cost and a probability of 203  
mortality (0–100%), and these parameters were then used as the basis for reclassifying 204  
the NLCD map into the other two input maps. 205

[AU3]

Model initialization, which involves reading the three maps as well as identifying 206  
and labeling contiguous habitat patches into habitats, takes several minutes and 207  
produces the image in Fig. 12.1. The 108 identified habitats are shown in medium 208  
gray, with edges outlined in darker gray and uniquely labeled. For this experiment, 209  
each walker was given 4,000 units of energy before its crossing attempt and was 210  
assigned a maximum turn angle of 20° after each step. Five hundred walkers were 211  
arbitrarily initialized at the same time, started at a habitat edge and randomly faced 212  
away from the habitat. The total leaving any habit was based on that habitat's relative 213  
size. Each walker moved ahead until it ran out of energy or successfully reached 214



Fig. 12.2 Successful migration density after three million attempts

215 a new habitat. Once these walkers were finished, a new set of 500 was initialized  
 216 and the process continued over and over. In 1 min of “wall-clock time,” the model  
 217 generated 1.25 million walker attempts, with about 10% successfully migrating  
 218 from 1 of the 108 habitat patches to another. After three million habitat-crossing  
 219 attempts were simulated, the patches were assigned a color along a log-adjusted  
 220 gray scale based on the relative number of successful crossings in which they were  
 221 used (Fig. 12.2). The specks in the image identify locations at which travelers ran  
 222 out of energy in their final attempt. The maximum number of successful crossings  
 223 supported by any one patch was 2,932 and is represented in black. Numerous patches  
 224 participated in one crossing, and these are shown in the form of white sinuous lines  
 225 against the darker background.

226 Just 357,328 of the 3 million crossing attempts were successful. This value was  
 227 derived from the inter-habitat migration success table, which can be displayed by  
 228 selecting NetLogo’s Interface tab. For this simulation, four strong metapopulations  
 229 emerged, with three of them being tenuously linked (inspect Fig. 12.2). With lower  
 230 initial energy levels, the number of successful migrations decreased, the number of

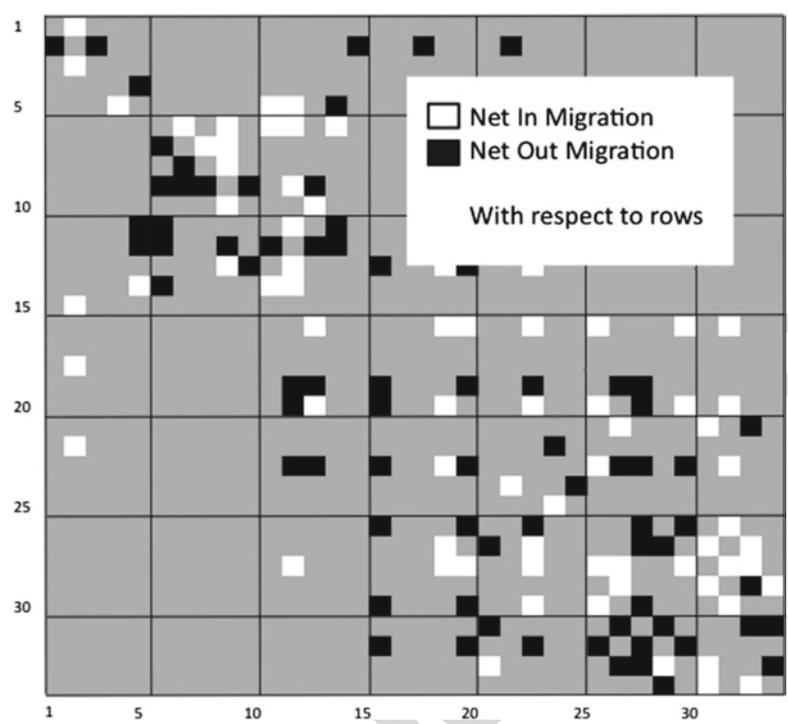


Fig. 12.3 Net in- and out-migration among habitats 1 through 34

separated metapopulations increased, and the number of habitats unconnected to other habitats increased. In terms of species conservation and survival, higher numbers of metapopulations and disconnected habitats are less desirable; and higher numbers of individuals and larger metapopulations are more desirable.

One output of this application is a table that shows the number of successful migrations between all pairs of habitats. By subtracting out-migrations from in-migrations, the user can discover which habitats in each pair are net population sources or sinks. Figure 12.3 shows the net migration from every habitat to every other habitat for habitats 1–34 (out of 108 total). Note that habitat 2 is a net source to habitats 1, 3, 15, 18, and 21 while habitat 16 is a net sink for 7 other habitats.

### 12.5 Discussion

This PATH application reveals that high-quality interstitial habitat is more likely to be associated with corridors than less-preferred habitat, and that short connectors develop more often than longer ones. The model assumes that movement through non-habitat areas is semi-random, with the walker's current heading having some

246 persistence. Actual animals may functionally select resources at a finer scale than is  
247 used in this model, and thus may not follow the same route as one optimized by  
248 PATH at a coarser resolution. However, animals also may respond to coarser-grained  
249 landscape cues than are represented by this model's habitat map, especially when  
250 migrating or dispersing across long distances. Animal movement choices and  
251 behaviors may vary with age, gender, pregnancy and nutrition status, and the nature  
252 and composition of traveling groups. The importance of those factors may differ  
253 between species.

254 The implementation of PATH described here attempts to illuminate patterns  
255 of successful inter-habitat migration with a computationally low-overhead model-  
256 ing approach. It encapsulates essential migration activities and costs into bare  
257 fundamentals—a binary habitat indicator, a movement parameter, a randomness  
258 parameter, an energy-accounting function, and a mortality probability. The model  
259 also includes output basic functions to track and display successful crossings. The  
260 map interface shows only the metapopulations and the strength of population con-  
261 nections within them. This information can be concisely output to reveal whether  
262 given populations are likely sources and sinks (Fig. 12.3).

263 Although this PATH-based model is very simple, it is important to note that it is  
264 technically sufficient to capture the essential elements of real-world migration path-  
265 formation for a variety of species. While simpler analytical approaches are possible,  
266 such as a least-cost method for predicting path formation, they do not account for  
267 multiple terrain types that differ in terms of crossing-energy costs or lethality prob-  
268 ability, and are too simplistic to capture all essential considerations. More impor-  
269 tantly, because least-cost path modeling methods show the solution to be a single  
270 pathway, they illustrate only the current optimal route but do not show secondary  
271 routes that could be improved over the current best route through small modifica-  
272 tions to the habitat map. The PATH tool shows all feasible connectivity routes, not  
273 just the single current best one. Paths that have good potential, but are currently  
274 used as secondary routes by the metapopulation, are exactly the ones that resource  
275 managers need to know about in order to consider where strategic management  
276 alterations can dramatically improve habitat connectivity. Such routes are evident in  
277 a PATH output corridor map as strong potential corridors, which may be impeded  
278 only in one or two locations by passing through low-quality patches.

279 The walkers in a simulation, considered individually, have almost no sophistica-  
280 tion at finding migration paths as compared with individual real-world animals.  
281 However, considered collectively, the behavior of all successful walkers represents  
282 a spatial optimization process that can be used to reproduce the optimum pathways  
283 we would expect well-adapted individuals of the subject species to use most often.  
284 For this reason, it is not a problem that the walkers, endowed only with the ability  
285 to “see” land types immediately adjacent to their current location, represent animals  
286 that may have much greater sensory scope and range. The simplified walker mode  
287 of functioning in the model does not constrain the optimization of the potential cor-  
288 ridors found by PATH. The optimization in this model results from the collective  
289 action of the large number of successful dispersers and the weighting of the most  
290 efficient potential dispersal paths the most heavily. Even if individual walkers in the  
291 model had a greater look-ahead capability, the same optimal potential corridors

would be predicted by the PATH tool. Consider, for example, a situation in which the local environment is inhospitable, but just beyond this there is a high-quality habitat pathway to another patch. Although short-sighted, a few walkers will make rare, immediately suboptimal choices and cut through the inhospitable bottleneck to discover the optimized pathway beyond. Becoming successful dispersers, their tracks will become part of the final map, showing the connection just as surely as if they had been able to look beyond the local problem with terrain. A converse situation is also true: pockets of higher-quality habitat that are surrounded by barriers of poor-quality habitat will attract many individual walkers, but it is not likely that those walkers will successfully reach a second patch. Since only the travel paths of successful dispersers are used, no potential corridors will pass through this attractive dead-end area, just as if walkers had been able to see the barriers to migration that lie beyond.

For purposes of real-world application to habitat-management decisions, corridors identified using randomized walkers in this PATH tool must be verified against actual movement corridors that have been observed in the field. Radio tracking and telemetry studies would be appropriate for empirically testing walker-generated corridors against migration paths established by the subject species in the natural environment.

**12.6 Conclusions** 311

The original PATH model, designed to handle very large numbers of walkers on very large landscapes, was implemented on a supercomputer. Few working resource managers actually have access to a supercomputer. This implementation of the PATH algorithm as a simplified NetLogo model makes PATH available to a much wider user community because it works well on a standard desktop computer. This PATH-driven model identifies and highlights areas in a landscape that contribute to the natural connections among populations, identifies the metapopulation structure, and indicates the relative strength of connections holding a metapopulation together. This information is essential to making effective habitat-management decisions that support robust populations of species at risk.

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# Author Queries

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Queries	Details Required	Author's Response
AU1	Following references "Bennett (1999) and Hargrove, Hoffman, and Efroymson (2004)" are cited in text but not given in the reference list. Please provide complete details to add to the reference list.	
AU2	Citation "Hargrove, Hoffman, and Efroymson (2004)" is not given in the reference list. Please provide complete details to add to the list.	
AU3	Please check the edit to the sentence "Model initialization, which involves...".	
AU4	Please provide accessed date for the references Applied Biomathematics (2003) and Wilensky (1999).	