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Analytical Methods

USE OF MARKOV CHAINS IN ANALYSES OF FORAGING BEHAVIOR

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Abstract. For logistical reasons, observers often record sequential movements of birds among foraging resources. An appropriate method of analysis involves Markov chains, which summarize the frequency of movement from one resource to another. Such data are summarized into a transition matrix, where numbers of observations of movement of a bird from one habitat are tallied into all categories to which the bird subsequently moves. When such data are gathered for several species, or other groupings, tests of homogeneity can be performed using log-linear models. These data can also be used to generate tables of transition probabilities, and these in turn can be reduced, through eigenanalyses, to steady-state vectors that give the probability of use (over the long run) of each habitat. These vectors can be compared (through goodness-of-fit tests or tests of independence) to measures of habitat availability and measures of habitat selectivity can be calculated. Analyses are described for use with popular statistical computer packages.

Key Words: Birds; environmental grain; foraging behavior; log-linear models; Markov chain; transition probability.

For mostly logistical reasons, ornithologists usually record foraging behaviors of birds as a sequential series of observations. The reason data are gathered sequentially is valid: birds can be difficult to find and it is more efficient to follow a bird, once it is found, than to abandon it after one or two observations and search for another bird. However, analyses of such data using traditional chi-square or other similar techniques may not be valid because sequential observations are not necessarily independent, and independence of observations is a critical assumption of most statistical tests. Other methods of analysis are available that take advantage of the sequential structure of such data (e.g., time-series analyses). This paper describes one of these methods involving Markov chains and log-linear modeling.

First, a few definitions (following Vandermeer 1972) may be useful. *Operational habitat* denotes an identifiable habitat unit, for example, each of the s tree species in a study site. *Environment* denotes a specified set of operational habitats. *Environmental grain* denotes the way in which a particular species moves from one operational habitat to the next during a specified time interval that is short relative to the lifespan of the species (MacArthur and Levins 1964, Levins 1968). For example, one might observe two species of birds. Individuals of one species stay in one operational habitat for a long time (the birds forage mainly in one tree species), whereas individuals of another species forage in trees of all species at random. The environment is coarse grained for the first species and fine grained for the second. *Markov chain* denotes a series of operational habitats, and the probability of passing to a new one by some defined process (Keller 1978). To illustrate, suppose we have a system that moves from habitat i at time t to habitat j at time $t + 1$. At each time interval, the system can be in any one of s habitats. We define $p_{i,j}^{(1)}$ as the frequency (probability) of moving from habitat i at time t to habitat j at time $t + 1$, where the superscript (1) indicates a transition occurring in one, discrete time interval. For example, let the habitats be tree species in a forest. We observe frequencies of birds flying from one tree species to the next. Next, we observe the bird flying at two time intervals; from habitat i at time t to habitat k at time $t + 2$, with the resulting probability $p_{i,k}^{(2)}$. Thus:

$$\begin{aligned} p_{i,k}^{(2)} = p_{i,1}^{(1)}p_{1,k}^{(1)} &+ p_{i,2}^{(1)}p_{2,k}^{(1)} \\ &+ \dots + p_{i,j}^{(1)}p_{j,k}^{(1)} \\ &+ \dots + p_{i,s}^{(1)}p_{s,k}^{(1)} \end{aligned}$$

or

$$p_{i,k}^{(2)} = \sum_{j=1}^{s} p_{i,j}^{(1)}p_{j,k}^{(1)}.$$

This is the sum of all the different pathway-probabilities between habitat i and habitat k, each passing through exactly one intermediate habitat.

We can extend the last result to n consecutive time intervals to obtain $p_{i,j}^{(n)}$, and in general

$$p_{i,k}^{(m+n)} = \sum_{j} p_{i,j}^{(m)}p_{j,k}^{(n)},$$

where $p_{i,j}^{(m)}$ is the m-step transition probability from habitat i to habitat j, and $p_{j,k}^{(n)}$ is the n-step transition probability from habitat j to habitat k.

Now let

$$\lim_{n \to \infty} p_{i,j}^{(n)} = u_j.$$

It can be shown (Chiang 1980:123) that if the limit u_j exists, then u_j is independent of the initial state i, and the vector **u** is called a stationary distribution, with the sum of the vector elements equal to 1.0. Formally, if

$$u_j = \sum_i u_i p_{i,j}^{(1)},$$

u is a stationary distribution. As before, suppose $p_{i,j}^{(1)}$ defines the probability (frequency) of a bird of one particular species flying from tree species i to tree species j, during one time interval, in an environment that contains s tree species. The transition probabilities $p_{i,j}^{(1)}$ $(i, j = 1, 2, \ldots, s)$ define a one-step matrix $\mathbf{G}^{(1)}$, which is called the grain matrix (Vandermeer 1972, Colwell 1973); that is:

$$\mathbf{G}^{(1)} = \begin{array}{cccc} p_{1,1}^{(1)} & p_{1,2}^{(1)} & \cdots & p_{1,s}^{(1)} \\ p_{2,1}^{(1)} & p_{2,2}^{(1)} & \cdots & p_{2,s}^{(1)} \\ \cdot & \cdot & \cdots & \cdot \\ \cdot & \cdot & \cdots & \cdot \\ \cdot & \cdot & \cdots & \cdot \\ p_{s,1}^{(1)} & p_{s,2}^{(1)} & \cdots & p_{s,s}^{(1)} \end{array}$$

Given $\mathbf{G}^{(1)}$, one can obtain the grain matrix of the stationary distribution $\mathbf{G}^{(\infty)}$ that contains s identical row vectors composed of s elements:

$$\mathbf{G}^{(\infty)} = \begin{array}{cccc} u_1 & u_2 & \cdots & u_s \\ u_1 & u_2 & \cdots & u_s \\ \cdot & \cdot & \cdots & \cdot \\ \cdot & \cdot & \cdots & \cdot \\ \cdot & \cdot & \cdots & \cdot \\ u_1 & u_2 & \cdots & u_s \end{array}$$

Note that u_i is also the reciprocal of the mean return time to habitat i (Hoel et al. 1972:60). Thus, a large u_i also indicates a relatively small number of steps before a bird returns to u_i after having left.

If we denote the frequency of the jth operational habitat (e.g., relative frequency of tree species j in the study site) by e_j, we can then define the environmental matrix (**E**) composed of s identical row vectors, each with s elements:

$$\mathbf{E} = \begin{array}{cccc} e_1 & e_2 & \cdots & e_s \\ e_1 & e_2 & \cdots & e_s \\ \cdot & \cdot & \cdots & \cdot \\ \cdot & \cdot & \cdots & \cdot \\ \cdot & \cdot & \cdots & \cdot \\ e_1 & e_2 & \cdots & e_s \end{array}$$

As a scaler u_j approaches unity, the environmental grain becomes coarser; and, as u_j tends to e_j, the environment becomes fine grained. Therefore, we have upper and lower limits to grain coarseness. An index of grain coarseness (C) can be calculated as

$$C = \sum_{j=1}^{s} |u_j - e_j|,$$

where (Colwell 1973),

$$C_{\max} = \sum_{j=1}^{s} [1 - e_j + (s - 1)e_j]$$
$$= 2(s - 1).$$

Thus, C can vary between 0 and $2(s - 1)$. By dividing C by $C_{\max}$ one can calculate a relative index that is independent of s. One can also compare the vector **u** to a row vector from **E**, in which case $C_{\max} = 2.0$ (e.g., if $u_1 = 1$, then all other u_i are 0 since $\Sigma\, u_i = 1.0$; if $e_2 = 1.0$, then all other $e_i = 0$ and $\Sigma\, |u_j - e_j| = 2.0$).

AN APPLICATION

STUDY SITE AND METHODS

Field work was conducted within a 20-km radius of the University of California Sagehen Creek Field Station near Truckee, California. Birds were observed June and August of 1976 and 1977 at elevations varying from 1800 to 2300 m. The basin is dominated by Jeffrey pine (*Pinus jeffreyi*) and white fir (*Abies concolor*). Meadow stands with lodgepole pine (*Pinus contorta* var *murrayana*) and aspen (*Populus tremuloides*) occur in the moist areas near springs and streams. Red fir (*Abies magnifica*) and mountain hemlock (*Tsuga mertensiana*) dominate at higher elevations.

Bird observations

For this analysis, two types of data were collected: first, an index of relative abundance of operational habitat units (in this case relative frequency of tree species); and second, a record of sequential moves by individual birds between tree species. A single observation started when a bird left one tree and ended when it landed on the next. An individual bird was sometimes followed as it flew from one tree to the next for up to 10 moves.

I tabulated the movements of four species of woodpeckers and three species of nuthatches among the four most common tree species (operational habitats) (Table 1). For this example, I eliminated all observations of birds landing on or departing from rarer tree species because sample sizes in these species were too small for analysis.

I also estimated the availability of stems of each tree species from a randomly located sample of 100, 0.04-ha circular plots. All stems >8 cm dbh were tallied among the four tree species.

Data analysis

Environmental (**E**) and grain (**G**) matrices were obtained from the data in Table 1 by dividing each cell

TABLE 1. ONE-STEP TRANSITION FREQUENCIES FOR MOVEMENTS AMONG TREE SPECIES BY FORAGING WOODPECKERS, SAGEHEN CREEK, CALIFORNIA

Species	Tree species[a] at t_i	Tree species[a] at t_{i+1}				
		LP	JP	WF	RF	Totals
Williamson's Sapsucker	LP	16	2	1	0	19
	JP	3	12	4	0	19
	WF	1	5	14	2	22
	RF	1	2	1	11	15
Red-breasted Sapsucker	LP	36	0	1	0	37
	JP	0	8	2	1	11
	WF	0	3	11	1	15
	RF	1	1	2	3	7
Hairy Woodpecker	LP	38	1	2	1	42
	JP	0	29	15	0	44
	WF	2	13	38	4	57
	RF	0	0	2	18	20
White-headed Woodpecker	LP	3	1	1	0	5
	JP	1	47	5	1	54
	WF	1	5	24	2	32
	RF	0	1	1	13	15
Pygmy Nuthatch	LP	0	0	0	0	0
	JP	0	33	3	0	36
	WF	0	3	5	1	9
	RF	0	1	0	3	4
Red-breasted Nuthatch	LP	20	1	2	1	24
	JP	1	53	5	1	60
	WF	3	4	10	2	19
	RF	0	1	2	40	43
White-breasted Nuthatch	LP	0	0	1	0	1
	JP	0	87	11	1	99
	WF	0	10	10	1	21
	RF	1	2	0	3	6
Random sample[b]		142	95	139	97	473

[a] LP = lodgepole pine, JP = Jeffrey pine, WF = white fir, RF = red fir.

[b] Frequency of each tree species counted on 100, 0.04 ha circular plots, randomly located on the study area.

value by its corresponding row total (Table 2). Stationary grain vectors **u** were calculated for each bird species so that $\mathbf{uG} = \mathbf{u}$. The row vector **u** is the eigenvector associated with the dominant eigenvalue of the transposed grain matrix, which in this case is always equal to unity (Vandermeer 1972:115). This calculation was accomplished using a FORTRAN program (available from the author on request) incorporating the EIGRF subroutine of the IMSL library (IMSL 1982). The eigenvector was normalized so that all values summed to 1.0. Harlow (1986a, b) provided a BASIC program that could also be used for the eigenanalysis.

Statistical inferences regarding the similarity of transition frequencies among bird species, and between each species and the randomly sampled trees (environmental matrix), were tested using log-linear models (Bishop et al. 1975) and chi-square tests (Neu et al. 1974, Riley 1986). Because these analyses assume a one-step, stationary, Markov process (i.e., the habitat unit occupied by a bird at time t depends only on its habitat occupied at time $t - 1$, and probabilities do not change over time), Bishop et al. (1975:265) discuss a goodness-of-fit approach for testing the assumption of one-step stationarity. I tested the grain matrices for symmetry ($G_{ij} = G_{ji}$ for all species) prior to computing among-species comparisons (Bishop et al. 1975:282).

To compare grain matrices of each species (**G**) to the environmental matrix (**E**), I used a chi-square test of independence based on the row frequencies of **G** and a row vector from matrix **E**. Interspecific comparisons were computed using a log-linear model that included main effects (row, column, species) and the interaction of row and column. All computations were performed using the HILOGLINEAR module of the SPSS/PC+ statistical program (Norusis 1986). Full descriptions of statistical inference tests are provided by Bishop et al. (1975), Basawa and Prakasa Rao (1980), and Chatfield (1973).

RESULTS

I recorded a total of 736 foraging transitions of seven bird species (Table 1). Birds were most likely to move to another tree of the same species rather than to another tree species in all cases except White-breasted Nuthatches using white fir. In the latter case, White-breasted Nuthatches were equally likely to switch to Jeffrey pine.

TABLE 2. COMPUTATION OF TRANSITION PROBABILITIES FROM TRANSITION FREQUENCIES FOR WILLIAMSON'S SAPSUCKER (TABLE 1)

	Tree species at t_{i+1}			
Tree species at t_i	Lodgepole pine	Jeffrey pine	White fir	Red fir
Lodgepole pine	16/19 = 0.84	2/19 = 0.11	1/19 = 0.05	0/19 = 0.00
Jeffrey pine	3/19 = 0.16	12/19 = 0.63	4/19 = 0.21	0/19 = 0.00
White fir	1/22 = 0.05	5/22 = 0.23	14/22 = 0.64	2/22 = 0.09
Red fir	1/15 = 0.07	2/15 = 0.13	1/15 = 0.07	11/15 = 0.73

The overall test of symmetry, based on the entire 4 rows × 4 columns × 7 species contingency table (Table 1), was not significant (χ^2 = 11.03, df = 36, P > 0.50), indicating that birds were equally likely to move from tree species *i* to species *j* as from species *j* to *i*.

Comparisons of tree-species use by each bird species with tree availability estimated from randomly sampled plots showed that all birds, except Williamson's Sapsucker, departed significantly from expected frequencies of use (Table 3). This was evident both from direct comparisons of the steady-state vectors **u** with the environmental vector e_j (assessed using the index of grain coarseness [Table 3]), and by chi-square tests of independence between the marginal row frequencies of each bird and the numbers of randomly sampled trees of each species (Table 1). White-breasted and Pygmy nuthatches differed most from the random sample; Williamson's Sapsucker differed least.

Interspecific comparisons, based on tests of homogeneity (Table 4), revealed significant differences among all pairs of species except Williamson's versus Red-breasted sapsuckers, Williamson's Sapsucker versus Hairy Woodpecker, White-headed Woodpecker versus Pygmy Nuthatch, and White-breasted versus Pygmy nuthatches. Significant differences indicated that birds differed in their probabilities of moving to a particular tree species at time t_i, given the tree species they used at time t_{i-1}.

DISCUSSION

DESIGN CONSIDERATIONS

Analyzing sequences of behavior using Markov chains appears to be a useful technique, primarily because such chains allow explicit recognition of the potential interdependence of sequential observations. The technique can be applied to any type of behavior—including spatial distribution—that can be categorized into discrete units. For example, Colwell (1973) used the method to analyze visit frequencies of hummingbirds to flower species and used the results to predict the relative abundance of phoretic mites in the various flowers. Cane (1978) used Markov chains to examine grooming behavior of a blowfly (*Calliphora erythrocephala*) in which sequences of 10 different types of behavior were analyzed, and to analyze 11 social behaviors (aggregated from 123 original categories) of rhesus monkeys (*Macaca rhesus*). Raphael and White (1984) used Markov chains to compare the use of snags, living trees, and other substrates among

TABLE 3. STEADY-STATE VECTORS OF TREE SPECIES USE DERIVED FROM EIGENANALYSES OF GRAIN MATRICES (TABLE 1), AND INDEX VALUES OF DEPARTURE FROM FREQUENCIES OF AVAILABLE TREE SPECIES

	Steady-state vector (**u**) of relative use of tree species					Significance[b]	
Bird species	Lodgepole pine	Jeffrey pine	White fir	Red fir	Index of grain coarseness[a]	χ^2	P
White-breasted Nuthatch	0.005	0.785	0.177	0.033	0.584	160.32	0.000
Red-breasted Nuthatch	0.155	0.354	0.125	0.367	0.315	43.01	0.000
Pygmy Nuthatch	0.000	0.787	0.147	0.065	0.587	70.53	0.000
Williamson's Sapsucker	0.391	0.288	0.239	0.081	0.062	1.35	>0.500
Hairy Woodpecker	0.129	0.244	0.351	0.276	0.171	9.10	0.027
Red-breasted Sapsucker	0.389	0.250	0.288	0.074	0.138	15.12	0.002
White-headed Woodpecker	0.019	0.499	0.268	0.214	0.205	55.71	0.000
Random sample[c]	0.300	0.201	0.294	0.205			

[a] $(\frac{1}{2}\sum_{j=1}^{s}|u_j - e_j|)$. Values can vary from 0 to 1, with greater values indicating greater departure from the fine-grained limit (random use of habitat units).

[b] Significance of chi-square test of independence based on data in Table 1 comparing row frequencies (marginal totals) of each bird species to random frequencies (df = 3).

[c] Proportional abundance of each tree species estimated from 100, randomly selected, 0.04 ha plots (e_j).

foraging cavity-nesting birds. Following techniques of Colwell (1973), they computed steady-state vectors of substrate use but did not conduct any tests of statistical significance of patterns; they simply described the values obtained. Investigators have used Markov analyses to examine sequences of song phrases in wood pewees (*Contopus* sp.) and cardinals (*Paroaria* sp.) (Chatfield and Lemon 1970), and to compare foraging-substrate use between male and female Emerald Tocanets (*Aulacorhynchus prasinus*) (Riley 1986). Mangel and Clark (1986) based their development of a unified foraging theory on what they call "Markovian decision processes," which are analyzed using Markov models.

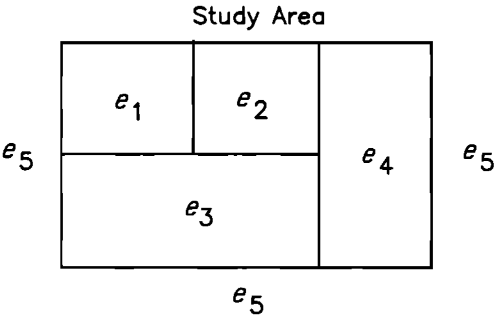
Most of these analyses were based upon first-order or one-step chains, but analyses of higher order processes are also possible. Suppose that the following are five successive observations of habitat units (or behavior), A, B, and C:

A B A C B C.

In this sequence there are five pairs of first-order observations (A–B, B–A, A–C, C–B, B–C) and four second-order triplets (A–B–A, B–A–C, A–C–B, C–B–C). The data could be arranged in a 3 × 3 × 3 table that contains the frequencies of each unit (A, B, or C) at time t_i that lead to each of the next two possible combinations at times t_{i+1} and t_{i+2}:

		t_{i+2}		
t_i	t_{i+1}	A	B	C
A	A	x_{111}	x_{112}	x_{113}
A	B	x_{121}	x_{122}	x_{123}
A	C	x_{131}	x_{132}	x_{133}
B	A	·	·	·
B	B	·	·	·
B	C	·	·	·
C	A	·	·	·
C	B	·	·	·
C	C	·	·	x_{333}

Chi-square tests of goodness-of-fit of such higher-order models compared to lower-order alternatives can be assessed using log-linear analyses described by Bishop et al. (1975:269).



Study Area

Transition Matrix

	e_1	e_2	e_3	e_4	e_5
e_1	0	1/4	1/4	0	1/2
e_2	1/4	0	1/4	1/4	1/4
e_3	1/6	1/6	0	1/6	3/6
e_4	0	1/6	1/6	0	4/6
e_5	2/10	1/10	3/10	4/10	0

Steady–state Vector

$\mathbf{u} = 0.133 \quad 0.133 \quad 0.200 \quad 0.200 \quad 0.333$

FIGURE 1. Hypothetical study area composed of four habitat patches (e_j) and surrounded by a fifth (e_5). The probability that an animal will move from e_i to e_j from time t_i to t_{i+1} is the ratio of the perimeter that abuts against e_j and the total perimeter of e_i. The matrix **E** represents the matrix of probabilities of transition from any patch e_j along a row to any other patch, and the vector **u** represents the long-term probability (after an infinite number of transitions) of an organism being observed in each of the five patch-types.

Another important assumption of these analyses, especially important in interpreting the steady-state vector **u**, is that transition probabilities are stationary. In reality, these probabilities may shift during different times of day, times of year, across different years, or among subgroups within the animal population (e.g., age groups, sexes, demes), as described by other authors in this symposium. This temporal heterogeneity of resource use or behavior is not a unique concern in Markov analyses; indeed, any behavioral study must consider these effects and must restrict conclusions to the appropriate season or time period. Under a Markov analysis, one could collect observations within each relevant time unit and then compute and compare transition matrices between units to explicitly test for differences. If none is found, the units may be grouped for further analyses. If they do differ, all subsequent analyses must be restricted to comparisons across animal groups within the same time unit.

Sample size is another important issue in these analyses. Although I am aware of no explicit treatment of sample size requirements for Markov analyses, the considerations appropriate for contingency table analyses probably apply. In general, the study should be designed so that none of the expected values of cells in the table

TABLE 4. COMPARISONS[a] OF TRANSITION MATRICES (TABLE 1) AMONG ALL BIRD SPECIES. CHI-SQUARE VALUES ARE GIVEN WITH SIGNIFICANCE IN PARENTHESES

Bird species	WISA[b]	RBSA	HAWO	WHWO	PYNU	RBNU
White-breasted Nuthatch (WBNU)	83.47 (0.00)	106.50 (0.00)	104.33 (0.00)	34.93 (0.00)	3.82 (<0.50)	73.95 (0.00)
Red-breasted Nuthatch (RBNU)	30.34 (0.01)	59.36 (0.00)	50.14 (0.00)	29.62 (0.01)	29.07 (0.02)	
Pygmy Nuthatch (PYNU)	41.31 (0.00)	56.76 (0.00)	53.52 (0.00)	12.17 (>0.50)		
White-headed Woodpecker (WHWO)	31.86 (0.01)	68.62 (0.00)	42.15 (0.00)			
Hairy Woodpecker (HAWO)	17.57 (0.29)	30.65 (0.01)				
Red-breasted Sapsucker (RBSA)	22.44 (0.10)					

[a] Chi-square tests of homogeneity, df = 15.

[b] Williamson's Sapsucker.

is <1 and no more than 20% of the cells should be <5 (Cochran 1954). Thus, a rough guide is that one should collect at least 5 times the number of cells in the analysis. For the bird data I used to illustrate the technique, I used a 4 × 4 × 7 table (=112 cells), which would require a sample size of at least 5 × 112 = 560 observations. This is a minimum estimate; greater numbers of observations (up to some asymptotic sample size) will lead to more robust results.

As in any study of animal behavior, an observer's actions must not influence the behavior of the observed animal. Because one is most interested in the movement among habitat units, it is critical that the observer does not disturb the animal, forcing it to move to a new location that it might not otherwise have chosen.

REFINEMENTS AND OTHER APPLICATIONS

The methods described here do not take into account the time spent in each habitat unit before moving to the next unit. It is certainly realistic to believe that an organism might spend more time in some habitat units (or behavior) than in others. For example, Raphael and White (1984: 38) reported that foraging time on a tree increased from averages of 30–73 s as tree diameter increased. Cane (1959) described methods to incorporate time effects into what she calls "semi-Markov" chains.

Another important improvement on the technique I have described involves a better sample-design and analysis of the distribution of available habitat units or environmental matrix (**E**). Most applications I have described assume a homogenous distribution of habitat units so that, at any time t_i, the choices available at time t_{i+1} are estimated from the habitat units that were randomly sampled over the entire environment (study area). However, if habitat units are patchily distributed, then the choices presented to the organism differ from one time to the next. Suppose, for example, that a study area contained only 10% lodgepole pine, occurring in one patch. If a woodpecker flew into the patch of lodgepole pine, its next choice of tree would probably be another lodgepole pine. The grain matrix for this bird could show a strong tendency to remain in lodgepole pine, even though the bird's actual behavior may have been random with respect to tree species when the environmental matrix was estimated from the overall study area. There are two solutions to this problem. First, one could estimate the total area occupied by each habitat-patch unit and then record the transitions between patch types and the transitions between units within patches. Colwell (1973) encountered a similar situation where hummingbirds foraged in patches of flowers; his techniques should be followed where resources are patchily distributed. If there is "preference" for one or more patch-types the observed transition probabilities will differ from expected transition probabilities.

A second approach would involve resampling the available habitat units at each successive location. From a bird's perspective, the available habitat probably lies in some radius (average distance flown between habitat units at time t_i and t_{i+1}) around its current location. Thus, selection should really focus on the units in this immediate environment rather than the whole study area. An observer could follow the birds from point to point, mark the successive locations (without disturbing the bird), and then estimate frequency of available habitat units in an area bounded by, say, a circle of radius r, which could be determined from pilot studies of movement distances. A grain matrix could be calculated as usual from the observed transition data, but the environmental matrix would be calculated from the sample of available units recorded at each foraging stop. Such an approach should provide a reasonable picture of the bird's selection of habitat units.

Markov analyses might also be useful in analyses of an organism's spatial distribution among geographically defined patches of habitat. To illustrate such an analysis, consider a hypothetical study area (Fig. 1). Each habitat unit e_j is a recognizable patch, such as a timber type or any mapped area. The question to be addressed is "What is the probability that an animal will be found in any unit e_j after n trials?" Note that a trial consists of a move from one unit to another. The probability that an animal will move from, say, patch e_1 to e_2, might be estimated from the proportion of the perimeter of e_1 that abuts against e_2 (in this case $1/4 = 0.250$). Similar values can be computed for each combination of units (Fig. 1). Over the long run, the expected distribution of animals in each habitat unit can be calculated using the eigenanalysis described above. In this example, the steady-state vector **u** equals 0.133, 0.133, 0.200, 0.200, and 0.333 for e_1 to e_5, respectively. One could then compare the observed distribution of animals to the steady-state vector using the chi-square goodness-of-fit or log-linear analyses described earlier. Such an approach could be used in radio-telemetry studies or any other studies where the spatial distribution of mobile organisms is investigated over time.

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