

Discrimination and classification of foraging paths produced by search-tactic models

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Search tactics are cognitive processes, or decision mechanisms, that organisms use to locate available resources such as food, mates, refugia, and high-quality habitats. However, our knowledge of the actual tactics that animals use while searching for resources is limited, and very little empirical evidence has been accumulated. Therefore, we developed a suite of search-tactic models (1) to simulate possible searching behaviors of mobile organisms so that inferences can be made about their decision mechanisms, and (2) to determine the extent to which different models produce paths that approximate a globally optimal solution. The search-tactic models included deterministic and probabilistic searches in attempt to characterize biologically plausible searching behaviors. Classical linear multivariate methods (discriminant function analysis, Mahalanobis distances) and nonlinear artificial neural networks were used to discriminate the paths produced by the different models and to classify “unknown” foraging paths into one of the search-tactic models, based on the geometry of the resulting paths. Both linear and nonlinear analyses suggested that it is possible for animals to use a nearest-neighbor search tactic to search with near-optimum efficiency without having complete knowledge of the specific locations of all available resources. Furthermore, both methods of analyses demonstrated that it might be possible to use characteristics of foraging paths in an experimental setting to make inferences about the actual decision mechanisms animals use while searching for resources. *Key words:* computer simulation, discrimination, foraging paths, multivariate analysis, neural networks, searching behavior, search tactics. [*Behav Ecol* 15:248–254 (2004)]

Searching behavior is defined as the active movement of individuals to locate or attempt to locate available resources such as food, mates, refugia, and high-quality habitats (Bell, 1991). Behavioral ecologists, foraging ecologists, and landscape ecologists have considered patterns of searching behavior to better understand how organisms move and the effect of their movements on the environment. However, each field has focused on different aspects of searching behavior with little attempt to integrate them (Lima and Zollner, 1996). For example, behavioral ecologists are interested in the decision-making processes associated with searching, landscape ecologists emphasize the relationship between searching behavior and environmental heterogeneity, and foraging ecologists focus on how individuals maximize benefits or minimize costs associated with searching. Furthermore, behavioral ecologists are concerned with the cognitive abilities of animals but do not currently have a means of delineating the decision mechanisms that animals use while searching for resources. Landscape ecologists generally use diffusion theory to model the dispersal of individuals within the environment to characterize the spatial distributions of foragers and resources (Farnsworth and Beecham, 1999; Turchin, 1991; Zollner and Lima, 1999). Although diffusion theory enables comparisons to be made among the searching behaviors of different species while minimizing behavioral interactions in the models, it might not be applicable to behaviorally complex organisms such as vertebrates because of their sophisticated cognitive skills. In contrast, foraging ecologists generally use optimality models that assume individuals are omniscient, having complete knowledge of the resources within their environment. Even though these models have a strong conceptual underpinning, the omniscience assumption is probably not valid because of limita-

tions in animal cognitive abilities. Although natural selection may act to optimize cognitive ability, factors such as structural, developmental, and phylogenetic limitations may keep the cognitive ability far from the theoretical optimum (Arnold, 1994; Dukas, 1998; Gould and Lewontin, 1979).

Search tactics are cognitive processes, or decision mechanisms, that organisms use to elicit a group of related and sequential behaviors that allow them to locate available resources (Bell, 1991; Ydenberg, 1999). Search tactics may be related to innate mechanisms, may reflect the ability of the organism to perceive environmental stimuli, or may more than likely manifest into some combination of the two. In addition, different organisms may use different search tactics depending on their diets, modes of locomotion, sensory abilities, levels of satiation, abilities to learn, and even their interspecific environments. Because animals are not omniscient and generally do not have complete knowledge of resource location, they must move in such a way as to maximize their chances of locating resources while minimizing the probability of returning to patches they have already visited (assuming a low turnover rate for the resources). For randomly distributed resources, variations of random walks are thought to be the most efficient searching methods (Viswanathan et al., 1999), whereas systematic searches are thought to be most efficient for uniform distributions of resources (Dusenbery, 1989; Zollner and Lima, 1999). However, application of different search tactics may involve tradeoffs. For example, one advantage of using random walks is that they imply little in the way of cognitive skills to perform the searching behavior; however, the disadvantage is the high probability of path crossings, which detracts from the optimality of the search, thereby increasing the time and energy spent in searching for resources. In fact, the only way to optimally search among any distribution of resources is to use the equivalent of the traveling-salesman path or Hamiltonian circuit (Anderson, 1983), which in this context is the shortest distance required to find and consume all available resources, producing a foraging path with no crossings.

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However, the number of computations required to solve this problem for N food items is proportional to $\exp(N)$ (Klein and Subramanian, 1998; Platzman and Bartholdi, 1989), which exceeds the expected cognitive abilities of animals, including primates, for more than just a few food items (Cramer and Gallistel, 1997; Menzel, 1973).

Random walks and Hamiltonian circuits are the extremes in terms of cognitive requirements and optimality of the resulting foraging path, and both are unlikely to be used frequently by animals. Therefore, these search tactics should not be incorporated uncritically into theoretical models because they may violate critical assumptions and minimize the applicability of the models. In the current study, we attempted to contribute to our understanding of searching behavior by simulating the performance of different classes of search tactics. Specifically, we attempted to determine (1) whether different search tactics produce foraging paths that have consistent and recognizable geometric properties within a realistic experimental setting, (2) whether foraging paths produced by different tactics can be distinguished from those of a globally optimal solution, and (3) whether underlying tactics might be inferred from the characteristics of the observable foraging paths they produce. If successful, such an experimental approach will provide behavioral ecologists with a means of inferring the actual decision mechanisms animals use while searching for resources. Once we have a better understanding of the actual mechanisms associated with particular searching behaviors, we can then incorporate those search tactics into the models produced by both foraging and landscape ecologists to produce more realistic models that are applicable to a wider array of biological situations.

SEARCH-TACTIC MODELS

The theoretical search tactics used in the current study included three deterministic and four probabilistic tactics and were simulated by using computer algorithms written for MATLAB v.5.2 (Mathworks, 1997). The deterministic models used were (1) minimum path-length search (MINI), (2) maximum path-length search (MAXI), and (3) nearest-neighbor search (NEAR). The probabilistic models were (4) trajectory-directed search (TRAJ), (5) reciprocal-distance search (RECI), (6) inverse-squared-distance search (INVE), and (7) uniformly random search (RAND).

This set of search-tactic models was intended to be representative rather than exhaustive and was chosen to include various kinds of searches from the shortest possible path (MINI) to the longest possible (MAXI) to put lower and upper bounds on the length and geometry of the resulting sets of foraging paths. Because they are globally optimal solutions, the MINI and MAXI models require that the individual have a priori knowledge of the specific locations of all available resources. The remaining search-tactic models relax this assumption to be more biologically realistic. The nearest-neighbor (NEAR) model simulated the idea that an animal will determine which of the available food items is closest to its current location, move to and consume that item, and iterate the same task from its new position. This tactic requires only that the nearest food item be within the perceptual range of the organism; if not, the rules of the search-tactic model change such that the tactic models a random walk. That is, once the organism consumes all of the resources within its perceptual range, it must move randomly until it locates another patch of resources before it continues the nearest-neighbor search. Therefore, our simulation of NEAR assumed that at least one resource is within the perceptual range at all times.

Among the probabilistic models, the trajectory-directed (TRAJ) model was based on the idea that an animal will choose an average direction of movement based on environmental stimuli and pick up the food as it travels along the linear transect. This tactic also requires that the resources lie within the perceptual range of the individual along the transect for the same aforementioned reasoning. Two other models were biased toward selecting nearby resources at a distance d , but allowed an organism to bypass them to capture resources farther away at smaller probabilities: the reciprocal-distance (RECI) model, based on a linear deterioration of perceptual range, and inverse-squared-distance (INVE, $1/d^2$) model, based on an areal deterioration of perceptual range. If food items were bypassed, then the animal was forced to return on a different pass to consume the point resources. The uniform-random (RAND) model generated uniformly random foraging paths with no biological basis by randomly permuting the sequence in which the 15 point resources were consumed. RAND implicitly served as the null model for the set of search-tactic models. Although additional kinds of systematic searches have been empirically observed in nature (e.g., spirals and petals), for comparative purposes it was important that the set of tactics be mutually consistent in their configurations. The models we used were defined to have a starting point at the bottom-left corner of a square domain outside the distribution of resources, whereas spirals and petals begin their searching in the center of a distribution of resources.

The search-tactic models were simulated with a design that might be used in an experimental study of searching behavior. Each of the search tactic models was simulated with 1000 iterations to find and consume the same set of 15 point resources, assuming neither satiation nor learning, so that comparisons among the tactics could be made, and to characterize the sampling variation for each of the theoretical search tactics. The number of resources was chosen so that there would be enough points to generate foraging paths that would characterize the search tactics adequately and still allow "organisms" the opportunity to search with a globally optimal solution by limiting the number of resources, which in turn limits the number of required calculations. The positions of point resources were determined by random sampling from a bivariate uniform distribution within a square domain (50 units \times 50 units); this sampling scheme ensured that each location within the domain was equally likely to have a resource located on it. Because we modeled only the linear path-segments among point resources rather than the actual path that an organism might take (as in the random-walk model), we could ignore boundary effects.

Path descriptors

For each iteration, the foraging paths produced by the different search-tactic models were measured by using 14 path descriptors (Bell, 1991; London, 1999): (1) total path length, (2) minimum step length, (3) maximum step length, (4) standard deviation of step lengths, (5) lag-1 autocorrelation of step lengths, (6) number of path crossings, (7) standard deviation of distances between path crossings, (8) lag-1 autocorrelation of absolute angular deviations, (9) minimum absolute angular deviation, (10) maximum absolute angular deviation, (11) mean absolute angular deviation, (12) standard deviation of absolute angular deviations, (13) mean signed angular deviation, and (14) standard deviation of signed angular deviations (Bell, 1991). For two consecutive steps, the angular deviation was defined to be the minimum angle between the

second step and the line extrapolating the first step; signed angular deviations were coded as positive if counterclockwise and negative if clockwise. This set of descriptors was chosen because they provide numerous correlated measures of crucial path characteristics without producing linear combinations.

Data analysis

To measure differences among the foraging paths produced by the different search-tactic models, we used discriminant function analysis (DFA) and artificial neural networks (ANNs). We chose to implement both kinds of analyses because classical statistics allow for linear discrimination among groups of observations while neural networks allow for nonlinear discrimination (Smith, 1993).

DFA is a classical multivariate statistical tool that is designed to predict group membership from a set of correlated variables by maximizing the linear separation among groups (Hand, 1981). When performing DFA, we do not have to specify how to combine variables in order to form different discriminant functions. Rather, DFA automatically determines the optimal combination of variables such that the first function provides the most overall discrimination among groups, the second provides second most, and so on (Hand, 1981). Moreover, the discriminant functions are orthogonal, so their contributions to the discrimination among groups will not overlap (Sokal and Rohlf, 1995); thus, each function accounts for a percentage of the total variance among groups. In addition to the percentages of the total variation, DFA produces several key results that aid in the understanding of the discrimination of the groups. For example, DFA provides the discriminant scores, which are the original data transformed into discriminant space and projected onto discriminant axes. Discriminant scores are useful because they allow us to visually examine the maximum separation of groups by plotting the scores as a function of the first two, or more, discriminant functions. DFA also produces the loadings (expressed as vector correlations between the variables and the discriminant functions), which indicate how and how well each variable discriminates the groups. In addition, DFA allows us to reclassify the original data to measure the ability of DFA to classify groups according to the preselected variables and to classify unknown observations (Hand, 1981). Both types of classification are conducted using the Mahalanobis distances between observations and group centroids. Mahalanobis distances are measures of the distance between two points in the space defined by two or more correlated variables in the original space; they are equivalent to Euclidean distances among discriminant scores. DFA does have key assumptions associated with it, such as multivariate normality and homogeneity of covariances; however, DFA is rather robust to the underlying assumptions for larger sample sizes (Hand, 1981; Tabachnick and Fidell, 1996), particularly if formal hypothesis tests are avoided.

ANNs are statistical information-processing systems that are based on generalizations of human cognition and are composed of subunits that are analogous to biological neurons. McCulloch and Pitts (1943) first described a neural network as a computer model of a biological neuron that could generate binary output. The McCulloch-Pitts neuron calculated the weighted sums of its input and produced an output of either zero or one depending on whether or not the total exceeded a threshold value. Rosenblatt (1962) extended the McCulloch-Pitts model to include stochastic events by organizing the ANN into layers with feed-forward connections between one layer and the next (Figure 1). This type of organization, which allows for the training of the network, is

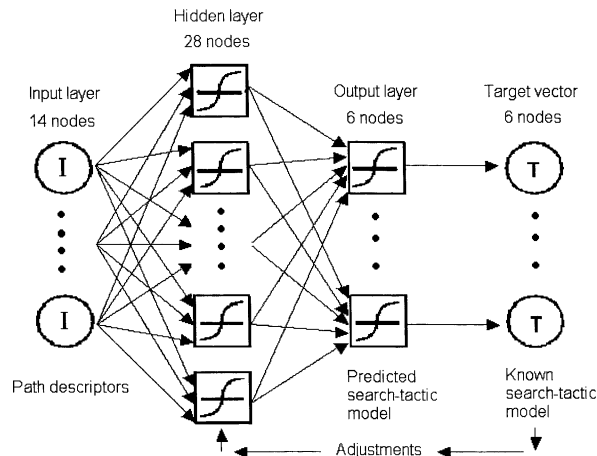


Figure 1
Diagram of the basic construction of a fully connected artificial neural network. Each circle or box represents a node within an input, hidden, or output layer. The arrows represent the transmission of information from node to node, and each arrow has an associated weight coefficient. The output is compared to the target vector; and the weights and biases are adjusted accordingly, so as to minimize the difference between predicted values and target output.

called a perceptron. Although Rosenblatt's one-layer perceptron applied only to elementary computations (Minsky and Papert, 1969), it provided the foundation for today's multi-layered perceptrons that are capable of learning through processes such as backpropagation.

Backpropagation provides a systematic way of using a known target vector to adjust the weights and biases of an ANN so that the output produced is as close as possible to the target vector (Smith, 1993). Backpropagation is usually conducted on a three-layer feed-forward network consisting of the input, hidden, and output layers although additional hidden layers can be added as needed (Hertz et al., 1991). The nodes of the input layer perform no calculations; they simply send the input values to the hidden nodes. Each node in the hidden layer calculates a numeric activation level that is determined from the weighted sum of the input variables plus or minus a bias value, which is analogous to a regression intercept. The weights can be either positive or negative depending on their excitatory or inhibitory effect, which is analogous to the synaptic efficacy of a biological neuron. Once each node has calculated the activation level, the hidden node then transforms the scalar value into an output signal with the use of a transfer function (Smith, 1993). Once output is generated, ANNs then compare the actual output to the target output and calculate an error coefficient (Hertz et al., 1991). This error coefficient is then propagated back to the hidden nodes, and the weights and biases are adjusted accordingly to reduce the amount of error. This cycle is referred to as an epoch, and it is generally repeated with enough iterations so that the error term reaches a minimum. There is no guarantee that the minimum will be globally stable, but as the number of hidden nodes and hidden layers are increased, the network fits the data more closely, minimizing the probability of them settling in local minima.

Data set

The data from the simulations were divided into three subsets to produce a training set, a validation set, and a testing set. The training set consisted of the first 500 sets of path descriptors for each of the seven search-tactic models and was used in the DFA to determine the discriminant functions and

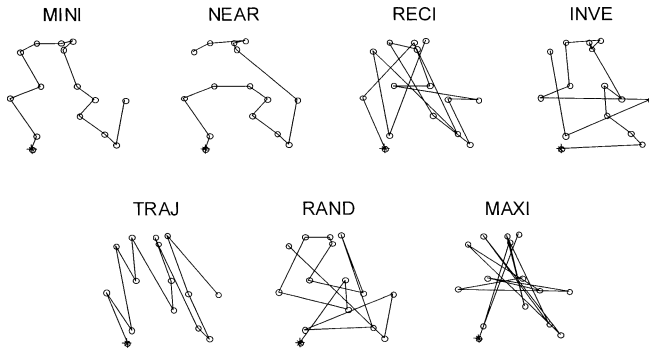


Figure 2

Comparison of foraging paths produced by the theoretical search tactics for the same set of randomly placed resources. Each empty circle represents a resource, and the asterisk inside the circle represents the first resource consumed, or the starting point. Each search tactic begins with the same resource to facilitate comparisons.

in the ANN to adjust the weights and biases of the network. The validation set consisted of the next 250 paths and was used only in the ANN to stop training early if further training would diminish the generalization ability of the network. The final subset of 250 paths was used as a testing set to measure the performance of the DFA and ANN at generalizing to new observations. Because the sets of path descriptors corresponded to paths among randomized point coordinates (point resources), the training, validation, and testing sets effectively comprised random samples of observations.

Discriminant function analysis

We used functions written for Matlab version 5.2 (Mathworks, 1997) to carry out the discriminant analyses. DFA (Matlab function “discrim”) was performed on the training set, and a plot of the hulls and centroids of the discriminant scores was produced to visually portray the discriminatory abilities of the analysis. The vector correlations (correlations of path descriptors with discriminant functions) and proportion of variance accounted for by each discriminant function were bootstrapped with 1000 iterations to generate corresponding 95% confidence intervals (CIs). Mahalanobis distances (function “mahal”) among groups of paths were calculated to quantify the differences among tactics, and they too were bootstrapped with 1000 iterations to generate 95% confidence intervals. The Mahalanobis distances were used to classify (function “classify”) the paths in the testing set to determine the reliability of DFA at classifying new, or “unknown,” paths that were not used in the analysis. Each path in the testing set was classified into one of the theoretical search tactics based on the centroid to which it was closest in the full discriminant space. As a result, some of the paths may have been misclassified if they were closer to another centroid rather than their own. Finally, the Mahalanobis distances were used in an unweighted pair-group hierarchical cluster analysis (function “upgma”), bootstrapped with 1000 iterations, to visually examine the relationships among search tactics.

Artificial neural network

Neural networks were constructed by using Matlab version 6 and the Neural Network Toolbox version 4. A fully connected ANN consisted of an input layer with 14 nodes each corresponding to a path descriptor, six hidden layers (one layer for each discriminant function) with 28 nodes per layer to provide adequate learning rates without overfitting the data, and an output layer with one node for each search-tactic model in the analysis. A hyperbolic-tangent transfer function

was used for all nodes within the network; this function accepts input values from negative to positive infinity and produces output values ± 1 , inclusive. A fully connected neural network was trained by using resilient backpropagation, which eliminates the detrimental effects of small slopes at the extreme ends of a sigmoidal transfer function (small slopes slow down the learning process) by using the sign of the gradient descent rather than the magnitude (Demuth and Beale, 2000). Training on the network continued until the mean squared error between the output values of the validation set and the known target vector stabilized. The network classified the foraging paths within the testing set based on a \pm threshold criterion. For a path to be classified, all but one of the variables produced by nodes in the output layer must have been negative; the node that produced the positive variable corresponds to the underlying search tactic. Thus, unlike classifications based on Mahalanobis distances, these observations were not forced to fit into a search tactic if the above criterion was not met. If many observations could not be classified, this was a sign of overlap between the tactics because the ANN could not reliably distinguish among them.

RESULTS

The search-tactic models used in this study produced distributions of paths that were notably different from one another based on appearance alone (Figure 2). For example, MINI resulted in the shortest total path lengths, producing paths having no path crossings and very low turn rates. TRAJ also resulted in paths with no crossings, but on average were longer and had much higher turn rates. In contrast, MAXI resulted in the longest paths with the highest turn rates and the maximum numbers of path crossings. In fact, DFA revealed that paths produced by MAXI did not overlap results from any of the other search-tactic models in the discriminant space, and the shortest Mahalanobis distance to another centroid was 937.7 (95% CI: 842.7, 1041.9) variance units. As a result, the MAXI data were removed from the analysis, and the remaining paths were reanalyzed to increase the resolution in discriminating among those tactics that were close to the globally optimal solution.

Reanalysis of the search-tactic models demonstrated that paths produced by all models except RAND (the null model) and RECI overlapped the globally optimal solution in their characteristics (Figure 3). However, this figure is somewhat misleading because only 89.1% of the total variation among models is portrayed. The Mahalanobis distances among the search-tactic models revealed a considerable distinction between MINI paths and those produced by the remainder of the models, but they also revealed that paths from several of the search-tactic models overlapped extensively (Table 1). For example, the search-tactic model that produced paths closest to the globally optimal solution, as measured by Mahalanobis distances, was NEAR ($D^2 = 6.80$ [95% CI: 5.90, 7.99]). RECI and INVE are separated by a relatively small Mahalanobis distance of 2.29 (95% CI: 1.92, 2.88) variance units. Such a small Mahalanobis distance might be nonsignificant in certain contexts; however, the design of this study did not allow for statistical testing of significance because the results are highly dependent on sample size, which was arbitrary in these computer simulations. The Mahalanobis distances were used to create a dendrogram to visualize the relationships among the various theoretical search tactics based on the resulting path characteristics (Figure 4).

The variation in foraging paths produced by the different models was geometrically characterized by the path descriptors, which within their respective categories (path length variables, step length variables, path crossing variables, and

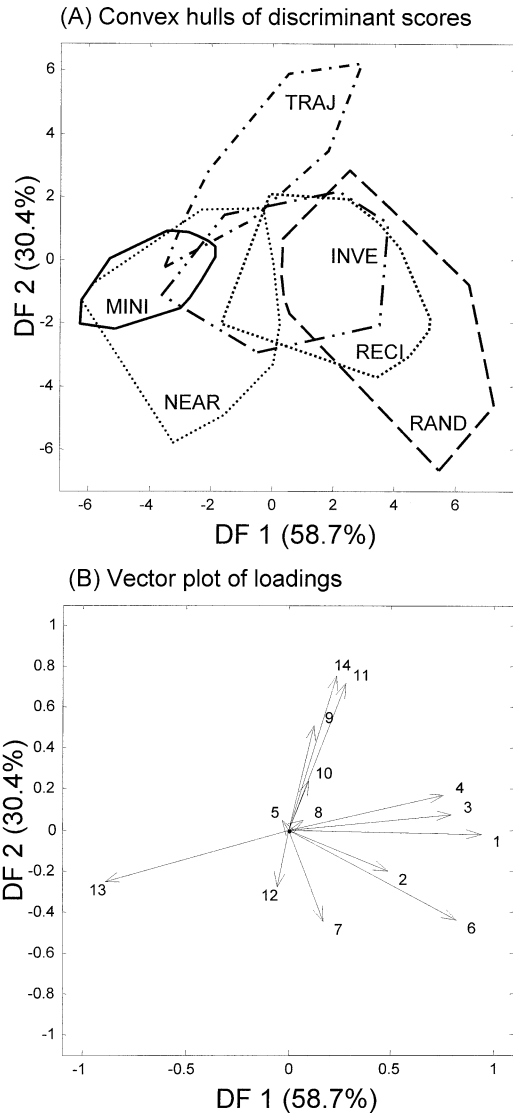


Figure 3
 Visual representation of how the path descriptors discriminated the search-tactic models, excluding MAXI. (A) Plot of the convex hulls of the discriminant scores. (B) Plot of the vector correlations between path descriptors and discriminant functions. The number in parentheses represents the percentage of the total among-group variance accounted for by the corresponding discriminant function.

angular deviation variables) discriminated among the search-tactic models in roughly the same manner; that is, they discriminated them along the same directions within the discriminant space (Figure 3). However, the individual path descriptors did not perform equally well in discriminating among the various search-tactic models. For example, total path length had a vector correlation of 0.94 (95% CI: 0.93, 0.95) for the first discriminant function, whereas the lag-1 autocorrelation of step lengths had a nonsignificant loading of -0.03 (95% CI: $-0.06, 0.01$). Four path descriptors were the primary discriminators along the first discriminant function with vector correlations greater than 0.75; these were (1) total path length, 0.94 (95% CI: 0.93, 0.95); (2) number of path crossings, 0.82 (95% CI: 0.78, 0.85); (3) maximum step length, 0.80 (95% CI: 0.78, 0.81); and (4) standard deviation of step lengths, 0.76 (95% CI: 0.74, 0.78).

Although it was not possible to test whether the foraging

Table 1
 Mahalanobis distances for search-tactic models, excluding MAXI

	MINI	NEAR	RECI	INVE	TRAJ	RAND
MINI	0	6.80	33.61	25.88	33.85	49.17
NEAR	6.80	0	22.14	13.53	33.02	37.87
RECI	33.61	22.14	0	2.29	23.07	5.61
INVE	25.88	13.53	2.29	0	19.22	13.72
TRAJ	33.85	33.02	23.07	19.22	0	37.01
RAND	49.17	37.87	5.61	13.72	37.01	0

paths produced by the different search-tactic models were significantly different from one another, we were able to quantify the probability of correctly classifying “new” observations, which provided some insight into the overlap of the tactics. The proportions of correct classification based on Mahalanobis distances revealed that a few of the paths generated by the search-tactic models were correctly classified with some degree of reliability: MINI, 99.6%, TRAJ, 96.4%, and RAND, 76.0% (Table 2). The performance based on ANNs also revealed that these paths were reliably classified: MINI, 94.8%, TRAJ, 97.6%, and RAND, 73.2% (Table 3). However, classification of the foraging paths produced by the different search-tactic models revealed that some paths were incorrectly classified by both methods of classification. For example, NEAR paths were misclassified as MINI paths 44.0% of the time based on the Mahalanobis distances, which further demonstrated the overlap with the globally optimal solution. The ANN also misclassified NEAR paths as MINI paths, but at 38.0% rather than at 44.0%. The lower misclassification rate was probably attributable to the nonlinear discriminatory ability of the ANN, but could have been attributable to the

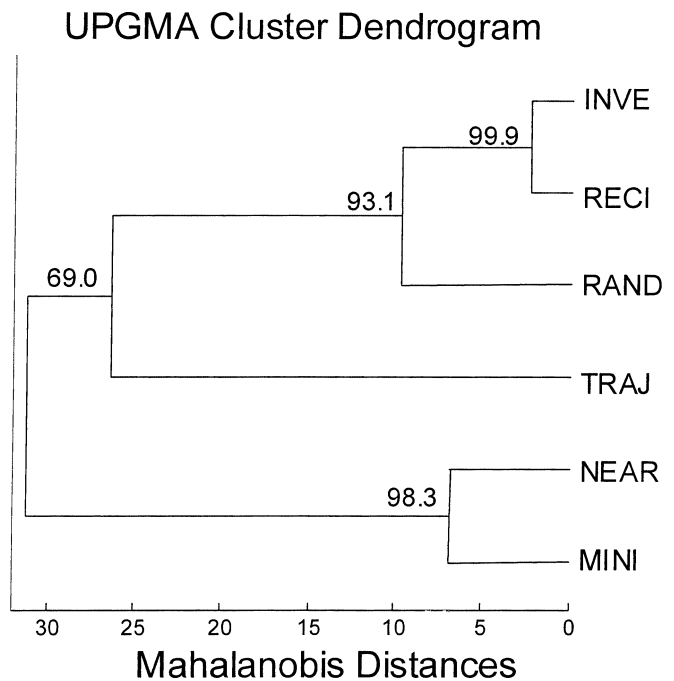


Figure 4
 Unweighted pair-group hierarchical cluster analysis (UPGMA) of the search-tactic models, excluding MAXI, based on Mahalanobis distances. The nodes connect those search-tactics that produce relatively similar paths, and the numbers represent the bootstrapped support value of the corresponding node.

Table 2
Percentage of classifications for the search-tactic models, excluding MAXI, based on Mahalanobis distances

Actual tactic	Classification					
	MINI	NEAR	RECI	INVE	TRAJ	RAND
MINI	99.6	0.4	0.0	0.0	0.0	0.0
NEAR	44.0	51.2	0.0	4.4	0.4	0.0
RECI	0.0	1.2	57.6	24.8	0.4	16.0
INVE	0.4	5.2	20.8	72.4	0.8	0.4
TRAJ	2.8	0.4	0.0	0.4	96.4	0.0
RAND	0.0	0.0	21.6	2.4	0.0	76.0

The percentage in boldface is the correct classification.

fact that the ANN did not force any path to be classified. Both methods of classifying observations resulted in misclassifications and both had difficulty in distinguishing paths produced by RECI from those produced by INVE, implying that there was a large amount of overlap in those paths generated by the different search-tactic models.

DISCUSSION

This study was based on a suite of search-tactic models that were developed to simulate biologically plausible searching behaviors. The first goal was to determine whether the various models produced paths having consistent, predictable path characteristics. The path of a searching animal can be characterized by geometric measurements that describe the pattern of movement (Bell, 1991). When all movements are consistent among replicate paths generated by a particular search-tactic model, the geometric measurements of the resulting paths have low variability and appear compact within a multidimensional space, such as the discriminant space portrayed in this study. When movements are inconsistent, the path characteristics are highly variable and will appear dispersed. The foraging paths produced by the various theoretical tactics in this study revealed that not all tactics have the same degree of consistency of movements; some of the distributions of path descriptors are more compact than are others within the projection space of the first few discriminant functions. As expected, the probabilistic search-tactic models demonstrate less consistency than do the deterministic tactics. All models exhibit more consistency than does the null model, RAND.

Groups of foraging paths overlapped considerably within the discriminant space, implying either that the models were too similar mathematically to be separated by discriminant analysis or that there were an inadequate number of path descriptors to accurately characterize the geometry of the foraging paths. Although there is no universal set of path descriptors that work well for every research design, Bell (1991) provides details regarding the measures that are useful in quantifying foraging paths. The measures he discussed included locomotory and turning rate, compass heading, turn bias, turning rate per unit distance, path straightness, displacement, thoroughness, autocorrelation, and stopping frequency. Although some of these measures do not apply to the current study, they provide an estimate of the number of descriptors needed to capture the biologically important aspects of a foraging path. Increasing the number of correlated path descriptors will generally provide greater discriminatory ability in the analyses as long as none of the descriptors form linear combinations with one another. Therefore, if we increase the discriminatory ability, then we

Table 3
Percentage of classifications for the search-tactic models, excluding MAXI, based on the artificial neural network

Actual tactic	Classification					
	MINI	NEAR	RECI	INVE	TRAJ	RAND
MINI	94.8	0.8	0.0	0.0	0.0	0.0
NEAR	38.0	51.6	0.0	4.0	1.2	0.0
RECI	0.0	0.8	44.8	21.2	0.0	16.4
INVE	0.0	7.6	15.2	61.2	1.6	0.4
TRAJ	0.8	0.0	0.0	0.0	97.6	0.0
RAND	0.0	0.0	19.6	1.6	0.0	73.2

The percentage in boldface is the correct classification.

are more likely to be able to recognize the paths produced by the various search-tactic models as different based on their resulting path characteristics.

The second goal was to determine the degree to which different search-tactic models could be distinguished from the globally optimal solution (i.e., are suboptimal). Classical models of optimal foraging predict that searching behavior should maximize net energy intake and minimize search time; therefore, optimal foraging models would predict searching behavior that closely mimics the globally optimal solution because it results in the shortest possible path length and has no path crossings. This optimal searching behavior does, however, require the maximum amount of cognitive ability, and only primates searching for a limited number of resources have demonstrated the ability to use it (Cramer and Gallistel, 1997; Menzel, 1973). Therefore, omniscience, which is an important underlying assumption of many optimal foraging models, is generally not a valid assumption. However, in this simulation study we found that various search-tactic models produce paths that overlap broadly in their geometry with the globally optimal searching solution, without invoking the assumption of omniscience (Figure 3). The NEAR model, in particular, overlapped the globally optimal solution to the greatest extent and represents a behavior that both invertebrates and vertebrates could use extensively, for it simply involves choice of the closest resource.

The third goal was to determine whether “unknown” foraging paths (i.e., paths for which the tactics generating them are unknown to the analysis) could be classified into one of the search-tactic models reliably to gain a better understanding of the decision mechanisms that real organisms might use while searching for resources. The current study did determine that unknown foraging paths could be allocated to the search-tactic models, but with varying degrees of reliability. Some of the search-tactic paths had higher probabilities of correct classification than others owing to the overlapping of distributions. The probabilistic search-tactic models generally had fewer correct classifications than did the deterministic models because of the inconsistency in movement patterns. However, we cannot eliminate probabilistic models from consideration because data on animal searches are currently too poor to tell if they use deterministic or probabilistic tactics. Our goal, however, should be to incorporate only those models that truly represent a distinct and biologically plausible searching behavior, whether deterministic or probabilistic, into the underlying set of theoretical tactics.

The protocol simulated in this study (square domain, randomly placed point resources to eliminate learning, and multivariate descriptors of foraging paths) may provide an experimental basis for associating the foraging paths of real

animals with the theoretical search tactics that produce them, and might allow inferences to be made about the decision mechanisms that animals utilize while searching for resources. The parameters of the search tactics actually used by a particular set of animals can then be incorporated into models produced by both landscape and foraging ecologists to make the models more biologically realistic and more applicable to a wider array of situations.

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