SELECTING THE BEST HOME RANGE MODEL: AN INFORMATION-THEORETIC APPROACH

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Abstract. Choosing an appropriate home range model is important for describing space use by animals and understanding the ecological processes affecting animal movement. Traditional approaches for choosing among home range models have not resulted in general, consistent, and unambiguous criteria that can be applied to individual data sets. We present a new application of information-theoretic model selection that overcomes many of the limitations of traditional approaches, as follows. (1) It alleviates the need to know the true home range to assess home range models, thus allowing performance to be evaluated with data on individual animals. (2) The best model can be chosen from a set of candidate models with the proper balance between fit and complexity. (3) If candidate home range models are based on underlying ecological processes, researchers can use the selected model not only to describe the home range, but also to infer the importance of various ecological processes affecting animal movements within the home range.

Key words: Akaike's information criterion; exponential power function; home range; information-theoretic approach; Kullback-Leibler distance; likelihood cross-validation criterion; model selection; utilization distribution.

INTRODUCTION

When animals confine their movements to a particular area, we typically define this area as the home range (Burt 1943). The size, shape, structure, and location of the home range may be affected by predator–prey relationships (Stamps 1995), competition (Bowers et al. 1979, Minta 1992), location of important resources (Powell 2000), or social pressures and mating systems (Conner et al. 1999). Therefore, accurate portrayal of the home range can provide vital insight into important ecological processes, and ecologists have been challenged to develop methods for its estimation.

Home ranges are usually modeled (i.e., approximated) from a sample of locations that are used to infer where an animal occurred but was not observed. The number of methods for estimating the home range is large and increasing. For example, Harris et al. (1990) reviewed four methods, Robertson et al. (1998) assessed the performance of seven, and Kernohan et al. (2001) evaluated 12 methods. Because of the importance of accurately depicting the home range in ecological studies, it is important to have objective criteria for evaluating their performance and choosing the best method for a set of location data.

Home range models are usually evaluated by comparing assumptions and methodology, using computer simulations, and testing goodness of fit. However, these approaches have not produced consistent, unambiguous, and generally applicable criteria for identifying the best home range model for a particular data set. We present a new application of information-theoretic model selection (i.e., choosing the best home range model) that overcomes many of the limitations of traditional approaches.

CHOOSING A HOME RANGE MODEL

A common approach to evaluating home range models has been to qualitatively compare assumptions and methodology and then summarize the strengths and weaknesses of each home range method (Anderson 1982, Harris et al. 1990, White and Garrott 1990, Kernohan et al. 2001). Although methodological comparisons have been beneficial in providing a thorough description of available methods, they fail to incorporate one of the most important criteria in selecting the most appropriate model; that is, how close a particular model is to the true home range (i.e., fit). To assess model fit, several authors have used computer simulations to generate known home ranges and then have compared the fit of various home range models to the simulated distribution (e.g., Boulanger and White 1990, Seaman et al. 1999, Worton 1995). Despite the power of using simulations to evaluate home range models, these studies often show that the performance of a particular home range model depends on the characteristics of the assumed true distribution. An alternative to using methodological comparisons or computer simulations is to "let the data speak" by using statistical tests to determine whether a set of locations is consistent with an assumed statistical model (e.g., Samuel and Garton 1985). However, these tests have not been extended as a general approach beyond the bivariate uniform and bivariate normal distributions, and this approach is

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open to criticisms of testing trivial null hypotheses and the associated problems of power and biological significance (Anderson et al. 2000).

An information-theoretic approach

We suggest that a better approach for choosing the best home range model is to apply the theory and methods of information-theoretic model selection (Johnson and Omland 2004). Model selection is built on the philosophy that all models are only estimates of reality and that no single model is ever "true" or likely to perform well in all situations (Hilborn and Mangel 1997). Thus, a more appropriate question would be which of a set of approximating home range models has the most support from the data.

Many scientific investigations rely on finding the best model out of a set of competing models with "*best*" defined as the smallest discrepancy between the approximating and the true model (Linhart and Zucchini 1986). Kullback-Leibler (KL) distance, described as the "information lost" when a fitted model ($\hat{f}(x)$) is used to approximate the true model ($f(x)$) (Burnham and Anderson 1998:37), is commonly used as a measure of discrepancy because of its connection with information theory (Kullback 1959). Model selection based on minimizing KL distance has been used increasingly in other areas of ecological research (e.g., Anderson et al. 1994, Harig and Fausch 2002), and we show how this approach can be used for home range model selection as well.

The goal of information-theoretic model selection is to choose the model with the smallest Kullback-Leibler (KL) distance, defined as

$$KL(f,\hat{f}) = \int f(x)\ln\left(\frac{f(x)}{\hat{f}(x)}\right)dx$$

where f is the true probability density of random variable(s) x and $\hat{f}$ is the probability density of the approximating model. Because the true underlying distribution, f, is unknown, direct calculation of $KL(f,\hat{f})$ is impossible. Therefore, various criteria have been developed to estimate the relative expected KL distance. One such is Akaike's information criterion (AIC) (Akaike 1973, Sakamoto et al. 1987):

$$AIC = -2\ln(\hat{f}(x)) + 2K$$

where $\ln(\hat{f}(x))$ is the maximized log-likelihood of the approximating model and K is the number of estimated model parameters. When the ratio of sample size/K is small (i.e., <40), Burnham and Anderson (1998) suggest using the second-order variant of AIC (AIC$_c$):

$$AIC_c = AIC + \frac{2K(K+1)}{n-K-1}$$

where n is the sample size. The relative support for model j can be determined by the difference (ΔAIC_j) in AIC (or AIC$_c$) between model j and the lowest AIC.

A less familiar, but more general, criterion for selecting the model with the smallest KL distance is likelihood cross-validation (Stone 1974, Geisser 1975, Linhart and Zucchini 1986). The likelihood cross-validation criterion is defined as

$$CVC = -2 \times \sum_{i=1}^{n} \ln\hat{f}_{-i}(x_i)$$

for $i = 1$ to n samples, where $\hat{f}_{-i}(x_i)$ is the density calculated for sample x_i without that sample being used to estimate $\hat{f}$. Cross-validation was a technique originally employed for assessing the performance of a single model. However, Stone (1974) showed that it could also be used for choosing among models and later demonstrated asymptotic equivalence with AIC (Stone 1977). Analogous to AIC, the relative support for model j can be determined by the difference (ΔCVC_j) in CVC between model j and the lowest CVC. Unlike AIC, the number of model parameters (i.e., complexity) is not explicit in CVC. To understand how CVC favors models with fewer parameters, it is important to understand the problem of overfitting. Overfit models are the result of having too many parameters for the amount of data used to specify those parameters. The result of overfitting is highly variable models that fit closely to the data used to construct the model, but predict novel observations poorly. By holding one sample out, constructing the model with the rest of the data, and then evaluating the fit of the model at the held-out location, CVC essentially evaluates the predictive ability of a model. Thus, highly variable models with too many parameters relative to n are penalized for poor predictions.

The home range as a probability density function

To use AIC or CVC, the approximating model must be defined in terms of a probability density function. Therefore, it is important to emphasize the equality among the concepts of home range, utilization distribution, and probability density function (Anderson 1982). Home range was recently defined as "the extent of area with a defined probability of occurrence of an animal during a specified time period" (Kernohan et al. 2001:126). This definition follows directly from that of previous authors who described the home range in a probabilistic manner (Hayne 1949, Calhoun and Casby 1958, Jennrich and Turner 1969). Calhoun and Casby (1958:2) introduced the "density function" as "a mathematical expression representing the probability of an animal being present in some arbitrarily small area" and Jennrich and Turner (1969:232) later described this density function as the "utilization distribution." The important connection is that the definition of the utilization distribution (i.e., home range) is the same as a bivariate probability density function. For continuous variates (i.e., x, y), the volume under a bivariate probability density function in some defined area describes the probability that an unrealized random "location" will occur in that area (Hastings and Peacock 1975).

Application to Real and Simulated Data

Animal location data

We applied information-theoretic home range model selection to location data representing a variety of sample sizes, taxa, and possible patterns of space use (Supplement 1). For each animal, we calculated home range estimates using six home range models. Three of these are common home range estimation methods, including the bivariate normal (BVN) (Jennrich and Turner 1969), and the nonparametric fixed (FK) and adaptive kernel (AK) methods (Worton 1989). For the kernel models, we used likelihood cross-validation to choose the smoothing parameter (Horne and Garton, *in press*). In addition to these, we developed three other home range models. Two of these were based on the "multinuclear" home range suggested by Don and Rennolls (1983:71) and the third was based on a uniform distribution of space use (e.g., Schoener 1981).

To accommodate animals that might have two centers of activity, we developed a two-mode bivariate circular normal mix (2CN) and a more general two-mode bivariate normal mix (2BVN). The 2CN model was defined as

$$\hat{f}_{2CN}(x,y) = D_1 \times m + D_2(1-m)$$

where D_i is a bivariate circular distribution and m is the proportional contribution of D_1. The 2BVN was a generalized version of the 2CN with each D_i component defined as a bivariate normal distribution. Parameters for 2CN and 2BVN were estimated by maximum likelihood using the simplex algorithm (Press et al. 1986).

It is likely that many animals would not conform to the aforementioned home range models if their space use were more uniform (e.g., territorial animals in uniform habitat) than unimodal, bimodal, or multimodal. Because of the absence of home range models that describe a uniform distribution, we used a bivariate exponential power model (CU) to allow for a circular uniform distribution of space use. The CU was defined as

$$\hat{f}_{CU}(x,y)$$
$$= \frac{2}{c2\pi a^2\Gamma(c)} \exp\left[-\left(\frac{\sqrt{(x-\mu_x)^2 + (y-\mu_y)^2}}{a}\right)^{2/c}\right]$$

where Γ is the gamma function, μ is the center of the distribution, $a > 0$ is the scale parameter, and $c > 0$ is the shape parameter (Robledo-Arnuncio and Gil 2005). Parameters were estimated using maximum likelihood (Mineo 2003). A particular case of the exponential power model is the normal distribution (i.e., $c = 1$), but it also allows for leptokurtic (i.e., $c > 1$) and platykurtic (i.e., $c < 1$) distributions. It is the platykurtic nature of the distribution that makes it useful for modeling uniform distributions. In fact, as c tends to 0, the exponential power model tends toward a circular uniform distribution with radius $= a$ (Fig. 1). Because we wanted a model
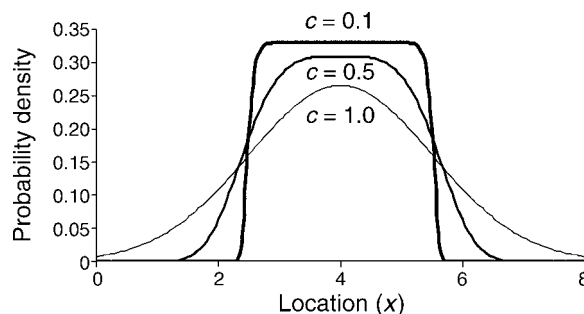

Fig. 1. Probability density function for one-dimensional exponential power model showing the effect of the shape parameter (c). For all three distributions, the location parameter (x) = 4, and the scale parameter (a) = 1.5.

for uniformly distributed space use, we bounded c by $0 < c < 1$.

Results of model selection

We calculated CVC for all home range models and AIC$_c$ for all parametric models (i.e., all except nonparametric kernel models) using a program written in Visual Basic (see Supplement 2). The best model was determined by the lowest CVC or AIC$_c$, but we considered models with ΔCVC or ΔAIC$_c$ < 3 to be competing best models (Burnham and Anderson 1998). When AIC$_c$ was used to determine the best model, we found a relationship between sample size and complexity (i.e., number of parameters) of the best model. As sample size increased, models with greater complexity were generally more likely to be the best model (Table 1). When CVC was used, we were able to compare the performance of the nonparametric kernel methods against the parametric models and found that kernel methods were often selected as the best model (Table 2). Indeed, there was only one (elk) out of six species for which either the adaptive or fixed kernel model was not a competing best model. Within the kernel models, neither fixed nor adaptive was consistently best.

Simulated data: AIC vs. CVC

Because of few direct comparisons between the performance of AIC and CVC, we were interested in comparing AIC vs. CVC model selection when a true distribution of space use was known. Therefore, we generated a unimodal bivariate normal and a bimodal bivariate normal mix to represent an animal's true space use (Appendix A). We then simulated animal location data by drawing 100 replicate random samples of size 30, 50, 100, and 200 from each distribution. For each sample of locations, we calculated AIC$_c$ and CVC for the four parametric home range models (i.e., CU, BVN, 2CN, 2BVN) and determined the percentage of the 100 replicate samples where each model was considered a competing best model (i.e., ΔCVC or ΔAIC$_c$ < 3). We found that AIC and CVC performed similarly in choosing the true data-generating model as the best

TABLE 1. Application of Akaike's information criterion (AIC_c) to determine the best parametric home range model ($\Delta AIC_c = 0$, boldface) for six animals.

Model	np†	ΔAIC_c					
		Bobcat (20)	Warbler (32)	Turtle (35)	Elk (51)	Black bear (64)	Hawk (102)
CU	4	**0**	16.9	23.0	8.4	100.4	130.1
BVN	6	3.3	**0**	12.8	**0**	53.2	20.3
2CN	7	9.5	10.8	16.2	4.4	9.2	32.0
2BVN	11	28.5	13.2	**0**	12.4	**0**	**0**

Note: The number of locations for each animal is given in parentheses.

† The number of parameters for each model.

model, although there was more model selection uncertainty at smaller sample sizes (i.e., 30), and especially for the more complex bimodal distribution (Appendix B).

DISCUSSION

An important goal of home range estimation is to gain insight into the underlying distribution of space use of a particular animal or group of animals. However, specifying the true distribution is a lofty endeavor because of the complexity of ecological systems and because of limited data for model specification. An alternative is to build simplified approximating models, sufficiently close to the true distribution, that are useful for prediction and inference. The goal of information-theoretic model selection is to assist in deciding which approximating models are closer to truth than others.

Selection criteria must take into account two components that cause an approximating model to deviate from the true distribution (Linhart and Zucchini 1986). First, if the approximating model is a poor description of the process, or assumptions about the underlying distribution are too rigid (i.e., too few parameters), then that particular model will have a high error of approximation. The second component contributing to the overall discrepancy is the result of having limited data with which to estimate model parameters. When too many parameters are fit with too few data, models will be inconsistent. That is, repeated sampling under the same conditions would lead to widely varying home range estimates. The benefit of using AIC and CVC as selection criteria is that both components of discrepancy

are taken into account, resulting in a model that fits the data well (i.e., small error due to approximation) and yet is not overly variable (i.e., small error due to estimation) (Fig. 2).

Implementing AIC and CVC model selection

In choosing whether to use AIC or CVC, results from our simulations did not suggest favoring AIC or CVC. Additionally, we found no compelling theoretical arguments favoring one vs. the other (Shibata 1989, Burnham and Anderson 1998). There are subtle differences. (1) AIC, as a measure of the relative expected KL distance, was developed under the assumption that one of the approximating models is either equal to or very close to the true model, whereas CVC is not restricted by this assumption (Shibata 1989). (2) Because model parameters are estimated using $n - 1$ data, CVC has been criticized for the accompanying loss of information in model development (Picard and Cook 1984). However, in the context of home range estimation, we feel that neither of these differences would invalidate the use of AIC or CVC as a general, objective way to choose the best home range model. We do suggest that future research should more thoroughly investigate the performance of AIC vs. CVC home range model selection with particular emphasis on variability, sensitivity to outliers and sample size, as well as robustness to model misspecification. Variability of each criterion could be assessed using straightforward application of bootstrap methods (Burnham and Anderson 1998:127–130).

Incorporating AIC and CVC as standard output of home range software would be relatively straightfor-

TABLE 2. Application of cross-validation score (CVC) to determine the best home range model ($\Delta CVC = 0$, boldface) for six animals.

Model	np†	ΔCVC					
		Bobcat (20)	Warbler (32)	Turtle (35)	Elk (51)	Black bear (64)	Hawk (102)
CU	4	27.8	17.5	48.2	3.0	144.3	141.9
BVN	6	12.3	**0**	44.2	**0**	97.5	33.6
2CN	7	7.1	8.0	43.4	0.2	48.0	54.9
2BVN	11	20.3	21.1	27.4	6.2	44.6	11.2
FK		**0**	0.5	0.8	4.8	3.8	**0**
AK		0.4	0.4	**0**	4.1	**0**	1.5

Note: The number of locations for each animal is given in parentheses.
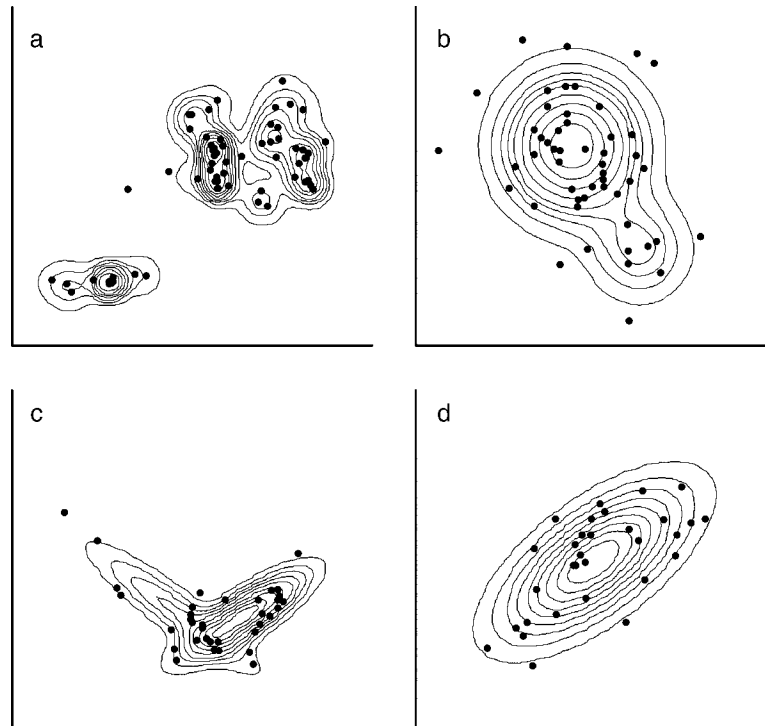
† The number of parameters for each model.

FIG. 2. Example of different space use patterns by (a) black bear, (b) elk, (c) Blanding's turtle, and (d) Golden-cheeked Warbler. Best models determined by information-theoretic criteria were (a) the adaptive kernel, (b) two-mode circular normal mix, (c) two-mode bivariate normal mix, and (d) bivariate normal.

ward. For AIC, the log-likelihood of each model can be calculated directly from estimates of the utilization distribution. After the log-likelihood is determined, one needs only to specify the number of parameters. For CVC, an iterative loop can be employed to sum the log-likelihoods at each location without that location being used to estimate the model. Although computations are more intensive for CVC (i.e., parameters must be estimated n times), we did not find that computation time prevented using this approach.

Beyond computational ease, using AIC as a relative measure of KL distance is supported by well-developed statistical theory (see Akaike 1973, Sakamoto et al. 1987, Burnham and Anderson 1998) as well as practical guidelines for implementing AIC in ecological studies (Anderson and Burnham 2002, Johnson and Omland 2004). If there is significant model selection uncertainty, an AIC-based model-averaging approach can be used to estimate parameters and make predictions. The main limitation of using AIC for home range model selection is that the number of estimable parameters must be specified. Thus, kernel methods cannot be included as competing models. When kernel models are included in the set of approximating models, CVC may be used as a naïve approach to evaluate models by means of their forecasts (Hjorth 1994).

As a final practical consideration, it is important to realize that AIC and CVC are only *approximations* of the relative expected KL distance. Therefore, despite asymptotic equivalence, we should not expect them to be equivalent for a given set of locations (see Tables 1 and 2). Indeed, AIC and CVC might not even agree on which is the "best" model in every situation. Although this result is possible, it only happened for one of our example animals (bobcat), and our simulations demonstrated that agreement was quite likely, especially at sample sizes ≥50. We do not think these discrepancies to be a failure of AIC or CVC, but believe that they only strengthen the point that, without knowledge of the truth, there will be model selection uncertainty and this may be exacerbated at small sample sizes.

Beyond home range description

Kernohan et al. (2001:160) suggested that our understanding of an animal's ecology is limited when "home range estimation does not examine meaningful hypotheses about factors underlying an animal's movements and behavior." A major benefit of using information-theoretic home range model selection is that it encourages us to ask questions about the ecological processes affecting animal space use. If candidate models are chosen to reflect different hypotheses about how certain ecological processes affect space use, then the degree to which different models are supported by the data reflects the strength of support for their corresponding hypotheses (Hilborn and Mangel 1997).

For this approach to realize its full potential, we should move beyond the convenience of using a single model to describe home ranges and begin exploring multiple models for both describing the home range and understanding important ecological processes that affect animal space use. For example, each home range model that we considered, except kernel models, was derived from hypotheses about ecological factors affecting space use. The BVN model approximates the space use of an animal that "wanders" out but must continually return to a central place (e.g., nest or den site) (Dunn and Gipson 1977). Similarly, the 2BVN is based on the idea that an animal has two foci of activity and wanders out from these. The CU model, characterized by a uniform distribution of space use within a sharp boundary, is theoretically the result of low-density, territorial animals in relatively homogeneous environments (Grant 1968, Covich 1976). One could use information-theoretic model selection to answer the question of whether a particular animal's space use was consistent with a central-place wanderer or the result of territorial behavior.

We see no need to limit the possible home range models to the ones that we considered. With objective criteria for deciding among home range models, new models based on other hypotheses of space use are encouraged. In the future, we see a great opportunity to incorporate additional spatially explicit variables, other than x–y coordinates, into home range models. For example, space use of many animals is affected by the location of important resources, escape cover, and other organisms of the same and different species. By incorporating this information, we are likely to get home range models with better fit while enhancing our understanding of the ecological factors affecting space use. However, as additional variables are incorporated, home range models will increase in complexity and there will be a need to evaluate these more complex models against simpler ones. Use of information-theoretic criteria such as those presented here will greatly aid this development.

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APPENDIX A

Unimodal bivariate normal and bimodal bivariate normal mix distributions used to generate 100 replicate samples for comparing AIC vs. CVC model selection (*Ecological Archives* E087-066-A1).

APPENDIX B

Percentage of 100 replicate samples for which each home range model was a competing best model (i.e., ΔCVC or ΔAIC$_c$ < 3) (*Ecological Archives* E087-066-A2).

SUPPLEMENT 1

Animal location data used for home range analysis (*Ecological Archives* E087-066-S1).

SUPPLEMENT 2

Visual Basic source code containing the algorithms described in this paper (*Ecological Archives* E087-066-S2).

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