
14 Analysis of Movement and Habitat Use from Telemetry Data

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■ 14.1 INTRODUCTION

Telemetry in freshwater environments began in the 1950s (Trefethen 1956; Stasko and Pincock 1977; Mitson 1978), and a fairly extensive body of literature has developed since then. Unfortunately, the literature contains very few rigorous treatments of telemetry data. The data sets generated during a telemetry project quickly become so massive that analyses could not really flourish until personal computers became widespread. Now that personal computers are pervasive, the absence of complex analyses that produce quantitative results cannot be blamed on a lack of processing power. Though fish telemetry projects continue to proliferate, the dearth of quantitative analyses used in them is perhaps due to the absence of a readily available synopsis of the various approaches that can be employed and exposure to the various software packages that have been developed to perform such analyses. Fortunately, sophisticated personal computer programs that run on a variety of platforms are available free of charge from a variety of sources (e.g., White and Garrott 1990; Kenward 1992; Larkin and Halkin 1994; Hooge et al. 2001). Our objective for this chapter is to help provide a foundation for synthesizing some of the many divergent approaches and software that can be used in the analysis of telemetry data.

While we recognize that the emphasis of this book lies with data analysis, tackling telemetry analyses without first carefully considering an adequate study design can lead to untrustworthy results. Perhaps the first question that should be asked regarding proposed telemetry-based research is whether telemetry is really necessary to answer the question of interest. Some have implemented costly and labor intensive telemetry studies because of the high-tech allure when a more mundane approach would have yielded better results and been considerably less labor intensive. For instance, course-scale movement and range extent can often be examined with conventional mark–recapture programs that allow for the tagging of thousands of individuals. However, there are certainly many situations in which telemetry is the only realistic option for addressing the questions of interest. Fine-scale movement and habitat use studies often fall into this latter category.

If one is certain that all other options have been explored, one can find details on telemetry equipment in Henderson et al. (1966), Stasko and Pincock (1977), and Winter (1996). Specific methods of transmitter attachment are discussed in Hart and Summerfelt (1975), Ross (1981), Schramm and Black (1984), and Petering and Johnson (1991). Both radio and ultrasonic transmitters are used in fisheries work, each with its own benefits and limitations. In addition to the standard transmitters that provide horizontal locations of a fish's position, many specialized transmitters exist that can provide additional information. Perhaps the most commonly used specialized transmitters are temperature sensitive (Kelso 1978; Schulz and Berg 1992). Not only is ambient temperature important for bioenergetics work (see Chapter 12), but generally, if the lake is stratified, the depth of the fish can be inferred as well if a temperature profile of the lake has been obtained. Alternatively, several authors have used pressure-sensitive transmitters that measured depth directly (Warner and Quinn 1995; Lee and Bergersen 1996; Baldwin et al. 2002). Numerous authors have explored the use of heart rate telemetry (Priede and Young 1977; Armstrong et al. 1989; Lucas et al. 1991, 1993) and tail beat frequencies (Stasko and Horrall 1976; Ross et al. 1981; Johnstone et al. 1992) to try to assess energy budgets of host fish. Because heart rate can be affected by stimuli other than exercise, electromyogram transmitters have become increasingly popular for indirectly assessing oxygen consumption (Weatherley et al. 1982) and swimming speed and activity (Demers et al. 1996; Økland et al. 1997). Because these specialized techniques generally require specialized analyses, they will not be discussed here. Interested readers should consult the literature cited for each topic.

■ 14.2 FUNDAMENTAL CONSIDERATIONS IN TELEMETRY-BASED RESEARCH

14.2.1 Representative Samples

Paramount to any telemetry project is the underlying assumption that those animals carrying transmitters are representative of the population as a whole. Historically, this has been evaluated subjectively as in “the animals appeared normal.” More rigorous treatment of this assumption is warranted, however, as the repercussions can be severe if this assumption is violated. If, for example, the implantation procedure resulted in substantial internal infections of most fish that received transmitters and infection induced extreme lethargy, one would expect these fish to move significantly less than their untelemetered counterparts. If movement and habitat use by telemetered fish is uncharacteristic, then there is little point in conducting the study, as it will be uninformative about the population of interest. Unfortunately, this dilemma is difficult to resolve and is usually complicated by the absence of controls (Doerzbacher 1980). The assumption is difficult to test because telemetry is used presumably to gather information that one cannot obtain any other way, making it difficult to compare data with untagged controls. Numerous studies have been conducted with dummy

transmitters in laboratory settings and have failed to document negative effects on growth, feeding, condition, or swimming behavior (e.g., Moore et al. 1990; Martin et al. 1995; Swanberg and Geist 1997; Brown et al. 1999; Cote et al. 1999; Cooke and Bunt 2001). The program MARK (White and Burnham 1999) can be used to compare survival rates between fish carrying transmitters and those monitored with conventional tag recovery studies, allowing estimation of the impact of the transmitter on survival of telemetered fish compared with fish tagged in a conventional manner. Now that transmitter battery life has been greatly enhanced, merely documenting survival of fish carrying transmitters over an extended period of time may lend some support to the notion that they are behaving normally. Additionally, if no differences in growth or condition can be detected in the same waters between telemetered fish and conspecifics tagged with conventional methods, then transmitters are probably not negatively affecting the host fish.

There are several things one can do in order to minimize the potential negative influence of the transmitter, including using the smallest possible transmitter that will still allow collection of the required data. Some have advocated keeping the weight of the transmitter to less than 2% of recipient's body weight (Gallepp and Magnuson 1972; Ross and McCormick 1981), although Brown et al. (1999) found that transmitters weighing up to 12% of the body weight did not affect swimming performance. The transmitters, if not internal, should be inconspicuous and unobtrusive. Finally, data acquisition should be delayed until animals have had a chance to become accustomed to the extra ballast afforded by the transmitter, so that fish behavior can become representative. Activity patterns, growth, and condition may be abnormal at least 2 weeks following surgery (Smith 1974; Manns and Whiteside 1979; Knights and Lasse 1996; Paukert et al. 2001). If resources permit, monitoring the behavior and health of captive fish carrying transmitters in a controlled setting can also be helpful.

Additionally, one must be concerned that the approach used to capture fish will not lead to an unrepresentative sample and thereby biased statistics. For instance, gill nets sample moving fish more than they do stationary ones. If all fish used in the study were acquired from gill-net sets, one might run the risk of implanting transmitters in a more mobile subpopulation, biasing movement estimates for the population as a whole. The radio-marked sample must be representative of the entire population if correct inferences from radio-marked fish are to be applied to the entire population.

Timing of the study and data collection is critical as well; fish should be observed over a time frame that is representative of the question of interest. One's inference regarding behavior patterns is limited to the seasons in which one observed the fish. If one is exploring habitat use but only locates telemetered fish in the middle of the day, then one cannot infer what habitats these same fish use at night. This notion seems trivial, but telemetry studies have often extrapolated behavior patterns outside the window of observation. To do so is simply not supported by the data.

14.2.2 Data Format

Analysis of telemetry data requires that information be stored in a readily usable digital database because rigorous treatment of telemetry data cannot be addressed without a computer. The pervasiveness of geographic information systems (GISs) has greatly facilitated the analysis of spatial telemetry data (Rogers and Bergersen 1996) for both map generation and analysis. Conventional spreadsheet programs (e.g., Microsoft's Excel or Corel's Quattro Pro) are also very capable platforms for compiling data and performing some of the more rudimentary data analyses.

Basic telemetry data are at least three-dimensional (x and y in space and z in time), so that in addition to the tag number and date and time, some metric of horizontal position must be recorded in the database. A variety of mapping systems have been used for describing position, such as the township-range land-mapping system, the latitude–longitude system, and the Universal Transverse Mercator (UTM) system. The township-range land-mapping system is difficult to work with, and because of survey errors, distances between locations cannot be computed reliably (White and Garrott 1990). The latitude–longitude system is not rectangular, making calculation of the distance between any two points less intuitive. The UTM system is the coordinate system of choice for mapping locations in inland waters because subsequent analysis is so much easier than it is in a latitude–longitude system. The UTM approach is based on the metric system, which is the universal standard for science. It provides a Cartesian coordinate system within each zone, allowing easy calculation of distances between points and greatly simplifying triangulation to locate animals. Now that global positioning systems (GPSs) are widely used in telemetry projects, obtaining UTM coordinates is trivial as well.

In the UTM system, the world is divided into 60 zones between 80°S latitude and 84°N latitude that each span 6° of longitude and are bisected by a central meridian. The polar ice caps are not included because the width of the zones becomes zero at the North and South poles. In addition, the coordinate system is not continuous because coordinates from a spherical surface cannot be plotted on a Cartesian coordinate system without breaks. Though this projection spans the globe, its power lies in mapping finer scales because error and distortion increase for regions that cover more than one zone. The UTM coordinates consist of a zone descriptor and two seven-digit numbers with units in meters. The y -coordinate increases with distance from the equator. The x -coordinate describes the distance from the central meridian. Five hundred thousand meters (3° longitude) are added to each x -coordinate within each zone so that negative x -values don't result. As one heads east within a zone, x -coordinates increase; y -coordinates increase as one heads north.

14.2.3 Study Design

There are basically three kinds of telemetry studies that can be conducted. The first are exploratory descriptive studies that are very common in the early literature.

Usually there is no attempt at formulating testable hypotheses. Some include evaluations of home range size and movement, but they are limited to learning about what an animal does but not why (Sanderson 1966; White and Garrott 1990). Descriptive studies that simply map fish locations are of limited value. The second variety of telemetry studies are correlative in nature and are becoming increasingly prevalent. These studies try to link movement or habitat use to environmental features that may be important to the well being of the fish. Although relationships can be documented, they do not necessarily imply cause and effect. Manipulative experiments with both spatial and temporal controls make up the third type of telemetry study. These are the only ones that can establish why animals do what they do and are therefore preferred.

Careful study design is critical if useful results are to be obtained. The notion that analyses are restricted to summarizing data that has already been gathered is a major misconception. Consideration of analysis goals should precede data collection to ensure that the study is worthwhile and to ensure that the appropriate data will be collected (Kenward 1992). If the parameters to be estimated or hypotheses to be tested are not defined, then an optimum strategy for data collection cannot be formulated and sample sizes cannot be determined. Sample size and power calculations (see Chapters 1 and 3) are mandatory before initiating a study because they determine whether or not proposed experiments will adequately address the questions that are posed. Either literature searches or pilot experiments can provide the background information needed to make these calculations. Simply employing the latest technology does not guarantee that quality research will follow. If funding or time constraints will prevent one from achieving the sample sizes necessary to detect a biologically significant difference, then there is no point in conducting the study. Unfortunately, cost and labor must be factored in, as transmitters are expensive and monitoring them has historically been labor intensive. Precision of estimates should be adequate to answer the questions being addressed, even if attaining adequate precision means focusing on a narrower set of questions, such as a portion of the population (e.g., one species, one sex, or a single basin). To answer one question well is far better than to address many questions poorly. Experiments with low sample sizes can lead to variable results with little power to detect differences in metrics of interest.

14.2.4 Pseudoreplication

The independence of successive observations of a given fish has always been a big concern in telemetry work (Byers et al. 1984; Swihart and Slade 1985; Alldredge and Ratti 1986; Thomas and Taylor 1990; Cresswell and Smith 1992). The closer in time two locations occur, the more likely they are to be autocorrelated. Autocorrelation has received much attention because many of the statistical techniques used in telemetry work require that observations be independent. The assumption of independence is violated on two levels when locations are taken as the sampling unit and records for all individuals are combined or pooled (Aebischer et al. 1993), as is common in fish telemetry analyses. If locations are taken to be

the sampling unit, then points close in time are serially correlated (Swihart and Slade 1985). In addition, if locations are pooled across individuals, then the natural heterogeneity found between individuals is eliminated, resulting in statistical tests that yield significant results more often than they should. Pooling data across individuals is only justified if all individuals being monitored act similarly (Aebischer et al. 1993), which is rarely the case in natural systems.

This violation of observation independence, however, is largely an artifact of how the telemetry data are analyzed. If inferences are to be made about the population of animals, the experimental units in a telemetry project are the individual animals, not the individual location estimates (Aebischer et al. 1993; Winter 1996; Otis and White 1999). Though precise estimates of an animal's movement can be achieved by intensive sampling of an individual, we are generally interested in how the population as a whole behaves. Hypothesis tests should use the variation among individuals to assess significant effects. As such, the power of a given study will then be driven by the number of fish monitored more than the number of locations obtained for each fish (Otis and White 1999). Using each location as a sampling unit while analyzing telemetry data is pseudoreplication and is the equivalent of "statistical malpractice" (Hurlbert 1984). The perceived dilemma associated with autocorrelation is mitigated when the data are analyzed correctly and experimental unit assignment is restricted to individual fish only (Kenward 1992). In fact, serial correlation between locations of an individual fish is not necessarily a bad thing if sampling is representative, as increased sampling effort (resulting in points closer in time) will better describe what an animal is actually doing (Aebischer et al. 1993). The emphasis on obtaining uncorrelated location estimates has been misguided and has allowed the more egregious violation of pseudoreplication to persist.

■ 14.3 ESTIMATION OF TELEMETRY ERROR

Telemetry error is introduced into fish telemetry projects from two sources. The first potential introduction or error occurs when trying to determine the actual position of a telemetered fish. Unlike radio telemetry, ultrasonic telemetry can make this source of error negligible, especially in small basins. The second potential introduction occurs when converting that fish position to a pair of coordinates that can be used to plot the location on a map. The advent of GPS technology has greatly simplified this task. If fine-scale habitat work is needed, then one might consider setting up a differential GPS (Rogers and Bergersen 1996). By deploying a fixed GPS base station, one can subtract erroneous deviations in position recorded on the stationary unit from positions registered on a mobile unit to achieve added accuracy. For deeper-dwelling fishes living in lentic systems, one can maneuver the monitoring boat directly over the fish while obtaining a GPS reading (Wilkerson and Fisher 1997; Paukert and Fisher 2000). The primary concern with this approach in shallow systems is that continual harassment of the fish may actually alter the very behavior that one is hoping to monitor. In these situations, it may be advisable to maintain some distance between the observer and the

subject by employing a triangulation technique to determine fish location (Springer 1979; Lenth 1981; Nams 1989; Saltz and White 1990; White and Garrott 1990). For both approaches, it is imperative that experiments are conducted to verify the methodology and evaluate what accuracy can be expected (Box 14.1).

In addition to legitimate sources of error, simple data entry errors can dramatically alter the results of an analysis. It is imperative that the data sets are first subjected to algorithms that can identify potentially erroneous data points (White and Garrott 1990). Dates and times should increase chronologically, and movement between fish locations should be assessed to ensure that they are reasonable. Finally, the location of a fish should be reasonable as well (e.g., if a recorded observation has a fish on dry ground, then the raw data forms should be reviewed).

■ 14.4 SPATIAL DISTRIBUTION

The first step in the analysis of telemetry data should be the creation of location maps. With the rapid expansion of GIS technology, the generation of maps is trivial and greatly facilitates subsequent analyses. Generally, the time dimension is eliminated, and fish locations are overlaid on a map of the perimeter first, then on maps of other habitat features (e.g., depth, habitat type, and temperature) to evaluate use. Many of the subsequent analyses of telemetry data will focus on fusing spatial information into one dimension, which results in a loss of information. Often an examination of the raw data can be more revealing in terms of illustrating the importance of habitat features that do not show up in conventional summary statistics. This examination can lead to a better understanding of the system as a whole. In many packages, animated graphics can reintroduce the time dimension by portraying movement through time. Although it can be difficult to do quantitative work with these graphics, they can be instructive when combined with maps of habitat features.

Of interest is whether the distribution of fish locations on the map is random. Samuel and Garton (1985) propose a Cramér-von Mises statistic to test whether the distribution of fish locations follows a bivariate uniform distribution. White and Garrott (1990; their Appendix 7) provide SAS code to perform the test. Another conceptually simple approach to evaluate randomness compares the distribution of the fish locations to an equal number of random locations placed in the same basin (Rogers 1998), which is analogous to a randomization test. One metric to use as a test statistic would be the variance of the distances from each random point to the nearest fish location. If the distribution of the fish locations is fairly random, then the distances between fish locations and random locations should not be highly variable. On the other hand, if fish locations are highly clustered, then distances from each random point will be highly variable, depending on whether the point is near or far from the cluster. The entire process of generating the variance of these distances is then iterated 1,000 times to generate a mean variance estimate that is then used as a test statistic (Figure 14.1). Replacing the fish locations with an equal number of randomly placed “pseudolocations” generates the distribution of this test statistic. This process should be iterated at

Box 14.1 Estimation of Telemetry Error

Prominent landmarks were used to assess the location of 31 largemouth bass carrying ultrasonic transmitters in two small impoundments near Denver, Colorado, over a 4.5-year period (Rogers 1998). Because these landmarks were associated with the shoreline, it was assumed that error would be a function of distance to shore. This error was quantified by locating 50 random points on each lake's surface by means of prominent landmarks and by means of a differential global positioning system (GPS) with better than 1-m accuracy. If the GPS readings reflect true position, then error associated with using prominent landmarks was taken to be the distance between each pair of locations generated for each point by the two methods.

Distance from the 50 random locations to shore was calculated with the program FishTel (available at <http://wildlife.state.co.us/Research/Aquatic/Software/>) and a digitized map of the lake perimeter. Distance between each pair of locations (prominent landmark and GPS) was generated in a simple spreadsheet by use of the Pythagorean relation. As expected, error generally increased with distance from shore (see figure) with fitted regressions for both lakes having positive slopes ($P = 0.002$ in Lake Ladora and $P \leq 0.001$ in lower Derby Lake). Because fish tended to congregate offshore in winter seeking deeper warmer water, this analysis suggested that greater error was incorporated in estimates of winter movement than those movement estimates generated in summer.

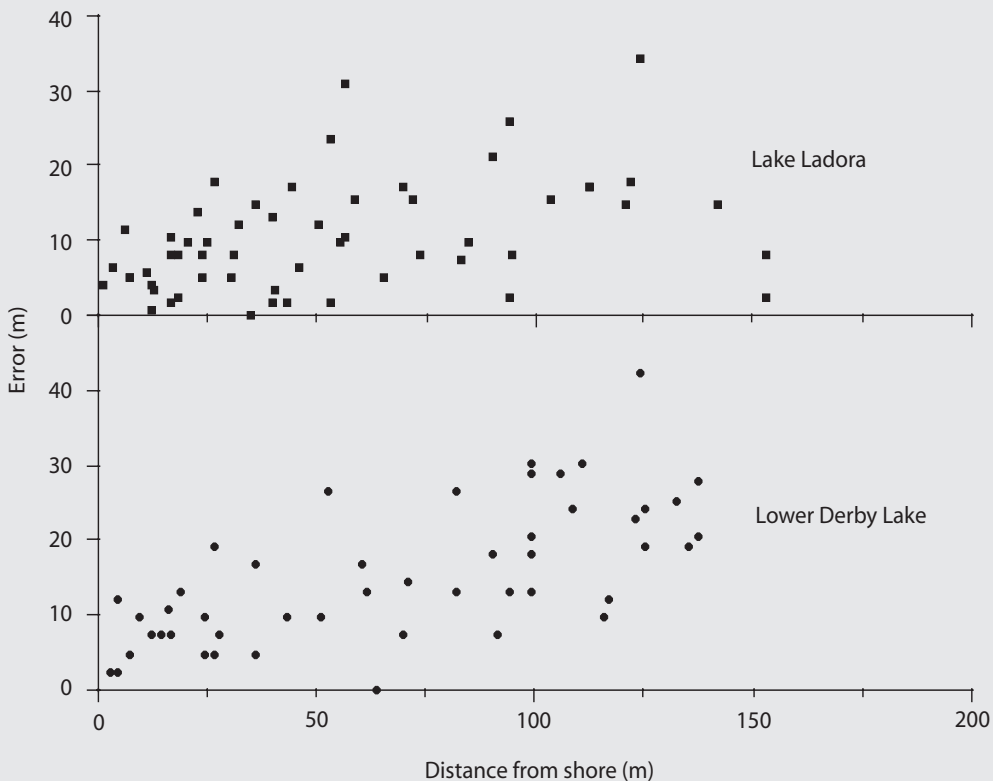


Figure Fifty random coordinates were located conventionally and with a differential GPS in each lake. The distance between these points was assumed to be a measure of telemetry error (in meters). This error was then plotted as a function of distance from shore in meters (from Rogers 1998).

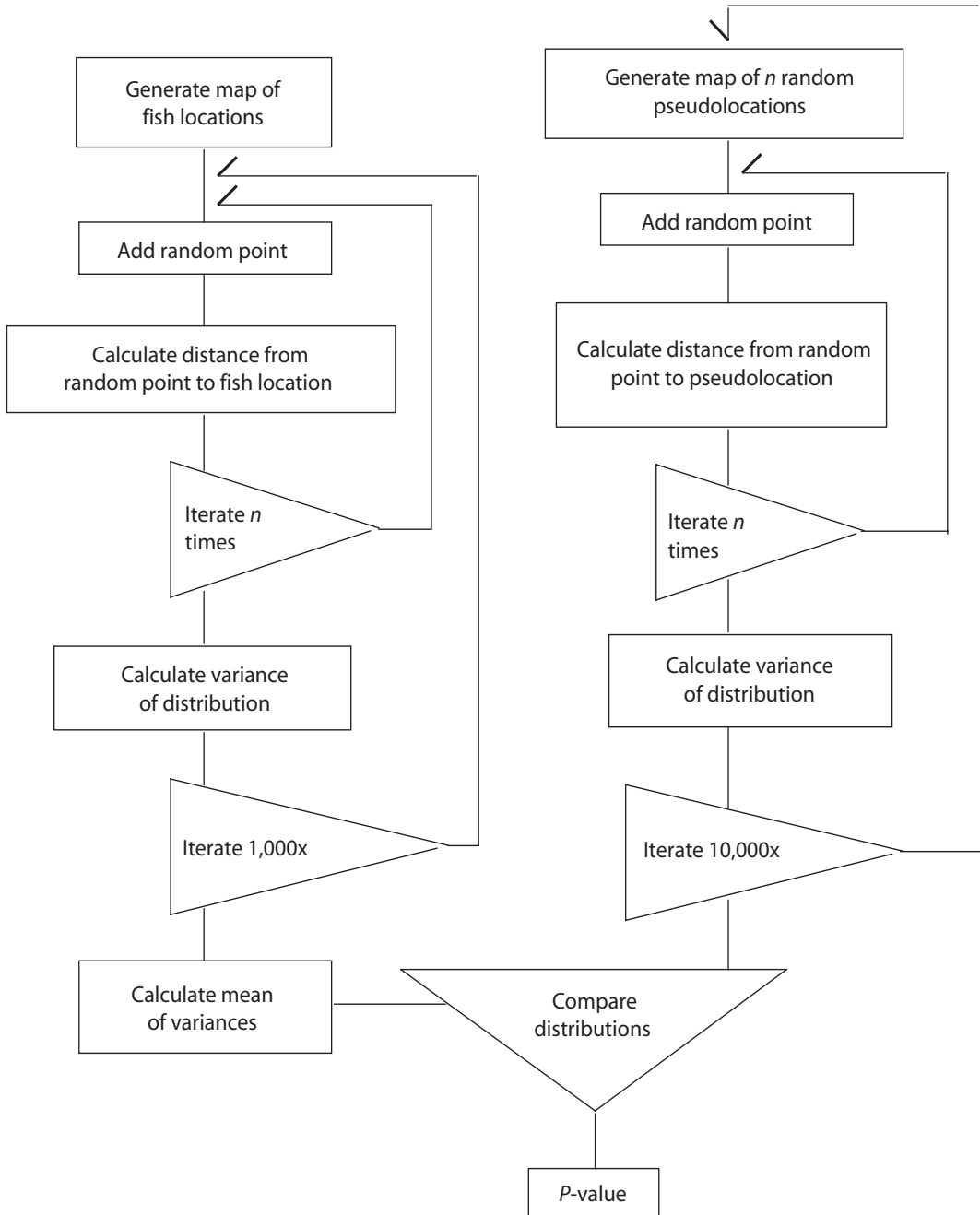


Figure 14.1 A flowchart demonstrating the process for evaluating if n fish locations are distributed randomly around a lake. The left arm calculates the mean of variance estimates for the each telemetered fish, whereas the right arm is used to generate the distribution of the test statistic so that a P -value can be assessed. If randomness of the population of fish is to be evaluated, then a grand mean can be calculated and compared to the same test statistic distribution.

least 1,000 times to generate a distribution for the expected mean variance statistic under the null hypothesis of random distribution. The actual mean variance statistic generated from the fish location data can then be compared with this distribution to determine the appropriate *P*-value (Box 14.2). Comparisons can be made between individuals, seasons, or basins, the only caveat being that the same number of fish locations must be considered in each group. If not, the group with more locations will display shorter distances on average than those groups with sparser data. A quick way to remedy this dilemma is simply to have a computer randomly drop fish locations out of each group to be compared until all groups have the same number of locations (Rogers 1998).

Usually, one is more interested in how the locations of all telemetered fish are distributed (population level). This can be achieved by averaging the mean variance for each fish across the population of telemetered fish to generate a grand mean variance that can then be compared with the sampling distribution (see figure Box 14.2) to yield a *P*-value. For this approach to be valid, one only has to ensure that all fish are located the same number of times. As mentioned previously, that goal can be easily achieved by randomly dropping observations from each data set until all fish register the same number of locations. Several alternative approaches are possible and could be substituted for this one based on the following considerations. The mean distance to the nearest fish location should be the same as the mean distance to a random location if fish locations are randomly distributed. Alternatively, the probability that the nearest location is a fish location should be 0.5 if fish locations are randomly distributed.

■ 14.5 MOVEMENT PATTERNS

Evaluations of movement by telemetered fish are pervasive in the literature, yet it is very difficult to compare metrics across studies because observed movement is a function of how often a fish was located (Baras 1998). Estimates of fish movement are minimum estimates of displacement. Fish do not move in a straight line (Guy et al. 1994; Rogers and Bergersen 1995), so the more times a fish is located in a day, the greater total movement will appear. Better estimates of true movement can therefore be obtained if continuous tracking schedules are employed or if fish are at least monitored frequently over a 24-h period.

If one wishes to compare movement between studies or lakes, or even within a population, it is critical that subjects be located the same number of times and the time interval between locations be approximately equal. Because fish movement is usually heterogeneous among individuals (Rogers 1998), if fish are not located consistently over a given time frame, contact bias can result (Jones and Rogers 1998). This bias can dramatically affect the outcome of a study if search routines are not rigorously applied to give all telemetered fish the best chance of being located every time they are sought. If more mobile fish tend to spend more time in open water while moving, they might be located more often than are their sedentary brethren. Movement estimates for the population would therefore be biased upward. If, on the other hand, sedentary fish are easier to locate because

Box 14.2 Evaluation of Spatial Distribution

In this example, we will explore the distribution of northern pike in Lake Ladora, Colorado, in summer (Rogers 1998). Colorado's plains' reservoirs represent the southern limit of this species' range, as water temperatures frequently approach the species' tolerance limits in summer. A spring that feeds a slough of this lake ensures that water temperatures in this shallow arm are cooler than the remainder of the lake basin. As the northern pike begin to experience thermal stress, they congregate in this region despite the marginal habitat that is available (Rogers 1998).

To quantify the nonrandom nature of this spatial distribution, we will examine the locations of a northern pike (number 96) that was observed on 43 occasions over a 3-month period in Lake Ladora. A data file containing the x - y positions on a Universal Transverse Mercator (UTM) grid were read by the program FishTel, which performs the functions described in Figure 14.1. The mean variance statistic generated for this fish was 6,095 m^2 . Using the spatial test statistic module of program FishTel and 43 random pseudolocations, a distribution of the test statistic was generated under a null hypothesis of random distribution (see figure).

The probability of obtaining a mean variance value of 6,095 m^2 or larger by chance was remote ($P = 0.008$). The distribution of northern pike 96 observations was therefore nonrandom.

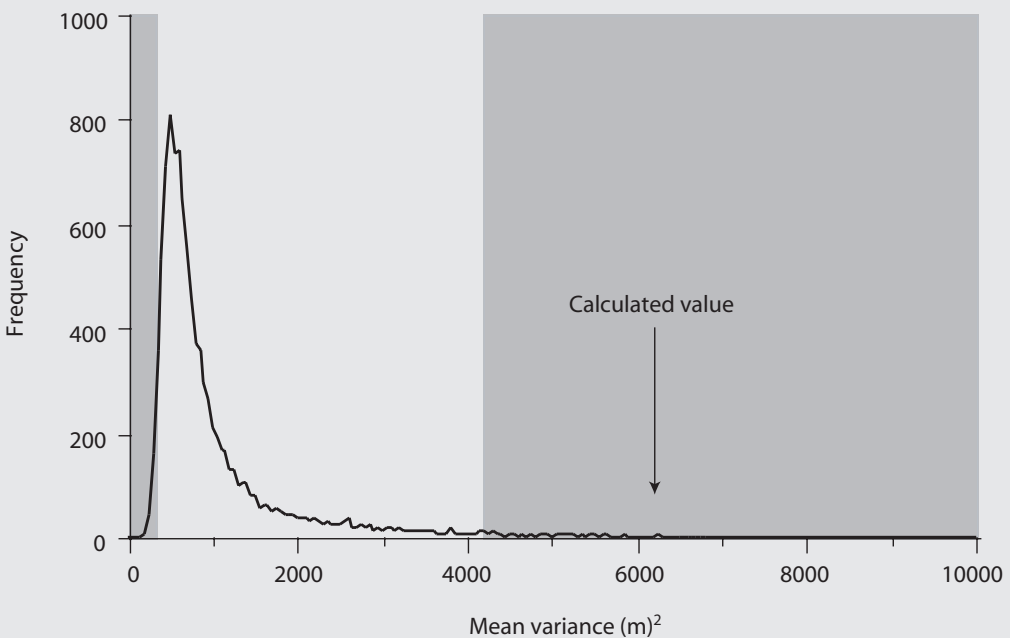


Figure The variance in distances from 43 random points to 43 randomly generated pseudolocations was calculated and iterated 10,000 times to generate a distribution of the mean of variance estimates under a null hypothesis of random distribution. The P -values for mean variance statistics calculated from fish locations can be assessed by determining where that value falls on this graph and evaluating what percent of the area under the curve falls to the right (or left) of the value calculated for the fish. The area under the curve in the shaded regions represents a two-tailed alpha of 0.05 (2.5% of the observations under each tail).

one already knows about where they are from the previous observation, then apparent movement may be biased downward.

Units of measure should reflect the precision that was conferred when the data were acquired. For instance, if fish were located numerous times over a 24-h period, then it might be fair to express movement as minimum displacement per hour (MDPH). If fish were located only several times per week, then movement should not be expressed in units of finer resolution than meters per day. The common practice of expressing fish movement in centimeters per second is usually absurd and implies precision that is simply not possible. Positional information cannot be accurately measured in centimeters, and reporting movement in seconds suggests that fish were followed (and locations recorded) continuously, which is rarely the case.

Quite often, as the values that describe various aspects of telemetry data, such as MDPH, increase in magnitude, the variance associated with those values increases as well. Because increasing variance conflicts with the equal variance assumption of many of the parametric statistics used in telemetry analysis, the data may first need to be transformed. A simple natural log transformation is usually all that is required (Jones and Rogers 1998; Rogers 1998) because the variance is a constant multiple of the mean. That is, the coefficient of variation is constant, and the natural log transformation creates a new variable that has constant variance. Other options exist (Ott 1988; Wilkerson and Fisher 1997). The important thing is to check to make sure that the variances have stabilized, and that they are no longer increasing with the metric of interest before the analyses are conducted.

14.5.1 Evaluation of Movement with Categorical Data

General linear models (GLMs) are very conducive to exploring variation in movement and allow for a broad spectrum of relationships to be examined (Ott 1988; Box 14.3). Heterogeneity among fish, or between seasons, years, and diel periods, can easily be evaluated in this fashion. Fish do not expend energy for swimming needlessly, so relationships between movement and other factors give some insight into which factors are associated with fish movement. As with all analyses presented here, it is important to remember that the fish carrying transmitters are the sampling units (Otis and White 1999).

14.5.2 Evaluation of Movement with Continuous Data

A variety of parameters are thought to influence movement. Because fish are poikilothermic, they tend to move less in winter when their metabolisms slow down (Casselman 1978; Cook and Bergersen 1988; Schulz and Berg 1992; Rogers 1998; Snedden et al. 1999; Bramblett and White 2001). Rogers and Bergersen (1995) documented more movement during a mild reservoir water level draw-down. Several authors have shown barometric pressure to influence fish move-

Box 14.3 Evaluation of Seasonal Movement Patterns

Variation in movement by largemouth bass in Lake Ladora, Colorado, is evaluated with a mixed-model analysis of variance (ANOVA). Seventeen largemouth bass carried transmitters during a 4.5-year study, and their movement (m/h) was evaluated on 49 consecutive full-moon 24-h tracks (Rogers 1998). Analyses were conducted with SAS version 6.

Table Portion of data set of minimum displacement per hour (m/h) by 17 largemouth bass in Lake Ladora. Fish represents unique largemouth bass; year is the last digit in 199*; seasons are given as (1) spring (March–May), (2) summer (June–August), (3) fall (September–November), and (4) winter (December–February); and minimum displacement per hour (MDPH) is given in m/h. The full data set is included in the Chapter 14 CD folder.

Fish	Year	Season	MDPH
1	4	2	18.74
1	4	3	34.55
1	4	3	32.05
1	4	3	17.76
1	4	4	0.68
1	5	4	4.83

The following SAS program is used to evaluate whether largemouth bass move differently between seasons and years (fixed effects), with the sampling unit of individual fish taken as a subject or random effect. Interactions between fish and season and fish and year are also treated as random effects. Notice that MDPH has been transformed by the natural logarithm to stabilize increasing variance found with increasing MDPH. Bonferroni's multiple-comparisons procedure was used to assess differences in MDPH between seasons.

Program

```
Options nodate ps = 40;
data LMB;
input FISH YEAR SEASON MDPH;
LNMDPH = LOG(MDPH);
proc mixed;
CLASS FISH YEAR SEASON; * These variables are categorical;
MODEL LNMDPH = SEASON YEAR; * Fixed effects in the model;
RANDOM FISH*SEASON FISH*YEAR/subjects = fish;
/* Above specifies which effects in the model are random */
lsmeans SEASON/ADJUST = BON;
run;
```

(Box continues)

Box 14.3 (continued)**Descriptive Output**

Table Mixed model output (partial) to evaluate whether largemouth bass move differently between seasons and years. Akaike's Information Criteria (AIC), small-sample corrected AIC (AICc), and Bayesian Information Criteria (BIC) are model fit statistics, for which smaller values reflect better fit (see Box 14.4 for additional explanation of AIC).

Covariance Parameter Estimates				
Covariance parameter	Subject			
Fish*Season	Fish	0.04282		
Fish*Year	Fish	0.07549		
Residual		0.6042		
Fit Statistics				
-2Residual log likelihood	414.4			
AIC	420.4			
AICc	420.5			
BIC	422.9			
Type 3 Tests of Fixed Effects				
Effect	Numerator <i>df</i>	Denominator <i>df</i>	F-value	<i>P</i> > <i>F</i>
Season	3	45	7.00	0.0006
Year	4	10	0.98	0.4629

ment (Warden and Lorio 1975; Markham et al. 1991; Guy et al. 1992; Jones and Rogers 1998). Jones and Rogers (1998) also documented a link between water clarity and movement. A simple way to explore the influence of these continuous variables is to model them against MDPH in a multiple regression framework (Box 14.4).

The Akaike's Information Criteria (AIC) model selection procedure (Burnham and Anderson 1998) provides an elegant way to resolve which variables are really important in describing movement. However, one should ensure that fish used in this sort of analysis are exposed to a biologically meaningful cycle or spectrum of values for each variable included in the model. One might not detect a significant relationship between water temperature and movement if fish were followed for only a couple of months when water temperatures were stable, and that result might have little biological relevance. Failure to detect a relationship does not imply that no relationship exists, especially in this scenario.

Least-Squares Means

Effect	Season	Estimate	SE	df	t-value	$P > t $
Season	1	2.5819	0.1642	45	15.72	<0.0001
Season	2	2.8455	0.1563	45	18.20	<0.0001
Season	3	2.7107	0.1750	45	15.49	<0.0001
Season	4	1.9358	0.1686	45	11.48	<0.0001

Differences of Least Squares Means

Effect	Season– season	Estimate	SE	df	t-value	$P > t $	Adjusted P^a
Season	1–2	–0.2636	0.2082	45	–1.27	0.2121	1.0000
Season	1–3	–0.1288	0.2180	45	–0.59	0.5577	1.0000
Season	1–4	0.6461	0.2057	45	3.14	0.0030	0.0179
Season	2–3	0.1348	0.1974	45	0.68	0.4982	1.0000
Season	2–4	0.9096	0.2105	45	4.32	<0.0001	0.0005
Season	3–4	0.7748	0.2186	45	3.55	0.0009	0.0056

^a Bonferroni adjustment for experimentwise error rate.

Interpretation

From this output (type 3 tests of fixed effects), it is clear that movement observed is very different between seasons ($P < 0.001$) but not from year to year ($P = 0.463$). The conservative Bonferroni multiple-comparisons test (controls experimentwise error rate) demonstrates that movement in winter (4) was significantly less than during the ice-free seasons.

■ 14.6 HABITAT USE

Interest in evaluating the habitat used by fishes has been a cornerstone of telemetry projects. The overriding question is whether fish spend more or less time in some habitats than would be expected based on the availability of those habitats. When this disproportionate allocation of time occurs, the behavior is said to be selective. Although selection and preference are often used synonymously, selection is the process by which an animal chooses a habitat. Preference is the likelihood that a resource will be chosen if all habitats are offered up equally (Johnson 1980; Manly et al. 1993). Animals are presumed to use habitats that confer fitness, so by studying habitat use biologists can hope to assess what habitat features may be limiting. By studying where animals allocate their time, one can gain insight into how they meet their requirements for survival. Such information is useful when considering the introduction of a species and

Box 14.4 Evaluation of Environmental Effects on Movement

The potential influence of water temperature, surface elevation, barometric pressure, and change in barometric pressure are modeled against MDPH (natural log transformed) of northern pike in a Colorado reservoir. Fish in this population were monitored on consecutive full-moon 24-h tracks for at least 1 year (Rogers 1998). A mixed-model ANOVA with a random coefficients model (Littell et al. 1996) and an AIC model selection (Burnham and Anderson 1998) was used to isolate significant effects. Akaike's Information Criteria is a useful tool for selecting the model that most closely fits the theoretical distribution of the data without overparameterization (Schisler and Bergersen 1996). This metric can be thought of as the relative distance between pairs of multiple candidate models (Burnham and Anderson 1998) and allows model selection to occur in an optimization framework similar to parameter estimation. By formulating the problem of model selection across a set of candidate models, AIC provides an objective means for the selection of the best approximating model for inference (Burnham and Anderson 1998), as well as allowing the user to rank other candidate models. This minimizes the practice of data dredging and overfitting models and provides an alternative to the traditional null hypothesis testing approach. For a complete analysis of these data, additional models would likely have been considered a priori, and values of AIC would be useful in selecting the most parsimonious model supported by the data.

Table Data for northern pike being located during a 24-h track in lower Derby Lake, Colorado (partial data set). Provided are the individual fish identification (Fish ID), the water temperature (temp, °C), the maximum lake depth (depth, m) for that date, the mean barometric pressure (BP, mm), the change in barometric pressure (DBP, mm) over the 24-h period, and the mean minimum displacement (MDPH, m/h). The full data set is included in the Chapter 14 CD folder.

Fish ID	Temp	Depth	BP	DBP	MDPH
2	21	4.4	630	-1.8	31.22
2	25	5.0	630	-2.3	43.25
2	23	4.6	634	0.2	28.06
2	27	4.1	630	-1.3	23.21
2	21	3.7	633	-2.8	16.72
2	12	3.5	630	-1.3	38.52

The following SAS program evaluates whether fish movement is correlated with the environmental variables listed. Again, we must transform the MDPH to stabilize increasing variance found with increasing MDPH. As AIC values will be used to isolate the most parsimonious model, all possible models should be entertained (or at least all that make biological sense).

Program

```

OPTIONS NODATE PS = 40;
data NOP;
INFILE 'DNOPEMV.TXT' FIRSTOBS = 3;
input FISH TEMP DEPTH BP DBP MDPH;
LNMDPH = LOG(MDPH);
PROC MIXED DATA = NOP;

```

```

CLASS FISH;
MODEL LNMDPH = TEMP DEPTH BP DBP/Solution;
/* Prints the solution to the model */
RANDOM INTERCEPT TEMP DEPTH BP DBP/TYPE = VC SUBJECT = FISH;
/* TYPE = VC sets the Variance-Covariance for each subject to a variance
components type*/
MAKE 'FitStatistics' OUT = ModelFit;
/* Saves the AIC value into the file MODELFIT */
DATA ModelSelection;
LENGTH MODEL $ 18;
SET ModelFit;
MODEL = 'TEMP DEPTH BP DBP';
/* The above DATA step adds the model name to the file
Now the process is repeated for another model */

PROC MIXED DATA = NOP;
CLASS FISH;
MODEL LNMDPH = TEMP/Solution;
RANDOM INTERCEPT TEMP/TYPE = VC SUBJECT = FISH;
MAKE 'FitStatistics' OUT = ModelFit;
DATA ModelFit;
LENGTH MODEL $ 18;
SET ModelFit;
MODEL = 'TEMP';
PROC APPEND BASE = ModelSelection DATA = ModelFit;
/* Append the new model's statistics to the file MODELSELECTION */

PROC MIXED DATA = NOP;
CLASS FISH;
MODEL LNMDPH = TEMP DEPTH/SOLUTION;
RANDOM INTERCEPT TEMP DEPTH/TYPE = VC SUBJECT = FISH;
MAKE 'FitStatistics' OUT = ModelFit;
DATA ModelFit;
LENGTH MODEL $ 18;
SET ModelFit;
MODEL = 'TEMP DEPTH';
PROC APPEND BASE = ModelSelection DATA = ModelFit;

```

Iterate last 10 lines here for all models entertained.

```

PROC SORT DATA = ModelSelection;
BY Value;
/* Sort by AIC value */
PROC PRINT DATA = MODELSELECTION;
WHERE DESCR = 'AICC (smaller is better)';
/* Print the summary table of sorted AICC values */
RUN;

```

(Box continues)

Box 14.4 (continued)**Descriptive Output**

Table Small-sample corrected Akaike's Information Criteria (AICc) model selection for dependent variable \log_e MDPH (LNMDPH). Smaller values of AIC, AICc, and BIC reflect better fit. Results for two best models are shown.

Selection method	
Model	AICc value
TEMP	384.4
TEMP DEPTH	387.5
TEMP BP	388.3
TEMP DEPTH BP	389.7
TEMP DBP	390.6
TEMP DEPTH DBP	393.6
TEMP BP DBP	394.4
TEMP DEPTH BP DBP	395.8
DEPTH	403.4
DEPTH BP	409.1
DEPTH DBP	409.4
DBP	409.9
BP	410.4
DEPTH BP DBP	415.1
BP DBP	416.3

Covariance Parameter Estimates

Covariance parameter	Subject	Estimate
Intercept	Fish	0.1816
Temp	Fish	0
Residual		0.5929

Fit Statistics

-2Residual log likelihood	380.4
AIC	384.4
AICc	384.4
BIC	384.8

Solution for Fixed Effects

Effect	Estimate	SE	df	t-value	$P > t $
Intercept	2.4878	0.1839	8	13.53	<0.0001
Temp	0.03906	0.007112	8	5.49	0.0006

Type 3 Tests of Fixed Effects

Effect	Numerator <i>df</i>	Denominator <i>df</i>	F-value	<i>P</i> > <i>F</i>
Temp	1	8	30.17	0.0006

Covariance Parameter Estimates

Covariance parameter	Subject	Estimate
Intercept	Fish	0.1655
Temp	Fish	0
Depth	Fish	0.003149
Residual		0.5870

Fit Statistics

-2Residual log likelihood	381.4
AIC	387.4
AICc	387.5
BIC	388.0

Solution for Fixed Effects

Effect	Estimate	SE	<i>df</i>	<i>t</i> -value	<i>P</i> > <i>t</i>
Intercept	3.0604	0.5955	8	5.14	0.0009
Temp	0.04392	0.008580	8	5.12	0.0009
Depth	-0.1517	0.1501	8	-1.01	0.3417

Type 3 Tests of Fixed Effects

Effect	Numerator <i>df</i>	Denominator <i>df</i>	F-value	<i>P</i> > <i>F</i>
Temp	1	8	26.20	0.0009
Depth	1	8	1.02	0.3417

Interpretation

The best model to predict $\log_e(\text{MDPH})$ based on the AIC model selection criterion is temperature and is better by 3.1 AIC units than the second-best model (it is the absolute rather than relative difference in values that matters). Temperature appeared in the top eight models, demonstrating the importance of this variable in the model. Depth appears in four of the top eight. For the best AIC model, temperature is positively related to $\log_e(\text{MDPH})$ with a slope of 0.0391 (SE = 0.0071). Thus, northern pike moved more at warmer water temperatures. In the second best model, in addition to temperature being positively correlated with movement, depth was negatively related with a slope of -0.1517 (SE = 0.1501). Under this model, northern pike moved more in warmer water but less as water levels were reduced.

its ability to persist or potentially explaining why a species is in decline. Note, however, that just observing how fish use habitat does not allow cause and effect to be inferred. Rather, inferences from these observational studies are strictly correlational. Cause and effect can only be isolated from experiments involving manipulation of habitat.

In order to assess habitat use, one must first document what habitat is available to the fish. Often, what the biologist perceives as available and what the fish deems as available may be quite different. Biologists typically consider the contiguous wetted area as available habitat for limnetic fish, though this may not always be warranted, as restrictions in fish movement may occur based on physical barriers such as inhospitable water temperatures, excessive aquatic vegetation growth, presence of other species, or shallow waters. The advent of GPS and GIS technologies has greatly enhanced the process and accuracy of mapping habitat types and has simplified the estimation of availability.

Typically, the habitat type a fish is using is recorded either when the fish is observed in the field, or it is determined in a GIS by overlaying fish distribution maps on habitat maps (Rogers and Bergersen 1996). A broad array of approaches can be used to evaluate habitat use and resource availability at the population and individual level. Some of the more prominent methods of evaluating whether fish spend more time in some habitats than would be expected based on the availability of those habitats are discussed elsewhere (White and Garrott 1990; Alldredge and Ratti 1992; and Manly et al. 1993). Here our focus will center on methods for which individual use is known (monitoring fish carrying transmitters) and the proportion of available resource units is also known. Though similar methods exist to evaluate resource selection when resource availability is only estimated or sampled (Thomas and Taylor 1990; Manly et al. 1993), the proliferation of mapping technologies (GIS and GPS) has probably limited the need for discussion of those approaches here.

14.6.1 Chi-Square Tests

The simplest and most pervasive approach to assessing whether fish are using habitats in proportion to their availability is the use of chi-square tests. Though the Pearson statistic is more common, the log-likelihood statistic is preferred because model selection based on AIC (Burnham and Anderson 1998) can be used and because more sophisticated models using logistic regression can be built compared with the use of simple contingency tables. In practice, both often yield similar results and are asymptotically equivalent.

Researchers traditionally pooled use data and did not maintain unique identification for each animal (Neu et al. 1974). For example, Rogers (1998) followed seven adult largemouth bass over a summer in a Colorado reservoir, locating these fish, in total, 128 times (Box 14.5). Historically, these observations might simply have been analyzed as 128 independent observations, though this clearly was not the case. Locations by the same individual are correlated in time and must be treated accordingly (section 14.2.4; Otis and White 1999). Pooling may be justified if a few

Box 14.5 Evaluation of Habitat Use

This example reports habitat use by seven largemouth bass carrying transmitters during the summer of 1994 on 27-ha Lake Ladora, Colorado (Rogers 1998). Maps of individual fish locations were overlaid on a 10 × 10-m raster map of bottom type in a GIS to evaluate habitat use by individual fish and to quantify available habitat. The frequency of habitat use along with the availability of the habitat is shown in the table below.

Table The number of locations each of seven largemouth bass frequented by habitat type in Lake Ladora. Fish are identified by transmitter identification numbers, habitat types are listed in the first column, and the last column represents the number of 10 × 10 m cells of a given habitat type that were available in the lake.

Habitat type and individual total	105	132	17	2,263	2,353	285	510	Total for habitat type	Available habitat type
Silt	0	2	3	22	4	9	9	49	959
Chara	0	0	1	2	0	0	0	3	155
Pondweed	0	0	0	0	2	10	1	13	57
Milfoil	1	0	2	3	4	0	1	11	988
Coontail	9	9	3	3	0	28	0	52	503
Total for fish	10	11	9	30	10	47	11	128	2,662

The following SAS code can be used to evaluate both relevant chi-square tests.

Program

```

data VEG;
length Habitat $8;
input Habitat fish1 fish2 fish3 fish4 fish5 fish6 fish7 Available;
cards;
Silt          0      2      3      22      4      9      9      9      959
Chara         0      0      1      2      0      0      0      0      155
Pondweed     0      0      0      0      2     10      1     13      57
Milfoil      1      0      2      3      4      0      1     11     988
Coontail     9      9      3      3      0     28      0     52     503
;
data VEG1;

/* The following rows read in the above data table and format it for
analysis */
array cnt{7} fish1-fish7;
set VEG;
do i = 1-7;
Fish = i;
Count = cnt[i];
keep Habitat Count Fish;
output;
end;
proc freq;
weight Count;

```

(Box continues)

Box 14.5 (continued)

```

tables Fish*Habitat/chisq;
proc transpose data = VEG out = TransposeVeg;
proc sort;
by _NAME_;
data Availability;

/* This portion determines the amount of habitat available */
array Habitat{5} COL1-COL5;

/* The data table is transposed, so habitat is given in columns */
array Available{5} Avail1-Avail5;
retain Avail1-Avail5;
retain ChiSq TotalChiSq TotalDF TotalLocs 0;
set TransposeVeg end = Last;
if _NAME_ = 'Available' then do;
SumAvailable = sum(of COL1-COL5);
do i = 1 to dim(Available);
Available[i] = Habitat[i]/SumAvailable;
end;
end;
else do;

/* The following generates the chi-square for the first test */
ChiSq = 0;
TotalLocations = sum(of COL1-COL5);
do i = 1 to dim(Available);
if Habitat[i]>0 then
ChiSq = ChiSq+Habitat[i]*log(Habitat[i]/
(TotalLocations*Available[i]));
end;
df = Dim(Available)-1;
Prob = 1-ProbChi(ChiSq, df);
format Prob PVALUE.;
keep _NAME_ TotalLocations ChiSq df Prob;
output;

/* Chi-square for the second test */
TotalChiSq = TotalChiSq+ChiSq;
TotalDF = TotalDF+df;
TotalLocs = TotalLocs+TotalLocations
if Last then do;
_NAME_ = 'Total';
TotalLocations = TotalLocs;
ChiSq = TotalChiSq;
df = TotalDF;

```

locations are obtained from many fish, but generally just the opposite is true, and many locations are obtained from just a few individuals. Use of habitat among fish in the same population can be highly variable. Not only can the availability of habitat to each individual vary, but there is inherent heterogeneity in use among individuals as well. This heterogeneity among individuals is eliminated if the location

```

Prob = 1-ProbChi(ChiSq, df);
output;
end;
end;
proc print;

```

Descriptive Output (Partial)

Table Statistics for fish by habitat.

Statistic	<i>df</i>	Value	Probability
Chi-square	24	93.6632	<0.0001
Likelihood ratio chi-square	24	107.1104	<0.0001
Mantel-Haenszel chi-square	1	6.5549	0.0105
Phi coefficient		0.8554	
Contingency coefficient		0.6500	
Cramer's V		0.4277	

Transmitter identification					
number	Chi-square	Name	Locations	<i>df</i>	Probability
105	25.473	Fish1	10	4	<0.0001
132	23.645	Fish2	11	4	<0.0001
17	2.180	Fish3	9	4	0.7026
2263	20.129	Fish4	30	4	0.0005
2353	10.373	Fish5	10	4	0.0346
285	98.854	Fish6	47	4	<0.0001
510	14.843	Fish7	11	4	0.0050
	195.498	Total	128	28	<0.0001

Interpretation

The resulting χ^2 value for the first test, χ_{L1}^2 (equation [14.1]), was 107.1 with 24 *df*. The resulting P (< 0.0001) indicates that fish are using the available habitats very differently. The value of the second test, χ_{L2}^2 (equation [14.2]), was 195.5 with 28 *df* and a P of 0.0001, also indicating that the largemouth bass were very selective in the types of habitat they used. The difference between these two chi-square tests is 88.4 with 4 *df* (P < 0.0001), which demonstrates strong selection for certain habitat types.

information is pooled across individuals. In the worst case scenario, two fish might select opposite habitats, but pooling would make the investigator think that no selection was occurring (White and Garrott 1990). With computer processing power no longer limiting, the integrity of the data should be maintained. The preferred approach is to consider the animal as the primary sampling unit, and statistical

inference should be based on use with individual fish as replicates (Manly et al. 1993; Otis and White 1999).

Several tests can be conducted in a situation for which individual fish habitat use is recorded and available habitat is known. First, we can check to see if fish are using the various habitat types in similar fashion. Following the notation presented by Manly et al. (1993), u_{ij} is the amount of habitat type i used by fish j ; u_{i+} is the amount of habitat type i used by all fish; u_{+j} is the total amount of habitat units used by fish j ; and u_{++} is the total number of habitat units used by all fish. The first log-likelihood test statistic (χ_{L1}^2) is

$$\chi_{L1}^2 = 2 \sum_{j=1}^n \sum_{i=1}^I u_{ij} \log_e [u_{ij}/E(u_{ij})], \quad (14.1)$$

where $E(u_{ij}) = u_{i+}u_{+j}/u_{++}$. If the value is sufficiently large compared with the chi-square distribution with $(I-1)(n-1)$ df (I being the number of habitat categories and n the number of fish), then there is evidence for heterogeneity, and fish are using the habitats differently.

To examine if selection is occurring for individual habitat types by some of the fish carrying transmitters, the second log-likelihood test statistic (χ_{L2}^2) is used:

$$\chi_{L2}^2 = 2 \sum_{j=1}^n \sum_{i=1}^I u_{ij} \log_e [u_{ij}/E(u_{ij})], \quad (14.2)$$

where, $E(u_{ij}) = \pi_i u_{+j}$, and π_i is the proportion of available resource units that are in category i . Selection for specific habitats is demonstrated if the chi-square is sufficiently large with $n(I-1)$ df. The difference between these two chi-squares ($I-1$ df) describes whether, on average, fish are using the various habitat types in proportion to their availability, regardless of which ones they are selecting.

Although it is recommended that the expected frequencies in a chi-square test be five or more, these tests are fairly robust to deviations from this rule (Ott 1988). Generally if 90% or more of the expected values are greater than two, there is not a serious problem (Ott 1988). However, the data shown in the example are more sparse than even this rule of thumb suggests is appropriate. Accordingly, we should be cautious in our interpretation of these results, as almost half of the expected counts are less than two. However, given the extreme significance of these three tests and their robustness to deviation, it would be difficult to maintain that the largemouth bass were not using habitats differently or displaying strong selection for certain habitat types (Manly et al. 1993).

14.6.2 Selection Ratios

Once selection has been established, we shift our attention to evaluating which types of habitats were selected. An old intuitive approach is with selection ratios (Manly et al. 1972, 1993; Hobbs and Bowden 1982). Selection is indicated with values greater than one, while avoidance of a habitat is demonstrated with ratios

less than one. Again, from Manly et al. (1993), the selection ratio for the j th fish and the i th habitat type is estimated by

$$\hat{w}_{ij} = u_{ij} / (\pi_i u_{+j}). \quad (14.3)$$

Generally, one is more interested in selection by the population as a whole, which is estimated by

$$\hat{w}_i = u_{i+} / (\pi_i u_{++}). \quad (14.4)$$

In order to generate confidence intervals (CIs) about these selection ratios, the SE can be calculated as (K. Gerow, University of Wyoming, personal communication)

$$\text{SE}(\hat{w}_i) = \sqrt{\frac{n}{(n-1)(u_{++})^2} \sum_{j=1}^n \left(\frac{u_{ij}}{\pi_i} - \hat{w}_i(u_{+j}) \right)^2}. \quad (14.5)$$

The selection ratio estimates are generated by pooling observations from all fish in the sample, but the equation takes variation in resource selection from individual fish into account (Manly et al. 1993). It is recommended that simultaneous Bonferroni CIs be constructed to ensure the probability of all intervals containing their true parameter values is $1 - \alpha$ (Thomas and Taylor 1990). The intervals around each selection ratio should therefore be constructed at the $100(1 - \alpha/I)\%$ level, where I is the number of intervals being constructed (one for each habitat type), such that

$$\hat{w}_i \pm z_{\alpha/2I} \text{SE}(\hat{w}_i), \quad (14.6)$$

where is the z -score corresponding to an upper tail probability of $\alpha/2I$. An example of the use of selection ratios is given in Box 14.6.

The results are summarized in Figure 14.2, along with the results that would have been obtained if we had used the historic approach of pooling all our location data and analyzed it with the traditional chi-square method (Neu et al. 1974; Byers et al. 1984; Manly et al. 1993). Although the results are similar, different conclusions are drawn, underscoring the need for conducting the analysis correctly. Under both scenarios, largemouth bass avoid milfoil, yet under the historic approach, they select strongly for pondweed. When analyzed with fish as the sampling unit, however, the sparse data prevent us from achieving the power necessary to infer selection for pondweed. The CI includes 1 (failure to demonstrate selection) at an overall $\alpha = 0.10$ (individual $\alpha = 0.02$).

14.6.3 Continuous Distribution of Availability

Occasionally the distribution of a habitat character of interest does not lend itself to categorization. Parameters such as temperature, dissolved oxygen, and depth,

Box 14.6 Application of Selection Ratios

Using the data from Box 14.5, we can use selection ratios to evaluate which habitats were selected for or against by the population of largemouth bass in Lake Ladora. Calculation of selection ratios is demonstrated based on equation (14.4) and the milfoil habitat data from Box 14.5. The proportion of available resource units that are in category i is given by

$$\hat{w}_{milf} = u_{milf} / (\pi_{milf} u_{++}) = 11 / (0.371 \times 128) = 0.232.$$

The SE is calculated as (equation [14.5])

$$\begin{aligned} SE(\hat{w}_{milf}) &= \sqrt{\frac{n}{(n-1)(u_{++})^2} \sum_{j=1}^n \left(\frac{u_{milf}}{\pi_{milf}} - \hat{w}_{milf}(u_{+j}) \right)^2} \\ &= \sqrt{\frac{7}{(7-1)(128)^2} \left[\left(\frac{1}{0.371} - 0.232(10) \right)^2 + \dots + \left(\frac{1}{0.371} - 0.232(11) \right)^2 \right]} = 0.122. \end{aligned}$$

The simultaneous Bonferroni confidence intervals (CIs) are generated as (equation [14.6])

$$\hat{w}_{milf} \pm z_{\alpha/2l} SE(\hat{w}_{milf}) = 0.232 \pm z_{0.10/2 \cdot 5} 0.122 = (-0.052, 0.516).$$

Because one cannot observe a negative value, the -0.052 should be replaced with 0.000 . The process can obviously be facilitated with the aid of a computer, and the appropriate code is available from several sources. The plug and play application FishTel also can perform these calculations.

to name a few, are continuous in nature. One common solution is to simply break the continuum up into categories. Whereas this is a legitimate approach, this method is not as efficient as treating the variable as continuous. Further, the approach is subjective because the biologist must then decide the cutoffs for categorization. A conceptually simpler approach would be merely to measure the parameter of interest and see if that parameter changes in response to some other factor by means of a GLM.

Numerous studies have demonstrated the importance of nearshore habitats to fishes in inland temperate lakes during summer (Winter 1977; Doerzbacher 1980; Betsill et al. 1988). Others have shown that some fishes move offshore in winter, presumably in search of deeper, warmer water when ice covers the lakes (Cook and Bergersen 1988; Rogers 1998). One option for evaluating this distribution would be to divide the habitat into, say, littoral and limnetic zones and then use the chi-square approach described in section 14.6.1, but then one would have to decide what constituted those two habitat types. Rather than make spurious assumptions, one could instead simply calculate the average distance to shore for each fish during each season and use a GLM to assess if distance from shore varied between seasons (Box 14.7).

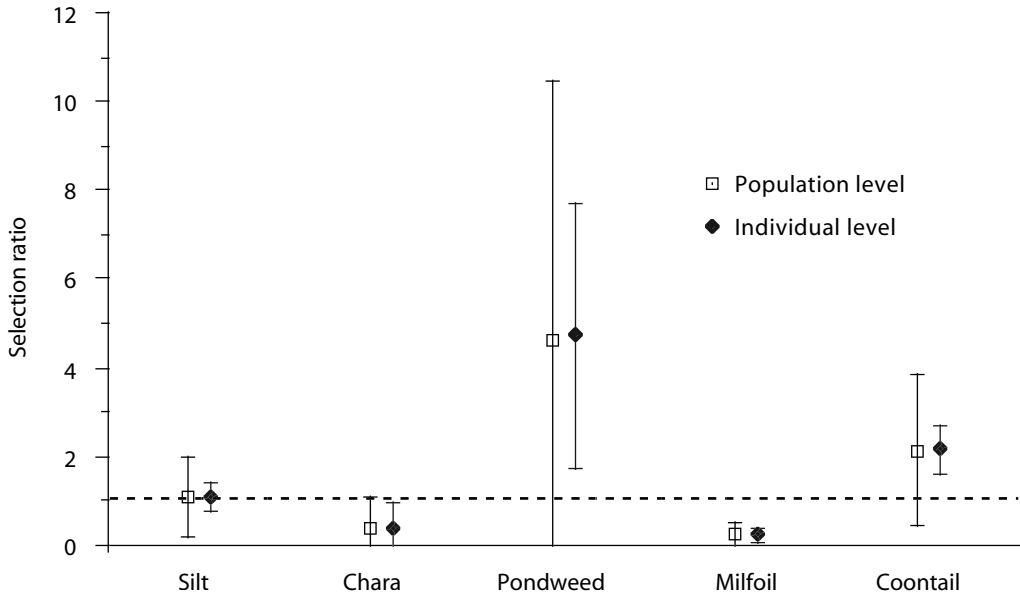


Figure 14.2 Seven adult largemouth bass were monitored during the summer of 1994 on Lake Ladora, Colorado, and their locations were plotted on a map of vegetation to assess habitat use. Selection ratios (W_i) and their associated Bonferroni-adjusted 90% confidence intervals (error bars) were used to determine if selection for (>1) or against (<1) a given habitat type was occurring. The intervals were calculated with both the traditional population level approach and the individual level approach advocated here, which uses the individual fish as sampling units.

The first two models in Box 14.7 (A and B in the SAS code) represent the traditional approach to this sort of analysis, where sources of variation are included for differences between fish and fish \times season. Though legitimate, they ignore the autocorrelation of the repeated measurements (distances) taken for each fish and therefore display relatively high values of the small-sample corrected Akaike's Information Criteria (AICc) values. We would expect that distances taken close in time would have a high correlation, whereas distances taken farther apart in time would be less correlated. Model A assumes a constant residual variance across all four seasons, with no covariance between distances for a fish, whereas model B assumes a different residual variance for each season, but still with no covariance. Model E assumes a constant residual variance across seasons and that the autocorrelation of distances is constant across all of the repeated measurements for a fish. Thus, model E ignores the fact that only distances taken close in time should have a high correlation, and therefore it also gives rise to a high AICc. Only models C, D, F, and G incorporate the autocorrelation of the distances in their structure (Littell et al. 1996). Models C and D assume equal time intervals, whereas F and G do not and are therefore rewarded with the lowest AICc values. Model G allows the variance structure to vary by season as well as modeling

Box 14.7 Evaluation of Habitat Use with Continuous Variables

To quantify whether largemouth bass really do move offshore in winter in search of warmer water at greater depth, we will use the same fish observed in Box 14.3. Seventeen adult largemouth bass in Lake Ladora were monitored on monthly 24-h tracks over a 4-year study.

Table Distances (m) from shore to each fish location (partial data set). The mean distance to shore for each fish was calculated with FishTel, which determines the distance from every location registered by a fish to the perimeter of the lake. Seasons are described in Box 14.3. The full data set is included in the Chapter 14 CD folder.

Season	Fish ID	Date	Time	Distance (m)
1	2	18 March 1992	13:04	6
1	2	18 March 1992	17:20	6
1	2	18 March 1992	20:20	33
1	2	19 March 1992	08:07	19
1	2	19 March 1992	00:08	36
1	2	19 March 1992	05:32	45
1	2	16 April 1992	20:59	7
1	2	17 April 1992	00:27	5

The distance to shore is again transformed by the natural logarithm to stabilize increasing variance associated with increasing distance from shore. Using a mixed-model ANOVA where FISH and FISH*SEASON are considered random effects, a variety of models can be developed that allow for autocorrelation in the repeated observations for each fish (Littell et al. 1996).

Program

```
proc format;
value season 1 = 'SPRING' 2 = 'SUMMER' 3 = 'FALL' 4 = 'WINTER';
data llmb;
infile 'NEARSHORE.TXT' firstobs = 3;
input SEASON FISH DATE : mmddy8. TIME : time5. DISTANCE;
format date date. time time. datetime datetime.;
DateTime = DHMS (DATE, hour (TIME), minute (time), second (time));
DateTIme1 = DateTime / (60 * 60 * 24); *Convert to days;
format season season.;
LNDIST = log (DISTANCE);

* MODEL A; /* Traditional approach with random effects and constant residual
variance across seasons */
PROC MIXED DATA = LLMB;
CLASS SEASON FISH;
MODEL LNDIST = SEASON / s;
RANDOM FISH FISH * SEASON;
*LSMEANS SEASON / ADJUST = BON;

* MODEL B; /* Traditional approach with different residual variance between
seasons */
PROC MIXED DATA = LLMB;
CLASS SEASON FISH;
```

```
MODEL LNDIST = SEASON/s;
RANDOM FISH FISH*SEASON;
repeated/type = vc/* Default type */group = season;
*LSMEANS SEASON/ADJUST = BON;

* MODEL C;/* Accounts for autocorrelation in distances assuming equal time
intervals */
PROC MIXED DATA = LLMB;
CLASS SEASON FISH;
MODEL LNDIST = SEASON/s;
RANDOM FISH FISH*SEASON;
Repeated/subject = FISH type = ar(1);
*LSMEANS SEASON/ADJUST = BON;

* MODEL D;/* Same as C while allowing different residual variance between
seasons */
PROC MIXED DATA = LLMB;
CLASS SEASON FISH;
MODEL LNDIST = SEASON/s;
RANDOM FISH FISH*SEASON;
Repeated/subject = FISH type = ar(1) group = season;
*LSMEANS SEASON/ADJUST = BON;

* MODEL E;/* Constant residual variance across seasons, constant
autocorrelation */
PROC MIXED DATA = LLMB;
CLASS SEASON FISH;
MODEL LNDIST = SEASON/s;
RANDOM FISH FISH*SEASON;
Repeated/subject = FISH type = cs;
*LSMEANS SEASON/ADJUST = BON;

* MODEL F;/* Accounts for autocorrelation in distances as a function of the
actual time interval */
PROC MIXED DATA = LLMB;
CLASS SEASON FISH;
MODEL LNDIST = SEASON/s;
RANDOM FISH FISH*SEASON;
repeated/subject = fish type = sp(pow)(datetime1);
*LSMEANS SEASON/ADJUST = BON;

* MODEL G;/* Same as F while allowing different residual variance between
seasons */
PROC MIXED DATA = LLMB;
CLASS SEASON FISH;
MODEL LNDIST = SEASON/s;
RANDOM FISH FISH*SEASON;
repeated/subject = fish type = sp(pow)(datetime1) group = season;
*LSMEANS SEASON/ADJUST = BON;
run;
```

(Box continues)

Box 14.7 (continued)**Descriptive Output**

Table Summary of mixed ANOVA output for all models (random effects for fish). The smallest value of AICc represents the model with the best fit.

Model	AICc	F-value
A) Variance components	2,227.4	8.88
B) Variance components/seasons	2,220.6	8.91
C) Autoregressive	2,053.4	8.21
D) Autoregressive/seasons	1,985.2	12.24
E) Compound symmetry	2,229.4	8.88
F) Spatial power	2,063.2	10.32
G) Spatial power/seasons	1,929.8	12.47

Table Mixed ANOVA output for the spatial power/seasons model that displayed the best fit. This model describes autocorrelation in distances as a function of the actual time interval (SP[POW]) by season as well as season-specific residual variances (variance).

Covariance Parameter Estimates

Covariance parameter	Subject	Group	Estimate
Fish			0.2511
Season*Fish			0.06000
Variance	Fish	Season winter	0.6089
SP(POW)	Fish	Season winter	0.5816
Variance	Fish	Season summer	0.6653
SP(POW)	Fish	Season summer	0.000534
Variance	Fish	Season spring	0.8392
SP(POW)	Fish	Season spring	0.01965
Variance	Fish	Season fall	0.8132
SP(POW)	Fish	Season fall	0.007301

Fit Statistics

-2Residual log likelihood	1,909.6
AIC	1,929.6
AICc	1,929.8
BIC	1,937.9

Solution for Fixed Effects

Effect	Season	Estimate	SE	df	t-value	P > t
Intercept		3.3492	0.1824	16	18.36	<0.0001
Season	Winter	0.5809	0.2060	26	2.82	0.0091
Season	Summer	-0.5647	0.1631	26	-3.46	0.0019
Season	Spring	-0.2104	0.1794	26	-1.17	0.2516
Season	Fall	0				

Type 3 Tests of Fixed Effects

Effect	Numerator df	Denominator df	F-value	P > F
Season	3	26	12.47	<0.0001

the correlation as a function of the time interval. It is clearly the most parsimonious model, with an AICc of 1,929.8. This result demonstrates the necessity of including the time element in telemetry data, as autocorrelation is pervasive. Furthermore, this autocorrelation varies across seasons. Examination of the variance-covariance parameter estimates reveals that not only do the variances appear different between seasons, but the only strong correlation between observations close in time occurs in winter ($\hat{r} = 0.5816$), also when the smallest residual variance was estimated ($\hat{\sigma}^2 = 0.6089$). This result is expected, as we have already demonstrated that these fish move least in winter (Box 14.3). When water temperatures drop close to freezing, these poikilotherms are less likely to move far enough from a previous location to remove the autocorrelation effect. The variation among fish (0.2511) and among fish \times season (0.0600) is considerably less than the residual variance within fish for each season.

The untransformed mean distance to shore for all the largemouth bass in summer was 26 m, which more than doubled in winter, with fish locations moving to 58 m from shore on average. Mean distance from shore was 39 m in spring and 41 m in fall. Largemouth bass moved offshore, presumably seeking out the deeper, warmer water found at the bottom of the ice-covered lake (Rogers 1998). This same approach can be used in a vertical plane to evaluate conveniently if fish are using various depths in proportion to their availability.

Nearly identical conclusions are obtained with this analysis if the natural logarithm transform is not applied to distance. The same autocorrelation structure, a spatial power autocorrelation function varying among seasons, was selected as the minimum AICc model. The highest autocorrelation was again estimated for winter. Because the residual variance is computed for each season, the heterogeneity of variances caused by distance is somewhat mitigated. Because the mean distance for winter was the largest, the residual variance for winter is greatest for the untransformed distances. The analysis results obtained with the untransformed distances are biologically easier to interpret, hence, in some ways preferred. However, in general, the effect of heterogeneity of variance on ANOVA results is to lower the power of the tests. We can better understand the structure of the data by performing an analysis on both the transformed and untransformed variable and examine similarity in results.

14.6.4 Alternative Approaches

Numerous approaches for analyzing resource selection have been developed over the years. Though most questions can be addressed with the methods we have already discussed, a brief summary of some of the more prominent historic approaches is presented, should the reader wish to explore other avenues.

The first approach to test resource selection rigorously was presented by Neu et al. (1974). They used chi-square analyses to examine the differences in the proportion of used versus available habitats. Analogous to the approaches presented in this chapter, chi-square tests are implemented to test the goodness-of-fit of used to available habitat considering both all habitats simultaneously and each

habitat separately. With their method, the influence of an animal's electivity is effectively weighted by the number of locations for each animal. Unfortunately, analysis is restricted to population level use data and does not allow the user to incorporate unique information for each individual fish in the analysis. As such, it assumes that locations are independent, with a lack of independence resulting in too many type I errors.

The approach developed by Marcum and Loftsgaarden (1980) is especially elegant if the availability of the habitat is only estimated. By doing a chi-square test of independence of habitat types from random locations and telemetry locations, a census of available habitat is not needed. As discussed earlier, with the proliferation of GIS and GPS available to inland fisheries professionals, conducting a census of available habitat is not difficult and does confer more power.

Johnson (1980) developed another approach that is less sensitive to availability concerns. His method ranks habitats by area so that precise estimates are not necessary and minor errors in habitat classification can be tolerated. The method does not test for habitat selection for each animal but rather uses each animal as an observation to test for a preference by the population. Unfortunately, the data from each telemetered fish is weighted equally, regardless of the number of observations recorded for each fish. This method also tends to have lower power than the chi-square approaches discussed earlier. We encourage the investigator instead simply to measure the available habitat.

Friedman's test is another rank-based approach (Allredge and Ratti 1986, 1992). Unlike Johnson's test, this approach ranks the actual differences between proportional use and availability. Like Johnson's test, fish are compared as if sample sizes are equal for each fish, which is usually not the case. Both tests cause much higher type I error rates if animals differ in their habitat selection because animals are assumed to be blocks. This is not a problem for the chi-square goodness-of-fit tests because those are performed for each individual fish.

Lastly, logistic regression models are gaining popularity in the evaluation of habitat use, especially in wildlife journals (Hudgins et al. 1985; Hosmer and Lemeshow 1989; Agresti 1990; Mace and Waller 1996; Conner and Leopold 1998; Mysterud and Ims 1998). Logistic regression methods represent a specialized form of regression models that are designed for the analysis of categorical data, which are the most common in habitat studies. Unlike the chi-square analyses, logistic regression can also incorporate continuous habitat variables such as water temperature or depth in the analysis. Logistic regression evaluates changes in the odds of habitat use where the odds are defined as the ratio between the probability of using a habitat and the probability of not using it. In a simple study where only three habitats are available to choose from, the model equation is

$$\text{odds} = \exp(\beta_0 + \beta_1 X_1 + \beta_2 X_2) = e^{\beta_0} e^{\beta_1 X_1} e^{\beta_2 X_2}. \quad (14.7)$$

When the predictor (X) is categorical with several categories (as would be the case when habitat is used as a predictor), one must represent that predictor by a

set of indicators (artificial variables set at 0 or 1). Given the above equation, suppose there are three habitats: A, B, and C. Then let X_1 be 1 to represent an observation in habitat A and be 0 otherwise. Observations in habitat B are given by $X_2 = 1$ and 0 otherwise. Possible values for this pair of variables is (1,0), (0,1), or (0,0), representing habitats A, B, and C, respectively. An important point is that we need only two indicators to represent three habitats. In general, the number of indicators required is one less than the number of categories. The choice of habitat that is referenced implicitly (habitat C) is arbitrary. One should simply select the habitat that makes the subsequent inferences simplest or most meaningful.

Most telemetry work is retrospective (K. Gerow, personal communication), necessitating the use of odds ratios defined by

$$\text{odds ratio} = \frac{e^{\beta_0} e^{\beta_1(X+1)}}{e^{\beta_0} e^{\beta_1 X}} = e^{\beta_1}. \quad (14.8)$$

In logistic regression, the influence of unit changes in the predictor (X) is manifested in the odds ratios for each predictor. Because we are interested in the ratio of odds, one habitat category must be selected as a baseline to which other habitat categories can be compared. The selection of the baseline category is again arbitrary, and one should just select the habitat that makes explaining the subsequent data most meaningful.

Implementation is straightforward when fish are used as the sampling unit. The chosen model is fit to each individual fish, and only the parameter estimates are recorded. We are only isolating the relative odds parameters for each fish (K. Gerow, personal communication). Once accomplished, standard parametric approaches can be used to explore the distribution of the independent estimates for each parameter. Like the chi-square analyses, this approach has trouble with categories that have zero use. In fact, CIs in habitat categories with very low observed or expected numbers may be suspect, because the standard normal distribution may not accurately represent the sampling distribution of the statistic (K. Gerow, personal communication).

Although logistic regression is a powerful modeling tool for data analysis, we prefer selection ratios when selection for only habitat categories is explored. Results derived from the selection ratio approach are both more intuitive and easier to interpret. The benefits associated with using logistic regression become apparent when habitat information contains continuous metrics.

14.6.5 Conclusion

Although the above approaches are powerful tools to elucidate if fish are using various habitat types in proportion to their availability, they do not tell us if the habitats are critical to survival or reproduction (Hobbs and Hanley 1990; White and Garrott 1990). Given that heterogeneity in habitat use is pervasive within a species in the same basin, even the link between habitat use and fitness may be tenuous. We do suspect that preferences that actually decrease fitness would be

rapidly eliminated from the population through natural selection (White and Garrott 1990). Telemetry studies are generally correlational and tell you only if a habitat is preferred or not, not if it is critical. Only manipulative experiments can reveal the true importance of underutilized habitats.

■ 14.7 HOME RANGE

Home range is defined as “that area traversed by the individual in its normal activities of food gathering, mating, and caring for young” (Burt 1943). The word normal unfortunately introduces ambiguity into the home range concept. An objective method is needed to define normal. Typically, it is defined as some probability level (95% of the locations), though selecting the appropriate probability is arbitrary as well. Evidence for the establishment of home ranges has been documented for several temperate piscivores (Lewis and Flickinger 1967; Malinin 1969; Winter 1977; Doerzbacher 1980; Ross and Winter 1981; Mesing and Wicker 1986), though the results have been questioned due to the very short duration of some of these telemetry studies (Diana et al. 1977; Diana 1980; Cook and Bergersen 1988). The time frame in which the fish are observed must be representative of the interval of interest, which is determined by the objective of the study. Despite the common practice of generating home range estimates, they rarely are related back to the original study objective. Alone, estimates of home range are of little use unless correlated with some additional parameter of importance. Even then, most approaches for determining home range are so vulnerable to criticism that their utility is questionable. Unfortunately, the most commonly used method of estimation (minimum convex polygon approach) is fraught with more problems than any other. Its persistence in the literature is presumably a tribute to its ease of calculation.

14.7.1 Minimum Convex Polygons

The oldest and most common method for evaluating home range size is the minimum-convex-polygon approach (Mohr 1947; Odum and Kuenzler 1955). In its most basic form, the locations for each fish are plotted, and the smallest convex polygon that encompasses all the locations is constructed. The area of this polygon is then an estimate of home range. This approach has several appealing attributes in that it is simple to calculate and allows for flexibility of home range shape.

As mentioned before, the original intent of the home range was to describe the area that an animal “normally” uses during a specified time frame (Burt 1943). The convex-polygon approach encompasses all points where a fish was recorded, including any rare forays. As such, the minimum-convex-polygon approach is really more of an estimate of the total range of an animal, rather than its home range. In addition, the estimate is a minimum estimate of range, because it is unlikely that fish never explored areas farther than where they were monitored. The range is also constrained to be a convex polygon with this method, which is

probably an unreasonable assumption especially in heterogeneous environments (Anderson 1982). This is especially true when studying fish in lakes with complex shorelines, as fish clearly cannot exploit the dry land that falls in their “home range.” Several authors (Winter 1977; Rogers and Bergersen 1995) have removed land areas by generating convex polygons with concave intrusions to reflect the wetted minimum area of the home range. One must be objective when defining such boundaries, but as fish need water to live, this approach is probably defensible.

The most glaring problem with this approach, however, is that estimated home range size increases with increasing sample size (Jennrich and Turner 1969; Schoener 1981). The home range size is a function of the duration of the study and the number of locations used to generate the estimate (Winter 1977). To demonstrate this, daily summer locations of 13 largemouth bass in two Colorado reservoirs (Rogers 1998) were used to generate a minimum-convex-polygon estimate of home range, excluding land area that intruded on the range. In addition to calculating the convex polygon for each fish over the course of the summer, a program was written that randomly dropped 10, 30, 50, and 70% of the locations and recalculated the minimum-convex-polygon home range. Each scenario for each fish was iterated 100 times to generate a mean value (Figure 14.3). Clearly, in all scenarios, documented home range sizes would have been substantially less had fish been located fewer times during that summer. This underscores the futility in comparing home range sizes of a species across studies that use different sampling protocols.

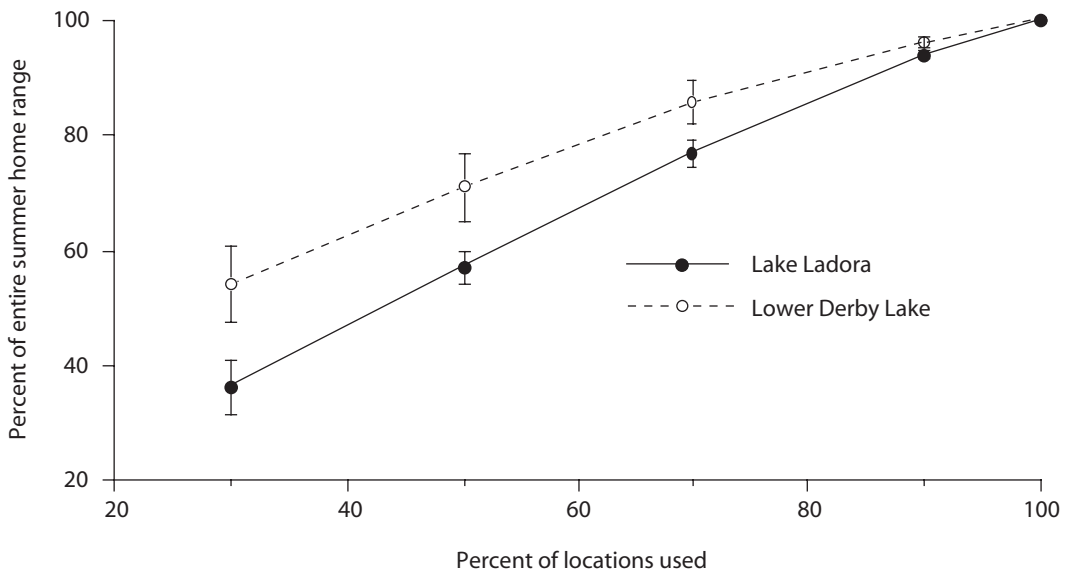


Figure 14.3 Minimum-convex-polygon home ranges were calculated for largemouth bass located in lakes Ladora and lower Derby in the summer of 1994. If the estimates are recalculated using only 30%, 50%, 70%, and 90% of those same locations, a reduction in estimated home range size is realized. Error bars represent the SE of the mean.

Odum and Kuenzler (1955) recognized this limitation and proposed a method to justify using the minimum-convex-polygon approach by plotting the size of the home range against increasing numbers of contacts used to generate the polygon. This “observation area” curve, or cumulative increase in maximum home range area with time, was drawn to determine whether home range size was stable or increasing. They defined stable as the point beyond which each additional observation produced less than 1% increase in area. If the curve did not level off, then either not enough observations were made or the animal in question did not set up a home range in the classic sense. When this approach is used, a staircased graph typically results (Figure 14.4). Although the estimated home range appears to stabilize in a number of places, it is apparent that the home range does not reach an asymptote until the locations fill the entire basin of this 27-ha lake. Terminating the study after the 20th, 40th, or 60th observation would have been made under the illusion that the home range area had stabilized, which was clearly not the case.

14.7.2 Bivariate Normal Models

According to a bivariate normal model, locations are assumed to be distributed independently; that is, fish move randomly around their home range, with their most probable location being the very center. Most models use the area of a 95% ellipse calculated around the mean location as an estimate of the animal’s home range. Although 95% has traditionally been used, the number is arbitrary, and any percentage could be used with adequate justification. By not including all of the points, these methods tend to be more robust to outliers. Points close to the mean are weighted greater than those far away (Jennrich and Turner 1969), and

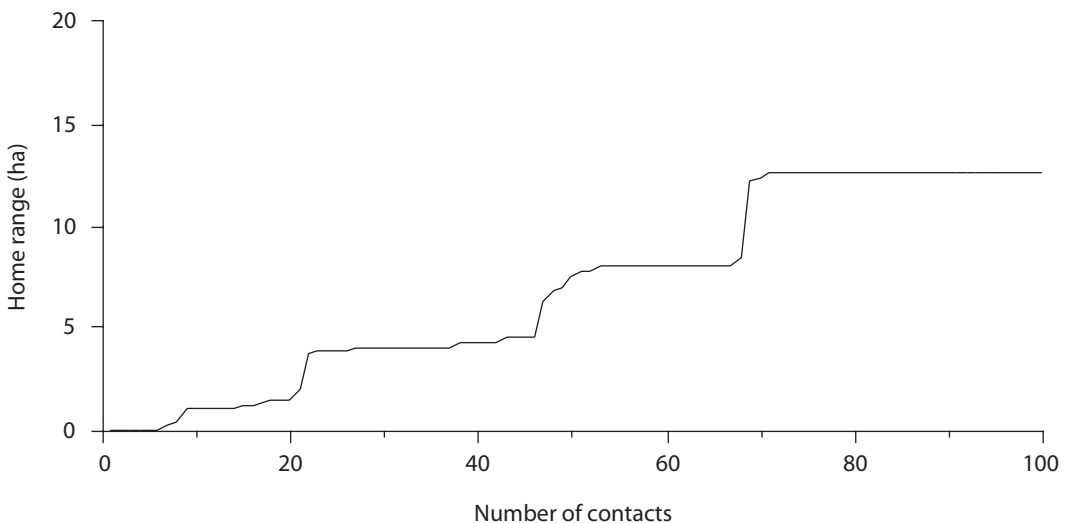


Figure 14.4 The area of the minimum convex polygon encompassing increasing numbers of consecutive contacts for the first 100 locations of largemouth bass #258 in Lake Ladora, Colorado (from Rogers 1998).

some models weight points close in time less than those far apart (Dunn and Gipson 1977). This results in home range estimates that are more consistent with the spirit of Burt's (1943) definition of the home range as the "area traversed by the individual in its normal activities of food gathering, mating and caring for young." Bivariate normal models generally do not include extreme forays that stray far from a center of activity. Numerous methods have been developed in an attempt to decouple the estimated home range size from sample size by this approach (Jennrich and Turner 1969; Dunn and Gipson 1977; Anderson 1982; Samuel and Garton 1985). The obvious benefit is that estimates of home range become more comparable between studies. Fisheries scientists have been reluctant to adopt these methods, presumably because the alternative was historically much easier to calculate. With personal computers now ubiquitous, and a plethora of software programs available (e.g., White and Garrott 1990; Kenward 1992; Larkin and Halkin 1994; Hooge et al. 2001), this should no longer be the case.

Unfortunately, bivariate normal models are still fraught with problems. Conceptually, they do not properly describe the movements of most free-living animals. Fish do not randomly bounce around their home range; they move through it with a purpose, finding food resources, shelter, and mates. Bivariate normal models assume a single center of activity and, hence, do not deal well with multiple centers of activity if a fish decides to change its movement patterns. Home ranges generated by these approaches still increase in size if a fish decides to relocate to new centers of activity on a regular basis, requiring the investigator to decide subjectively what location data to include in the analysis. Smith (1983) provides a chi-square goodness-of-fit test to evaluate whether the home range data are consistent with the assumption of bivariate normality. In addition, these models assume a bivariate normal probability distribution that may not be applicable in many biological settings. Even if range is based around one activity center, this approach is still problematic if you do not want the ellipse to overlap land that the fish cannot use. Clearly land-masses that protrude into a fish's home range would not be well represented by an elliptical home range. In these situations, estimates of home range can be highly biased (Boulanger and White 1990). Additionally, there is no reason a fish should spend most of its time in the center of its home range and little time at the periphery. In general, animal movements arise from strange sampling distributions more frequently than they arise from common, well-known distributions (Schoener 1981; Anderson 1982; Swihart and Slade 1985). Outlying locations, however, cause the ellipse to extend in the opposite direction from the outliers to compensate for their impact on the shape of the normal distribution. Although animal locations seldom fit a bivariate normal distribution, the use of the bivariate normal model for home range estimation is still worthwhile, as the incorporation of a probability model is conducive to robust estimators.

14.7.3 Other Nonparametric Approaches

Perhaps the area with the most promise in dealing with the limitations of home range analyses are the more recently developed nonparametric approaches. These

are more flexible in that they are not restricted to modeling home ranges of a particular shape. Numerous nonparametric approaches have been proposed over the years, including the minimum-convex-polygon approach (Mohr 1947) discussed earlier, as well as Fourier series estimation (Anderson 1982) and grid cell counts (Siniff and Tester 1965). With Fourier series smoothing, the location data are described by adding a finite number of sine waves of various amplitude and frequencies to generate a two-dimensional surface of the area an animal uses. The home range is then the smallest area that encompasses a given percent (e.g., 95%) of the volume of this surface (similar to the arbitrary cutoffs established with the bivariate normal models). The grid cell approach superimposes a grid on a map of the area a fish uses, and the number of locations in each cell is recorded. Although this approach makes no assumptions regarding the shape of the home range, it is very sensitive to the size of the grid cell selected for analysis and the sampling intensity (White and Garrott 1990). Recent developments have provided more robust methods for estimation and are discussed below. Software for the analysis of these methods and detailed instructions for their use can be obtained from a variety of sources (e.g., White and Garrott 1990; Kenward 1992; Larkin and Halkin 1994; Hooge et al. 2001)

14.7.3.1 *Dirichlet Tessellations*

When sample sizes are very large and autocorrelation is significant, Dirichlet tessellations provide a simple and robust technique for evaluating home range size (Wray et al. 1992; Hooge et al. 2001). This approach describes the spatial pattern of the locations in terms of their relative position only. The density of the locations is calculated without any assumptions about the underlying distribution of the data. The Dirichlet tessellation creates a polygon around each fish location, such that all parts of the polygon are closer to the enclosed location than any other location (Figure 14.5). Fish locations are joined by the dotted lines to form Delaunay triangles (Upton and Fingleton 1985). The perpendicular bisectors of the dotted lines then give rise to the polygons that form the tessellation (Wray et al. 1992). The home range is determined as the smallest possible area that includes 95% (or any other justifiable amount) of the polygons (location estimates). Using much smaller percentages will isolate the core areas within a home range. Areas of the home range where fish locations are concentrated then give rise to smaller polygons. The internal configuration of an animal's home range is therefore readily detected. This approach is sensitive to outliers, and the home range boundary can be difficult to establish at high inclusion percentages (Wray et al. 1992). Its use should be restricted to situations for which the location data sets are large.

14.7.3.2 *Harmonic Mean*

Dixon and Chapman (1980) proposed a home range estimator based on the harmonic mean of the spatial distribution of locations, using the distances from nodes on a grid to observed locations. The estimator uses the mean of the inverse distances from a node on a grid to all the locations (Seaman and Powell 1996). This mean is then inverted to generate a surface that is low where locations are most

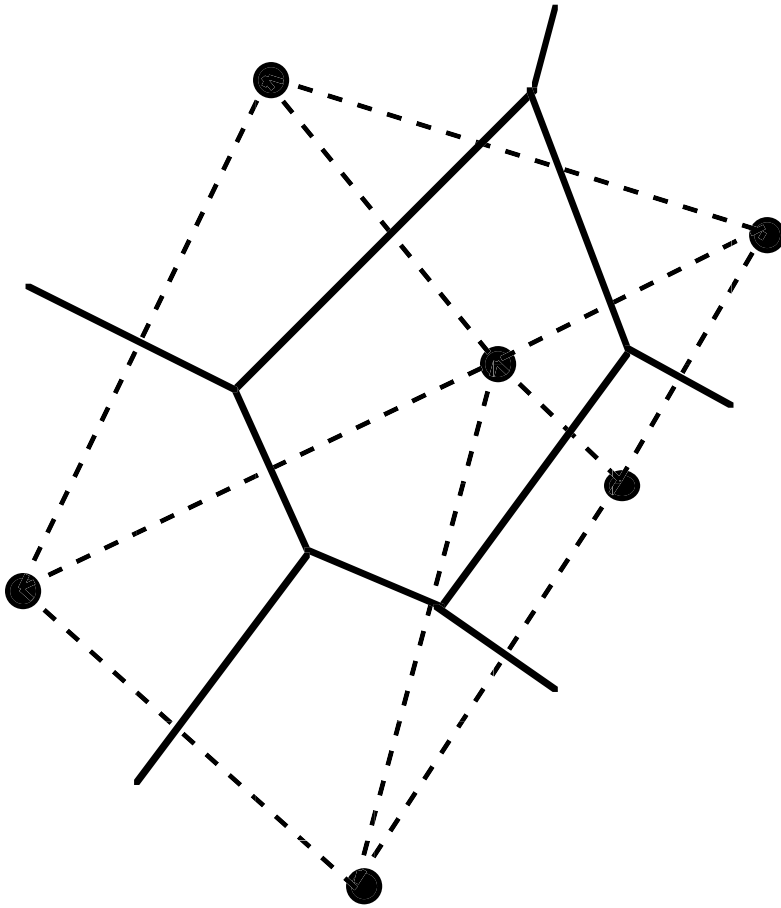


Figure 14.5 The Dirichlet tessellation is constructed from the perpendicular bisectors (solid lines) of the sides of the Delaunay triangles (dotted lines) that connect the fish location estimates. The home range is determined as the smallest possible area that includes 95% (or any other justifiable amount) of the polygons (fish location estimates).

clustered (low mean distance to observations) and high where locations are dispersed (high mean distance to other observations). The boundary of the home range can then be defined by calculating harmonic means at all locations, then at all nodes. All nodes that have harmonic mean values greater than any calculated at the locations are deemed outside the home range (Seaman and Powell 1996). The harmonic means can be converted to a frequency distribution by dividing the means at each node by the sum of the means in the home range. The area under the lowest 95% of this surface is then an estimate of home range (Seaman and Powell 1996). This estimator does not impose any particular shape on the estimated home range and can define ranges with multiple centers of activity properly. It has been shown to be less biased than the other methods presented up to this point (Boulanger and White 1990) and is useful for determining centers of

activity (Dixon and Chapman 1980). Unfortunately, the results are dependent on the origin and spacing of the grid used and the measurement units of the locations, all because a location that falls exactly on a node provides an undefined quantity. As such, the more robust kernel estimators (Worton 1987) have largely replaced this approach,

14.7.3.3 *Kernel Estimators*

These nonparametric density estimators represent perhaps the most intriguing of the probabilistic approaches to estimating home range (Worton 1989). They are preferred over the harmonic mean approach because they are much less sensitive to outlying locations and the choice of measurement units and the grid, and show very little bias (Worton 1995; Seaman and Powell 1996). Conceptually, the kernel method places a probability density (a mound-shaped kernel) over every location registered for a given fish that is to be used in the home range analysis. The density of the kernel is maximized directly over the fish location, but then tails off in all directions, similar to a bivariate normal function. The density is estimated at the nodes of a grid draped over this surface as the average density of all the kernels that overlap at that point. This density will be high in areas where fish are concentrated (and many kernels overlap), but low in less-frequented areas. Once this surface has been generated, contour lines can be inscribed on it that connect areas of equal density. For comparison purposes, usually the area that incorporates 95% of the utilization distribution is calculated as an estimate of home range. This value is arbitrary, however, and it is often useful to draw contour lines at multiple levels so that high-use areas can be rapidly identified.

Smoothing is critical for describing accurate home range sizes with kernel estimators (Worton 1995), and that is how the two kinds of kernel estimators are defined. In the fixed kernel estimator, the smoothing parameters are fixed over the entire surface (Worton 1989). The smoothing parameters are allowed to vary in the adaptive kernel estimator approach. Areas where the densities of fish are low receive more smoothing than do areas where fish are concentrated. Although adaptive kernel methods are thought to yield better estimates (Worton 1989; Silverman 1992), the fixed kernel approach gave the least-biased results and lowest error based on simulated data (Seaman and Powell 1996; Seaman et al. 1999) and is therefore recommended. Kernel estimates based on sparse data should be expected to overestimate true home range size, though home ranges that follow smooth unimodal distributions can be accurately described with fewer locations than can more complex distributions (Seaman and Powell 1996).

Though elegant nonparametric approaches have been developed to address some of the concerns with earlier methods of home range estimation, they still have several shortcomings. Perhaps the most problematic is that these approaches, like those that use minimum convex polygons, have no CIs around them. One cannot judge the quality of the estimate because only a point estimate is generated, without an estimate of its SE. However, SEs for the kernel estimators could be developed with a bootstrap procedure, resampling the original data with replacement to generate a distribution of calculated values (Good 1994; Edgington

1995; Manly 1997). Kernel estimators also ignore the time series nature of the data and tend to have lower precision than do parametric methods of estimation because fewer assumptions are made (White and Garrott 1990). However, the lower bias of these estimators still makes their use recommended.

14.7.4 Utility of the Home Range Concept

No one method for characterizing home range size is without flaws (Table 14.1). Many subjective decisions and assumptions must be made when generating home range estimates, limiting the biological insight they can provide (White and Garrott 1990). In particular, the sampling scheme to obtain the locations used to calculate a home range estimate must provide an unbiased picture of the animal's movements (Otis and White 1999). Many varied approaches for estimating home range size exist, but they are all vulnerable to criticism. All involve making subjective decisions that lack objective criteria, causing the resulting estimates to provide little biological insight. Home range estimates are often presented to disguise the fact that no hypotheses are being tested, providing a quantitative albeit insignificant summary of the data. Some have advocated abandoning the calculation of home range size altogether and using raw data to test hypotheses (Anderson 1982; White and Garrott 1990). This would eliminate the need to invoke spurious assumptions and biases inherent in home range estimates and confer more power to subsequent statistical tests.

Home range analyses provide an interesting exercise in data analysis but are of little interest, unless correlated with some additional parameters. Properties of the home range should have adaptive significance. For example, home range size

Table 14.1 A subjective summary of various traits associated with the minimum convex polygon (MCP), wetted MCP (MCPw), Jennrich–Turner bivariate normal (JT), Dunn–Gipson bivariate normal (DG), Fourier series (FS), grid cell count (GC), Dirichlet tessellation (DT), harmonic mean (HM), and kernel estimator (KE) methods for calculating home range. In general, only those methods that are particularly sensitive to a specific trait are included.

Trait	Method
Experiences range increases with sample size	MCP, MCPw
Experiences range increases with sampling duration	MCP, MCPw
Accounts for land intrusions	MCPw, GC, DT, HM, KE
Restricts home range to a particular shape	JT, DG
Includes arbitrary percent of locations in range	JT, DG, FS, DT, HM, KE
Assumes single center of activity	JT, DG
Accommodates multiple centers of activity	MCP, MCPw, FS, GC, DT, HM, KE
Is robust to outliers	JT, DG, DT, HM, KE
Accounts for time series nature of data	DG
Has robust statistical foundation	JT, DG
Isolates core areas	GC, DT, HM, KE
Experiences difficulty in defining boundary of home range	JT, DG, FS, DT
Depends on grid used	GC, HM

is considered an important aspect of an animal's feeding strategy and should be related to food density, metabolic needs, and the efficiency of movement, in addition to being inversely correlated with population density (Schoener 1981). Fish and Savitz (1983) attempted to use home ranges to compare trophic relationships between species in an Illinois lake. Their hypothesis was that largemouth bass would have larger home ranges than would bluegills or pumpkinseeds because the latter species were benthivores whereas largemouth bass were piscivores. The lower densities of piscine prey would necessitate that largemouth bass would have larger home ranges. Their fish were tracked on average for 43 d, and a home range was arbitrarily defined as the minimum-convex-polygon area that a fish occupied for at least 5 consecutive days. Not surprisingly, extreme variability kept them from detecting any differences in home range size between species. Usually, one can substitute raw location or movement data to test a hypothesis of interest, thereby avoiding the problems associated with home range analysis. Because movement (MDPH) and home range are highly correlated (Rogers and Bergersen 1995), Fish and Savitz (1983) may have been able to address the same relationships without having to make all of the spurious assumptions associated with analysis of home range by invoking MDPH instead. Savitz et al. (1993) used home range size to show that largemouth bass used reduced areas when given supplemental feed. Minns (1995) demonstrated that home range was correlated with fish size. Both would have drawn the same conclusions by measuring MDPH while avoiding criticisms of home range analysis.

The entire home range concept may not be as appropriate for fishes as it is for terrestrial mammals (especially those with altricial young). Burt's (1943) original home range concept was developed for mammals as the area used for foraging that surrounded a permanent home site. These areas were generally stable over long periods of time. In fact, before generating a home range estimate, it would be wise to determine if site fidelity even exists (Hooge et al. 2001). Fish seem to display more transitory ranges (Winter 1977; Cook and Bergersen 1988; Jones and Rogers 1998), perhaps due to short spawning seasons (Savitz et al. 1993) and limited or absent parental care. Changes in home range areas appear to occur with changes in prey, water temperature (Savitz et al. 1993), or body size (Minns 1995) rather than intraspecific competition. We may be stretching the original spirit of Burt's (1943) concept too far in fisheries research and should perhaps employ metrics other than home range in testing hypotheses of interest.

■ 14.8 SUMMARY

The methods presented here are only a sampling of the varied approaches used in telemetry studies, but we hope that they will provide a foundation for customizing analyses for specific applications. With the proliferation of software programs and powerful computers to run them, many of the traditional shortcomings of telemetry work can now be addressed. Researchers can now focus on study design aspects of their work prior to the initiation of the study by ensuring that representative samples of fish from the population of interest are obtained.

Power calculations should be conducted before the initiation of field work to ensure that proposed research will be able to address the questions that are posed. Early on, one should explore the error associated with telemetry system to be used to evaluate what influence or bias it will introduce to the results. Perhaps the strongest message that should be gleaned from this chapter regards the correct treatment of the sampling unit. Because we are interested in describing how fish in a population behave, the individual fish are the sampling units and not the individual locations, as is commonly reported. Using locations as sampling units is pseudoreplication (Hurlbert 1984). The attention focused on the serial correlation of location data taken close in time is misguided now that powerful statistics packages, such as SAS, allow for the integration of autocorrelation in the data structures. Autocorrelation of location estimates is largely irrelevant when telemetry data are analyzed correctly.

After ensuring that the study design is sound, one is encouraged to explore the spatial distribution of fish locations to determine if they are distributed in a non-random fashion. Movement is another metric that is often explored in telemetry literature and can often be correlated with environmental attributes. Often habitat use is the primary area of interest. Though numerous approaches have been developed to characterize use, they do not reveal whether the behaviors we observe are actually a critical reflection of what is needed for the fish to reproduce and survive. Cause and effect can be isolated only by conducting manipulative experiments.

A tremendous amount of effort has been expended on developing methods to evaluate home range size. The minimum-convex-polygon approach is certainly the most common but is problematic because home range size tends to increase with sample size or sampling duration. Bivariate normal models strive to minimize those limitations by including only a portion of the locations (usually 95%). Reducing the number of locations considered makes this type of approach less sensitive to outliers, but 95% is completely arbitrary, and a few percentage points either way can have a large effect on range size. Additionally, these models unrealistically restrict the shape a home range can assume. Shortcomings of the bivariate normal models have been addressed with nonparametric approaches that allow for multiple centers of activity and accurate reflections of odd-looking home range boundaries that typically occur in nature. Many nonparametric methods also entertain only a portion of the locations recorded to decrease sensitivity to outlying locations. Though these approaches represent the most promise in home range analyses, it is difficult to establish CIs with these methods, preventing the reader from assessing the quality of the estimate. Because all approaches have some flaws, we advocate substituting alternative metrics, such as movement per hour, for comparison to parameters of interest. These other metrics generally provide the same results without invoking the myriad assumptions and subjective criteria associated with home range estimation. In fact, the whole concept of a home range may not be as appropriate for freshwater fishes as it is for small terrestrial mammals with altricial young, for which the concept was developed (Burt 1943).

■ 14.9 A LOOK TO THE FUTURE

With improvements in technology, we expect to see increased diversity in types of telemetry applications that are implemented. We have witnessed an increase in the use of telemetry to isolate the importance of various parameters used in bioenergetics modeling in recent publications. In addition, we expect fisheries scientists to explore other applications of telemetry, such as survival rate estimation (Pollock et al. 1989; White and Garrott 1990; Bunck et al. 1995; Harmata et al. 1999; White and Burnham 1999; Skalski et al. 2001) and population estimation (Bartmann et al. 1987; White and Garrott 1990; Bowden and Kufeld 1995; White 1996; White and Shenk 2001), applications that see wide use in wildlife research but are just beginning to be deployed in inland fisheries work.

As technology advances, we also expect to see a greater emphasis on automated receiving systems. Some new innovative applications of telemetry require continuous monitoring to obtain meaningful results. This has spawned a proliferation of automated systems that either track or monitor fish 24 h/d (Hawkins et al. 1980; Pincock 1980; Armstrong et al. 1992; Lucas et al. 1992; Cooke et al. 2000, 2001; Cooke and Bunt 2001; Dieperink et al. 2001; Skalski et al. 2001). With continuous monitoring, many of the assumptions that had to be made with previous telemetry work can be validated. Not only is this approach much less labor intensive than traditional telemetry, it can yield orders of magnitude more information that personal computers can easily process. Though some of these applications are extremely specialized and will require specific types of data analyses, many will be able to expand on the approaches discussed in this chapter.

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