

MCDONALD

ANALYSIS PROCEDURES FOR HABITAT AND FOOD SELECTION STUDIES

Lyman L. McDonald, Departments of Zoology and Statistics,
University of Wyoming, Laramie, Wyoming 82071-3332 USA

Daniel J. Reed, Alaska Department of Fish and Game, 1300 College
Road, Fairbanks, Alaska 99701 USA

Wallace Erickson, Department of Statistics, University of
Wyoming, Laramie, Wyoming 82071-3332 USA

Abstract: Designs and data analysis procedures for studies of resource selection in field ecology are reviewed. These studies compare relative use of resources (habitat or food items) with relative availability. It is proposed that estimation of a resource probability selection function is the best analytical procedure to meet the objectives of many field studies. Estimation procedures are presented for the resource selection functions and are illustrated with data from the literature and with hypothetical data.

Key Words: habitat selection, resource selection, food selection, selection functions, use versus availability, selectivity indices, forage ratios.

Selection (or use) of a resource has been defined as the process in which an animal chooses a resource (Johnson 1980), or as choice among resources available (Peek 1986). Preference on the other hand is defined as the likelihood that a resource will be chosen if offered on an equal basis with others (Johnson 1980) and choice of one resource over another without regard to whether one may be

available or not (Peek 1986). This paper deals only with the estimation of a resource selection function defined by "...a function of variables measured on resource units, such that for each unit the value of the function is proportional to the probability of that unit being utilized (Manly et al. 1989)." An example of an estimated resource selection function for habitat selection by pronghorn (Antilocapra americana) is plotted in Fig. 1 (Ryder 1983, Manly et al. 1989). Ryder (1983) studied winter habitat selection by pronghorn in the Red Rim area in south-central Wyoming. He systematically sampled the land to obtain 256 study plots of 4 ha each, covering 10% of the total area. For the purpose of this example assume that this is equivalent to a 10% random sample of the 2,560 plots available in the entire region. On each study plot Ryder recorded the presence or absence of antelope in the 1980-81 and 1981-82 winters, the average slope, the aspect, and the distance to available water. In addition, he estimated the density and average height of big sagebrush (Artemisia tridentata), black greasewood (Sarcobatus vermiculatus), Nuttall's saltbush (Atriplex nuttalli) and Douglas rabbitbrush (Chrysothamnus viscidiflorus).

Manly et al. (1989) reanalyze Ryder's data defining a plot to be used if antelope are present in both winters. There are then 38 used and 218 unused plots. With this classification there is little evidence when testing hypotheses in the statistical analysis (to be described in more detail later) that the used and unused plots differ with regard to the slope or vegetation

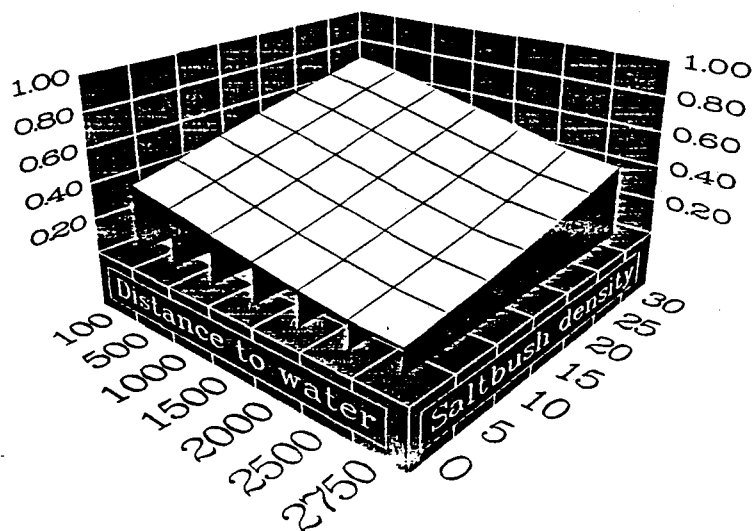


Fig. 1. Estimated probability of selection of a habitat unit with northeast aspect by antelope (*Antilocapra americana*) during two winters in south-central Wyoming (plotted as a function of the distance to the nearest available water and density of saltbush) (Ryder 1983, Manly et al. 1989).

parameters associated with big sagebrush, black greasewood or Douglas rabbitbrush. However, there are apparent differences related to the aspect, density of Nuttall's saltbush and the distance to water that are described by the estimated logistic regression model:

$$\hat{y} = \frac{\exp(-1.827 + 0.0486X_1 - 0.000521X_2 + 1.40X_3 + 0.441X_4 + 0.555X_5)}{1 + \exp(-1.827 + 0.0486X_1 - 0.000521X_2 + 1.40X_3 + 0.441X_4 + 0.555X_5)}, (1)$$

where \hat{y} is the estimated relative probability of selection of a plot, X_1 is the density of saltbush (plants/ha), X_2 is distance from water (meters), X_3 is 1 for a northeast-east direction (or otherwise is 0), X_4 is 1 for a southeast-south direction (or otherwise is 0), and X_5 is 1 for a southwest-west direction (or

otherwise is 0) (Manly et al. 1989). Probability of selection for the northwest-west aspect is estimated by setting $X_3 = X_4 = X_5 = 0$. Areas with the highest probability of use have a northeast-east aspect, have high density of saltbush, and are close to water. Fig. 1 shows a graph of the estimated probability of use for the northeast-east aspect ($X_3 = 1, X_4 = 0, X_5 = 0$) plotted as a function of saltbush density and distance to water. Similar plots could be constructed for the other three aspects.

Study design and sampling protocols dictate the procedures by which the resource selection function can be estimated. Three general study designs have been recognized in the wildlife ecology literature (Thomas and Taylor 1990):

Design I - variables on resource units available are measured or sampled for the entire study area and individual animals (or herds) are not identified in use of resource units,

Design II - variables on resource units available are measured or sampled for the entire study and use of resource units is identified by individual animals (or herds), and

Design III - variables on resource units available to each animal (or herd) identified in the study are measured or sampled and use of resource units is identified by individual animals (or herds).

Three sampling protocols have been identified in Table 1 (Manly et al. 1989). In addition to sampling available and used units, designs II and III implicitly assume that a simple random sample of animals is obtained from the population. The combination of study design and sampling protocol dictate the procedures by which the resource selection function is estimated and the degree Table 1.

Sampling protocols identified by Manly et al. 1989. Sampling

Protocol	Sample 1	Sample 2	
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SP1	Available	Used	Available units have a probability p_1 of being in sample 1; used units have a probability p_2 of being in the independent sample 2.
SP2	Unused	Used	Unused units have a probability p_1 of being in sample 1; used units have a probability p_2 of being in the independent sample 2.
SP3	Available	----	Case (a) A sample of available units is taken. Units are classified as unused or used. Case (b) Units with predetermined measurements for the independent variables are sampled and classified as unused or used.
SP4	Available	----	Census data. All available units are examined and classified as unused or used.

to which statistical inferences can be made to the study area and the animal population under consideration. Calculations for estimation of the resource selection function depend primarily on whether a comparison is made between available and used units or between unused and used units.

If individual animals are not identified (Design I, Thomas and Taylor 1990) each of the sampling protocols in Table 1 are possible and statistical inference is to the study area being sampled with its fixed population of animals. The units used to sample the study area may be quadrats, random points, belt transects, line transects, etc. and the sample sizes are the number of units chosen from the appropriate classifications.

If individual animals are identified (Designs II and III, Thomas and Taylor 1990) then two universes exist to be sampled. The philosophy of the scientific method for making statistical inferences does not easily handle two universes! We believe the best approach is to consider the animal as the primary unit of replication. First, the population of animals is sampled. Second, each of the protocols in Table 1 are candidates for sampling the universe of resource units available to the population of animals (Design II) or for sampling a subset of resource units uniquely available to animals chosen in the first step (Design III). Third, the resource units used by the i th animal in the sample must be sampled.

In Designs II and III, a resource selection function can be estimated for each animal and replications of the coefficients of the function are obtained. One set of coefficients is obtained for each animal (primary unit) in the sample. Logistic regression, a robust model fitting procedure, is recommended for estimating the selection function and to make statistical inferences toward the significance of the variables under study. Standard procedures are then available for testing the null hypothesis that a variable (or set of variables) does not contribute to the ability of the model to predict the probability that a resource unit will be selected. For example, the reanalysis of Ryder's data in the above example was made by using the standard BMDP statistical package PR1 (BMDP 1988) for stepwise logistic regression. Nonlinear terms and terms for interaction of variables can be included in the analysis.

DESIGN I

Consider a study following Design I where animals are not uniquely identified. Each of the Sampling Protocols are appraised for their effect on the analysis.

Sampling Protocol SP1

We make the assumption that the relationship between the relative probability of selection, $w(\underline{x}) = w(x_1, x_2, \dots, x_p)$, and the independent variables $\underline{x} = \{x_1, x_2, \dots, x_p\}$ is given by the log-linear model:

$$w(\underline{x}) = \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_p x_p),$$

i.e.,

$$\ln(w(\underline{x})) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_p x_p \quad (2)$$

where $\beta_0, \beta_1, \beta_2, \dots, \beta_p$ are the unknown regression parameters. If the sampling fraction from the population of available units (p_1) and the sampling fraction from the population of used units (p_2) are known then the absolute probability of selection of a plot is given by the formula

$$w^*(\underline{x}) = [p_1 / \{p_2(1-p_1)\}] \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_p x_p) \quad (3)$$

(Manly et al. 1989). If either of the sampling fractions is very small then estimates of the ratio $p_1/p_2(1-p_1)$ may be unreliable. Therefore it may be best not to attempt to scale the selection function to give absolute probabilities but instead to simply use the arbitrarily scaled function (arbitrary value of the term $\hat{\beta}_0 = b_0$) as an indication of the relative attractiveness of different resource units. Usually, the constant b_0 will be selected so that the maximum value of the function over the range of the independent

variables x_1, x_2, \dots, x_p is the number 1.0.

For simplicity, consider a hypothetical example of sampling protocol SP1 where the objective is to study the dependence of habitat selection by caribou on percent cover by willow and percent cover by tundra. Assume that Design I and Sampling Protocol SP1 are used. A random sample of plots available to the population of animals in a study area is obtained and the researcher measures two variables on each: x_1 = percent cover by willow, and x_2 = percent cover by tundra.

Define a plot to be "used" if at least one caribou has been on the plot during the period of interest. Assume that the collection of plots in the study area which have at least one relocation of radio tagged caribou is an independent sample of used plots. Design of the study to meet the assumptions of an independent sample of used plots is not a trivial matter. However, discussion of procedures to meet this assumption is highly dependent on a particular application and is beyond the scope of the present paper. Define the dependent variable y by:

$y = 0$, for all plots in the sample of available plots, and

$y = 1$, for all plots in the sample of used plots.

Note that the sample of available plots may contain plots that are used. Table 2 contains simulated data from the selection function

$$w(x_1, x_2) = \exp(-3.8 + 2.2x_1 + 3.8x_2) \quad (5)$$

where 3.8 is subtracted from the exponent so that the maximum value of the function is 1.0 over the permissible range $x_1 + x_2 \leq 1.0$.

The "true" probability of selection, $w(x_1, x_2) = \exp(-3.8 + 2.2x_1 + 3.8x_2)$,

is plotted in Fig. 2.

It has been shown (Manly et al. 1989) that for sampling protocol SP1, the probability of an individual with x values (x_1, x_2, \dots, x_p) coming from the population of used resources given that the individual is in one of the two samples is

$$\text{prob}(\text{used}|\text{sampld}, \underline{x}) = \frac{\exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_p x_p)}{1 + \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_p x_p)} \quad (6)$$

This is a logistic regression function with the desired selection function in the numerator. Estimates of the relative value of the selection function can be obtained by carrying out a logistic regression of $y = 0$ and $y = 1$ on the independent variables x_1, x_2, \dots, x_p . Once the coefficients $\beta_0, \beta_1, \dots, \beta_p$ have been estimated by $b_0, b_1, b_2, \dots, b_p$, the relative probability of selection of a plot with $X_1 = x_1, \dots, X_p = x_p$ is estimated by just the part in the numerator

$$\hat{w}(\underline{x}) = \exp(b_0 + b_1 x_1 + \dots + b_p x_p) \quad (7)$$

or any convenient multiple of it.

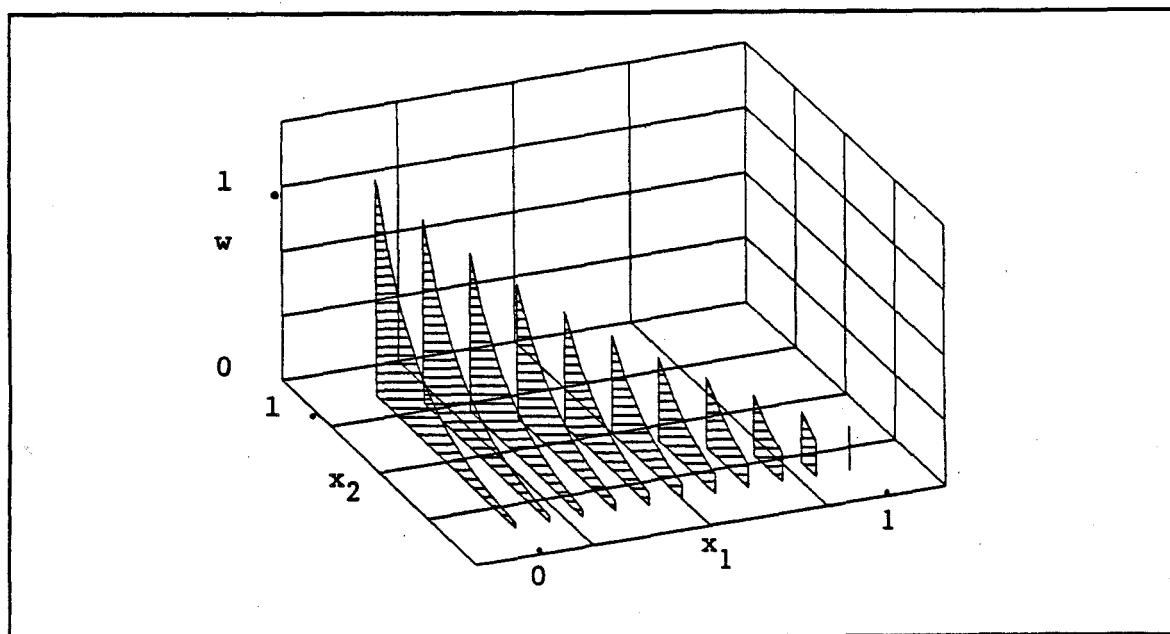


Fig. 2. Plot of the original relative probability of selection function $w(x_1, x_2) = \exp(-3.8 + 2.2x_1 + 3.8x_2)$.

Table 2. Simulated sample data for the selection function $w(x_1, x_2) = \exp(2.2x_1 + 3.8x_2 - 3.8)$ where x_1 = percent cover by willow and x_2 = percent cover by tundra, $y = 1$ indicates a plot in the sample of used plots, and $y = 0$ indicates a plot in the sample of available plots.

x_1	x_2	Y	x_1	x_2	Y	x_1	x_2	Y	x_1	x_2	Y
0.8	0.1	0	0	1	0	0	1	0	0	0.6	0
0	0.9	0	0	0	0	0.2	0.6	0	0.7	0.2	0
0.8	0.2	0	0.2	0	0	0.2	0.8	0	0.6	0	0
0.5	0.3	0	0.3	0.5	0	0.5	0.4	0	0.3	0.4	0
0.3	0	0	0.3	0.1	0	0.3	0.1	0	0.4	0.6	0
0.3	0.4	0	0.4	0.4	0	0.2	0.3	0	0.6	0.3	0
0.2	0.8	0	0.6	0.4	0	0.1	0.4	0	0.5	0.5	0
0.1	0.5	0	0.5	0	0	0.1	0.9	0	0.5	0.3	0
0	0.6	0	0.5	0.3	0	0.1	0.8	0	0.5	0.1	0
0.1	0.4	0	0.5	0.4	0	0.1	0.1	0	0.4	0.1	0
0.8	0.1	0	0.6	0.1	0	0.7	0.1	0	0.7	0.3	0
0.2	0.2	0	0.7	0.2	0	0.3	0.1	0	0.7	0	0
0.4	0.3	0	0.4	0.5	0	0.1	0.1	0	0	0.9	0
0.1	0.8	0	0.3	0	0	0.1	0.9	0	0.3	0.4	0
0.1	0.3	0	0.3	0.7	0	0.2	0.6	0	0	0.6	0
0.4	0.4	0	0	0.5	0	0.5	0.4	0	0	0.4	0
0	0.1	0	0.2	0	0	0.9	0.1	0	0.1	0.8	0
0.4	0.5	0	0.1	0.6	0	0.1	0.5	0	0.8	0.1	0
0.5	0	0	0.2	0.4	0	0	0.7	1	0	0.9	1
0	0.7	1	0.2	0.8	1	0	0.9	1	0.1	0.8	1
0	1	1	0	0.5	1	0.8	0	1	0.8	0.2	1
0.8	0.2	1	0.4	0.3	1	0.1	0.2	1	0.5	0.5	1
0.6	0.2	1	0.5	0.2	1	0.6	0.3	1	0.5	0.4	1
0.2	0.7	1	0.4	0.3	1	0.4	0.2	1	0.3	0.7	1
0.2	0.2	1	0.2	0.2	1	0.3	0.7	1	0.2	0.8	1
0.4	0.4	1	0.2	0.7	1	0.4	0.6	1	0.1	0.9	1
0.3	0.5	1	0.4	0.4	1	0.4	0.6	1	0.6	0.4	1
0.3	0.6	1	0.4	0.2	1	0.4	0.3	1	0.7	0.3	1
0.3	0.7	1	0	1	1	0.2	0.3	1	0.4	0.6	1
0.2	0.7	1	0.5	0.2	1	0.7	0.3	1	0.2	0.7	1
0.1	0.5	1	0.6	0.3	1	0.1	0.9	1	0.6	0.2	1
0.1	0.6	1	1	0	1						

Returning to the hypothetical data generated in Table 2, the logistic regression function

$$y = \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2) / \{1 + \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2)\} \quad (8)$$

was fitted to the data in Table 2 using the IBM-PC statistical package SOLO (BMDP 1988) to obtain $b_0 = -2.33$, $b_1 = 2.27$ and $b_2 = 2.79$. The graph of the estimated relative probability of selection function,

$$\hat{w}(x_1, x_2) = \exp(-2.79 + 2.27x_1 + 2.79x_2), \quad (9)$$

is plotted in Fig. 3. The constant $b_0 = -2.33$ is of no particular interest because the fraction of used units which are in the sample is unknown and the absolute probability of use cannot be estimated. The value -2.79 has been subtracted from the exponent of the selection function so that the maximum value of the estimated relative probability of selection is 1.0. The constants b_1 and b_2 are large compared to their standard errors (1.03 and 0.94, respectively). In practice, this would indicate a significant relationship between probability of use and x_2 = percent cover by tundra and x_1 = percent cover by willows.

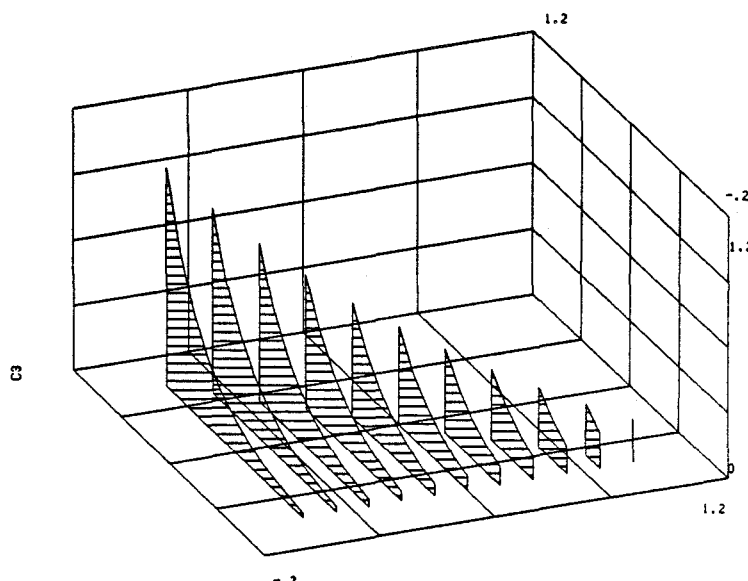
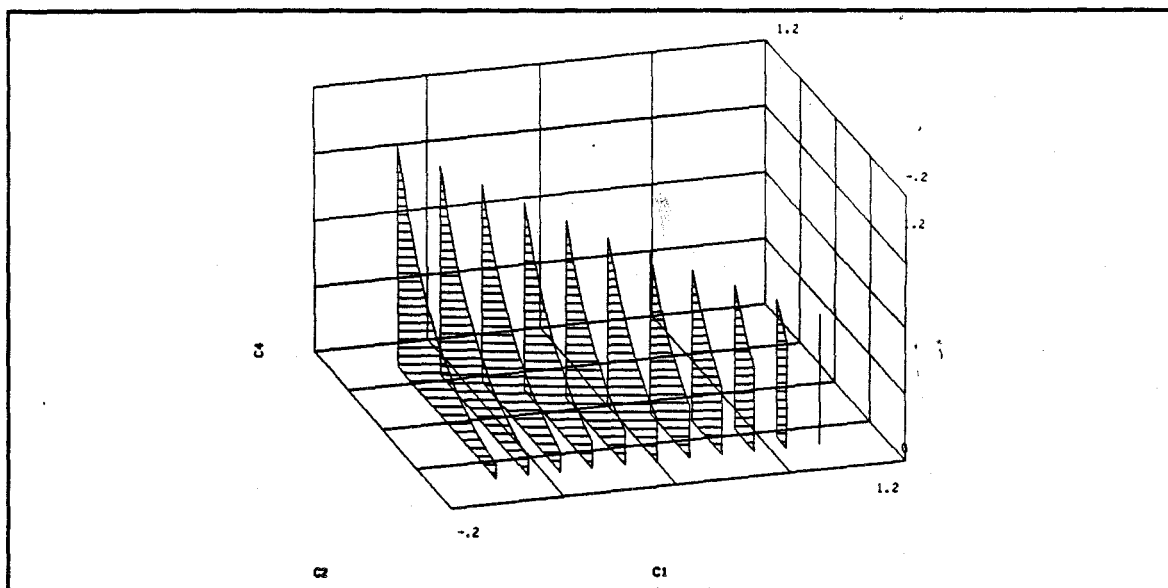


Fig. 3. Plot of the estimated selection function $\hat{w} = \exp(-2.33 + 2.27x_1 + 2.79x_2)$ obtained by logistic regression of y on x_1 and x_2 for the simulated sample data in Table 2.



Sampling Protocol SP2

In this sampling protocol, a sample of used units is compared to a sample of unused units. In many situations the fraction of the available resource units actually used will be very small so that the difference between the population of available resource units and the population of unused resource units will be negligible. In this case the sample of unused resources can be regarded as effectively being a random sample of available resources, which means that the approaches discussed in the previous section for sampling protocol SP1 can be used for the analysis.

If the fraction of the resources used is not small, then assume that p variables $\underline{x} = (x_1, x_2, \dots, x_p)$ are measured on each resource unit and conduct the logistic regression of $y = 0$ (for unused units) and 1 (for used units) on $\underline{x} = (x_1, x_2, \dots, x_p)$ to obtain the

estimated coefficients (b_0, b_1, \dots, b_p) as above. If p_1 , the fraction of unused units in the sample of unused units, and p_2 , the fraction of used units in the sample of used units, are known then the absolute probability of selection of a unit with $\underline{x} = (x_1, x_2, \dots, x_p)$ is estimated by the formula

$$w^*(\underline{x}) = \frac{(p_1/p_2) \exp(b_0 + b_1 x_1 + \dots + b_p x_p)}{1 + (p_1/p_2) \exp(b_0 + b_1 x_1 + \dots + b_p x_p)} \quad (10)$$

If the ratio, p_1/p_2 , is not known then estimation of the resource selection function is not possible! It will be difficult to estimate the ratio in many field studies and the sampling protocol SP2 is not recommended except in the special cases when the sizes of the universe of unused and the universe of used units are known and the ratio p_1/p_2 is accurately estimated. Only if used units naturally occur separately from unused units or are otherwise easy to sample separately using known sampling fractions p_1 and p_2 should sampling protocol SP2 be used.

For an example of Sampling Protocol SP2, consider a group of animals being released into a study region in an attempt to reestablish a population. If every animal is radio tagged then the combined home ranges of the animals might be defined as the "used" segment of the study region. The complement of the home ranges in the study region could be defined as the "unused" segment. The areas of the used and unused segments could be accurately measured on a map and each sampled independently by selecting a known number of units. Perhaps $p_1 = 15\%$ and $p_2 = 10\%$ of the used and unused segments are independently and randomly sampled. The key element

is that the ratio of the sampling fractions, p_1/p_2 (e.g., $0.15/0.1 = 1.5$), is known or accurately estimated. The values of the variables X_1, X_2, \dots, X_p would be measured on all sampled units and equation (10) would be used to estimate the resource selection function.

Sampling Protocols SP3 and SP4

Consider SP4, where all the resource units available to an organism are known, a definition is given for "used" units, and a complete record is available of used and unused units. For example, suppose a study area has been divided into 500 plots. In a study of habitat selection in winter, the researcher might wait for a certain period of time after a fresh snowfall and conduct an aerial survey of every plot to determine if tracks are present or not. Define plots with tracks to be "used". Variables such as x_1 = density of browse species and x_2 = exposure to wind are measured for every plot. Assume that the absolute probability of a unit with values $\{x_1, x_2, \dots, x_p\}$ will be used is given by:

$$w^*(\mathbf{x}) = \frac{\exp(b_0 + b_1x_1 + \dots + b_px_p)}{1 + \exp(b_0 + b_1x_1 + \dots + b_px_p)} \quad (11)$$

and estimate this function using regular logistic regression. Note that this is a special case of Sampling Protocol SP2 where $p_1 = p_2 = 100\%$ and $p_1/p_2 = 1.0$.

In this case there is no variance due to sampling habitat units because data are available on every unit in the universe. However, estimates of coefficients are still subject to statistical variation because of the other "universe", namely the population of

animals in the study area and selection of units over time. At one point in time, standard errors from the logistic regression analysis provide means to test hypotheses concerning which variables are significantly related to the probability of use during that period of time. Independent replication of the coefficients over time would also provide a general means for making inferences concerning which variables are important in determining habitat selection.

Consider sampling protocol SP3(a), where a random sample of available units is taken, and divided into used and unused units, or design SP3(b) where units with fixed values for the X variables are identified, stratified into subsets, and sampled. The function (11) can still be estimated directly by logistic regression because sampling protocol SP3(a) is a special case of SP2 where $p_1/p_2 = 1$ in equation (6), i.e., the sampling probability is the same for used and unused units. After available units are sampled with equal probability, they are split into used and unused subsets.

In sampling protocols SP3 and SP4, regular logistic regression can be conducted and the probabilities computed by the standard statistical packages are applicable. Care should be taken to observe the sign of the coefficients. In some packages it may be necessary to reverse the signs on all coefficients to achieve agreement with the notation in this paper.

The example presented earlier concerning habitat selection by antelope (Ryder 1983) is an application of Sampling Protocol SP3(a) where plots were randomly sampled with equal probability then

classified as used or unused. Equation (1) is the estimated logistic regression function relating probability of use to the independent variables and is plotted in Fig. 1 for one aspect.

DESIGNS II AND III

In Designs II and III, a resource selection function can be estimated for each animal and replications of the coefficients of the function are obtained. One set of coefficients is obtained for each animal (the primary unit) in the sample. Inductive inferences can then be made to the mean value of the coefficients using standard statistical procedures where the "sample size" is the number of animals chosen. Statistical inferences and standard errors of coefficients for unique animals may not be of any particular interest. Sample sizes in the sampling protocols of Table 1 are viewed as the size of subsamples necessary to adequately "measure" the resource function for a unique animal. Inferences based on replication of the primary unit, the animal, are of primary concern.

RESOURCE SELECTION BASED ON A SINGLE CATEGORICAL VARIABLE: RATIOS OF RANDOM VARIABLES

Ratios of certain random variables arise in the analysis of resource selection based on a single categorical variable. Procedures for estimation of the standard error of a ratio of random variables are not ordinarily presented in introductory textbooks and are reviewed here. Let (Y,W) denote an arbitrary pair of random variables where interest is in estimation of the ratio

$R = (\text{population mean of } Y) / (\text{population mean of } W).$

Given a random sample of size $N \{(Y_1, W_1), \dots, (Y_N, W_N)\}$ on the pairs, the recommended estimator of R is the ratio of totals (or means),

$$\begin{aligned}\hat{R} &= (\Sigma_j Y_j) / (\Sigma_j W_j) \\ &= \bar{y} / \bar{w}.\end{aligned}\tag{12}$$

The standard error of \hat{R} is estimated by

$$SE(\hat{R}) = [\hat{R}/N^{1/2}] [(s_y^2/\bar{y}^2) + (s_w^2/\bar{w}^2) - (2r_{yw}s_y s_w / \bar{y}\bar{w})]^{1/2}\tag{13}$$

where \bar{y} and s_y^2 are the mean and sample variance of $\{Y_1, Y_2, \dots, Y_N\}$, \bar{w} and s_w^2 are the mean and sample variance of $\{W_1, W_2, \dots, W_N\}$, and r_{yw} is the sample correlation coefficient of the pairs (Y_i, W_i) , $i=1, 2, \dots, N$.

In many applications, there is not a random sample on the pair (Y, W) but, rather Y and W are summary statistics computed from different sources of data. Given the pair (Y, W) with standard errors $SE(Y)$ and $SE(W)$, the ratio R is estimated by $\hat{R} = Y/W$ and its standard error is approximated by

$$SE(\hat{R}) = \hat{R} [(SE(Y))^2/Y^2 + (SE(W))^2/W^2].\tag{14}$$

This approximation is accurate when Y and W are uncorrelated. If Y and W are correlated and the correlation is estimated then an improvement can be made in the approximation (Reed et al. 1990).

Confidence intervals on the ratio can be approximated by use of the standard normal distribution to obtain, $\hat{R} \pm z_{\alpha/2}(se(\hat{R}))$, where $z_{\alpha/2}$ is the upper percentile of the standard normal curve with $100(\alpha/2)\%$ of the area in the upper tail. However, when comparing two selection indices with data from individual animals, this procedure can be improved by obtaining confidence intervals on the transformed statistic, $\hat{w} = \log(\hat{R})$, with standard error approximated

by $se(\hat{w}) = se(\hat{R})/\hat{R}$. An approximate confidence interval on $w = \log(R)$ is given by; $\hat{w} \pm z_{\alpha/2}(se(\hat{w}))$. The ratio \hat{R} will be declared significantly different from 1.0 (i.e., no significant selection for or against the corresponding category) if the confidence interval on w does not contain the number 0.0, because $\log(1.0) = 0.0$.

ANALYSIS PROCEDURES FOR A SINGLE CATEGORICAL VARIABLE: SAMPLING PROTOCOL

SP1 AND DESIGN I

Resource selection in wildlife science has commonly been evaluated by the study of a single categorical variable. For example, the selection of habitat might be studied as a function of the habitat type present at points in the study area. Such studies usually involve a single qualitative variable such as habitat type or a single quantitative but discrete valued variable. In other studies, the values of a quantitative variable may be grouped into intervals and analyzed as if the intervals were qualitative categories. Common analysis procedures recently reviewed by Alldredge and Ratti (1986) include: Chi-square goodness-of-fit tests (Neu et al. 1974, Byers et al. 1984), univariate nonparametric tests (Friedman 1937, Quade 1979), and a multivariate test based on rank order statistics (Johnson 1980). Thomas and Taylor (1990) review habitat and food selection papers published in the Journal of Wildlife Management during the period 1985-1988. A majority of the papers reviewed by Thomas and Taylor (1990) consider only a single categorical variable and analysis by the chi-square goodness-of-fit test. Thomas and Taylor comment that

many times the chi-square goodness-of-fit test is not an appropriate analysis procedure for the design used. In this section, we consider the analysis which arises when resource selection functions are applied to this most common study design.

Census of Available Resource Units

The most common sampling plan and analysis is a special case of Sampling Protocol SP1 where we have:

- (i) a simple random sample of used units,
- (ii) a census of available units (with respect to the single categorical variable),

and Design I where

- (iii) there is no unique identification of data collected from different animals.

The assumption of independence of used units in the sample of used units is very often violated and the chi-square goodness-of-fit test is not valid. Also, the test requires (ii), the census of available units. The percentage p_i of units in each category (availabilities) must be known constants, or be measured with very small errors (e.g., be measured from aerial photographs or maps), or be estimated from a very large sample of resource units.

Resource selection functions specialize to forage ratios (selection ratios, selection indices, or preference indices)

$$X_i = o_i/p_i \quad (15)$$

where o_i is percentage of occasions when the i th category is selected and p_i is the percent of the resource units belonging to the i th category. Under the assumption that the animals have unrestricted access to all categories of habitat, the i th selection

ratio is interpreted as the relative probability that the next item selected will be from the i th category.

Selection ratios are an old intuitive approach to analysis of a single categorical variable (e.g., Ivlev 1961, Manly 1972, or Hobbs and Bowden 1982) but generally have not been recognized as giving rise to relative probabilities of selection. The names have varied from selectivity indices (Manly 1972) to preference indices (Hobbs and Bowden 1982) but, the estimation formulas are equivalent. The fact that the selection ratios can be interpreted as relative probabilities of selection is a primary advantage over the more common analysis methods.

For an example, consider the selection ratios in Table 3 computed for a subset of data on selection of escape cover by quail (Stinnett and Klebenow 1986). Given unrestricted access to the entire distribution of habitat types, the shrubland habitat type was estimated to be selected with about twice the probability compared to riparian habitat, and field border was approximately 30 times more likely to be selected than was riparian.

Table 3. Relative probability of selection of escape cover by quail (Stinnett and Klebenow 1986). Selection ratios with the same letter the column labeled code are not significantly different when testing $H_0: X_i = X_j$ at the overall $\alpha=0.05$ level when using the Bonferroni procedure.

Escape cover	n_i	p_i	np_i	\hat{X}_i	Code	\hat{E}_i
Pasture	0	0.362	23.530	0.000 ¹	A	0.0
Disturbed	0	0.066	4.290	0.000	A	0.0
Farmstead	2	0.057	3.705	0.540	A	0.016
Riparian	19	0.249	16.185	1.174	A	0.034
Shrubland	36	0.262	17.030	2.114 ¹	B	0.061
Field border	8	0.004	0.260	30.769 ¹	C	0.889
Totals	65			35.597		1.0

¹Indicates $H_0: X_i=1$ is rejected at the 0.05 Level using the Bonferroni procedure.

Standardized Selection Ratios

A desirable method to present the results is to standardize the ratios so that the total is the number 1.0 (i.e., divide each by the sum of the original values)

$$B_i = X_i / (\sum_i X_i). \quad (16)$$

The value of B_i is interpretable as the probability that the next randomly observed selection will be from the i th category given unrestricted access to all categories. Thus, under the assumption that all habitats were available, the estimated probability of selection of field borders was 89% in Stinnett and Klebenow's study (Table 4).

Large Available, But Seldom Used Categories

Another important advantage of the selection ratios relative to the chi-square tests (Neu et al. 1974, Byers et al. 1984) is that the relative values of the ratios are not sensitive to decisions concerning which categories to include in the analysis. In the study of selection of escape cover by quail (Stinnett and Klebenow 1986) the researchers might have decided to drop pasture and disturbed habitat from the study because these types were never selected. This is a well known problem in use of the Neu et al. (1974) procedure for comparison of the observed counts n_i and the expected counts np_i because the relationship of n_i to np_i will change (e.g., Johnson 1980). Table 4 contains the resulting values of the statistics when pasture and disturbed habitat types are dropped. The selection ratios (B_i 's) do not change in this example

when pasture and disturbed habitat types are dropped. However, based on the relationship of n_i to np_i , the riparian habitat switches from being "preferred" to being "avoided" if the pasture and disturbed habitat types are discarded from the analysis.

Table 4. Relative probability of selection of escape cover by quail (Stinnett and Klebenow 1986) with the pasture and disturbed habitat types removed.

Escape cover	n_i	p_i	np_i	\hat{X}_i	\hat{B}_i
Farmstead	2	0.100	6.50	0.308	0.016
Riparian	19	0.435	28.08	0.677	0.034
Shrubland	36	0.458	29.77	1.209	0.061
Field border	8	0.007	0.455	17.582	0.889
Totals	65			19.766	1.0

Pearson's Chi-square Goodness-Of-Fit Test

The usual null hypothesis tested by the Pearson chi-square goodness-of-fit test is:

$$H_0: o_i = p_i \text{ for } i = 1, 2, \dots, k$$

(equivalent to $H_0: X_1 = \dots = X_k = 1.0$). This null hypothesis is that there is no selection for or against any of the categories, i.e., that selection is "random" and in proportion to availability given unrestricted access to all categories and independent observations. We recommend that hypotheses concerning the ratios be tested by first using Pearson's chi-square test of H_0 . If the hypothesis is rejected then it should be followed by tests of the components of the chi-square statistic (Rayner 1990).

For an example, consider Table 3 which contains a subset of data on quail habitat at use (Stinnett and Klebenow 1986). Pearson's chi-square statistic with $k-1 = 5$ degrees of freedom for this example is:

$$\chi^2 = \sum_i (o_i - np_i)^2 / np_i = 280.6.$$

This value is large compared to the upper tail percentage values of

the chi-square distribution with 5 degrees of freedom which indicates that there is significant departure from the null hypothesis that selection is "random", i.e., the selection ratios are not all equal to 1.0.

Assume that interest is in testing a single, preselected null hypothesis

$$H_{01}: X_i = 1.0$$

(i.e., that there is no selection for or against items in the i th category). The chi-square test statistic with one degree of freedom is:

$$\chi^2_{(1)} = (\hat{X}_i - 1)^2 (np_i / (1 - p_i)) \quad (17)$$

where $X_i = n_i / np_i$, n_i is the number of occasions a unit from the i th category is observed to be selected, and n is the number of independent occasions of selection which are observed. The null hypothesis would be rejected with a size α test if $\chi^2_{(1)} \geq \chi^2_{\alpha}$ ($\chi^2_{\alpha} = 3.84$ for $\alpha = 0.05$ and one degree of freedom).

Confidence Intervals On Selection Ratios

The standard error of \hat{X}_i is given by:

$$se(\hat{X}_i) = ((1 - p_i) / np_i)^{1/2}. \quad (18)$$

The standard error can be used to obtain the end points of an approximate $(1 - \alpha)100\%$ confidence interval on a single, preselected selection ratio X_i by the formulas

$$\hat{X}_i \pm Z_{\alpha/2} se(\hat{X}_i), \quad (19)$$

where $Z_{\alpha/2}$ is the upper standard normal table value corresponding to a probability tail area of $\alpha/2$. The selection coefficient X_i is declared significantly different from 1.0 if the confidence interval on X_i does not contain the number 1.0. This confidence interval is only approximate and if the lower limit from formula

(19) is negative, it should be replaced by the number 0.0.

However, the researcher is usually interested in the entire set of k selection ratios, X_i , $i = 1, 2, \dots, k$. When this is the case, approximate simultaneous confidence intervals or tests can be constructed by use of Bonferroni's inequality (e.g., Byers et al. 1984). One can be $(1-\alpha)100\%$ confident that the entire set of intervals contain their respective true ratios if $Z_{\alpha/2}$ is replaced in equation (19) by $Z_{\alpha/2k}$, the upper standard normal table value corresponding to a probability tail area of $\alpha/2k$. Similarly, the critical value for the chi-square statistic in equation (17) is obtained using the upper percentage value corresponding to a probability tail area of α/k . In Stinnett and Klebenow's study of escape cover selected by quail, there are $k = 6$ habitat types. For $\alpha = 0.05$, we have $\alpha/6 = 0.008$ and the critical value for the chi-square statistic is approximately $\chi^2_{0.008} = 7$. For example, the selection ratio for shrubland as escape cover is $\hat{X}_5 = 2.114$. The chi-square statistic for testing $H_0: X_5 = 1.0$ is $\chi^2_{(1)} = (2.114 - 1.0)^2 / 17.03 / (1 - 0.262) = 28.6$ which is significant using the Bonferroni procedure. This indicates that shrubland habitat is "preferred" as escape cover relative to availability. Three of the habitats have selection ratios which are declared significantly different from 1.0 using this simultaneous inference procedure with $\alpha = 0.05$ (Table 3). There is significant selection against pasture and selection for shrubland and field border as escape cover by quail in Stinnett and Klebenow's study.

Comparison Of Selection Ratios

For testing the single, preselected null hypothesis of no difference in the probabilities of selection of the i th and the j th categories, i.e.,

$$H_{02}: X_i = X_j$$

($i=1, 2, \dots, k$, and $j=1, 2, \dots, k$) the chi-square test statistic with one degree of freedom is:

$$\chi^2_{(1)} = (\hat{X}_i - \hat{X}_j)^2 (np_i p_j / (p_i + p_j)). \quad (20)$$

The standard error of $(\hat{X}_i - \hat{X}_j)$ is given by

$$se(\hat{X}_i - \hat{X}_j) = ((p_i + p_j) / np_i p_j)^{1/2} \quad (21)$$

and can be used to obtain the end points of a single, preselected approximate $(1-\alpha)100\%$ confidence interval on the difference $(\hat{X}_i - \hat{X}_j)$ by the formula

$$(\hat{X}_i - \hat{X}_j) \pm Z_{\alpha/2} se(\hat{X}_i - \hat{X}_j). \quad (22)$$

Again using Bonferroni's inequality, a procedure very similar to that used to compare means in analysis of variance can be suggested for comparing the selection ratios. Rank the selection ratios from the smallest to the largest and compare them two-at-a-time by use of the confidence intervals in equation (22) replacing $Z_{\alpha/2}$ by $Z_{\alpha/2k'}$ where k' is the total number of comparisons being made ($k' =$ number of combinations of k categories choosing two-at-a-time). The selection ratios X_i and X_j are declared significantly different if the confidence interval on $(X_i - X_j)$ does not contain 0.0.

The results of these tests are reported in Table 3 for the Stinnett and Klebenow (1986) study of selection of escape cover by quail. The column labeled "CODE" indicates the significant differences between habitats. Habitats with the same letter are judged not to be significantly different at the overall significance level of α

= 0.05 using the Bonferroni procedure. Given that the birds had unrestricted access to all escape covers, we can conclude that:

- (i) the probability of selection of shrubland or field border is significantly larger than probability of selection for one of the other habitat types,
- (ii) the probability of selection of field border is significantly larger than the probability of selection of shrubland, and
- (iii) there is no significant difference between probabilities of selection of the other habitats.

Standardized Analyses

An alternative analysis for the comparison of X_i and X_j would be to estimate the ratio $R_{ij} = X_i/X_j$ by $\hat{R}_{ij} = \hat{X}_i/\hat{X}_j = \hat{B}_i/\hat{B}_j$. The standard error of the ratio \hat{R}_{ij} can be approximated by use of equation (14) to obtain

$$se(\hat{R}_{ij}) = \hat{R}_{ij} [((1-p_i)(np_i)/n^2_i) + ((1-p_j)(np_j)/n^2_j)]. \quad (23)$$

The ratio $\hat{R}_{ij} = \hat{X}_i/\hat{X}_j$ gives the estimated relative value of the probabilities of selection of the two habitat types. Simultaneous inferences toward the ratios can be obtained by construction of approximate confidence intervals on R_{ij} using the standard error formula (23). Reject the hypothesis that $X_i = X_j$ if the confidence interval on R_{ij} does not contain the value 1.0.

Sample Of Available Units

In the more general situation for Design I and Sampling Protocol SP1, the proportions p_i are estimated from a sample of available units. For example, Marcum and Loftsgaarden (1980) consider estimation of the proportions p_i by placement of random points on

a map. In this case, the two-way chi-square test of homogeneity is applicable for testing hypotheses concerning equality of the percentages available and percentages used in the various categories. Marcum and Loftsgaarden (1980) assume that the proportion p_i of habitat type i in a study area is estimated by locating m random points on a map of the study area and counting the number of points m_i which "hit" habitat type i . The proportion p_i is estimated by $\hat{p}_i = m_i/m$, with estimated variance $\hat{p}_i(1-\hat{p}_i)/m$. The selection ratios are estimated by

$$\hat{X}_i = \hat{o}_i/\hat{p}_i \quad (24)$$

where $\hat{o}_i = n_i/n$ is defined as in the above section. The standard error of the estimated selection ratio \hat{X}_i can be approximated from the general formula (14) to obtain

$$se(\hat{X}_i) = (\hat{X}_i) [((1-\hat{o}_i)/n\hat{o}_i) + ((1-\hat{p}_i)/m\hat{p}_i)]^{1/2}. \quad (25)$$

Approximate simultaneous confidence intervals on the selection ratios can be constructed following the general procedures outlined above. Again, the selection coefficient X_i is declared significantly different from 1.0 if the confidence interval on X_i does not contain the number 1.0.

Sampling protocols which do not use random points as the basic sampling unit will require different formula for estimation of the standard errors of \hat{X}_i . For example, quadrats, or line transects might be used for estimation of availabilities p_i . Discussion of all possible cases is beyond the scope of the present paper.

ANALYSIS PROCEDURES FOR A SINGLE CATEGORICAL VARIABLE: SAMPLING PROTOCOL SP1 AND DESIGNS I AND II

In Designs II and III, data are available on selection of resource units by individual animals. For example, in Design II or III, the use of resource categories might be estimated in the home ranges of individual animals. In Design III, the availability of resource categories might also be estimated in individual home ranges. In both designs, selection ratios can be replicated over the random sample of animals.

As discussed earlier in this paper, there are three sampling plans operating simultaneously:

- (i) it is implicitly implied that a random sample of size N is obtained from the population of animals,
- (ii) the universe of available units may be censused or sampled to estimate the proportions p_i of units in each category, and
- (iii) the units used by the j th animal are sampled to obtain the proportions o_{ij} of selections of the i th resource category by the j th animal.

We prefer to consider the animal as the primary sampling unit, and to base the statistical inferences on variation of the selection ratios from animal to animal. Sampling in (iii) can be viewed as "subsampling" or measurement on the primary sampling unit, the animal. Sampling in (ii) to estimate the proportions p_i introduces sampling variance in the denominators of the selection ratios. Estimation of standard errors follows the general formulas (13)-(14).

Census Of Available Units

We first consider the case when a census of available units is available and consequently, the proportions p_i are known for the entire study area. For an example, Arnett et al. (1989) studied the selection of habitat types given a sample of $N = 6$ uniquely radio-tagged bighorn sheep (Ovis canadensis) in the Encampment River drainage of southeast Wyoming. The proportions p_i of $k = 10$ habitat types available in the study area were measured from maps. A subset of their data covering the period August through December 1988 is reported in Table 5. Each animal was

Table 5. Habitat type, proportion of study area in each type (p_i), and number of occasions a given bighorn sheep (Ovis canadensis) was observed in each habitat type (n_i). Data are from Arnett et al. (1989).

Habitat type	p_i	Bighorn sheep number						Total
		1	2	3	4	5	6	
Riparian	0.060	0	0	0	0	0	0	0
Conifer	0.130	0	2	1	1	0	2	6
Mt. shrub I ^a	0.160	0	1	2	3	2	1	9
Aspen	0.150	2	2	1	7	2	4	18
Rock-out-crop	0.060	0	2	0	5	5	2	14
Sage/bitterbrush ^b	0.170	16	5	14	3	18	7	63
Windblown ridges	0.120	5	10	9	6	10	6	46
Mt. shrub II ^c	0.040	14	10	8	9	6	15	62
Prescribed Burns	0.090	28	35	40	31	25	19	178
Clear cut	0.020	8	9	4	9	0	19	49
Total	1.000	73	76	79	74	68	75	445

^a(Cercocarpus/Amalanchier)

^bBig sagebrush/bitterbrush/grass

^c(Ceanothus/Prunus)

Each animal was "subsampled" during this time to obtain a sample of habitat points used. Let n_{ij} denote the number of independent observations of use of the i th habitat type by the j th animal, $i = 1, 2, \dots, 10$ and $j = 1, 2, \dots, 6$.

The selection ratio of the j th animal for the i th habitat type would be estimated by $\hat{X}_{ij} = n_{ij}/(p_i n_{.j})$, where $n_{.j} = \sum_i (n_{ij})$ is the

total number of observation on the jth animal. Given a random sample of N animals, the recommended estimator for the population selection ratio for the ith habitat is the "ratio of means" rather than the "mean of ratios", i.e.,

$$\begin{aligned}\hat{X}_i &= (n_{i.}/N) / (p_i n_{..}/N) \\ &= \Sigma_j (n_{ij}) / \Sigma_j (p_i n_{.j}) \\ &= (\Sigma_j Y_j) / (\Sigma_j W_j)\end{aligned}\quad (26)$$

where $n_{i.} = \Sigma_j n_{ij}$ is the total of observations of use of the ith habitat, $n_{..} = \Sigma_i \Sigma_j n_{ij}$ is the total of observations in all habitats, $Y_j = n_{ij}$, and $W_j = p_i n_{.j}$. Table 6 contains these estimated relative probabilities of selection for the 10 habitat types available to the population of bighorn sheep (Ovis canadensis) in the example. Conditional on known values for p_i , the standard error of \hat{X}_i is estimated by a special case of equation (13) where $Y_j = n_{ij}$ and $W_j = p_i n_{.j}$. Alternatively, one can use the equivalent equation:

$$\begin{aligned}se(\hat{X}_i) &= [(N/(N-1))^{1/2} / (p_i n_{..})] [\Sigma_j (n_{ij}^2) - 2\hat{X}_i p_i \Sigma_j (n_{.j} n_{ij}) + \\ &\quad \hat{X}_i^2 p_i^2 \Sigma_j (n_{.j}^2)]^{1/2}.\end{aligned}\quad (27)$$

Table 6. Relative probability of selection for the ith habitat with the lower limits (LL) and upper limits (UL) of simultaneous 90% confidence intervals on X_i computed by the Bonferroni inequality with $z_{(0.1)/2(10)} = 2.576$. Selection ratios with the same letter in the column headed "Code" are not significantly different when testing $H_0: X_i = X_j$ at the $\alpha = 0.10$ level using the Bonferroni method.

Habitat type UL	$n_{i.}$	$p_i n_{..}$	\hat{X}_i	Code	$se(\hat{X}_i)$	LL
Riparian 0.000	0.000	26.700	0.000 ¹	*	0.000	0.000
Conifer 0.198	6.000	57.850	0.104 ¹	A	0.037	0.009
Mt. shrub I ^a 0.220	9.000	71.200	0.126 ¹	A	0.036	0.033
Aspen 0.479	18.000	66.750	0.270 ¹	AB	0.081	0.061
Rock-out-crop 1.074	14.000	26.700	0.524	AB	0.213	0.000 ^d
Sage/bitterbrush ^b	63.000	75.650	0.833	B	0.211	0.289

1.376						
Windblown ridges	46.000	53.400	0.861	B	0.105	0.590
1.133						
Mt. shrub II ^c	62.000	17.800	3.483 ¹	C	0.471	2.270
4.696						
Prescribed Burns	178.000	40.050	4.444 ¹	C	0.407	3.397
5.492						
Clearcut	49.000	8.900	5.506 ¹	ABC	1.717	1.082
9.929						

Total	445.000	16.152
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^a(Cercocarpus/Amalanchier)

^bBig sagebrush/bitterbrush/grass

^c(Ceanothus/Prunus)

¹Intervals which do not contain 1.0 indicate that the corresponding habitat is not selected in proportion to availability.

If the numbers of observations on the animals are equal, (i.e., $n_{.1} = n_{.2} = \dots = n_{.N}$) then the standard error can be computed by the simple equation $se(\hat{X}_i) = (N)^{1/2} s_i / p_i n_{.}$, where s_i is the standard deviation of the set $\{n_{i1}, n_{i2}, \dots, n_{iN}\}$ of numbers of independent observations of use of the i th habitat by the N animals. The estimates of the selection ratios are computed by pooling observations across all animals in the sample. However, the procedure for estimation of the standard errors in equation (27) clearly takes variation in resource selection from animal to animal into account.

Simultaneous inferences toward the individual selection ratios in the hypotheses

$$H_0: X_i = 1.0, i = 1, 2, \dots, k$$

can be made by construction of the end points of Bonferroni confidence intervals,

$\hat{X}_i \pm z_{(\alpha/2k)} [se(\hat{X}_i)]$, where $z_{(N-1, \alpha/2k)}$ is the upper z -table value corresponding to a probability tail area of $\alpha/2k$, and k is the number of habitat types. Confidence intervals computed by this

procedure for the data from Arnett et al. (1989) are presented in Table 6. With $\alpha = 0.10$ for 90% confidence on 10 intervals the z-value is $z_{(0.005)} = 2.576$. Applying equation (13) or (27) the standard error of $\hat{X}_0 = 4.444$ is $se(\hat{X}_0) = 0.407$. The end points on the confidence interval for the selection ratio for prescribed burns X_0 are given by $4.444 \pm 2.576(0.407)$. The lower limit is $LL = 3.397$ and the upper limit is $UP = 5.492$ (Table 6). The number 1.0 is not in this interval which indicates that there is significant selection for prescribed burn habitat above what would be expected by chance. Also, mt. shrub II (Ceanothus/Prunus), and clearcut habitats have relative probabilities of selection which are above that expected under the hypotheses of "no selection". Similarly, there is significant selection against riparian, conifer, mt. shrub I (Cercocarpus/Amalanchier), and aspen habitat relative to the amount of habitat available. There is no apparent selection for or against the habitat types: rock-out-crop, sage/bitterbrush, and windblown ridges.

A simultaneous analysis of selection ratios can be made in much the same manner as means are compared in analysis of variance procedures. The ratios are ranked from the smallest to the largest in Table 6. Any two preselected categories i and j can be compared by computation of approximate end points of confidence intervals on the ratios

$$R_{ij} = X_i/X_j = B_i/B_j. \quad (28)$$

The ratio R_{ij} is preferred as the statistic for comparison of selection between resource categories i and j because it is not sensitive to decisions concerning which categories to include in

the universe of available units. For example, in Table 6 the riparian habitat type is certainly present in the study area and sheep do move through the riparian zones. However, none were observed in the riparian category during data collection. Also, based on knowledge of the behavior of bighorn sheep (Ovis canadensis) one might argue that riparian habitat is not "available" during the hours of the day while observations of use were being made. If this relatively large but seldom used category of habitat is dropped, estimates of the ratios R_{ij} do not change much.

The standard error of the estimated ratio \hat{R}_{ij} is approximated by noting that it involves the ratio of means

$$\begin{aligned}\hat{R}_{ij} &= \hat{X}_i / \hat{X}_j = \hat{B}_i / \hat{B}_j = \\ &= (p_j / p_i) (\bar{n}_i / \bar{n}_j)\end{aligned}\quad (29)$$

where \bar{n}_i and \bar{n}_j denote the mean number of observations of use of the i th and j th categories respectively.

For example, consider the comparison of the probability of selection of clear cuts ($\hat{B}_{10} = 0.341$) and the probability of selection of prescribed burns ($\hat{B}_9 = 0.275$). The null hypothesis is that the true ratio $R_{10,9} = 1.0$, i.e., that there is no difference in the relative probabilities of selection of the two habitat types. Note that the ratio of the selection probabilities is $\hat{R}_{10,9} = \hat{X}_{10} / \hat{X}_9 = \hat{B}_{10} / \hat{B}_9 = 1.239$ (Table 7). Also,

$$\begin{aligned}\hat{R}_{10,9} &= (p_9 / p_{10}) (\bar{n}_{10} / \bar{n}_9) = (0.09 / 0.02) (8.167 / 29.667) \\ &= 1.239 \text{ where } \bar{n}_{10} = 8.167 \text{ is the mean of the set } \{8, 9, 4, 9, 0, 19\} \text{ of}\end{aligned}$$

observations on the clear cut habitat ($s^2_{10} = 40.567$) and $n_9 = 29.667$ is the mean of the set $\{28, 35, 40, 31, 25, 19\}$ of observations on the prescribed burn habitat ($s^2_9 = 55.067$). The correlation of the two sets of observations is $r_{9,10} = -0.485$. The standard error of the ratio $\hat{R}_{10,9} = 1.239$ is approximated using the general equation (13) because it is the ratio of two sample means. The standard error of $\hat{R}_{10,9}$ is estimated by (Table 7)

$$\begin{aligned} \text{se}(\hat{R}_{10,9}) &= (1.239/6^{1/2}) [(40.567/8.167^2) + (55.067/29.667^2) \\ &\quad - 2(-0.485)(40.567^{1/2}55.067^{1/2}) / ((8.167)(29.667))]^{1/2} \\ &= 0.469. \end{aligned}$$

In this case, it is recommended that one transform to

$$\begin{aligned} w_{10,9} &= \log(\hat{R}_{10,9}) \\ &= 0.214 \end{aligned}$$

and compute

$$\begin{aligned} \text{se}(w_{10,9}) &= \text{se}(\hat{R}_{10,9}) / (\hat{R}_{10,9}) \\ &= 0.469/1.239 \\ &= 0.379. \end{aligned}$$

The distribution of the ratio transformed to logarithms is more symmetric than the distribution of the original ratio, thus yielding confidence intervals which are more robust. In computer simulations, this transformation performs well in comparing two selection indices when there are data on the individual animals. The approximate 95% confidence interval for the comparison of selection for these two habitat types is given by

$$0.214 \pm (1.96)(0.379)$$

or $[-0.165, .957]$

Because 0.0 is in the interval, one would conclude at the 95% confidence level for this single comparison that there is no significant difference in selection for burned areas vs clear cuts. End points of simultaneous confidence intervals on

$$w_{ij} = \log(\hat{R}_{ij}) \tag{30}$$

are approximated by

$$\hat{w}_{ij} \pm (z_{\alpha/2k'}) \text{se}(\hat{w}_{ij}) \quad (31)$$

where $(z_{\alpha/2k'})$ is defined earlier in this paper, $k' =$ the number of comparisons being conducted (combinations of k categories selecting two-at-a-time). The 90% family of confidence

confidence intervals for comparison of the relative probabilities of selection are given in Table 7. For example, the end points for an interval on

$w_{ij} = \log(\hat{R}_{ij})$ for comparing the relative probability of selection of clear cut versus probability of selection of prescribed burn are

$$0.214 \pm (3.09)(0.379)$$

or $[-0.957, 1.385]$

where $z_{\alpha/2k'} = z_{0.001} = 3.09$ because $k' = 36$ comparisons are possible between the top 9 habitat types. The number 0.0 is contained in this interval which indicates that there is no significant difference in the relative probability of selection of the prescribed burns compared to clear cuts using the conservative Bonferroni simultaneous inference procedure. Riparian habitat type is dropped from the family of simultaneous intervals because it was never selected, variances are zero and it is "significantly" below all of the other habitats in probability of selection.

Table 7. Illustration of the log transformed ratios of the relative probabilities of selection for 8 of the 36 possible comparisons in Table 5. The results of all 36 comparisons are given in the column "Code" of Table 6.

Habitat type i UL	Habitat type j	\hat{R}_{ij}	$w_{ij} = \log(\hat{R}_{ij})$	$\text{se}(w_{ij})$	LL
Conifer 1.243 1.630	Mt. shrub I	1.219	0.193	0.465	-
Mt. shrub I 0.123 1.639	Aspen	2.133	0.758	0.285	-
Aspen 0.318 1.648	Rock out crop	1.944	0.665	0.318	-
Rock out crop 1.126 2.050	Sage/bitter-brush	1.588	0.462	0.514	-

Sage/bitter-brush	Windblown ridges	1.034	0.033	0.251	-
0.744	0.810				
Windblown ridges	Mt. shrub II	4.043	1.397	0.241	
0.652	2.142				
Mt. shrub II	Prescribed Burns	1.276	0.244	0.208	-
0.399	0.887				
Prescribed Burns	Clear cut	1.239	0.214	0.379	-
0.956	1.384				

The habitat types are ranked in Table 6 from the smallest probability of selection to the largest probability. Comparing each of the habitat types with the next one below it, 8 of the 36 possible comparisons (confidence intervals) are presented in Table 7. One of the intervals does not contain the number 0.0, namely the one corresponding to the comparison of probability of selection for windblown ridges and probability of selection for Mt. shrub II (Ceanothus/Prunus). The results of all comparisons are indicated in Table 6 under the heading "Code". Selection ratios with the same letter are not significantly different using the Bonferroni procedure ($\alpha = 0.10$). The two habitat types: mt. shrub II, and prescribed burns are selected with significantly higher probability than are lower ranking habitat types. Use of clear cuts has high variance and even though clear cuts have the largest estimated probability of selection it is not significantly larger than the probability of selection for the lower ranking habitat types.

Estimated Availabilities: Design II

If the proportion p_i of the i th resource category available is estimated for the entire study area (Design II) or if the proportion p_{ij} of the i th category available to the j th animal is estimated (Designs III) then an additional source (or sources) of

variation is introduced to the estimates. In Design II, the probability of selection of the i th habitat by the j th animal is estimated by

$$\begin{aligned}\hat{X}_{ij} &= n_{ij} / (\hat{p}_i n_{.j}) \\ &= (1/\hat{p}_i) (n_{ij}/n_{.j})\end{aligned}\quad (32)$$

where n_{ij} is the number of independent observations of animal j in habitat i , $n_{.j} = \sum_i n_{ij}$ is the total number of observations of animal j , and \hat{p}_i is the estimated proportion of resource category i available in the study area. For example, in Table 4 the selection ratio for prescribed burns by sheep number 1 is

$$\hat{X}_{91} = 28 / (0.09)(73) = 4.26.$$

In some studies, the proportion $p_9 = 0.09$ might be based on a sampling procedure, e.g., measurement of the habitat type present at a sample of random points in the area. All three terms in \hat{X}_{91} are random variables if this is the case.

For Design II, the recommended estimators for the selection ratios are:

$$\begin{aligned}\hat{X}_i &= (\sum_j n_{ij} / \sum_j n_{.j}) / \hat{p}_i \\ &= \hat{V}_i / \hat{p}_i,\end{aligned}\quad (33)$$

for the i th habitat type. There are two ratios of random variables in \hat{X}_i . First, the variance of the ratio $\hat{V}_i = (\sum_j n_{ij} / \sum_j n_{.j})$ can be estimated by noting that $\hat{V}_i = \bar{Y} / \bar{W}$ where $Y_j = n_{ij}$ and $W_j = n_{.j}$ and using equation (13). The correlation of n_{ij} and $n_{.j}$ is taken into account by equation (13). Given that \hat{p}_i is estimated from an independent source of data with standard error $se(\hat{p}_i)$, then equation (14) can be used to estimate the variance of the final ratio $\hat{X}_i = \hat{V}_i / \hat{p}_i$. Simultaneous inferences toward a set of selection

ratios can proceed as in previous sections.

In Design III, assume that the estimates of p_{ij} are independent among animals (i.e., an independent sample is taken for the j th animal to estimate the proportion of habitat type i available to that unique individual). Combining data for all N animals in the sample, the estimator for the selection ratio of the i th habitat is given by:

$$\hat{X}_i = (\sum_j n_{ij}) / (\sum_j [\hat{p}_{ij} n_{.j}]), \quad (34)$$

for $i = 1, 2, \dots, k$. To estimate the variance of \hat{X}_i for this design, associate $Y_j = n_{ij}$ and $W_j = (\hat{p}_{ij} n_{.j})$ then compute $\hat{X}_i = \bar{y}/\bar{w}$ and its standard error by equation (13).

Simultaneous inferences toward a set of selection ratios can proceed as in previous sections.

Comparison Of Selection Ratios: Design II

To compare X_i with X_j in Design II, one would compute the ratio

$$\hat{R}_{ij} = \hat{X}_i / \hat{X}_j$$

and its approximate standard error, then transform to $w_{ij} = \log(\hat{R}_{ij})$, $se(w_{ij}) = se(\hat{R}_{ij}) / \hat{R}_{ij}$, and proceed as before. For any two habitat types, say {1 and 2}, the ratio \hat{R}_{12} can be written in the form

$$\begin{aligned} \hat{R}_{12} &= (\hat{p}_2 / \hat{p}_1) (\sum_j n_{1j} / \sum_j n_{2j}) \\ &= (\hat{V}_1) (\hat{V}_2) \end{aligned} \quad (35)$$

The standard error of the first term, $\hat{V}_1 = (\hat{p}_2 / \hat{p}_1)$, can be approximated by the general formula

$$\begin{aligned} se(\hat{V}_1) &= \hat{V}_1 [((se(\hat{p}_1))^2 / \hat{p}_1^2) + ((se(\hat{p}_2))^2 / \hat{p}_2^2) - \\ &\quad 2cov(\hat{p}_1, \hat{p}_2) / (\hat{p}_1 \hat{p}_2)]^{1/2}. \end{aligned} \quad (36)$$

where $\text{cov}(\hat{p}_1, \hat{p}_2)$ denotes the covariance of the estimates \hat{p}_1 and \hat{p}_2 . Probably the most common procedure for estimation of the p_i 's is by location of say M random points in the study area (or on a map of the study area) and recording the habitat type encountered by each point. The proportion of points encountering habitat type i , \hat{p}_i , is then taken as the estimate of p_i . The sampling distribution of the \hat{p}_i 's follows a multinomial distribution and the following formulas are applicable:

$$\text{se}(\hat{p}_i) = [\hat{p}_i(1-\hat{p}_i)/M]^{1/2}, \text{ and}$$

$$\text{cov}(\hat{p}_i, \hat{p}_j) = -[\hat{p}_i\hat{p}_j/M].$$

If the availabilities, p_i , are estimated by other procedures such as quadrat or line intercept sampling then the appropriate formulas for $\text{se}(\hat{p}_i)$ and $\text{cov}(\hat{p}_i, \hat{p}_j)$ should be used.

The standard error of the second term, $\hat{v}_2 = (\sum_j n_{ij} / \sum_j n_{2j})$, can be computed by equation (13) or more directly by

$$\text{se}(\hat{v}_2) = [(N/(N-1))^{1/2} / (\sum_j n_{2j})] [\sum_j (n_{1j}^2) - 2\hat{v}_2 \sum_j (n_{1j}n_{2j}) + \hat{v}_2^2 \sum_j (n_{2j}^2)]^{1/2}. \quad (37)$$

Under the assumption that \hat{v}_1 and \hat{v}_2 are estimated from independent sources of data, the standard error of the product, $\hat{x}_{12} = \hat{v}_1\hat{v}_2$, can be estimated by the formula (Reed et al. 1990)

$$\text{se}(X_{12}) = [\hat{v}_1^2(\text{se}(\hat{v}_2))^2 + \hat{v}_2^2(\text{se}(\hat{v}_1))^2 - (\text{se}(\hat{v}_1))^2(\text{se}(\hat{v}_2))^2]^{1/2}. \quad (38)$$

Comparison Of Selection Ratios: Design III

To compare X_i with X_j one would compute the ratio, $\hat{R}_{ij} = \hat{X}_i / \hat{X}_j$, and its approximate standard error, then transform to $w_{ij} = \log(\hat{R}_{ij})$, $\text{se}(w) = \text{se}(\hat{R}_{ij}) / \hat{R}_{ij}$, and proceed as in section 6.1. For any two habitat types, say {1 and 2}, $\hat{R}_{12} = \hat{X}_1 / \hat{X}_2$ is the "ratio of ratios",

where

$$\hat{X}_1 = (\sum_j Y_{1j}) / (\sum_j W_{1j}),$$

$$\hat{X}_2 = (\sum_j Y_{2j}) / (\sum_j W_{2j}).$$

Equation (13) can now be used to estimate the standard errors of \hat{X}_i , for $i = 1, 2$, where we identify $Y_{ij} = n_{ij}$, and $W_{ij} = \hat{p}_{ij}n_{.j}$. There are four random variables in the statistic \hat{R}_{12} and estimation of $se(\hat{R}_{12})$ requires the covariance term (Cochran 1963, p. 182)

$$\begin{aligned} cov(\hat{X}_1, \hat{X}_2) = & [(N/\{N-1\}) / (\{\sum_j W_{1j}\} \{\sum_j W_{2j}\})] [(\sum_j Y_{1j} Y_{2j}) - \\ & X_1(\sum_j Y_{2j} W_{1j}) - \hat{X}_2(\sum_j Y_{1j} W_{2j}) + \hat{X}_1 \hat{X}_2 (\sum_j W_{1j} W_{2j})] \end{aligned} \quad (39)$$

Finally, incorporation of $cov(\hat{X}_1, \hat{X}_2)$ from equation (39) into the generic formula (13) for the standard error of the ratio of \hat{X}_1/\hat{X}_2 yields the estimated standard error of \hat{R}_{12} ,

$$\begin{aligned} se(\hat{R}_{12}) = & \hat{R}_{12} [(se(\hat{X}_1))^2 / \hat{X}_1^2 + (se(\hat{X}_2))^2 / \hat{X}_2^2 - \\ & 2(cov(\hat{X}_1, \hat{X}_2)) / (\hat{X}_1 \hat{X}_2)]^{1/2}. \end{aligned} \quad (40)$$

Estimation of $se(\hat{R}_{12})$ by equation (40) requires the assumption that the estimates \hat{p}_{1j} and \hat{p}_{2j} are computed from independent data for the N animals. Violation of this assumption will usually yield a biased underestimate of the standard errors.

DISCUSSION AND ASSUMPTIONS

1. The distributions of the measured x variables (proportion p_i of category i available for a single categorical variable) do not change during the sampling period. For example, this assumption might be violated if caribou eat most of the "preferred" food during the first two weeks of a four week study. This requirement is difficult to satisfy with many studies. If it is not fully satisfied then inferences are made with respect to the "average"

available, used and unused distributions during the sampling period. Generally, the period of sampling should be held at the minimum necessary to achieve desired sample sizes. In rapidly changing populations, the researcher should attempt to obtain several snapshots of the populations and hence snapshots of the selection function over time.

2. Resource units are sampled randomly and independently. This requirement might be violated if tagged animals are in the same herd or if detectability of animals varies with habitat type. Estimates of the coefficients of a selection function may still be meaningful if this assumption is not satisfied, but standard errors may not reflect the true variation in the populations. For the sake of illustration, our example analyses were made on the assumption of random independent samples of resource units. It will be difficult to insure this especially in cases when animals occur in herds or when resource units are collected in batches. For example, consider collection of stomach samples of caribou in a food selection study. In this case the food items are obtained in batches and the selections of individual food items may not have been independent events because of different food "preferences" for different animals. Another common but difficult situation is in analysis of relocations of radio-tagged animals. Relocations come in a batch recorded at a series of points in time. Care must then be taken to ensure that the time interval between recordings is sufficient to assume that observations of used habitat points are independent events. In the presence of these problems, one approach is to estimate a separate resource selection function for

several independent replications of batches of dependent units. Thus, one might estimate the selection function for each of several randomly selected areas in a large calving grounds for caribou. Inference toward mean values of coefficients of the selection function over the entire study area can then proceed by standard statistical procedures, using the replicates to determine standard errors. Alternatively, one might consider the selection of individual animals as independent events, and estimate a separate selection function for each animal by randomly sampling the units available and the units used by each animal (Designs II and III). This may be the only reasonable approach for study of food and habitat use by highly territorial animals. Discussion of all situations is beyond the scope of the present paper; however, the reader should be aware of the difficulties in making proper statistical inferences when individual resource units cannot be independently collected.

3. In Design III experiments, estimates of p_{ij} may not be truly independent among animals. For example, a sample survey of habitat available in the overall study area may be conducted. Then the observations falling into an individual animal's home range might be used to estimate habitat available to specific animals. If there is considerable overlap of home ranges, then some data points will influence the estimate of habitat availabilities for several different animals. At this time, the procedures presented above are recommended for estimation of variances of \hat{X}_i , $i = 1, 2, \dots, k$; but, it is noted that the true sampling variance of \hat{X}_i is probably underestimated.

When possible, it is recommended that estimates of p_{ij} be estimated independently for each animal in Design III so that the estimates of sampling variance are approximately unbiased.

4. The universe of resource units available to the animals and the universe of used resource units have been correctly identified and sampled. For example, this requirement may be violated if caribou are eating food items which are not detectable in fecal samples. This is probably the most crucial and most difficult assumption of the study design. Specific problems must be addressed separately and a general discussion does not seem to be possible at this time.

5. The x variables which actually influence probability of selection have been correctly identified, measured and modelled. For example, this assumption is violated if percent cover by willows is measured, but caribou are actually selecting plots on the bases of height of willows. Hopefully, variables under study will be highly correlated with those which actually influence probability of selection. Also, all of the problems associated with regular regression analysis are present in the process of selection of a best set of variables for the logistic regression model. It is particularly difficult to model nonlinear effects and interactions.

6. Animals have free and equal access to the entire distribution of available resource units. If animals are territorial then a few aggressive individuals may control all of the "preferred" habitat to violate this assumption. The assumption is most easily justified when the subpopulation of used units is small relative to the population of available units. Also, changes in the density of

animals or in the availability of resource units may change the underlying selection strategies and the selection function. Thus, statistical inferences are made with respect to the specific conditions present in the study area over the time period of interest.

ACKNOWLEDGEMENTS

Computer graphics in Fig. 1 were conducted by Mr. Brent J. Esmoil, Wyoming Cooperative Wildlife Research Unit, University of Wyoming. His expert contribution is appreciated. We thank Edward B. Arnett and Thomas J. Ryder for providing us with 'original data for two of our examples. Dr. Lyman L. McDonald was partially supported in this work by the Alaska Wildlife Research Center, U.S. Fish and Wildlife Service, Anchorage, Alaska, and the Arctic National Wildlife Refuge, Fairbanks, Alaska.

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4th NORTH AMERICAN CARIBOU WORKSHOP
ST. JOHN'S, NEWFOUNDLAND
OCTOBER 31 - NOVEMBER 3, 1989

PROCEEDINGS

Edited by: Charlie Butler and Shane P. Mahoney

Technical Editors: John Blake, Margo Hoban and Brian Tucker

Artist: Frank LaPointe

Newfoundland and Labrador Wildlife Division

February 1991

Citation example:

Eastland, W.G. 1991. Correlations of weather and autumn caribou movements in Butler, C.E. and Mahoney, S.P. (eds.). Proceedings 4th North American Caribou Workshop. St. John's, Newfoundland. pp 143 - 145.