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A Comparison of Two Modeling Approaches for Evaluating Wildlife–Habitat Relationships

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ABSTRACT Studies of resource selection form the basis for much of our understanding of wildlife habitat requirements, and resource selection functions (RSFs), which predict relative probability of use, have been proposed as a unifying concept for analysis and interpretation of wildlife habitat data. Logistic regression that contrasts used and available or unused resource units is one of the most common analyses for developing RSFs. Recently, resource utilization functions (RUFs) have been developed, which also predict probability of use. Unlike RSFs, however, RUFs are based on a continuous metric of space use summarized by a utilization distribution. Although both RSFs and RUFs predict space use, a direct comparison of these 2 modeling approaches is lacking. We compared performance of RSFs and RUFs by applying both approaches to location data for 75 Rocky Mountain elk (*Cervus elaphus*) and 39 mule deer (*Odocoileus hemionus*) collected at the Starkey Experimental Forest and Range in northeastern Oregon, USA. We evaluated differences in maps of predicted probability of use, relative ranking of habitat variables, and predictive power between the 2 models. For elk, 3 habitat variables were statistically significant ($P < 0.05$) in the RSF, whereas 7 variables were significant in the RUF. Maps of predicted probability of use differed substantially between the 2 models for elk, as did the relative ranking of habitat variables. For mule deer, 4 variables were significant in the RSF, whereas 6 were significant in the RUF, and maps of predicted probability of use were similar between models. In addition, distance to water was the top-ranked variable in both models for mule deer. Although space use by both species was predicted most accurately by the RSF based on cross-validation, differences in predictive power between models were more substantial for elk than mule deer. To maximize accuracy and utility of predictive wildlife–habitat models, managers must be aware of the relative strengths and weaknesses of different modeling techniques. We conclude that although RUFs represent a substantial advance in resource selection theory, techniques available for generating RUFs remain underdeveloped and, as a result, RUFs sometimes predict less accurately than models derived using more conventional techniques. (JOURNAL OF WILDLIFE MANAGEMENT 73(2):294–302; 2009)

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Studies of resource selection form the basis for much of our understanding of wildlife habitat requirements (Morrison et al. 1998, Manly et al. 2002, Scott et al. 2002). Information about relationships between wildlife populations and their habitat is used for many purposes, including characterization of long-term resource requirements (Forsman et al. 1984, Schoen and Kirchhoff 1985) and prediction of potential impacts of habitat change (Edwards and Collopy 1988, Green and Stowe 1993). Although simple analytical techniques such as selection ratios and goodness-of-fit tests are available for quantifying resource use (e.g., proportion of time spent in a particular habitat type) and selection (amount of use of a resource relative to its availability; Alldredge and Ratti 1986, 1992; Manly et al. 2002; Thomas and Taylor 2006), more complex models have become the primary means of assessing wildlife–habitat relationships and generating predictions about the consequences of habitat change (Morrison et al. 1998, Wiens 2002, Marzluff et al. 2004). An evaluation of how new habitat modeling techniques perform relative to more traditional approaches is important for advancing methodology in wildlife ecology and for increasing our understanding of resource selection and habitat management.

Manly et al. (2002:ix) proposed the resource selection function (RSF) as "a unified theory for the analysis and interpretation of data on resource selection." An RSF predicts relative probability of use of different resource units based on measured characteristics of those units (Manly et al. 2002). As such, RSFs can be used to predict relative probability of use across a landscape based on mapped distributions of resources or to evaluate the relative influence of different habitat characteristics on species distributions. One of the most common techniques for producing an RSF is logistic regression, which contrasts used versus available or used versus unused resource units (e.g., Mace et al. 1996, Johnson et al. 2000, Osborne et al. 2001, Anderson et al. 2005). Use of logistic regression for this purpose, however, has been criticized for a variety of reasons, including arbitrary definition of resource availability (Aebischer et al. 1993), use of relocation points rather than individual animals as the sampling units (Aebischer et al. 1993, Gillies et al. 2006, Thomas and Taylor 2006), lack of sensitivity to changes in the value of habitat variables that results from dichotomous characterization of the response variable (i.e., either used or not used; O'Connor 2002), and model

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development that does not consider the spatial arrangement of resources (Klute et al. 2002). In addition, validity of using logistic regression to estimate an RSF based on a use-availability design recently has been debated in the literature (Keating and Cherry 2004, Johnson et al. 2006).

A new approach to modeling resource selection recently was proposed by Marzluff et al. (2004). Rather than a simple binary characterization of resource units, the approach of Marzluff et al. (2004) considers use as a continuous variable summarized by a utilization distribution (UD). Multiple regression techniques are used to produce a spatially explicit resource utilization function (RUF), which relates the UD to a suite of continuous or categorical resource variables. The height of the UD at each location within its extent provides a measure of relative use and may be used as the response variable in the model (Marzluff et al. 2004). In addition, because RUFs for individual animals are averaged to produce a population-level model, the individual animal is the sampling unit. Millspaugh et al. (2006) noted that the RUF technique developed by Marzluff et al. (2004) represented a new approach to calculating a resource selection probability function (Manly et al. 2002) for individual animals. Nevertheless, to maintain consistency with Marzluff et al. (2004), we refer to resource selection models derived from individual UDs as RUFs.

Although RUFs may represent a theoretical improvement over use of logistic regression to model resource selection, a direct comparison of the 2 modeling approaches is lacking. Our goal was to compare and contrast the results of using RUFs versus RSFs to model resource selection by Rocky Mountain elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) at the Starkey Experimental Forest and Range (Starkey) in northeastern Oregon, USA. Starkey represents an ideal model system for such a comparison because a detailed habitat database is available for the study site (Rowland et al. 1998) and patterns of resource use by elk and mule deer have been documented extensively by previous research (Johnson et al. 2000, Stewart et al. 2002, Ager et al. 2003). Specifically, we addressed the following 4 questions: 1) Do the 2 models identify the same variables as being important predictors of space use? 2) Is the direction of the relationship between use and each habitat variable (indicated by the sign of the regression coeff) consistent between models? 3) Do maps of predicted probability of use differ between the 2 models? and 4) Does predictive power differ between the 2 models?

STUDY AREA

We conducted our study on the Starkey Experimental Forest and Range in northeastern Oregon, USA. Starkey (45°12′N, 118°3′W) was a 101-km^2 research area located 35 km southwest of La Grande, Oregon, in the Blue Mountains and managed by the United States Forest Service. A 2.4-m-high New Zealand woven-wire fence enclosed Starkey and prevented immigration or emigration of large herbivores (Rowland et al. 1997). This ungulate-proof fence also divided Starkey into 5 research areas, 4 of which were used for telemetry studies of mule deer, elk, and cattle during spring to fall. We used location data collected in Main Study Area (77.6 km^2), which was 2–4 times larger than the average home range size reported for elk in the Blue Mountains (Leckenby 1984). Habitat choices available to elk and mule deer were similar to those available outside of Starkey. Traffic levels, recreational activities, and timber management also were similar to patterns of use on nearby public lands (Rowland et al. 1997, Preisler et al. 2006). Elevations at Starkey ranged from 1,120 m to 1,500 m, and the site supported a mosaic of coniferous forests, shrublands, and grasslands, with moderately sloping uplands dissected by numerous drainages (Johnson et al. 2000, Stewart et al. 2002). Detailed descriptions of Starkey are provided by Skovlin (1991), Wisdom et al. (1993), and Rowland et al. (1997, 1998).

METHODS

Animal Locations and Habitat Variables

We radiocollared and released adult female elk and mule deer into Main Study Area during early spring (Mar–Apr) of 1999–2001. We typically recovered collars in winter (Nov–Jan) and we placed new collars on a different sample of animals the following spring so that we generally monitored individuals for only 1 year. All animal handling was in accordance with protocols approved by an established Animal Care and Use Committee (Wisdom et al. 1993). We determined animal locations using a LORAN-C automated telemetry system (Findholt et al. 1996, Rowland et al. 1997). We collected telemetry data 24 hours/day with occasional exceptions due to equipment maintenance or repair, and we obtained a location for each radiocollared animal every 1–5 hours. Mean position error of animal locations was 53 $\pm$ 5.9 (SE) m (Findholt et al. 1996).

We limited our analyses to locations collected during spring (30 Apr–14 Jun) because this represents a critical period for both elk and mule deer due to the need to recover from the physiological stresses of winter and to meet energetic demands of reproduction (Johnson et al. 2000, Cook 2002). In addition, we only used locations collected during crepuscular hours ($\pm$1 hr of sunrise and sunset) when habitat selection was assumed to be strongly influenced by forage distribution (Johnson et al. 2000). We included in our analysis animals with $\geq$30 locations during this period, although mean number of locations per animal was substantially higher (89 for elk, 85 for mule deer). Our dataset included 107 elk (9,569 locations) and 44 mule deer (3,761 locations). We evaluated spatial independence of individual animals within species and years using association matrices (Weber et al. 2001), which indicated within-year independence of all animals in our dataset.

We included the following habitat variables with demonstrated potential to influence distribution of elk and mule deer at Starkey (Rowland et al. 1998, Johnson et al. 2000, Stewart et al. 2002) as predictor variables in our analyses: aspect (transformed with sine and cosine functions to measure east–west and north–south aspects, respectively); distance to permanent water (m); convexity (m; a measure of topographical complexity); slope (%); canopy closure of trees >12 cm diameter at breast height (%); and distance to open (open to public access) and restricted (access restricted to authorized personnel) roads (m). Each of these variables can influence space use by elk and mule deer by affecting energy balance, risk of predation, or proximity to humans. For example, green-up of forage at Starkey following winter occurs first on south-facing slopes with an open canopy, which may attract both elk and mule deer to those areas in spring. In addition, energetic costs of locomotion are substantially greater in steep terrain (Parker et al. 1984), yet predators often favor easily traversable terrain (Ozoga and Harger 1966, Farmer et al. 2006). Consequently, slope (and potentially convexity) can alter patterns of space use by influencing trade-offs between energy expenditure and risk of predation. Previous research at Starkey also has indicated that elk strongly avoid roads, whereas mule deer tend to be located close to roads (primarily to avoid elk; Johnson et al. 2000, Rowland et al. 2000). We note, however, that although previous studies at Starkey largely have evaluated resource selection within the boundary of the Experimental Forest (second-order selection; Johnson 1980), models we developed describe resource selection within individual home ranges (third-order selection; Johnson 1980). The RUF approach described by Marzluff et al. (2004) was designed primarily to evaluate resource selection within the home range boundary, and therefore we developed both RUFs and RSFs at this scale to facilitate our comparison of the 2 modeling approaches. We obtained values for all habitat variables except canopy closure from a 30 × 30-m pixel basis from the Starkey habitat database for ungulate research (Rowland et al. 1998). The habitat database consists of a series of raster-based Geographic Information System layers, details of which are given by Rowland et al. (1998). We derived canopy closure from photo interpretation of 1:12,000 color aerial photos. We examined a correlation matrix (PROC CORR; SAS Institute 2002) to detect collinearity between predictor variables; we eliminated no variables due to collinearity (greatest $|r| = 0.37$ between slope and distance to open road).

Model Development and Validation

We calculated RUFs for individual elk and mule deer as described by Marzluff et al. (2004). The first step in this process was to estimate individual UDs using location data for each animal. We used the ANIMAL MOVEMENTS extension of ArcView 3.3 (Hooge and Eichenlaub 1997) with fixed-kernel home range estimation and the least squares cross-validation option for bandwidth selection (Silverman 1986, Kernohan et al. 2001) to estimate individual 99% UDs. We chose this extension because it provides the values of the UD as a response surface or kernel grid, information needed to construct RUFs. In addition, Marzluff et al. (2004) used ANIMAL MOVEMENTS in developing the RUF technique. We opted to output the kernel grid for each UD with a 30 × 30-m cell size to match the resolution of our habitat data.

We estimated relative use at each 30 × 30-m grid cell within 99% UDs using the FOCAL PATCH extension of ArcView 3.3, which measured the height of the kernel density estimate over each cell (Marzluff et al. 2004). The result was a point file containing the *x*- and *y*- coordinates for the center of each grid cell and the associated relative use value. To account for spatial bias in the rate at which we obtained telemetry locations in our study area (Johnson et al. 1998), we multiplied relative use values by the inverse of the observation rate for each grid cell and then rescaled them to their original range of 1–99. We also clipped UDs at the fence marking the Starkey boundary, although <5% of the volume of each UD was typically located outside the fence. The number of cells in each UD ranged from 4,725 to 53,663 for elk and from 756 to 14,727 for mule deer.

We estimated RUFs for each animal in our dataset using multiple regression in an RUF analysis package designed for use in the statistical program R (Marzluff et al. 2004). Each RUF represented the relationship between the UD of an individual animal and either 7 (elk) or 6 (mule deer) unique habitat variables. For each species, we only included variables with demonstrated potential to influence space use at Starkey based on previous research at that site (Johnson et al. 2000, Stewart et al. 2002). The RUFs also accounted for spatial autocorrelation inherent in each UD with 2 spatial parameters that we estimated jointly with the coefficients for each habitat variable (Handcock and Stein 1993, Marzluff et al. 2004). Further details on estimation of spatial parameters and on the specific spatial correlation structure applied in the RUF analysis package are provided by Marzluff et al. (2004).

We systematically subsampled 10% of grid cells in each elk UD and 33% of cells in each mule deer UD prior to analysis because of computational constraints. With one gigabyte of random access memory (RAM) available, the number of predictor variables we used combined with the size and complexity of the matrices that must be constructed to estimate the 2 spatial parameters in the RUF analysis package limited the number of grid cells that we could include in each model to roughly 5,500. We began our sampling routine at the northwestern-most grid cell in each UD and, moving across the UD from left to right and from top to bottom, we selected every 10th cell for elk and every third cell for mule deer for inclusion in our analyses. In addition, for some animals ($n = 32$ elk and 5 mule deer) the maximum likelihood procedure applied in the RUF analysis package was unable to estimate a variance for one or both of the spatial parameters. The reason for this problem was unclear, but because estimates of regression coefficients in those cases were questionable (M. S. Handcock, University of Washington, personal communication), we chose not to include those animals in further analyses. Final reduced sample sizes for comparison of RUFs to RSFs were 75 elk and 39 mule deer.

Once we calculated the RUF for each animal, we averaged unstandardized coefficients for each habitat variable across animals to produce a population-level RUF for each species (Marzluff et al. 2004; Sawyer et al. 2006, 2007). We calculated variance estimates for average unstandardized coefficients according to Marzluff et al. (2004, eq 2), which quantified uncertainty in the average value of each coefficient for the animals in our sample but did not include interanimal variation. We used a t-statistic to determine which variables would remain in the final model for each species ($\alpha \leq 0.05$). We then used average unstandardized coefficients for those variables to map predicted probability of use by elk and mule deer across the Starkey landscape. We calculated standardized partial regression coefficients for individual models according to Marzluff et al. (2004, eq 1). In addition, we averaged standardized coefficients for significant variables across individuals, and we used the absolute value of the averaged coefficients to rank the relative importance of each variable to the 2 species (Marzluff et al. 2004). We obtained variance estimates for average standardized coefficients using standard sampling statistics and were therefore conservative due to inclusion of interanimal variation in the calculation (Marzluff et al. 2004).

We calculated RSFs for individual elk and mule deer based on a use-availability design as described by Manly et al. (2002). The 99% UD boundary for each animal represented the spatial extent of our analyses. We assigned locations for each animal (75 elk, 39 mule deer) to a 30 × 30-m grid cell to determine values of associated habitat variables. We then cast an equal number of random locations within each 99% UD to determine availability of habitat characteristics. We fit a logistic regression model to the dataset for each animal (PROC LOGISTIC; SAS Institute 2002) and used the resulting coefficients to estimate an RSF (Manly et al. 2002, eq 5.11).

Our approach to calculating population-level RSFs for elk and mule deer was similar to the approach we used to calculate population-level RUFs. We averaged unstandardized regression coefficients for each habitat variable across individuals and used a t-statistic to determine which variables would remain in the final model for each species. We calculated variance estimates for average coefficients in the same manner as for the RUFs and used the final population-level models to map predicted probability of use by each species across the Starkey landscape. We averaged standardized regression coefficients for each habitat variable across animals to rank the relative importance of each variable to the population. We also calculated variance estimates for those coefficients in the same way as for the RUFs. Averaging regression coefficients across animals allowed us to develop RUFs and RSFs in a comparable manner and to give each animal equal weight in the final models for each species. In addition, although actual values of both unstandardized and standardized coefficients from RUFs and RSFs were not directly comparable as a result of the different procedures used to produce each type of model (i.e., linear vs. logistic regression), evaluating the sign of those coefficients (+, −, or nonsignificant) at the population level, as well as their relative rank, provided a useful comparison of the 2 model types.

We mapped predicted probability of use by elk and mule deer across the Starkey landscape by calculating relative selection probabilities for all grid cells in the study area using RUFs and RSFs with unstandardized coefficients. We assigned each cell and its associated predicted value to 1 of 4 categories based on the quartiles of the distribution of predicted values for each map (Sawyer et al. 2007). We classified cells with the highest 25% of predicted values as high-use areas (4), cells in the 51 to 75 percentiles as areas of medium-high use (3), cells in the 26 to 50 percentiles as areas of medium-low use (2), and cells in the 0 to 25 percentiles as low-use areas (1). We evaluated similarity between maps generated by each model type qualitatively based on the spatial distribution of cells in each category.

We used k-fold cross-validation (Boyce et al. 2003) to evaluate predictive strength of the RUF and RSF for each species. In each iteration of the procedure, we withheld one animal as test data and used the remaining animals (74 elk or 38 mule deer) as model training data. This procedure was appropriate for the scale of our analyses (third-order selection; Johnson 1980), because population-level models were designed to predict relative probability of use by an individual animal in our sample within its home range regardless of where that home range was located in the study area. A similar procedure was used by Anderson et al. (2005) to validate third-order models of resource selection. The data we used to generate each type of model were inherently different (RSFs were generated directly from location data whereas RUFs were based on estimated UDs), and hence the cross-validation procedure for the RUFs differed slightly from that of the RSFs.

We based the cross-validation procedure for the RUFs on the methods of Johnson et al. (2000). In our case, however, the test dataset in each iteration of the cross-validation was the UD of an individual elk or mule deer. We obtained RUF values (predicted values of relative use) for each grid cell in the test dataset using the model derived from the training data. We then associated an observed relative use value (actual UD ht) and a predicted relative use value with each grid cell in the test data. We sorted those data from lowest to highest based on the RUF (predicted) values and binned them into 8 groups, each containing an equal number of grid cells. We then regressed the sum of the observed values in each bin against the sum of the predicted values in each bin and recorded the coefficient of determination and slope. We considered the combination of a high coefficient of determination and a positive slope to be indicative of a model that predicted well (Johnson et al. 2000, Anderson et al. 2005). Therefore, we averaged coefficients of determination and slopes across 75 cross-validation iterations for elk and 39 iterations for mule deer to provide a measure of the overall predictive strength of the RUF for each species. As an additional measure of overall predictive strength, we calculated the ratio of positive to negative slopes and positive and significant to negative and significant slopes across all cross-validation iterations for both species. We determined significance of the regression in each iteration based on $\alpha \leq 0.05$.

We used the cross-validation procedure described by Anderson et al. (2005) to evaluate predictive strength of the RSF for each species. In each iteration of the procedure, we used the model derived from the training data to obtain RSF values (predicted values of relative use) for the random

Table 1. Parameter estimates and relative ranking of habitat variables for a resource utilization function (RUF) and a resource selection function (RSF) for elk ($n = 75$) at the Starkey Experimental Forest and Range, Oregon, USA. We based models on location data collected with a LORAN-C automated telemetry system during spring (30 Apr–14 Jun) of 1999–2001 within 1 hour of sunrise or sunset.

	Elk RUF					Elk RSF				
Variable	β	SE	Standardized β	Standardized β SE	Relative rank[a]	β	SE	Standardized β	Standardized β SE	Relative rank[a]
Intercept	3.39	0.17	8.61	1.27						
Distance to water	-8×10^{-4}	2×10^{-5}	−0.16	0.12	1	NS[b]				
Distance to restricted road	-4×10^{-4}	1×10^{-5}	−0.16	0.20	2	NS				
Distance to open road	-2×10^{-4}	1×10^{-5}	−0.12	0.26	3	NS				
Convexity	0.01	3×10^{-4}	0.05	0.06	4	0.04	6×10^{-3}	0.10	0.02	2
Sine of aspect	−0.06	2×10^{-3}	−0.04	0.05	5	−0.08	0.03	−0.04	0.02	3
Canopy closure	-1×10^{-3}	7×10^{-5}	−0.04	0.11	6	NS				
Percent slope	3×10^{-4}	1×10^{-4}	0.01	0.06	7	−0.02	3×10^{-3}	−0.10	0.02	1

[a] Ranking based on absolute value of standardized coeff. (β).
[b] NS, not significant ($P \geq 0.05$).

locations for each species. We then sorted random locations from lowest to highest based on their RSF values and binned them into 8 groups, each of which contained an equal number of locations (Boyce et al. 2003, Anderson et al. 2005). Next we obtained RSF values for the test data and placed locations in the test dataset into the bins we created with the random data based on their associated RSF values (Anderson et al. 2005). We then regressed the number of locations from the test dataset in each bin against the median RSF value of the random locations in each bin and recorded the coefficient of determination and slope. As in the RUF cross-validation procedure, we considered the combination of a high coefficient of determination and a positive slope to be indicative of a model that predicted well. Therefore, we also used mean coefficient of determination and slope values across the entire set of cross-validation iterations and the ratio of positive to negative slopes and positive and significant to negative and significant slopes to evaluate overall predictive strength of the RSF for each species.

Although the cross-validation procedure for each model type differed slightly, the underlying assumption in both cases was that observed use should increase with predicted use in a linear fashion (Johnson et al. 2000). Furthermore, the perfect model in both cases should have resulted in $R^2 =$ 1 and a significant positive slope for the regression in each iteration. We therefore considered the results of the cross-validation for each model type to be directly comparable, with the exception of the mean slope values.

RESULTS

Considerable differences were evident between the 2 population-level models for elk. Only 3 habitat variables (i.e., convexity, sine of aspect, and % slope), all related to topography, were statistically significant in the RSF for elk, whereas all 7 variables were significant in the RUF (Table 1). In addition, the coefficient for percent slope was positive in the RUF for elk, indicating selection for steeper slopes, and negative in the RSF, indicating selection for gentle slopes (Table 1). Differences between models were less substantial for mule deer. Four of six habitat variables (i.e., distance to water, distance to restricted road, % slope, and convexity) were significant in the RSF, whereas all 6 variables were significant in the RUF for mule deer (Table 2). Of the 4 variables that were significant in both models, only distance to restricted roads had a coefficient that differed in sign between models (positive in the RUF, indicating avoidance of areas located close to restricted roads, and negative in the RSF, indicating selection of those areas; Table 2).

Table 2. Parameter estimates and relative ranking of habitat variables for a resource utilization function (RUF) and a resource selection function (RSF) for mule deer ($n = 39$) at the Starkey Experimental Forest and Range, Oregon, USA. We based models on location data collected with a LORAN-C automated telemetry system during spring (30 Apr–14 Jun) of 1999–2001 within 1 hour of sunrise or sunset.

	Mule deer RUF					Mule deer RSF				
Variable	β	SE	Standardized β	Standardized β SE	Relative rank[a]	β	SE	Standardized β	Standardized β SE	Relative rank[a]
Intercept	3.91	0.34	6.95	2.17						
Distance to water	4×10^{-3}	4×10^{-5}	0.80	0.34	1	1×10^{-3}	3×10^{-4}	0.12	0.03	1
Distance to restricted road	5×10^{-4}	2×10^{-5}	0.18	0.31	2	-4×10^{-4}	1×10^{-4}	−0.06	0.03	3
Cosine of aspect	−0.24	4×10^{-3}	−0.15	0.07	3	NS[b]				
Percent slope	-7×10^{-3}	2×10^{-4}	−0.09	0.06	4	-9×10^{-3}	4×10^{-3}	−0.03	0.03	4
Sine of aspect	−0.05	4×10^{-3}	−0.04	0.06	5	NS				
Convexity	3×10^{-3}	7×10^{-4}	6×10^{-4}	0.07	6	0.04	8×10^{-3}	0.09	0.02	2

[a] Ranking based on absolute value of standardized coeff. (β).
[b] NS, not significant ($P \geq 0.05$).

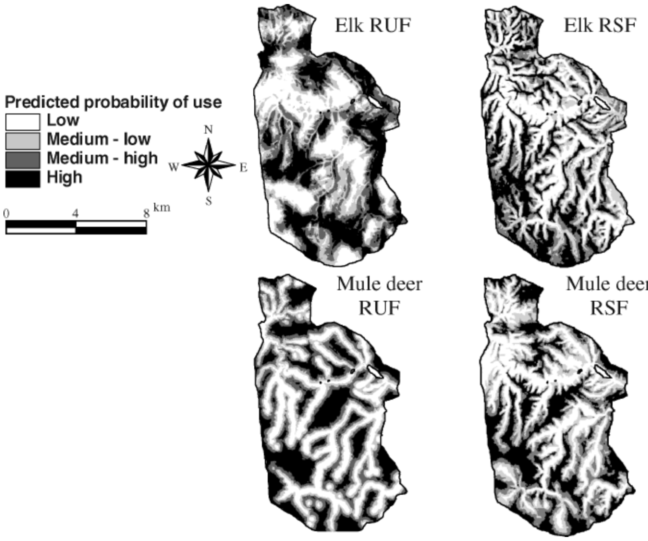

Figure 1. Predicted relative probability of use by elk ($n = 75$) and mule deer ($n = 39$) in Main Study Area, Starkey Experimental Forest and Range, Oregon, USA, generated from resource utilization functions (RUFs) and resource selection functions (RSFs). We based models of resource selection on location data collected with a LORAN-C automated telemetry system during spring (30 Apr–14 Jun) of 1999–2001 within 1 hour of sunrise or sunset.

Similar to modeling results based on unstandardized coefficients, relative ranking of habitat variables based on standardized coefficients differed substantially between model types for elk but not mule deer. The highest ranking variable in the RUF for elk was distance to water, which was not significant in the RSF for this species; the highest ranking variable in the RSF for elk was percent slope, which ranked last in the RUF (Table 1). In addition, none of the 3 variables that were significant in the RSF for elk ranked among the top 3 in the RUF (Table 1). Ranking of variables for mule deer, however, was more consistent between model types. Distance to water was the highest ranking variable in both the RUF and RSF for mule deer (Table 2). In addition, of the 4 variables that were significant in the RSF for mule deer, 3 also ranked among the top 4 in the RUF (Table 2). The biggest discrepancy between model types for mule deer with respect to variable ranking was convexity, which ranked sixth in the RUF but second in the RSF (Table 2).

Maps of predicted probability of use generated from RUFs and RSFs also differed markedly between model types for elk but not mule deer (Fig. 1). In contrast to elk, the spatial pattern of predicted probability of use generally was similar between models for mule deer. In other words, locations of grid cells predicted to have the highest and lowest relative probabilities of use were comparable between models for mule deer but were noticeably different between models for elk (Fig. 1). We also note that predictive maps generated from RUFs for both species appeared smoother with less spatial variability than maps generated from RSFs.

Cross-validation tests indicated that RSFs performed better than RUFs for both elk and mule deer. The magnitude of the difference in predictive strength between model types, however, differed between species. Mean coefficients of determination across 75 cross-validation iterations for elk were comparable between the 2 model types, but mean slope of the regression line across all iterations was negative for the RUF, indicating that predicted relative use values from that model frequently were inversely related to observed use values (UD ht). Mean slope of the regression line for the RSF, however, was positive (Table 3). Similarly, the ratio of positive to negative slopes was nearly 3 times greater for the RSF than the RUF for elk, and the ratio of positive and significant to negative and significant slopes for the RSF was nearly 4 times greater than that of the RUF (Table 3). In contrast, the mean coefficient of determination of the RUF for mule deer was nearly double that of the RSF for that species across 39 cross-validation iterations, and mean slope of the regression line across all iterations was positive for both models (Table 3). In addition, the overall ratio of positive to negative slopes was comparable between model types for mule deer, whereas the ratio of positive and significant to negative and significant slopes for the RSF was >7 times greater than that of the RUF (Table 3).

DISCUSSION

Much of our understanding of wildlife habitat selection is based on RSF models often developed using logistic regression. Resource selection models based on UDs offer alternatives that address some of the limitations identified in RSF analyses (Millspaugh et al. 2006). Reconciling results from these 2 modeling approaches is necessary to link past and future studies of habitat selection. Our work provides a direct comparison between approaches.

Results of our RUF-based analyses of resource selection differed markedly from those of the RSF-based analyses, particularly for elk. Although differences between the 2

Table 3. Cross-validation results for resource utilization functions (RUFs) and resource selection functions (RSFs) for elk ($n = 75$) and mule deer ($n = 39$) at the Starkey Experimental Forest and Range, Oregon, USA. We based models on location data collected with a LORAN-C automated telemetry system during spring (30 Apr–14 Jun) of 1999–2001 within 1 hour of sunrise or sunset.

	Mean		Slope frequency				Ratio[a]	
Model	R^2	Slope	Positive	Negative	Positive (significant)	Negative (significant)	P:N	PS:NS
Elk RUF	0.52	−1.95	37	38	20	23	0.97	0.87
Elk RSF	0.46	4×10^{-7}	55	20	20	6	2.75	3.33
Mule deer RUF	0.61	1.49	22	17	17	9	1.29	1.89
Mule deer RSF	0.36	1×10^{-7}	25	14	14	1	1.79	14.00

[a] P:N, ratio of positive to negative slopes; PS:NS, ratio of positive and significant to negative and significant slopes.

model types consistently were greater for elk than mule deer, the RSF performed better for both species with respect to predictive strength. Differences in the relative ranking of habitat variables also are noteworthy because substantially different ecological conclusions and management implications follow from them. For example, the population-level RUF for elk indicated that proximity to water was the most important factor influencing space use decisions by females. This result could lead to management actions designed to increase availability of water for elk. In contrast, proximity to water did not enter the population-level RSF, and thus it is unlikely that water management would be considered based on that model. Based on our results, we suggest that although RUFs may represent a substantial advancement in resource selection theory (Marzluff et al. 2004, Millspaugh et al. 2006), more work is necessary to make the models broadly applicable. Specifically, we identify avenues for future refinement that fall into 2 broad categories: 1) improvements in the techniques used to estimate the UD and 2) improvements in the statistical models used to link the UD to underlying habitat characteristics.

Several techniques are available for estimating UDs, and none perform best under all circumstances (Millspaugh et al. 2006). Yet, choice of the UD estimator likely affects results of resource selection models that use the UD to define space use. Although fixed-kernel analysis is a common method for estimating the UD, other methods might more accurately represent space use under differing conditions. For example, space use for territorial species for which UDs should have abrupt edges might more appropriately be quantified using the home range model based on an exponential power function (Horne and Garton 2006*a*). Similarly, the Brownian Bridge approach to UD estimation might be most appropriate when location data are collected at relatively frequent intervals (Horne et al. 2007). Horne and Garton (2006*a*) provided a review of different home range models and a method for assessing the fit of various home range estimators to a given dataset. Such an approach would facilitate selection of the most appropriate method for estimating the UD and hence, the best framework for evaluating habitat selection using the RUF approach.

When kernel analyses are used to produce the UD, the method for selecting the bandwidth (and the resulting smoothing parameter) might affect how well the UD characterizes space use (Kernohan et al. 2001, Gitzen and Millspaugh 2003, Millspaugh et al. 2006) and, as a result, how well an RUF characterizes the relationships between use and various underlying habitat characteristics. We used the least squares cross-validation (LSCV) method of bandwidth selection to estimate UDs. The LSCV approach, however, suffers from high sampling variability and, in some instances, selects bandwidth values that are too small, resulting in under-smoothing of the UD (Silverman 1986, Millspaugh et al. 2006). In contrast, the LSCV option in ANIMAL MOVEMENTS potentially over-smoothes estimates of the UD by consistently fixing the bandwidth at roughly 90% of the reference bandwidth (A. Rogers, Ontario Ministry of Natural Resources, personal communication). Either scenario could negatively affect performance of RUFs. For example, over-smoothing the UD might decrease the ability of the RUF to detect subtle relationships between the height of the UD and underlying habitat characteristics (Millspaugh et al. 2006). Other bandwidth selection methods might provide better estimates of the UD. Techniques such as plug-in and solve-the-equation methods (Wand and Jones 1995, Kernohan et al. 2001) and likelihood cross-validation (Horne and Garton 2006*b*) may prove useful in UD-based analyses of resource selection.

In addition to the choices of a UD estimator and bandwidth selection method, RUFs could be sensitive to the size of the UDs on which they are based. In an RUF analysis, the height of a UD at each grid cell is used as the response variable in a multiple regression model (Marzluff et al. 2004). The distribution of use values (cell-specific UD ht) derived from a large UD will often be more heavily skewed towards low use values than those derived from a smaller UD. A high degree of skewness in the distribution of the response variable in a linear regression model could introduce bias into estimates of regression coefficients and predicted values (Neter et al. 1996). Therefore, smaller UDs might sometimes lead to less biased estimates of regression coefficients in an RUF analysis.

The size of a UD (in addition to available RAM) also might affect the proportion of a dataset that can be included in the modeling process. In our study, the average area covered by mule deer UDs was roughly 33% of that covered by elk UDs. As a result, distributions of relative use values for mule deer UDs tended to be less skewed than those for elk, and we were able to subsample roughly 30% of mule deer UDs but were limited to 10% of elk UDs. This could help to explain why modeling results were more similar between model types for mule deer than for elk. Regardless of estimation techniques, the size of a UD or home range is largely a function of the biology of the species under study, and our results indicate that RUFs might be most useful for evaluating resource selection by species with small home ranges.

The second category of improvements necessary to make RUF analyses more broadly applicable relates to the techniques used to link the UD to underlying habitat characteristics. Theoretically, one of the major benefits of RUFs is that they account for spatial autocorrelation among grid cells in the UD. Marzluff et al. (2004) accounted for spatial autocorrelation by incorporating a maximum likelihood procedure into their RUF analysis package that jointly estimates RUF coefficients and 2 spatial parameters that describe the degree of autocorrelation in a dataset. Therefore, coefficients for models produced in the RUF analysis package were adjusted for the effects of spatial autocorrelation (Marzluff et al. 2004, Millspaugh et al. 2006). This likely explains why predictive maps generated from RUFs appeared smoother than maps generated from RSFs. Individual RUFs are constructed such that predicted values for specific locations are a function not only of the values of habitat variables at those locations, but also of the values of the response variable (UD ht) associated with nearby grid cells. This spatial dependency of the predicted values also is reflected in the population-level model. One potential problem with the estimation procedures used in the RUF analysis package, however, is the assumption of one underlying spatial correlation structure and associated correlation function. A number of different correlation structures are available for describing spatial dependence. For example, exponential, Gaussian, linear, rational quadratic, and spherical correlation structures are described for use in linear mixed-effects models by Pinheiro and Bates (2000). No correlation structure is universally best for describing spatial dependence. Therefore, we suggest that allowing the user to fit different correlation structures would represent a positive step towards more fully realizing the theoretical benefits of accounting for spatial autocorrelation when modeling resource selection using UDs.

An additional challenge is that RUFs are multiple linear regression models that must adhere to the standard assumptions of linear regression analysis (Marzluff et al. 2004). For example, constancy of error variance and normally distributed residuals are both assumed in RUF analysis (Neter et al. 1996). Diagnostics designed to assess validity of those assumptions, however, cannot be performed for the population-level RUF because there is no observed response variable for that model. This characteristic also precludes use of an information-theoretic approach to model selection at the population level. Consequently, diagnostics and transformations can only be carried out at the level of the individual animal. Because the models for individuals are averaged to produce the population-level RUF, all of the same variables and transformations of variables must be present in each individual model. Transformation of a variable may be appropriate or even necessary for some animals and entirely inappropriate for others. In such cases it is unclear whether the transformation should be performed for all animals or none of the animals. In a broader sense, how diagnostics and remedial measures should proceed in an RUF analysis needs to be defined. At the very least, we suggest that criteria be developed for determining whether or not a transformation is likely to improve the overall fit or validity of a population-level RUF if the measure is performed for all individuals in a dataset. For example, if a specific transformation appears appropriate for >50% of the individuals in a dataset, then applying that transformation to all individuals may improve predictive power of the population-level model.

MANAGEMENT IMPLICATIONS

We offer several suggestions to managers interested in modeling wildlife–habitat relationships. First, managers should consider the average home range size of the species under study before choosing a modeling approach. The RUF approach may be most useful for evaluating resource selection by species with small home ranges. In the case of large herbivores, which tend to have relatively large home ranges, traditional RSF approaches may provide more reliable information on patterns of resource selection than the RUF approach, and therefore, until the RUF approach is further refined, we suggest that managers of large herbivore populations continue to use traditional approaches to modeling resource selection. Second, managers should carefully consider the spatial scale of interest when choosing an approach to modeling resource selection. If resource selection within a larger study area is of interest rather than resource selection within the home range, then the proportion of a dataset that can be included in construction of an RUF may be reduced even further than we reported, which could limit the utility of RUF analyses in such cases. Finally, regardless of which modeling approach is used, we strongly encourage managers to evaluate the predictive power of their models using cross-validation; neither RUFs nor RSFs with low predictive power should serve as a basis for making management decisions.

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