Using Multilevel Models to Quantify Heterogeneity in Resource Selection

TYLER WAGNER, *United States Geological Survey, Pennsylvania Cooperative Fish and Wildlife Research Unit, Pennsylvania State University, University Park, PA 16802, USA*

DUANE R. DIEFENBACH,[1] *United States Geological Survey, Pennsylvania Cooperative Fish and Wildlife Research Unit, Pennsylvania State University, 404 Forest Resources Bldg., University Park, PA 16802, USA*

SONJA A. CHRISTENSEN,[2] *Pennsylvania Cooperative Fish and Wildlife Research Unit, Pennsylvania State University, University Park, PA 16802, USA*

ANDREW S. NORTON,[3] *Pennsylvania Cooperative Fish and Wildlife Research Unit, Pennsylvania State University, University Park, PA 16802, USA*

ABSTRACT Models of resource selection are being used increasingly to predict or model the effects of management actions rather than simply quantifying habitat selection. Multilevel, or hierarchical, models are an increasingly popular method to analyze animal resource selection because they impose a relatively weak stochastic constraint to model heterogeneity in habitat use and also account for unequal sample sizes among individuals. However, few studies have used multilevel models to model coefficients as a function of predictors that may influence habitat use at different scales or quantify differences in resource selection among groups. We used an example with white-tailed deer (*Odocoileus virginianus*) to illustrate how to model resource use as a function of distance to road that varies among deer by road density at the home range scale. We found that deer avoidance of roads decreased as road density increased. Also, we used multilevel models with sika deer (*Cervus nippon*) and white-tailed deer to examine whether resource selection differed between species. We failed to detect differences in resource use between these two species and showed how information-theoretic and graphical measures can be used to assess how resource use may have differed. Multilevel models can improve our understanding of how resource selection varies among individuals and provides an objective, quantifiable approach to assess differences or changes in resource selection. © 2011 The Wildlife Society.

KEY WORDS *Cervus nippon*, heirarchical models, logistic regression, multilevel modeling, *Odocoileus virginianus*, resource selection function.

Most often, when a sample of individual animals is monitored and their habitat use measured, these data are used to make inferences about population-level habitat selection (Manly et al. 2002). For each individual, a resource selection function (RSF) can be modeled even though the objective is to make inferences about population-level habitat selection. One solution to obtaining a population-level model of habitat use is to average coefficients of the RSF across individual animals (e.g., Sawyer et al. 2006). Although this 2-stage approach has some advantages, including intuitive appeal (see Fieberg et al. 2010 for details); this approach does not account for sample size differences among individuals,

animals with insufficient data for fitting models must be excluded, and heterogeneity in habitat use (i.e., variation of estimated coefficients) is not easily modeled (Fieberg et al. 2010). Furthermore, individuals may not share common parameters among their respective RSFs. An alternative approach that circumvents the aforementioned limitations of averaging coefficients across individuals, while allowing for the quantification and modeling of heterogeneity in habitat use, is multilevel modeling.

Multilevel models, also known as hierarchical models, are being used more as an analytical framework for studying resource selection by animals (Gillies et al. 2006, Hebblewhite and Merrill 2008, Belant et al. 2010, Duchesne et al. 2010, Singleton et al. 2010). These models are considered multilevel because they explicitly model the multilevel structure of the data (e.g., multiple measurements [level 1] nested within individuals [level 2]) by considering both within- and among-individual variation. Thus, multilevel models provide the ability to include covariates measured at multiple spatial and temporal scales. The increased use of multilevel models, as opposed to fitting fixed effects models, is due in large part to their ability to 1) accommodate

repeated observations made on individual animals while retaining the animal as the experimental unit (i.e., avoid pseudoreplication) and an unbalanced number of observations (e.g., locations) made across individuals through the inclusion of a random intercept and 2) allow for heterogeneity in the responses of individuals to resource availability through the inclusion of random slopes (Hebblewhite and Merrill 2008, Duchesne et al. 2010). Quantifying the heterogeneity in responses of individuals provides information about how individuals differ with respect to preference for specific habitat characteristics. In addition, multilevel models simultaneously allow for inferences about population resource selection (i.e., marginal inferences), which is described by the population-average RSF, and for inferences about individual animal resource selection (i.e., conditional inferences).

Details of the properties of multilevel resource selection models have been presented elsewhere (e.g., Gillies et al. 2006), but one feature of multilevel resource selection models is currently underutilized: the ability to model among-individual heterogeneity in resource selection coefficients (i.e., individual animal slopes and intercepts). Because multilevel models can have slopes and intercepts that are themselves given a model (i.e., covariates can be included at multiple levels of the model; Gelman and Hill 2007), they easily can be extended to model (explain) variability in functional responses in resource selection. This is important because we expect, in many cases, that individual animals or groups of animals differ in their selection for specific habitats. This heterogeneity could be driven by characteristics of an individual animal such as age, sex, or species or by characteristics of an individual's home range. In fact, the presence of cross-scale interactions, where the probability of resource use is affected by both predictors at the scale of individual resource units and at larger spatial scales, is likely a common occurrence. Understanding what drives variability in resource selection and at what spatial scale it occurs can provide valuable information to both managers and ecologists. Furthermore, the ability to detect differences or changes in resource selection from both an ecological (e.g., Indermaur et al. 2009) or a conservation perspective (e.g., Sawyer et al. 2009) is important to understanding both the ecological drivers of resource selection and the impact of human activities on wildlife behavior. Without a multilevel modeling approach, the ability to make inferences about biological and statistical differences or changes is not possible without the use of ad hoc decision rules.

To the best of our knowledge, very few resource selection studies have taken advantage of this ability to model coefficients, with Hebblewhite and Merrill (2008) and Indermaur et al. (2009) being notable exceptions. For example, Hebblewhite and Merrill (2008) modeled parameter variation in wolf pack use of locations near areas of human activity as a function of each pack's home range-scale proximity to human use. Indermaur et al. (2009) modeled coefficients in a multilevel logistic model to investigate differences in resource selection between 2 sympatric toad populations.

Our goal was to demonstrate the use of multilevel resource selection models to explain heterogeneity in resource selection. We used 2 examples to investigate 1) whether home range characteristics of individual white-tailed deer (*Odocoileus virginianus*) can explain heterogeneity in habitat use in response to the distance to roads (a cross-scale interaction) and 2) whether resource selection differs between sika (*Cervus nippon*) and white-tailed deer. Both of these examples use multilevel logistic models; however, the approach can easily be extended to RSF models that assume other distributions, including the negative binomial distribution (e.g., Belant et al. 2010).

METHODS

We conducted 2 case studies to illustrate modeling individual heterogeneity in resource selection. The first example is a simple illustration of how multilevel models can incorporate information at multiple scales to model resource selection. We examined resource selection as a function of distance to road in which this relationship was dependent on local road density. The second example is more realistic in that we model resource selection of 2 sympatric species and use multilevel models to evaluate whether resource selection differed between species. Both examples used study designs in which we identified individual deer and measured the use of resources for each, but we measured availability at the population level (Manly et al. 2002). For both analyses, we used Akaike's Information Criterion (AIC) to compare models with differing fixed effects. Although the application of AIC for multilevel models is not straightforward, largely because of difficulty determining the effective number of parameters, we used AIC corrected for sample size (AICc) because we were interested in making inferences about population-level parameters as opposed to inferences about particular groups in our dataset (i.e., we were interested in marginal as opposed to conditional inferences; Vaida and Blanchard 2005). Accordingly, for a marginal focus, the number of parameters is the number of fixed effect parameters (population average effects) plus the variance estimates for the random effects (Vaida and Blanchard 2005). We performed all analyses using the R (R Version 2.10.1, http://www.r-project.org, accessed 27 June 2011) function lmer (lme4 Package Version 0.999375-17, http://lme4.r-forge.r-project.org/, accessed 27 Sep 2010; see Supporting Material, available online at www.onlinelibrary.wiley.com).

Example 1: Effects of Roads and Road Density on White-Tailed Deer Resource Selection

We predicted that female white-tailed deer would avoid roads; specifically, that resource selection increases with increasing distances to roads. Also, we expected this relationship would vary among individual deer and that some of this variability would be a function of local road density (i.e., road density in an individual deer's home range). For example, if a deer has few roads in its home range we would expect the effect of distance to roads to be large and positive compared to a deer with a home range with high road

density. In the latter case, we would expect the effect of distance to roads to be either small and positive or negative because of the inability to avoid roads in a high road density area.

We captured 148 female white-tailed deer on a study area (1,304 km^2) in wildlife management unit 2G in Pennsylvania, 2005–2007, and we fitted each deer with very high frequency (VHF) or Global Positioning System (GPS) radiocollars (Norton 2010). Capture and handling protocols were approved by The Pennsylvania State University, Institutional Animal Care and Use Committee (IACUC No. 26886). The study area included forest lands managed by the Pennsylvania Game Commission and Pennsylvania Department of Conservation and Natural Resources, and privately-owned land to the south and west; 29% of the study area was privately owned and most of the landscape was forested. We divided the study area into 30-m × 30-m resource units in a Geographic Information System (ArcGIS 9.3, Environmental Research Systems Institute, Redlands, CA) and for each unit we calculated the distance to the nearest public road open to vehicular travel. We systematically selected every 400th resource unit with a random starting location to create a dataset of available habitat ($n = 1,480$). As a measure of road density in a deer's home range, for each deer, we summed the meters of road within 1,004 m of the median x–y location for each deer. We based the 1,004-m radius on the size of a circle equivalent to the average home range of 38 deer with fitted with GPS collars. We use the term "home range" in this example to represent habitat characteristics measured at a spatial scale that is representative of what deer experience in their area of use. Too few x–y locations for many deer precluded the estimation of the actual home range for individual deer.

We used software LOAS (Location of a Signal; Ecological Software Solutions, Hegymagas, Hungary) to triangulate estimated deer locations with ≥2 bearings using Andrew's estimator (White and Garrott 1990). For each deer, we defined a resource unit as used if ≥1 estimated location fell within the boundaries of the resource unit. For this example, we did not account for telemetry error but could assign a weight to used resource units according to the probability of the deer being located in the given resource unit (Samuel and Kenow 1992). A given resource unit should be classified as either used or available, but because we classified few resource units (<1%) as both used and available, we did not prevent the same resource unit from being included in both the used and available datasets (Manly et al. 2002).

We used multilevel logistic regression models to evaluate resource selection. A standard approach to modeling habitat use within a multilevel model framework is to include a random intercept to accommodate the lack of independence associated with multiple observations made on the same individual over time (i.e., a varying intercept model). For this example, we can view a varying intercept model that predicts use ($y_i = 1$ if resource unit i was a used, 0 otherwise) as a function of the distance to the nearest road (DIST) as a

2-level model as follows (the notation $j[i]$ in equation 1 indexes deer j for observation i):

Level-1: $\Pr(y_i = 1) = \text{logit}^{-1}(\alpha_{j[i]} + \beta_1 \text{DIST}_i)$, for $i = 1, \ldots n$,
Level-2: $\alpha_j \sim N(\mu_\alpha, \sigma_\alpha^2)$, $j = 1, \ldots J$

$$(1)$$

where α_j is the intercept for the jth deer, β_1 is the coefficient for effect of DIST, μ_α is the population-average intercept, and σ_α^2 is the estimated variance of deer-specific intercepts. We natural log transformed DIST and centered it to aid model convergence ($\log[\text{DIST}_i] - \overline{\log[\text{DIST}_i]}$). Although this model accommodates the lack of independence among observations taken on the same deer, we can expand it to allow the effect of DIST to vary among deer (i.e., varying slopes). For example, we hypothesized the effect of DIST on resource use would vary among deer based on deer-specific attributes, such as local landscape characteristics.

We then modified the model to allow for the effect of DIST on resource use to vary among individuals (i.e., a varying-intercept, varying-slope model). The multilevel model we used was:

Level-1: $\Pr(y_i = 1) = \text{logit}^{-1}(\alpha_{j[i]} + \beta_{j[i]} \text{DIST}_i)$, for $i = 1, \ldots n$,
Level-2: $\alpha_j \sim N(\mu_\alpha, \sigma_\alpha^2)$, $j = 1, \ldots J$,
$\quad\quad\quad \beta_j \sim N(\mu_\beta, \sigma_\beta^2)$, $j = 1, \ldots J$

$$(2)$$

where α_j is the intercept for the jth deer, β_j is the slope for the jth deer, μ_α is the population-average intercept, μ_β is the population-average effect of distance to the nearest road, and σ_α^2 and σ_β^2 are variance estimates of among deer-specific intercepts and among deer-specific slopes, respectively. A parameter that describes the between-group correlation in random effects (ρ) also is estimated.

The level-2 model in equation 2 is unconditional, which is a common practice because emphasis traditionally has been placed on estimating population average effects of covariates on resource use. However, the deer-level slopes and intercepts can themselves be modeled to provide further insight into resource use heterogeneity and to examine cross-scale interactions. We modeled slopes and intercepts as a function of the road density (RD) in each deer's home range as:

$$\alpha_j = \gamma_0^\alpha + \gamma_1^\alpha RD_j + \varepsilon_j^\alpha, \quad j = 1, \ldots, J \quad (3a)$$

$$\beta_j = \gamma_0^\beta + \gamma_1^\beta RD_j + \varepsilon_j^\beta, \quad j = 1, \ldots, J \quad (3b)$$

where $\gamma_0^\alpha, \gamma_0^\beta, \gamma_1^\alpha$, and γ_1^β are the coefficients for the intercept, the effect of DIST, and the effect of RD, on intercepts and slopes, respectively. Errors, ε_j^α and ε_j^β, have mean zero and variances σ_α^2 and σ_β^2. Also, ρ, as described in the model based on equation 2 is estimated (Gelman and Hill 2007). We report all means ±1 SE unless otherwise noted.

Example 2: Modeling Differences in Resource Selection Between Species

Assateague Island is a 59.2-km long barrier island located on the Atlantic coast of Maryland and Virginia that not only hosted native white-tailed deer but also exotic sika deer and

feral horses (*Equus caballus*). To document the effect of ungulate herbivory on Assateague Island, Sturm (2008) conducted an exclosure study to document the effect of no ungulate herbivory, deer-only, and horse and deer herbivory on plant communities. Sturm (2008) found that herbivory on some plant species could be directly attributable to either horse or deer; however, the separate effects of sika and white-tailed deer herbivory could not be identified via exclosures because of the inability to passively exclude one deer species but not the other. Thus, we modeled habitat use of sika and white-tailed deer to examine whether differences in habitat use existed and possibly attribute herbivory on specific plant species to either deer species.

We conducted this study on the Maryland portion of the island under the administration of the National Park Service, designated as Assateague Island National Seashore (3,234 ha), and the Maryland Park Service, Assateague State Park (368 ha). This portion of the island was approximately 35.5 km long from the north inlet to the Maryland–Virginia border. No agricultural activity occurred on the island and vegetation was typical of undeveloped barrier islands of the eastern coast of North America. The ocean side beach was the easternmost habitat, and to the west one encountered a primary dune system, an interdune meadow, and then a secondary set of dunes. The western side of the island typically contained shrubs and forested areas adjacent to salt marsh.

We defined the study area as the perimeter of the island itself (including salt marsh). We divided the study area into 360,181 10-m × 10-m resource units. We assigned each resource unit 1 of 6 land cover categories (sand and herbaceous areas, low shrub, tall shrub, forest, developed land, and salt marsh) based on the land cover type that covered the greatest area within each 10-m × 10-m resource unit. We calculated a distance (m) to nearest cover and defined cover as areas classified as tall shrub or forest because cover has been found to be a predictor of cervid habitat use (Mysterud and Ostbye 1999). Of the available resource units, we systematically selected every 400th resource unit with a random starting location to create a dataset of available habitat ($n = 901$).

We captured and radiocollared 11 white-tailed deer and 24 sika deer. Capture and handling protocols were approved by The Pennsylvania State University, Institutional Animal Care and Use Committee (IACUC No. 21758). In August–September 2007 we systematically located each deer up to 4 times/week, using ground based VHF telemetry, in the morning (0400–1000 hours), mid-day (1000–1700 hours), and evening (1700–2300 hours). We used LOAS to triangulate estimated deer locations with a 95% error ellipse of <1.0 ha using Andrew's estimator (White and Garrott 1990). We used the intersection of ≥3 telemetry bearings collected within 20 min to minimize location error caused by animal movement. For each deer, we defined a resource unit as used if ≥1 estimated location fell within the boundaries of the resource unit. For this example, we did not account for telemetry error but could assign a weight to used resource units according to the probability of the deer being located in the given resource unit (Samuel and Kenow 1992). A given resource unit should be classified as either used or

available, but because we classified few resource units (<1%) as both used and available we did not prevent the same resource unit from being included in both the used and available datasets (Manly et al. 2002).

We used the general model structure described in equations 1–3 to evaluate whether differences in resource selection differed between white-tailed and sika deer. Two notable differences between the models fitted in Example 1 were that instead of using a continuous covariate to model slopes and intercepts (e.g., home range road density), we used a categorical predictor (species: 1, white-tailed deer; 0, sika deer). In addition, instead of a single varying slope parameter as in Example 1 there were 6 (one for distance to nearest cover and 5 for the habitat indicator variables). We defined sand and herbaceous habitat as the reference category. The multilevel model we used was:

$$\text{Level-1: } \Pr(y_i = 1) = \text{logit}^{-1}\left(\alpha_{j[i]} + \sum_{k=1}^{6} \beta_{kj[i]} X_{ki}\right), \quad (4)$$
$$\text{for } i = 1, \ldots, n$$

where y_i is as defined in Example 1, α_j is the intercept for the jth deer and β_{kj} are the slopes for the jth deer for covariate X_{ki}. The X_{ki} represents the log-transformed and centered distance to nearest cover ($\log[X_{ki}] - \overline{\log[X_{ki}]}$) and each of the 5 habitat index variables.

$$\text{Level-2: } \alpha_j = \gamma_0^\alpha + \gamma_1^\alpha \text{Species}_j + \varepsilon_j^\alpha, \quad j = 1, \ldots, J \quad (5a)$$

$$\beta_{kj} = \gamma_0^{\beta_k} + \gamma_1^{\beta_k} \text{Species}_j + \varepsilon_j^{\beta_k}, \quad j = 1, \ldots, J \quad (5b)$$

where γ_0^α, $\gamma_0^{\beta_k}$, γ_1^α, and $\gamma_1^{\beta_k}$ are the coefficients for the intercept, the effect of covariate X_{ki}, and the effect of species on intercepts and slopes, respectively. Errors, ε_j^α and $\varepsilon_j^{\beta_k}$, had mean zero and variances σ_α^2 and $\sigma_\beta^2 k$.

RESULTS

Example 1: Effects of Roads and Road Density on White-Tailed Deer Resource Selection

For the 148 deer we used in the analysis, the number of times an individual was located ranged from 1 to 127 ($\bar{x} = 61$, SD = 37). For both used and available habitats, the distance to the nearest road ranged from 0.05 m to 3,189 m ($\bar{x} = 522$, SD = 490), whereas road density ranged from 0 m to 14,580 m ($\bar{x} = 3,636$, SD = 2,632). The first model was a varying intercept, varying slope model to estimate the population-average effect of distance to the nearest road and to examine variability in the effect of the distance to the nearest road among individual deer. We found a positive effect of distance to the nearest road on resource selection ($\hat{\mu}_\beta = 0.14 \pm 0.06$; Table 1). However, there was substantial variability in the effect of distance to the nearest road on resource selection among individual deer ($\hat{\beta}_j$ ranged from -0.62 ± 0.09 to 3.49 ± 0.29), and the slopes exhibited a skewed distribution (Fig. 1). One advantage of multilevel modeling is that we can attempt to explain variability in

Table 1. Fixed effect parameter estimates and 85% CI, and random effect parameter estimates from a varying intercept, varying slope model and a model with a deer-specific covariate to model heterogeneity in resource selection for white-tailed deer, Pennsylvania, 2005–2007.

Varying intercept, varying slope				Variation among slopes and intercepts			
Parameter	Estimate	SE	85% CI	Parameter	Estimate	SE	85% CI
Intercept ($\hat{\mu}_\alpha$)	−3.74	0.86	−4.98 to −2.50	Intercept ($\hat{\gamma}_0^\alpha$)	−5.22	0.23	−5.55 to −4.89
Distance to road ($\hat{\mu}_\beta$)	0.14	0.06	0.05–0.23	Distance to road ($\hat{\gamma}_0^\beta$)	2.22	0.09	2.09–2.35
				Road density ($\hat{\gamma}_1^\alpha$)	0.20	0.03	0.16–0.24
				Road density ($\hat{\gamma}_1^\beta$)	−0.29	0.01	−0.30 to −0.28
$\hat{\sigma}_\alpha^2$	1.04			$\hat{\sigma}_\alpha^2$	0.68		
$\hat{\sigma}_\beta^2$	0.61			$\hat{\sigma}_\beta^2$	0.05		
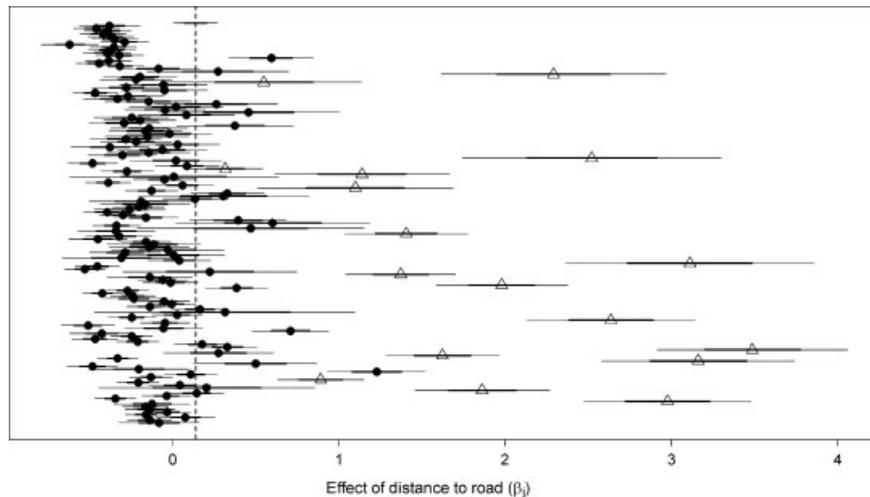
Figure 1. Deer-specific slopes (circles and triangles = mean, thick line = ±1 SE, thin line = ±2 SE), from a varying intercept, varying slope multilevel model (see equations 1 and 2), for the effect of distance to the nearest road on habitat use for 148 white-tailed deer, Pennsylvania, 2005–2007. Dashed vertical line is population-average effect. Open triangles indicate deer with zero road density in home range.

resource selection among individual deer. We predicted that this variability might be explained by the road density in an individual's home range and, in fact, the skewed distribution (Fig. 1) is caused by a few deer with home ranges that contain no roads (i.e., as predicted, deer with no roads in their home range have a large positive effect of distance to the nearest road).

In the second model, the addition of the deer-specific covariate to the varying intercept, varying slope model decreased AICc by 284 units (varying intercept, varying slope number of parameters $K = 5$, maximized log likelihood = −34,824, AICc = 69,658; model with deer-specific covariate $K = 7$, maximized log likelihood = −34,680, AICc = 69,374), indicating a substantial improvement in model fit (Table 1). The effect of road density on deer-specific slopes was negative ($\hat{\gamma}_1^\beta = -0.29 \pm 0.01$), suggesting that the effect of the distance to the nearest road decreases in magnitude as the density of roads in a home range increases (Fig. 2). However, if deer with no roads in their home range were excluded from the analysis the strong negative relationship between slopes and road density remained (Fig. 2 inset).

Example 2: Modeling Differences in Resource Selection Between Species

For the 35 deer we used in the analysis, the number of times an individual was located ranged from 1 to 34 ($\bar{x} = 28$,

SD = 7). For used and available habitats, the distance to cover ranged from 0 m to 1,032 m ($\bar{x} = 70$, SD = 127). Resource use for sika and white-tailed deer varied as a function of habitat type and distance to cover (Table 2). Relative to sand and herbaceous habitat, low shrub, salt
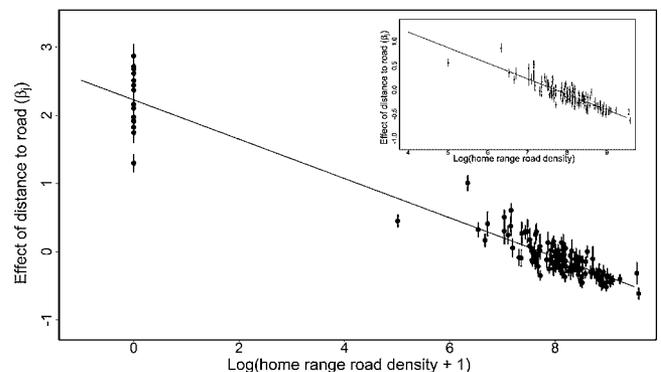
Figure 2. Deer-specific slopes for the effect of distance to the nearest road as a function of log home range road density for white-tailed deer, Pennsylvania, USA, 2005–2007. Circles are means and vertical lines are ±1 SE. The line is the estimated multilevel regression line. Inset shows the analysis when we excluded deer with no roads in their home range from the analysis.

Table 2. Fixed and random effect parameter estimates from a multilevel resource selection function for white-tailed deer and sika deer, Assateague Island, Maryland, 2007. The reference level for species is sika deer and for land cover type is sand and herbaceous habitat.

	Fixed effects			Random effects ($\hat{\sigma}_k$)
Parameter	Estimate	SE	85% CI	
Intercept ($\hat{\gamma}_0^{\alpha}$)	−4.63	0.34	−5.12 to −4.14	0.89
Species ($\hat{\gamma}_0^{\beta}$)	0.20	0.62	−0.69–1.10	
Low shrub ($\hat{\gamma}_0^{\beta 1}$)	1.23	0.39	0.67–1.80	1.08
Salt marsh ($\hat{\gamma}_0^{\beta 2}$)	0.39	0.32	−0.07–0.86	0.58
Tall shrub ($\hat{\gamma}_0^{\beta 3}$)	−0.81	0.54	−1.59 to −0.02	1.37
Forest ($\hat{\gamma}_0^{\beta 4}$)	−0.83	0.60	−1.69–0.04	1.81
Developed ($\hat{\gamma}_0^{\beta 5}$)	1.09	0.55	0.30–1.89	1.97
Distance to cover ($\hat{\gamma}_0^{\beta 6}$)	−0.89	0.14	−1.09 to −0.69	0.48
Species:low shrub ($\hat{\gamma}_1^{\beta 1}$)	0.28	0.70	−0.73–1.30	
Species:marsh ($\hat{\gamma}_1^{\beta 2}$)	−0.12	0.60	−0.98–0.75	
Species:tall shrub ($\hat{\gamma}_1^{\beta 3}$)	−0.18	0.97	−1.58–1.23	
Species:forest ($\hat{\gamma}_1^{\beta 4}$)	0.24	1.07	−1.30–1.80	
Species:developed ($\hat{\gamma}_1^{\beta 5}$)	0.07	0.99	−1.36–1.51	
Species:distance to cover ($\hat{\gamma}_1^{\beta 6}$)	−0.08	0.24	−0.43–0.27	

marsh, and developed were used more and tall shrub and forest were used less. Also, relative use decreased as distance to cover increased (population-average estimate $(\hat{\gamma}_0^{\beta 6}) = -0.89 \pm 0.14$). However, the magnitude of the effect of the covariates also varied among deer (Table 2). The primary goal of this analysis was to evaluate whether species could explain some of the observed variability. In this case, there was little evidence to suggest that habitat use differed between species (Fig. 3). All species effects in the model had large standard errors (Table 2) and the model that included species effects had an AICc that was 7 units greater than the varying intercept, varying slope model without species effects.

DISCUSSION

Our goal was to illustrate the extension of multilevel resource selection models, beyond the simple random intercept model, to quantify and explain heterogeneity in resource selection. Quantifying and explaining heterogeneity in resource selection is important because heterogeneity is likely common within and among species (Duchesne et al. 2010), and understanding this heterogeneity potentially can lead to better conservation and management decisions. In Example 1, we illustrated how the effect of distance to the nearest road varied among white-tailed deer and that the magnitude of the effect for individuals was largely driven by local-scale landscape characteristics. Consequently, deer behavior changes with road density and management decisions based on the assumption that deer avoid roads may not be warranted, even though the population level response indicates deer avoid roads. This example emphasizes the importance of examining cross-scale interactions and considering habitat at multiple spatial scales when fitting RSFs because local habitat conditions often are constrained by

larger-scale landscape characteristics (Boyce 2006, Mayor et al. 2009).

If we ignored the constraint home range road density imposes on the effect of distance to road on white-tailed deer resource selection (Fig. 4A), we would have concluded that resource selection in areas of high road density is lower than in areas with low road density. However, by incorporating information about road density at the home range scale (3.2 km^2) we see that only in areas with low road density do deer avoid roads and that road use is even slightly greater in areas with greater road density (Fig. 4B). If we had not used a multilevel model to incorporate road density at the home range scale to modify the function of distance to road in the RSF, we would have failed to identify what seems to be plasticity in deer behavior with respect to road density and incorrectly concluded that deer avoid roads.

Example 2 illustrates a quantitative approach to identify differences in resource selection between groups. The use of multilevel models to examine differences in resource selection among groups allows for the use of information theoretic approaches for assessing competing hypotheses about resource selection and provides uncertainty estimates for an estimated difference. Other approaches require ad hoc methods to assess whether resource selection differences exist between species. Our results of the sika–white-tailed deer analysis agree with the conclusion reached by Christensen (2010) where she created a map of sika resource selection and white-tailed resource selection and used the difference in RSF values to evaluate whether resource selection differed between species. However, Christensen (2010) could not assess whether these differences were statistically significant, assess the strength of competing hypotheses, or quantify uncertainty in estimated RSF differences. Regardless of whether an ad hoc method or multilevel modeling is used, the biological significance of any difference in resource selection must still be evaluated. We argue, however, that
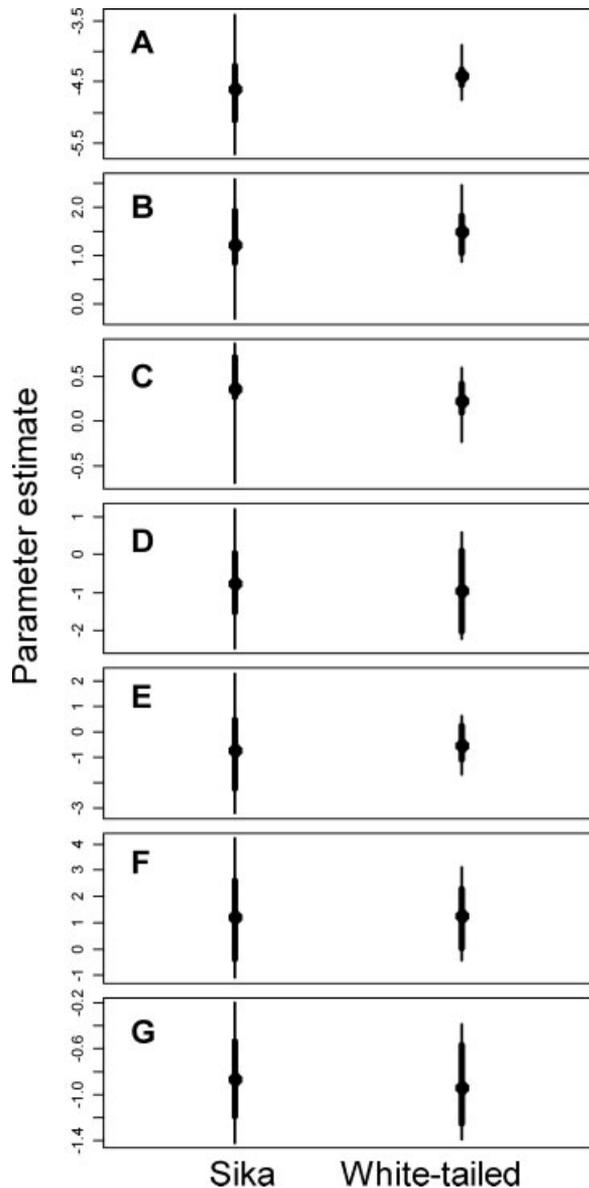
Figure 3. Species-specific predicted effects of beach and dune habitat for deer at a distance to cover equal to the mean distance to cover (A; approx. 40 m; deer-specific intercepts), low shrub (B), marsh (C), tall shrub (D), forest (E), developed land (F), and distance to cover (G) on resource use for white-tailed and sika deer, Assateague Island, Maryland, USA, 2007. Circles are means, thick lines are 25th and 75th percentiles, and thin lines are 5th and 95th percentiles.

the multilevel modeling approach provides a much more flexible and objective method for assessing differences in resource selection.

Multilevel modeling also permits graphical representations of modeled relationships to interpret results, such as the effect of distance to road as related to road density in a deer's home range (Fig. 2). Similarly, differences in resource selection between sika deer and white-tailed deer were assessed graphically (Fig. 3).

The details of estimation and the properties of multilevel models are described elsewhere (e.g., Gelman and Hill 2007), however, one property of multilevel models in par-

ticular is worthy of discussion within the context of RSF modeling. As described by Gelman and Hill (2007), multi-level models share information across individual deer to improve precision of the population level model of resource selection. There are 2 alternatives to this approach in which 1) complete pooling of data across deer provides a single RSF (e.g., Neu et al. 1974) or 2) an RSF is modeled separately for each deer (e.g., Sawyer et al. 2006). When data are pooled to estimate a single RSF, the assumption is that every deer has the same resource selection or else unequal sample sizes among deer will introduce bias. Also, the experimental unit becomes the animal location rather than individual deer. When a separate RSF is modeled for each deer, unequal sample sizes are less of a problem even though the experimental unit (e.g., individual deer) is appropriate. However, sparse data may preclude estimation of an RSF for some individuals.

Sharing of information across experimental units in multi-level estimation is possible with the assumption that individual-specific parameters belong to a probability distribution, e.g., $\alpha_j \sim N(\mu_\alpha, \sigma_\alpha^2), j = 1, \ldots, J$. As a result, deer-specific parameter estimates based on few data will be estimated closer to the mean. The advantage is that the relative contribution of data from each individual (i.e., sample size) is incorporated into the population-level parameter estimates. This is not possible when data across deer are pooled and or when individual RSFs are modeled (or at least methods that address unequal samples sizes are less efficient). In addition, this property of multilevel modeling allows for the estimation of individual-specific models even with small sample sizes for some animals. For example, in both of our examples there were a few deer with only a single location and several deer with <10 observations. Outside of a multi-level modeling framework (e.g., estimating separate RSF models for each deer), animals with as few as 10 locations would have to be excluded from the analysis, which is an inefficient use of data and could result in the exclusion of a large number of individuals.

The effect of unequal sample sizes among animals is apparent in the influence on individual-specific parameter estimates. Animals with larger sample sizes will be less affected by the population mean, whereas animals with sparse data, and thus greater uncertainty in resource selection, will have individual-specific parameters estimated closer to the mean. This characteristic of multilevel models is termed a shrinkage effect because the variation among individual-specific parameter estimates is closer to the mean than if they were estimated independently of other animals. For example, in Example 1, the population average intercept and slope for the effect of distance to nearest road was −3.74 and 0.14, respectively. A deer with 117 observations had an estimated intercept and slope of −2.54 and 0.002 independent of other deer (i.e., parameter estimates derived from a model fitted to only that deer's data), which is similar to the slope and intercept of −2.55 and 0.004 in the multilevel model (i.e., parameters estimated from a model using data from all deer). In contrast, the intercept and slope estimates for a deer with 3 observations were −6.20 and −0.045 independent of other
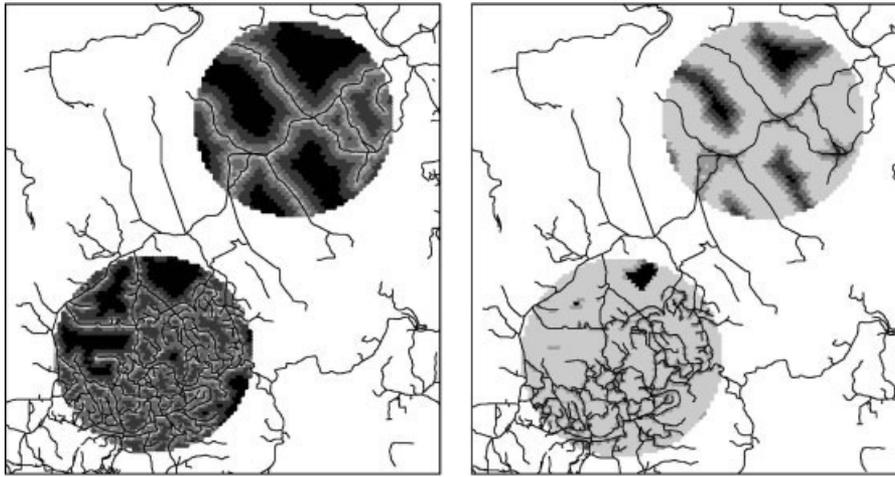
Figure 4. Chorograph of relative habitat use (darker shading indicates greater use) as (A) a function of distance from road and (B) distance from road and road density within the surrounding 1,004 m for female white-tailed deer in northcentral Pennsylvania, 2005–2007. Note that because the measure of resource selection is relative, it is inappropriate to compare intensity of use between (A) and (B).

deer but were much closer to the population average in the multilevel model (−5.59 and 0.21).

Although we have presented methods for estimating parameters using frequentist methods, Bayesian methods can also be used to estimate RSF parameters. For example, Thomas et al. (2006) fitted a Bayesian random effects discrete-choice model for caribou (*Rangifer tarandus*) on an Arctic coastal plain. Although the model allowed for random slopes, they did not explicitly model variation among slopes using individual-level covariates as presented here. Based on our experience, although fitting multilevel logistic regression models in a Bayesian framework is relatively straightforward in theory, in practice it may not be practical or possible with large data sets, which are common in resource selection studies. For example, we attempted to fit the model presented in equation 1 using WinBUGS (MRC Biostatistics Unit, Cambridge, United Kingdom) on a notebook computer with an Intel® Core i5 central processing unit with a clock rate of 2.67 gigahertz (Intel Corp., Santa Clara, CA) and 4 gigabytes of random access memory. The model ran for just over 11 hr and did not converge (we used 500 iterations as a burn-in period and 16,000 iterations total as a test run simply to assess the amount of time required to fit the model). Although fitting multilevel resource selection models may not always be practical using Bayesian methods, in many cases (i.e., with a large numbers of animals and a relatively large among-animal variance) parameter estimates should be similar to those obtained using the R function lmer.

MANAGEMENT IMPLICATIONS

Models of resource selection are being used increasingly to predict or model the effects of management actions (e.g., Sawyer et al. 2006) rather than simply quantifying habitat selection (e.g., Verner et al. 1986). Multilevel models can improve our understanding of how resource selection varies among individuals and provide objective, quantifiable

approaches to assess differences or changes in resource selection.

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