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Habitat selection of rodents along a piñon–juniper woodland–savannah gradient

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The biodiversity of piñon–juniper (P-J) woodlands of western North America has received increasing attention from conservationists because of concerns about woodland invasion into adjacent shrub-steppe communities. Small mammals contribute substantially to the faunal diversity of P-J woodlands, but the responses of small mammals to the inherent structural complexity of these woodlands have not been well described. We used occupancy modeling and ordination to describe habitat selection along a woodland–savannah gradient of 4 species of rodents, including 2 putative P-J woodland specialists, *Peromyscus truei* and *Tamias dorsalis*. We accounted for the influences of season and prior conspecific capture on detectability. *P. truei* and *T. dorsalis* preferred old-growth woodland sites near rock outcrops with high canopy and bare-ground cover and low herb and shrub cover. *Tamias minimus* preferred savannah sites with high shrub and grass cover farther from rock outcrops. We found no evidence of resource selection along the gradient by *Perognathus parvus*. Our results provide insight into the role of habitat selection in facilitating coexistence among closely related species within P-J woodlands and suggest that management efforts that better discriminate between old, presettlement stands and young, invasive stands may enhance regional biodiversity. We demonstrate an effective application of occupancy modeling for describing habitat selection of cryptic rodents, which are particularly prone to imperfect detection. DOI: 10.1644/09-MAMM-A-060.1.

Key words: detection probability, habitat selection, Idaho, occupancy modeling, *Peromyscus truei*, piñon–juniper woodland, principal component analysis, rodents, *Tamias dorsalis*

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The piñon–juniper (P-J) woodlands of western North America have received increasing attention because of concerns about woodland invasion into adjacent shrub-steppe communities (Baker and Shinneman 2004). Although the woodland–shrubland boundary has been highly dynamic over the Holocene, the rate of infilling and expansion is believed to have increased during the mid-19th century as a result of altered fire regimes and climatic conditions (Burkhardt and Tisdale 1976; Miller and Rose 1995; Miller and Wigand 1994; Soulé et al. 2004). The management emphasis has been on controlling woodland expansion and, especially, tree removal, and very little consideration has afforded the conservation of these woodlands for biodiversity (Baker and Shinneman 2004; Brockway et al. 2002; Waichler et al. 2001; Willis and Miller 1999).

Although presettlement, old-growth P-J woodlands have been recognized as important, the inherent structural and compositional complexity of these woodlands have complicated efforts to distinguish between pre- and postsettlement

stands (Jacobs et al. 2008; Miller et al. 2000; Waichler et al. 2001; Weisberg et al. 2008). As a result of topoedaphic and historical factors, P-J woodlands occur as a complex mosaic of older and younger stands with attributes best characterized as a gradient (Jacobs et al. 2008; Waichler et al. 2001). However, woodland removal efforts involving mechanical methods or prescribed fire often have been indiscriminant with respect to stand age or structure (Baker and Shinneman 2004; Brockway et al. 2002; Miller et al. 2000). Likewise, studies of fauna associated with P-J woodlands have not adequately addressed differences in stand age and complexity nor the effects of different woodland management practices on animal communities (Willis and Miller 1999). This is particularly relevant in Idaho, where the P-J woodland vegetation type reaches its northern geographic extent in conjunction with several state species of concern, including 2 putative P-J woodland rodent



specialists, *Peromyscus truei* (piñon mouse) and *Tamias dorsalis* (cliff chipmunk—Idaho Department of Fish and Game 2005).

Small mammals contribute substantially to the faunal diversity of P-J woodlands, and a number of experimental studies have compared small-mammal species richness and abundance among treated and untreated woodland stands, with mixed results (Willis and Miller 1999). Woodland removal treatments such as chaining or prescribed burning have been associated with increases in small-mammal richness and abundance in some cases and opposite patterns in others (O'Meara et al. 1981; Severson 1986; Willis and Miller 1999). Willis and Miller (1999) attributed these discrepancies to inadequate replication across the range of successional conditions encountered.

Studies of habitat selection offer an alternative approach for addressing management and conservation concerns for wildlife populations and their critical habitats. Habitat selection at the local scale enables closely related organisms to coexist, thereby contributing to broader patterns of biodiversity (Morris 2003; Rosenzweig 1981). Knowledge of habitat selection strategies of P-J woodland specialists such as *P. truei* and *T. dorsalis* can provide a better understanding of how P-J woodlands actually contribute to regional species pools and may help managers make informed decisions about how to control woodland expansion. However, few habitat selection studies have been conducted on P-J woodland rodent communities, particularly within a management context. In Wyoming, Rompola and Anderson (2004) showed that *P. truei* selected woodlands with higher canopy cover, lower forb cover, far from rock outcrops, whereas *T. dorsalis* was less selective and was associated more with sites with low bare-ground cover, high grass cover, and taller shrubs. Previous habitat descriptions have noted a general association with P-J overstory and proximity to rocks for both species (Hart 1992; Hoffmeister 1981).

Identifying patterns of habitat selection is complicated by the inherent plasticity in habitat selection, which is a function of population density, resource availability, and species interactions (Morris 2003; Schooley 1994). Models that are used to estimate species–habitat relationships therefore must account for spatiotemporal variability in these factors, and, ideally, should reflect the unique community characteristics and environmental conditions in which management decisions are to be made. Estimates of habitat selection also can be biased by detection error, particularly when cryptic species such as small mammals are involved (Gu and Swihart 2004; MacKenzie et al. 2002; Tyre et al. 2003). An efficient approach to modeling habitat selection is needed that can support the needs of conservation and resource management programs to identify critical habitats for local populations and account for imperfect detection of target species.

MacKenzie (2006) suggested that a recently developed class of occupancy models (MacKenzie et al. 2002, 2003) could be used as a type of resource selection function to estimate habitat selection from random samples of used and unused

locations (Manly et al. 2002). This approach is noteworthy because it relies only on presence–absence surveys, rather than on other, more informative but costly metrics of abundance, and can account for imperfect detection. We used occupancy models to describe habitat selection of rodent species across a landscape of P-J stands in southern Idaho. Our objective was to develop resource (habitat) selection functions for a suite of common species in P-J woodlands, including *P. truei* and *T. dorsalis*, *Tamias minimus* (least chipmunk), and *Perognathus parvus* (Great Basin pocket mouse). We were particularly concerned with *P. truei* and *T. dorsalis* and sought to ascertain whether these 2 species selected for woodland characteristics that could be targeted by land managers involved in the management and restoration of P-J woodlands for biodiversity conservation. We evaluated 2 general hypotheses for each of the 4 species: a null model describing random use of attributes of P-J woodlands; and an alternative model of nonrandom, selective use along the woodland–savannah environmental gradient, described through ordination. We accounted for heterogeneity in detection probabilities with capture- and season-specific covariates and obtained site-use probabilities for each species along the environmental gradient, inferring evidence of habitat selection when a trend was present in those probabilities.

MATERIALS AND METHODS

Study area and site selection.—Our study area included portions of City of Rocks National Reserve and adjacent Castle Rocks State Park, located in the Albion Mountains of Cassia County, Idaho (113°39–43'N, 42°3–8'W; Fig. 1). The area is situated in a unique biogeographic setting in which *Pinus monophylla* (single-leaf piñon pine) and *Juniperus osteosperma* (Utah juniper) reach their northern distributional limits in conjunction with massive granitic domes and pinnacles that dominate much of the landscape. Vegetation conditions in the sample area ranged from dense woodland with sparsely vegetated understory to open savannah–steppe ecotones dominated by *Artemisia tridentata* (big sagebrush) and bunchgrasses. Areas of bare ground occurred beneath dense stands of piñon pine and juniper and were covered in duff and mineral soil. The substrate of some sites was exposed granite rock.

We chose survey sites from approximately 300 ha of scattered stands of P-J woodland within a 1,100-ha study area that was drawn as a 500-m buffer around the 2 unpaved roads that traversed the northern portion of the reserve and state park (Fig. 1). A recent park land-cover map was used to identify target P-J woodland map alliance classes (Wilson 2005). The map classification followed the National Vegetation Classification System (Bourgeron and Engelking 1994; Comer et al. 2003; NatureServe 2009), and target classes included a range of alliances dominated by *P. monophylla* and *J. osteosperma*. Canopy cover conditions of target classes ranged from open-canopy savannah (canopy cover from 5% to 20%) to closed-canopy woodlands (cover > 25%—Bourgeron and Engelking

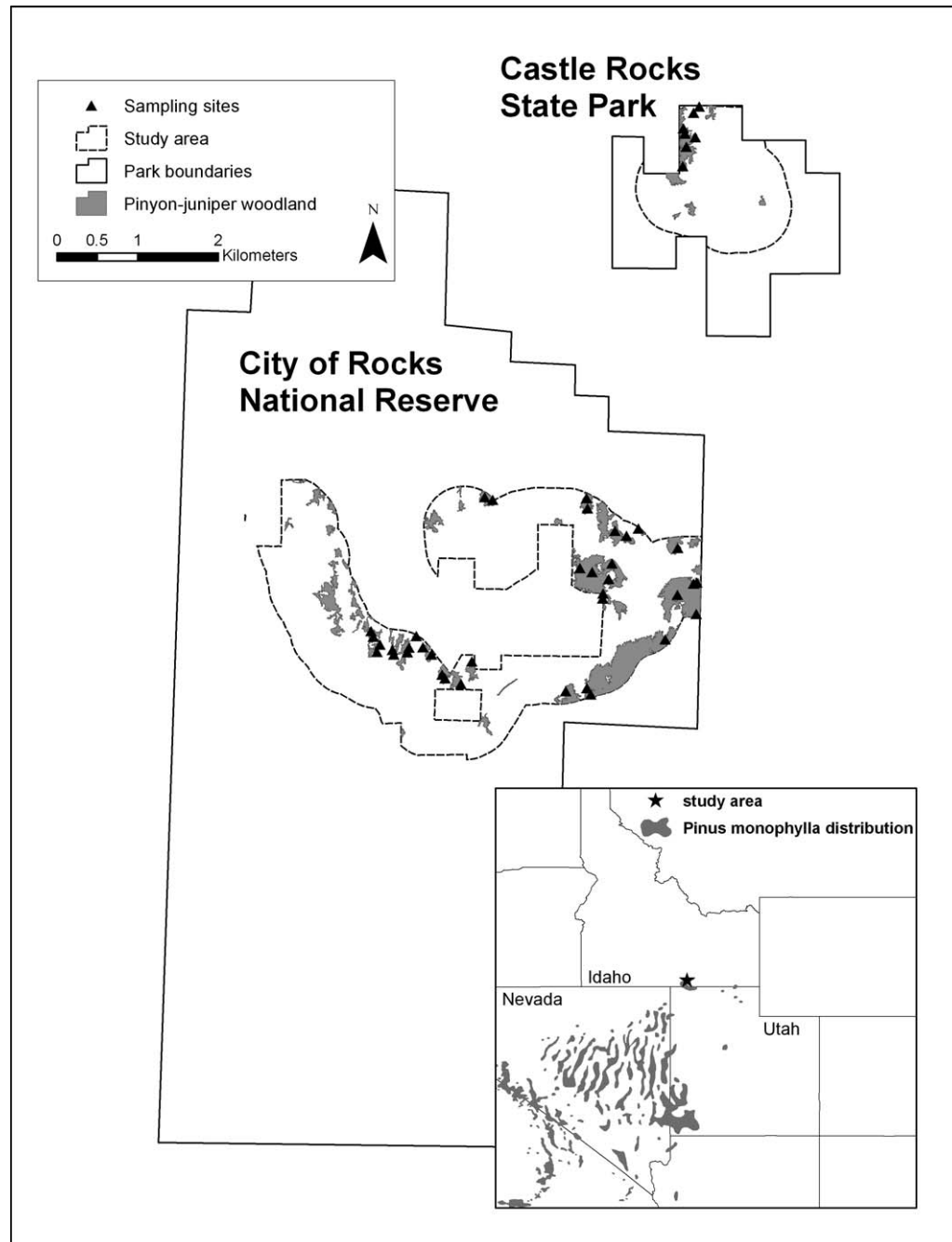


FIG. 1.—Study area within the City of Rocks National Reserve and Castle Rocks State Park, southcentral Idaho. Sampling sites were determined from a random sample of global positioning system coordinates within areas of mapped piñon–juniper within the study area (dashed line). Nontarget land cover was mostly shrubland dominated by *Artemisia tridentata*. The map inset shows the study area in relation to the approximate distribution of *Pinus monophylla* in the western United States (data from Little [1971]). The distribution of *Juniperus osteosperma* shows a similar pattern and also reaches its northern limit in southern Idaho.

1994; NatureServe 2009). We selected 44 point locations (sites) within these stands drawn from a simple random sample using a geographic information system (ArcGIS, version 9.1; ESRI, Inc., Redlands, California; Fig. 1). Not all sites were sampled each trapping session, but the occupancy models we used were robust to missing data, with the net effect being a loss of information for estimating model parameters (MacKenzie et al. 2006). Only 36 sites were sampled in all sessions

because of logistical constraints, but we added 8 sites as additional project resources became available. The average nearest-neighbor distance between sites was 150 m, and none were closer than 50 m. The spatial configuration of the sample locations was constrained by the patchy distribution of target vegetation (Fig. 1).

Capture methods and site characterization.—We trapped small mammals during the periods 9 June–20 July and 1–28

September 2006 (sessions 1 and 2, respectively) and 1–28 June 2007 (session 3). Each trapping session lasted 4 or 6 weeks. We assumed closure to changes in site-use status by each species within each session. We assumed that sufficient time existed between each of the 3 trapping sessions to allow for changes in site use. The closure assumption is fundamental to the occupancy modeling structure and tenable for our study given our interpretation of model parameters in terms of use rather than occupancy (MacKenzie 2006). Our trapping periods coincided with periods of reproductive activity and occurred outside periods when prolonged torpor could have influenced detection probabilities (Hart 1992; Hoffmeister 1981; Verts and Carraway 2001; Verts and Kirkland 1988).

At each site we placed 20 folding Sherman live traps ($8 \times 9 \times 23$ cm; H. B. Sherman Traps, Inc., Tallahassee, Florida) arrayed along 2 perpendicular 20-m transects centered on the random point. Pairs of traps were placed at 5-m intervals along each 10-m transect arm. This layout established a 14×14 -m square sample unit with transects running diagonally through the unit, resulting in the placement of 4 traps in the center and 4 traps along each arm. We assumed that detection of a species within one of these units indicated site use. The 200-m^2 sampling units were small enough to fall within the individual home ranges of target species but large enough to be encountered regularly during activities such as foraging. This helped us meet the closure assumption requirement that units were either always used or always unused by a target species during a trapping session (MacKenzie 2006). We also assumed that the sampling unit dimensions were large enough to describe the patchy habitat conditions present in the study area. Our intent was to match the grain of study with the range of regular movement of target species and scale of patchiness present within woodland stands. This design also represented our best effort at balancing the costs of overall sample size with information gathered at each site. Because our interest was in species-level detections, we reduced the amount of information collected at each site so as to increase sample size.

Traps were prebaited and locked open for 3 nights and set to trap for 3 consecutive nights. We assumed that prebaiting reduced some of the site-use bias inherent in a luring program by allowing animals to acclimatize to the presence of the new food supply. We baited traps with pieces of peanut butter balls rolled in black oil sunflower seed. Traps were washed between each of the 3 trapping sessions. Polyfiber batting was provided in each trap for added thermal protection. Traps were set in late afternoon, checked after dawn, and closed during the day. Captured animals were identified quickly to species and sex and released. Animals were not marked because our interest was in recapturing target species rather than individuals to estimate species detection probabilities. We used the binary pattern of species detections from captures to construct detection history matrices for each 3-night trapping session for subsequent occupancy modeling. A small subset of captured animals was collected as voucher specimens to confirm species identification. Specimens were prepared and curated by the University of Washington Burke Museum of

Natural History (UWBM). All capture and handling procedures were approved by the University of Idaho Animal Care and Use Committee (protocol 2007-38) and followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

False-positive identification of target species is a problematic source of bias in occupancy modeling (MacKenzie et al. 2006). To minimize misidentification of animals in the field, particularly of cryptic *Peromyscus* and *Tamias*, we followed keys provided by Fitzgerald et al. (1995) and Verts and Carraway (1998) and examined study skins of target species. We compared our field identifications with identifications of voucher specimens by UWBM curators between sampling sessions. We also confirmed identification of 7 *Peromyscus* from a genetic analysis of cytochrome-*b* sequences conducted by Portland State University (GenBank accession numbers FJ800578–FJ800584; J. Zinck, Portland State University, pers. comm.).

Studies of vegetation characteristics and rodent use of P-J habitats typically have included measures of tree canopy cover and understory vegetation and proximity to rock outcrops (Jacobs et al. 2008; Rompola and Anderson 2004; Waichler et al. 2001; Weisberg et al. 2008). We measured similar variables to facilitate comparisons with previous studies. We estimated the cover of vegetation, bare ground, and rock at each site by characterizing the vegetation and substrate at 1-m point intervals along each 20-m trapping transect (Elzinga et al. 2001). We assigned cover types using the following categories: bare cover, which included rock, bare ground, and litter; herbaceous cover, which included grasses and forbs; shrub cover; and tree cover. We estimated the distance from the intersection of the 2 transects to the nearest large rock judged in the field to be $\geq 5\text{ m}^2$ in area and also to the woodland edge. We corrected field distance estimates using 1-m resolution orthophotographs of sites in a geographic information system.

Data analyses.—We derived the most biologically meaningful environmental gradients represented in the sample using principal component analysis (PCA) with PC-ORD software (MJM Software, Gleneden Beach, Oregon). PCA is an efficient method to synthesize correlated attributes of sampling units, reducing the number of model covariates to consider, and providing a description of important features of habitat in terms of gradients (McCune and Grace 2002). Values of habitat variables were divided by the maximum value so that all were scaled between 0 and 1. Distance to rock was arcsine-square root transformed to reduce skewness. We examined axes scatterplots to detect arch effects and compression and to establish that relationships between variables were generally linear. We also considered outliers that were >2.5 SD units from the mean, although none were found. We evaluated the relative importance of PCA axes by considering the percent variance explained and the broken-stick eigenvalue criterion (McCune and Grace 2002). We based our interpretation of important axes on eigenvector loadings $> |0.55|$ (McGarigal et al. 2000), although we

considered potentially meaningful variables with smaller loadings. Finally, we used the scores from the most important and interpretable axes as covariates in occupancy models to generate site-use probabilities.

We evaluated a set of 6 models for each species that focused on the 2 central hypotheses of interest: a null model of random site use along the woodland–savannah gradient, and an alternative model of nonrandom, selective use along the gradient represented by the sample. The model set also enabled us to evaluate the relative importance of seasonal variation in detectability among the 3 trapping sessions and the effect of previous capture of conspecifics within the same session on detectability. We modeled seasonal variation with binary indicator variables for each session. An $n \times 9$ survey-specific indicator covariate matrix denoting prior conspecific capture within each 3-night session for a given site provided an additional parameter to account for the effects of prior capture. In our approach, several mechanisms could produce such an effect. For example, capture of an individual of a species at 1 trap could produce a species-specific scent cue that affects captures of conspecifics at this and other traps throughout the site (e.g., Heske 1987). In addition, detectability could be affected by individuals becoming habituated to traps (i.e., trap-happy or trap-shy). Finally, the territorial behavior of a species relative to the effective size of the sample unit could reduce the chance of detecting >1 individual at a given site, causing detectability to decline after prior capture, particularly if a territorial individual becomes trap-shy after 1st capture. Because we did not mark individuals, however, we cannot easily distinguish between these and other possible explanations.

We included both single-season and multiseason model parameterizations developed by MacKenzie et al. (2002, 2003) in model sets. The single-season model assumed no change in use throughout the study. This model was notated as $\Psi(\text{PCA axes})p(\text{session, prior capture})$, where Ψ represents site-use probabilities as a function of dominant PCA axes, and where p represents detection probabilities as a function of session and prior capture. We also included models of nonrandom change in site use between sessions using an alternative parameterization of the multiseason model developed by MacKenzie et al. (2003) that describes a stationary Markov process with the additional parameter ϵ included to account explicitly for local “extinction,” or, in this case, a change from used to unused site status between sessions (i.e., $\Psi(\text{PCA axes})\epsilon(.)p(\text{session, prior capture})$). This model structure assumes equilibrium between rates of change in site use over the 2-year study period and allows for sites used in a prior session to be unused in subsequent sessions. Therefore, the extra parameter ϵ accounted for additional site-use variability not accounted for by PCA scores. Our null model, notated as $\Psi(.)\epsilon(.)p(\text{session, prior capture})$, included only an intercept for site use but was fully parameterized for detectability and also included ϵ .

Candidate models were fit to the observed site detection histories from all 3 sessions for each individual species using PRESENCE software (version 2.0; United States Geological

Survey Patuxent Wildlife Research Center, Laurel, Maryland) and evaluated using Akaike’s information criterion adjusted for small sample size (AIC_C —Burnham and Anderson 2002). *P. truei* and *T. dorsalis* were our primary species of interest, and we included other common species that were well represented in the data set (e.g., $0.2 < \text{naïve } \Psi < 0.8$ —MacKenzie et al. 2006). Species encountered rarely or constantly (given a fixed sampling unit dimension) are not well addressed in an occupancy modeling framework.

Model parameters were estimated by maximum-likelihood procedures, and covariates were modeled using the logit link (i.e., logistic regression) following procedures outlined by MacKenzie et al. (2002, 2006). We evaluated goodness-of-fit for the fully parameterized single-season model $\Psi(\text{PCA axes})p(\text{session, prior capture})$ by estimating an observed chi-square statistic and comparing it against a bootstrapped distribution of 1,000 chi-square statistics, a procedure also implemented in PRESENCE (MacKenzie and Bailey 2004). Typically, goodness-of-fit is measured with the global model, which in our case also would include the parameter ϵ , but a procedure for estimating multiseason model goodness-of-fit is not supported in PRESENCE, and no agreement has been reached as to how this should be done (D. MacKenzie, Proteus Wildlife Research Consultants, pers. comm.). Therefore, our measure of goodness-of-fit is based on a model with similar structure and with 1 less parameter than the global model but with more parameters than other competing models evaluated for each species. According to this procedure, goodness-of-fit was adequate for all species ($P > 0.5$, overdispersion parameter $\hat{c} \approx 1$), except for *P. parvus* ($P = 0.08$, $\hat{c} = 1.9$). Because of the ad hoc nature of our goodness-of-fit test, we did not use a quasiliikelihood adjustment for this species (e.g., $QAIC_C$ —Burnham and Anderson 2002).

Finally, we evaluated the evidence for habitat selection by generating probabilities of site use and their confidence intervals from each best fitting model, or, when faced with model selection uncertainty, from averaged models for each species. We averaged models with AIC_C values within 2 units of the top model following recommendations from Burnham and Anderson (2002). Site use probabilities were obtained from the equation:

$$\hat{\Psi}_{\text{site}} = \frac{\exp[\tilde{\beta}_0 + \tilde{\beta}_1(x_{\text{site}})]}{1 + \exp[\tilde{\beta}_0 + \tilde{\beta}_1(x_{\text{site}})]},$$

where $\tilde{\beta}$ indicates averaged parameters from top-ranked models and x_{site} indicates the PCA scores for each site. Confidence intervals were estimated with SE computed using the delta method outlined by MacKenzie et al. (2006). Because distances between some sampling units were relatively short and easily traversed by target species, we tested for residual spatial autocorrelation after accounting for the effect of habitat by computing Moran’s I spatial correlation index. Moran’s I ranges from -1 to 1 , where these values indicate perfect negative and positive spatial correlation and 0 indicates no spatial correlation. Residuals

were computed from observed values (either 0 or 1) minus the probability of observing the species at least once from model-averaged estimates (Moore and Swihart 2005). We used the “ape” library in the R statistical software and environment (R version 2.8.0, 2008; R Foundation for Statistical Computing, <http://cran.r-project.org>) to calculate Moran’s *I* with inverse distance weights. We evaluated prediction errors associated with model-averaged probabilities by computing the area under the receiver operating characteristic curve (AUC) for each model. The receiver operating characteristic curve plots false-positive prediction rates against true-positive prediction rates. AUC scores range from 0.5 to 1.0 and represent the percentage chance that a randomly selected site where the target species was encountered at least once will have a higher site use probability than a site where the target species was not encountered at all during the study. An AUC score of 0.5 indicates that the model discriminated among sites no better than random chance, whereas a score of 1.0 indicates that the model discriminated among sites perfectly. Generally, an AUC score > 0.7 indicates acceptable performance (Fielding and Bell 1997; Swihart et al. 2007). AUC scores were computed in R with the “ROCR” library.

RESULTS

Capture results and relative abundances.—We sampled 36 sites in summer 2006 (session 1), 38 sites in fall 2006 (session 2), and 44 sites in summer 2007 (session 3), resulting in a total of 7,080 trap nights. Overall trapping success (number of traps filled) averaged 42% and ranged from 15% to 68% per night. We recorded 2,483 captures representing 12 species, but only captures of *P. truei*, *T. dorsalis*, *T. minimus*, and *P. parvus* were included in subsequent occupancy modeling. *P. truei* was recorded at 16 (36%) of the 44 sites over the course of the entire study. *T. dorsalis*, *T. minimus*, and *P. parvus* were recorded at 63%, 59%, and 84% of sites, respectively. *Peromyscus maniculatus* (deer mouse) was encountered at every site (100%) in almost every session, effectively swamping any ability to relate occupancy patterns to habitat attributes. The remaining 7 species, which included *Tamias amoenus* (yellow-pine chipmunk), *Spermophilus lateralis* (golden-mantled ground squirrel), *Neotoma cinerea* (bushy-tailed woodrat), *Microtus montanus* (montane vole), *Lemmus curtatus* (sagebrush vole), *Dipodomys ordii* (Ord’s kangaroo rat), and *Sorex vagrans* (vagrant shrew), were encountered much less frequently. Based on analysis of vouchers, we found some evidence of confusion of *T. amoenus* and *T. minimus* in the field but no evidence of identification errors for other genera.

Ordination.—Principal component analysis revealed only 1 important environmental gradient among the habitat variables. The 1st principal component (axis 1) had a significant eigenvalue and moderate to large eigenvector loadings across all variables (Table 1). Shrub and herbaceous cover had loadings of -0.86 and -0.83 , respectively, and bare cover had a loading of 0.90 on this axis. Bare-ground cover ranged

TABLE 1.—Results of ordination along 6 principal component axes from a sample of habitat variables from 44 sites. Only axis 1 was significant according to the broken-stick criterion (observed eigenvalue > expected broken-stick eigenvalue).

Axis	Observed eigenvalue	% variance	Broken-stick eigenvalue
1	3.037	50.63	2.45
2	0.899	14.99	1.45
3	0.858	14.30	0.95
4	0.705	11.75	0.62
5	0.317	5.28	0.37
6	0.184	3.06	0.17

across the sample from 2.5% to 85%. Distance to rock also was strongly loaded on axis 1 (-0.62), and distance to rock outcrops of sample sites ranged from 0 to 300 m. Distance to the woodland edge and tree canopy cover also loaded moderately on this 1st axis (0.45 and 0.47 , respectively), and tree canopy cover ranged from 15% to 80%. Axis 1 captured 50% of the variation in the habitat variables and described well the woodland–savannah gradient of interest. Axis 1 represented a gradient from closed-canopy woodland with sparsely vegetated and rocky understory to open-canopy savannah with dense shrub and grass-dominated understory conditions farther from rock. Therefore, sites with high scores on axis 1 were those rocky interior woodland sites with high overstory canopy and little to no understory vegetation. The remaining axes had low eigenvalues and were not included in occupancy models (Table 1).

Detection and extinction probabilities.—The relative importance of session and prior conspecific capture on detection probabilities varied among species and was subject to considerable model selection uncertainty (Tables 2 and 3). A combination of session and prior capture was included in the top-ranked models for *P. truei* and *T. minimus*. The reduced model $p(\cdot)$, representing constant detectability across sessions and capture histories, was included in top-ranked models for *T. dorsalis* and *P. parvus*, although averaged models retained prior capture parameters for both species and session parameters for *T. dorsalis* (Table 3). Both *P. truei* and *T. minimus* exhibited the strongest seasonal patterns of detection, but in contrasting directions (Table 3). The odds of detection in session 2 (September 2006) declined for *P. truei* but rose sharply for *T. minimus*. Detection for the other 2 species remained relatively constant throughout the study. Detection probabilities were influenced positively by prior within-session capture of conspecifics for all species except *T. minimus*, which exhibited a negative response to prior capture (model-averaged odds ratio [OR] = -0.12). *P. truei* exhibited a particularly strong positive response to prior capture and was twice as likely to be detected following a prior conspecific capture ($OR = 0.70$, $e^{0.7} = 2$). *T. dorsalis* and *P. parvus* were 1.3 and 1.2 times as likely to be detected following prior capture, respectively. After accounting for session and prior capture, model-averaged detection probabilities ranged from approximately 0.50 to 0.86 for *P. truei*, 0.44 to 0.53 for *T. dorsalis*, 0.54 to 0.78 for *T. minimus*, and 0.69 to 0.74 for *P.*

TABLE 2.—Occupancy model selection results for A) *Peromyscus truei*; B) *Tamias dorsalis*; C) *Tamias minimus*; and D) *Perognathus parvus*. Model notation refers to site-use probabilities (Ψ) as either constant (.) or varying along the 1st principal component analysis axis, extinction probabilities (ϵ) as constant or not included (i.e., a single-season model), and detection probabilities (p) as constant or varying by trapping session, prior conspecific capture within trapping sessions, or both (full). Presented are differences in corrected Akaike's information criterion values for each model from the top-ranked model (ΔAIC_C), model weights (w_i), and the number of model parameters (k).

Model	ΔAIC_C	w_i	k
A. <i>P. truei</i>			
Ψ (axis1), ϵ (.), p (full)	0.00	0.37	7
Ψ (axis1), p (full)	0.75	0.26	6
Ψ (axis1), ϵ (.), p (session)	1.49	0.18	6
Ψ (axis1), ϵ (.), p (prior capture)	2.00	0.14	5
Ψ (axis1), ϵ (.), p (.)	3.94	0.05	4
Ψ (.), ϵ (.), p (full)	11.43	0.00	6
B. <i>T. dorsalis</i>			
Ψ (axis1), ϵ (.), p (.)	0.00	0.41	6
Ψ (axis1), p (full)	1.00	0.25	4
Ψ (axis1), ϵ (.), p (prior capture)	2.12	0.14	5
Ψ (axis1), ϵ (.), p (session)	2.37	0.13	6
Ψ (axis1), ϵ (.), p (full)	3.82	0.06	7
Ψ (.), ϵ (.), p (full)	8.43	0.01	6
C. <i>T. minimus</i>			
Ψ (axis1), ϵ (.), p (session)	0.00	0.52	7
Ψ (axis1), ϵ (.), p (full)	1.52	0.25	6
Ψ (axis1), ϵ (.), p (.)	2.48	0.15	6
Ψ (axis1), ϵ (.), p (prior capture)	4.04	0.07	5
Ψ (.), ϵ (.), p (full)	8.16	0.01	4
Ψ (axis1), p (full)	20.15	0.00	6
D. <i>P. parvus</i>			
Ψ (axis1), ϵ (.), p (prior capture)	0.00	0.44	6
Ψ (axis1), ϵ (.), p (.)	0.45	0.35	7
Ψ (.), ϵ (.), p (full)	2.54	0.12	6
Ψ (axis1), ϵ (.), p (session)	4.41	0.05	5
Ψ (axis1), ϵ (.), p (full)	5.32	0.03	4
Ψ (axis1), p (full)	16.74	0.00	6

parvus. Estimated extinction probabilities (ϵ) were 0.02 for *P. truei*, 0.35 for *T. dorsalis*, 0.28 for *T. minimus*, and 0.23 for *P. parvus*. However, only for the latter 2 species did strong support exist for inclusion of this parameter in models (Table 2). The single-season model was within 1 AIC_C value for both *P. truei* and *T. dorsalis*, suggesting that little information was gained by retaining ϵ for those species.

TABLE 3.—Model-averaged parameter estimates and *SE* (parentheses) of the PCA axis 1 effect on site use ($\hat{\Psi}_{\text{axis 1}}$), and session ($\hat{P}_{\text{session}}$) and prior conspecific capture effects on detectability ($\hat{P}_{\text{prior capture}}$).

Species	$\hat{\Psi}_{\text{axis 1}}$	$\hat{P}_{2006 \text{ June}}$	$\hat{P}_{2006 \text{ September}}$	$\hat{P}_{2007 \text{ June}}$	$\hat{P}_{\text{prior capture}}$
<i>Peromyscus truei</i>	0.78 (0.25)	0.87 (0.44)	0.02 (0.36)	1.19 (0.54)	0.70 (0.52)
<i>Tamias dorsalis</i>	0.32 (0.19)	−0.21 (0.58)	−0.14 (0.19)	−0.14 (0.19)	0.29 (0.36)
<i>Tamias minimus</i>	−0.26 (0.10)	0.36 (0.34)	1.28 (0.45)	0.31 (0.28)	−0.12 (0.20)
<i>Perognathus parvus</i>	−0.01 (0.06)	0.83 (0.27) ^a	—	—	0.22 (0.27)

^a Session-specific estimates of detection probability were not included in top-ranked models for *P. parvus*.

Habitat selection.—Sites with detections of *P. truei* and *T. dorsalis* had, on average, >50% canopy closure and were within 30 m of rock outcrops (Table 4). Conversely, detections of *T. minimus* and *P. parvus* occurred in sites with less canopy closure and that averaged ≥ 30 m from rock. Average shrub cover of *T. minimus* detection sites was 3.5 times higher than in nondetection sites (Table 4). A similar difference of shrub cover was observed among sites for *P. parvus*. The opposite pattern was observed for *P. truei* and *T. dorsalis*, and average shrub cover at detection sites was <50% of nondetection sites for those 2 species (Table 4). Patterns observed among sites for bare ground and herbaceous cover also resembled those of shrub cover for each species. Detection sites of *T. minimus* and *P. parvus* averaged farther from the woodland edge than those of the 2 putative woodland species (Table 4), but this pattern dissolved after accounting for imperfect detection.

Occupancy models that accounted for imperfect detection revealed patterns of resource selection along the woodland–savannah gradient that varied among the 4 species (Fig. 2). Top-ranked models for each species included a parameter for PCA axis 1, although this was only weakly the case for *P. parvus* ($\Delta AIC_C = 2.5$, $OR = -0.01$; Tables 2 and 3). We found no support for the null model Ψ (.) for *P. truei*, *T. dorsalis*, and *T. minimus* ($\Delta AIC_C > 8$; Table 2). Therefore, *P. parvus* used sites along the gradient with equal probability ($\hat{\Psi} \approx 0.65$ across all sites; Fig. 2). *P. truei* and *T. dorsalis* were much more likely to use sites with positive PCA scores for axis 1 ($OR = 0.78$ and 0.32 , respectively; Table 3; Fig. 2). The odds of site use by these 2 species increased by 2 and 1.3 times, respectively, for each unit increase along the gradient for interior woodland sites far from the edge, near large rock outcrops, and with high bare-ground cover and low herb and shrub cover. Site-use probabilities increased along the gradient from approximately 0.05 to 0.75 for *P. truei* and 0.30 to 0.73 for *T. dorsalis*. *T. minimus* showed evidence of selection for sites with negative scores for axis 1 ($OR = -0.26$; Table 3; Fig. 2). Site-use probabilities declined along the gradient from approximately 0.65 to 0.26, and the odds of site use by this species increased by 1.25 times for brushy sites near the woodland edge farther from rock, a pattern that differed somewhat from naive estimates (Table 4).

Residual spatial correlation of averaged models was low, with Moran's *I* estimated to be 0.12 for *P. truei*, 0.09 for *T. dorsalis*, 0.11 for *T. minimus*, and 0.08 for *P. parvus*. Only the estimates for *P. truei* and *T. minimus* were significantly

TABLE 4.—Means ($\bar{X}$) and SEs (in parentheses) for individual habitat variables, grouped by sites with and without target species detections. Units of distance variables are meters, whereas cover variables are percentages.

Variable	<i>Peromyscus truei</i>		<i>Tamias dorsalis</i>		<i>Tamias minimus</i>		<i>Perognathus parvus</i>	
	$\bar{X}_{\text{undetected}}$	$\bar{X}_{\text{detected}}$	$\bar{X}_{\text{undetected}}$	$\bar{X}_{\text{detected}}$	$\bar{X}_{\text{undetected}}$	$\bar{X}_{\text{detected}}$	$\bar{X}_{\text{undetected}}$	$\bar{X}_{\text{detected}}$
Distance rock	42.0 (10.8)	29.5 (8.1)	57.1 (13.3)	26.2 (6.8)	46.5 (12.6)	30.5 (7.04)	49.5 (13.2)	35.1 (9.2)
Distance edge	247.4 (23.4)	154.7 (15.8)	243.7 (27.2)	193.2 (17.9)	182.6 (17.0)	233.6 (24.5)	248.5 (18.6)	204.5 (22.3)
Bare cover	0.47 (0.03)	0.73 (0.04)	0.49 (0.04)	0.63 (0.04)	0.78 (0.03)	0.41 (0.03)	0.81 (0.03)	0.52 (0.04)
Herb cover	0.46 (0.03)	0.28 (0.02)	0.46 (0.03)	0.35 (0.03)	0.29 (0.02)	0.47 (0.02)	0.32 (0.03)	0.40 (0.03)
Shrub cover	0.24 (0.02)	0.07 (0.01)	0.25 (0.03)	0.13 (0.02)	0.08 (0.01)	0.25 (0.02)	0.07 (0.01)	0.20 (0.44)
Tree cover	0.44 (0.02)	0.52 (0.02)	0.40 (0.02)	0.50 (0.02)	0.53 (0.02)	0.43 (0.03)	0.60 (0.01)	0.44 (0.02)

different from 0 ($\alpha = 0.05$). Predictive accuracy of model-averaged parameters varied among the 4 species, but AUC values from receiver operating characteristic plots were within acceptable ranges and highest for the 2 species with strongest evidence of selection (0.82, *P. truei*; 0.70, *T. dorsalis*; 0.79, *T. minimus*; 0.76, *P. parvus*).

DISCUSSION

We used occupancy models as resource selection probability functions and evaluated the strength of evidence for habitat selection by 4 species of rodents along a P-J woodland-savannah gradient, described through ordination (PCA).

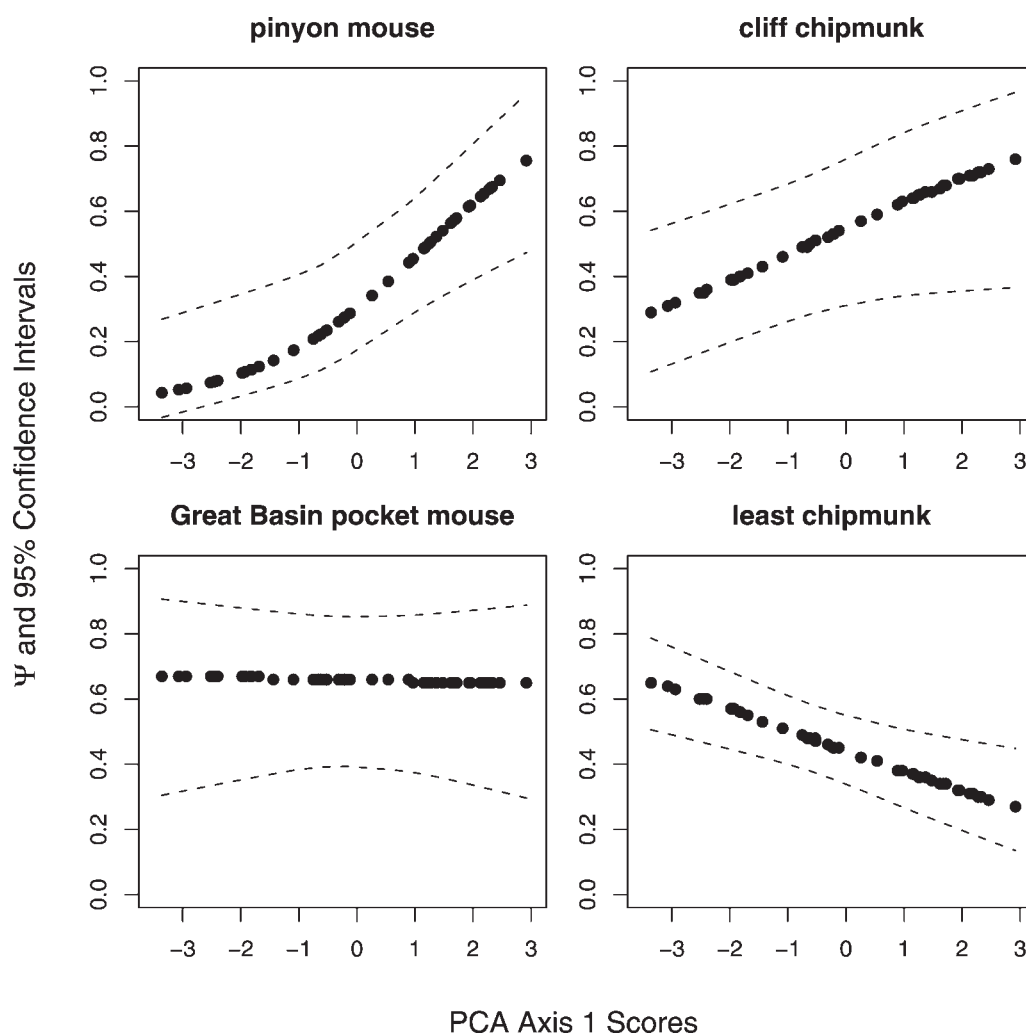


FIG. 2.—Site-use probabilities (Ψ) and 95% confidence intervals (dashed lines) versus principal component analysis axis 1 scores (the woodland-savannah gradient). Probabilities and intervals were computed from model-averaged parameter estimates for each of the 4 rodent species. Axis 1 represented a gradient from piñon-juniper savannah with dense shrub and grass-dominated understory conditions farther from rock on the negative end, to closed-canopy woodland conditions with sparsely vegetated and rocky understory on the positive end of the gradient.

Habitat attributes ranged from open-canopy savannah far from rock outcrops, represented on the negative end of the PCA axis, to rocky interior woodlands with well-developed canopies and sparsely vegetated understories on the positive end. The characteristics of our habitat gradient resembled those often used as a proxy to discriminate older, presettlement stands from younger invasive stands (Jacobs et al. 2008; Waichler et al. 2001; Weisberg et al. 2008). Old-growth P-J woodlands typically occur among rock outcrops where they have been protected from fire (Miller and Rose 1995; Weisberg et al. 2008). Canopy cover along P-J woodland-savannah gradients typically range from 5% to 80%, with >25% cover in older stands (Bourgeron and Engelking 1994; Jacobs et al. 2008; NatureServe 2009). Canopy cover in our sample ranged from 15% to 80% and was inversely correlated with distance to rock and percent cover of bare ground, reflecting descriptions of the structure of old and young stands elsewhere (Jacobs et al. 2008; Weisberg et al. 2008).

We found evidence that *P. truei* and *T. dorsalis* select for interior old-growth-type P-J woodland stands. These 2 species were substantially more likely to choose woodland sites on the positive end of the ordination gradient. Conversely, *T. minimus* was more likely to use savannah sites along the negative end of the gradient. *P. parvus* was the least selective of the species we studied and was encountered with equal probability across the habitat gradient. The apparent lack of selection by *P. parvus* along the woodland-savannah gradient was surprising. Throughout much of the Intermountain West this species is considered to be a specialist of sandy shrub-steppe habitats with considerable amounts of exposed soil (e.g., >40%—Verts and Kirkland 1988). Based on this description, we had expected *P. parvus* to remain outside the core woodland sites and select savannah sites with negative PCA scores.

Our results are consistent with other studies that showed that rock and P-J habitat attributes are important to *P. truei* and *T. dorsalis*, and that *T. minimus* prefers open, shrub-dominated areas (Hart 1992; Hoffmeister 1981; Rompola and Anderson 2004; Verts and Carraway 1998, 2001). However, our study is the 1st to model habitat selection along a woodland-savannah gradient relevant to woodland management, and is the 1st to account for detection error for these species. The shared preferences exhibited by *P. truei* and *T. dorsalis* in our study contradict the findings of Rompola and Anderson (2004), who reported differences in the amount of rock, bare ground, and shrub cover used by the 2 species in Wyoming. They reported that *T. dorsalis* was more likely to use sites with low cover of bare ground, high grass cover, and with taller shrubs. In our study we found the opposite pattern, with apparent selection for sites high in bare ground and low in grass and shrub cover. *T. dorsalis* was apparently much less selective in their study, because it was found in 92% of their study sites compared to 63% in ours. Likewise, they found that *P. truei* was captured farther from rock outcrops, whereas we found close proximity to outcrops to be an important habitat factor for *P. truei*.

Differences in study design and the local assemblage of interacting species may account for some of these disparities. Rompola and Anderson (2004) also did not account for imperfect detection. Failure to account for detection probabilities < 1 negatively biases estimates of occupancy and subsequent inferences of habitat selection (Ball et al. 2005; Gu and Swihart 2004; MacKenzie et al. 2006; Tyre et al. 2003). In our own study, for example, naive estimates of site use of *P. truei* and *T. dorsalis* unadjusted for imperfect detection (Table 4) indicated that these species used sites that were on average closer to the woodland edge than the other 2 species, patterns opposite those of subsequent habitat models. Naive estimates of site use of *T. minimus* also differed from the habitat selection model for the species' relationship to distance to rock. Studies of small mammals that use live trapping methods are particularly prone to nondetection error because of seasonal population fluctuations and unequal response to traps previously used by conspecifics (Heske 1987). In our study we explicitly modeled detection probabilities as a function of trapping session and prior within-session conspecific capture. Although the relative importance of these factors varied among species, one or both factors were retained in averaged models for all 4 species. Detection probabilities changed following prior capture for each of the 4 species included in our study. Effects were particularly strong for *P. truei*, which was twice as likely to be detected following prior capture.

The probability of occupancy or use of an area is a fundamental population attribute and one more readily measured than other abundance metrics. Presence-absence data require less intensive sampling and are therefore less costly and more likely to be implemented widely by research and monitoring programs. We designed our study with this in mind. Small-mammal trapping studies traditionally have been conducted with large and costly grids involving dozens of traps per replicate site. In the case of an occupancy modeling study, fewer within-unit samples can be taken in favor of more extensive replication across independent sampling units. The number of traps per sampling unit should be driven by considerations of species detectability rather than by concerns over individual recapture rates because interest is focused on population-level responses. Most detection probabilities estimated from our study were >0.50, suggesting that 3 trapping nights and 20 traps per site were sufficient for determining occupancy patterns for the 4 most common species in our study area (MacKenzie and Royle 2005). Given our goals, we would have improved study precision most by increasing the number of sites sampled rather than by increasing the number of repeat surveys (i.e., trapping nights) or traps per site (MacKenzie and Royle 2005). However, this would not have been the case with lower detection probabilities, and the recommended number of surveys can increase rapidly to as many as ≥ 15 for rarely encountered species (Gorresen et al. 2008; MacKenzie and Royle 2005).

The patterns identified in our study provide insight into the role of habitat selection in facilitating coexistence of closely

related species in P-J woodlands and the contribution these woodlands make to regional species pools. P-J woodlands provide important habitat for not only small mammals, including bats (Chung-MacCoubrey 2005), but also other vertebrates such as birds (Pavlacky and Anderson 2001). Prescribed fire and mechanical removal efforts directed at slowing the expansion of woodland trees into adjacent shrub-steppe often ignore stand age and structure (Baker and Shinneman 2004; Brockway et al. 2002; Miller et al. 2000). The rocky, high overstory and low understory cover characteristics apparently favored by *P. truei* and *T. dorsalis* in our study are similar to descriptions of presettlement P-J woodlands that were maintained by fire (Burkhardt and Tisdale 1976; Miller and Rose 1995; Soulé et al. 2004; Weisberg et al. 2008) and fit the habitat requirements of some P-J woodland specialist bird species (Pavlacky and Anderson 2001). Efforts aimed at controlling P-J invasion into shrub-steppe that discriminate among woodland and savannah structural conditions (e.g., with canopy cover and proximity to rock measures), and, by proxy, old and young stands (Jacobs et al. 2008; Waichler et al. 2001; Weisberg et al. 2008), will better allow for both woodland control and biodiversity objectives to be achieved.

Our study was conducted along the northern boundary of geographic distribution of P-J woodlands. Increased environmental variability at the periphery has been implicated as a mechanism for elevated or otherwise unique biodiversity in these zones, and peripheral areas are increasingly important places to observe accelerated ecological change and for conservation (Kark et al. 2005; Spector 2002; Thomas et al. 2001). P-J woodlands are clearly dynamic, and have not only exhibited rapid expansion into new areas but also dramatic die-offs in some areas as a result of disease and drought (Breshears et al. 2005). Given the potential for climate change to exacerbate these shifts, particularly in the periphery, additional studies of habitat selection and distribution of P-J woodland fauna, such as *P. truei* and *T. dorsalis*, are warranted. Climate-induced habitat shifts already have been demonstrated for *P. truei* (Cameron and Scheel 2001; Moritz et al. 2008). The occupancy modeling approach that we have taken here provides an efficient framework for detecting change in the periphery, particularly for imperfectly detected cryptic species.

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