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Persistence of Allegheny woodrats *Neotoma magister* across the mid-Atlantic Appalachian Highlands landscape, USA

W. Mark Ford, Steven B. Castleberry, Michael T. Mengak, Jane L. Rodrigue, Daniel J. Feller and Kevin R. Russell

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We examined a suite of macro-habitat and landscape variables around active and inactive Allegheny woodrat *Neotoma magister* colony sites in the Appalachian Mountains of the mid-Atlantic Highlands of Maryland, Virginia, and West Virginia using an information-theoretic modeling approach. Logistic regression analyses suggested that Allegheny woodrat presence was related positively to distance to the nearest occupied colony site and was influenced by location within physiographic subprovince. Colony sites were more likely to be active to the west (Allegheny Plateau) than the east (Blue Ridge/Piedmont), and colony sites were less likely to be active north of the Potomac River where land use and human disturbance patterns in the region were more intensive. Support also was generated for a presence-absence model that included forest cover within a 1-km radius of colony sites, although its importance was equivocal in this heavily forested region. Allegheny woodrats rely on emergent rock habitats for denning, and mast-bearing forest communities for foraging, and appear to display a metapopulation structure that is sensitive to a combination of natural and anthropogenically-induced isolation pressures that are recognizable but difficult to manage or mitigate.

W. M. Ford (mford@fs.fed.us) and J. L. Rodrigue, USDA, Forest Service Northeastern Research Station, Parsons, WV 26287, USA. – S. B. Castleberry and M. T. Mengak, Warnell School of Forestry and Natural Resources, Univ. of Georgia, Athens, GA 30602, USA. – D. J. Feller, Maryland Dept of Natural Resources, Natural Heritage Program Frostburg, MD 21532, USA. – K. R. Russell, College of Natural Resources, Univ. of Wisconsin-Stevens Point, Stevens Point, WI 54481, USA.

Habitat parameters that influence metapopulation dynamics such as habitat patch size and fragmentation commonly are examined to gain an understanding of the past, current, and potential future distribution relative to isolation and population status for sensitive, threatened, and endangered species (Fahrig and Merriam 1985, Lawes et al. 2000). Loss of corridors among suitable patches or alteration of the permeable matrix surrounding those patches can be linked to reduction in a local and landscape distributional extent for many small mammal species (Henein and Merriam 1990, Anderson and Danielson 1997). Even if patch suitability remains constant in terms of quality and spatial extent, loss or alteration of the inter-patch matrix permeability makes recolonization following localized extinction more challenging (Marsh and Trenham 2001). Although highly variable based on species and habitat type, these metapopulation processes of persistence and extirpation have increasingly been quantified empirically for many small mammal species (Kozakiewicz 1993, Rodríguez

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and Andrén 1999, Van der Ree et al. 2003, Walker et al. 2003, Franken and Hik 2004). Research approaches that can elucidate potential causes of spatially-correlated extinction patterns that lead to reduced biodiversity are critical for conservation management efforts (McCarthy and Lindenmayer 2000, Terborgh et al. 2001, Noss 2004).

The Allegheny woodrat *Neotoma magister* is a medium-sized (ca 200–350 g) nocturnal rodent that occurs in the central and southern Appalachian Highlands and Interior Low Plateau regions from central Pennsylvania south to north-central Alabama and west to southern Indiana of the eastern USA (Castleberry et al. 2006). The species' local distribution is confined to forested areas with rock outcrops, cave entrances, and large colluvial talus slopes where individuals den in deep crevices, overhangs, and narrow passageways (Mengak 2002a). As a forest obligate, the Allegheny woodrat has a substantial dietary reliance on oak *Quercus* spp. mast (Castleberry et al. 2002a). Moreover, Allegheny woodrats are constrained by patterns of surficial geology further limited by their small, sedentary home ranges (Castleberry et al. 2001). The species appears to display a classic metapopulation structure linked both to emergent rock quality and extent and numbers of emergent rock capable of harboring woodrats per unit area within forested landscapes (Balcom and Yahner 1996, Castleberry et al. 2002b). Although Allegheny woodrats are solitary and moderately intolerant of conspecifics, several individuals may occur within 1 rock outcrop site, and hence this often is referred to as a colony (Castleberry et al. 2001).

The Allegheny woodrat has experienced drastic range contraction in the past 3 decades in the United States (Balcom and Yahner 1996, Castleberry et al. 2001). It has been extirpated in Connecticut and New York, and reduced to disjunct populations listed as state-endangered in New Jersey, Ohio, and Indiana by their respective wildlife agencies (Castleberry et al. 2006). In the core of their distribution, Allegheny woodrats are considered rare or "In Need of Management" by either state wildlife agencies or Natural Heritage programs in Pennsylvania, Maryland, Virginia, West Virginia, North Carolina, Tennessee, and Alabama (Anon. 2006). The species is considered secure from a conservation perspective only in Kentucky (S. Thomas, USDI National Park Service, pers. comm., Castleberry et al. 2006). The reasons for decline are numerous and many factors may operate in an additive fashion. These include: 1) widespread deforestation from exploitative logging and loss of annually abundant hard mast crops following removal of the American chestnut *Castanea dentata* by the introduced chestnut blight *Cryphonectria parasitica* in the early 20th century, 2) reduced oak acorn production from repeated defoliation by the introduced gypsy moth *Lymantria dispar* and other agents contributing to oak decline such as widespread fire suppression, 3) concomitant increases in shade-tolerant tree species with low wildlife food value, i.e. sugar maple *Acer saccharum*, red maple *Acer rubrum*, and white pine *Pinus strobus*, 4) greater interspecific competition for hard mast, soft fruits, and forages from increased game populations such as white-tailed deer *Odocoileus virginianus* and black bear *Ursus americanus* and 5) continued anthropogenic disturbance from forest management, surface mining, vacation, and recreational development (Balcom and Yahner 1996, Mengak 2002a, Dickson 2004, Chamblin et al. 2004, LoGiudice 2006, Castleberry et al. 2006). However, within the northern portion of the Allegheny woodrat distribution, infection by the ascarid roundworm *Baylisascaris procyonis* is believed most responsible for the species' extirpation. As a larder-hoarder that relies on overwinter food caches, woodrats will collect or consume undigested seeds from raccoon *Procyon lotor* feces that contain highly infective second-stage *B. procyonis* larvae (LoGiudice 2003). Rodents are aberrant secondary hosts that typically succumb to a fatal neurological disease produced by *B. procyonis* infection (Davidson and Nettles 1997).

Similar to the pattern described by Balcom and Yahner (1996) within Pennsylvania, the Allegheny woodrat extirpation process appears to be correlated with human population density and overall forest habitat alteration or loss, with declines more widespread to the east and to the north in the mid-Atlantic Highlands. However, these perceived patterns have largely remained unquantified and undoubtedly are confounded by differences in patterns of forest ownership, forest use and forest condition among public, corporate, and private entities, and by surficial geologies that vary across the 3 physiographic subprovinces. By understanding geographic patterns of presence and absence and identifying both proximate and ultimate factors responsible for extirpation at both local and regional scales, natural resource managers could begin to develop comprehensive strategies for maintaining extant woodrat populations and/or re-introducing them to inactive sites. Herein, we examined landscape and macro-habitat characteristics of the presence or absence of Allegheny woodrat colonies at 417 currently occupied or inactive sites across the three physiographic subprovinces of the Appalachian Mountains in the mid-Atlantic Highlands using an information-theoretic approach. We generally hypothesized that active woodrat colonies in the region would be aggregated near other colonies (Castleberry et al. 2002b) and also positively linked to more completely forested and mountainous landscape conditions with less local disturbance around the colony (Castleberry et al. 2001, 2002c). Accordingly, we secondarily hypothesized that these patterns would manifest themselves along perceived extirpation gradients from north to south (Balcom and Yahner 1996, LoGiudice

2006) and east to west (Castleberry et al. 2006) along defined landforms and physiography.

Materials and methods

Study area

We compiled spatial information on 417 active and inactive Allegheny woodrat colony sites within the Blue Ridge/Piedmont, Ridge and Valley, and Allegheny Plateau across a ca 80 000 km^2 portion of the mid-Atlantic Highlands from the Washington D.C. area west to central West Virginia (Fig. 1). Colony sites were surveyed or re-surveyed between 1991 and 2001 by Maryland Dept of Natural Resources, Virginia Dept of Game and Inland Fisheries, West Virginia Dept of Natural Resources, U.S. Dept of Agriculture (USDA) Forest Service, U.S Dept of the Interior (USDI) National Park Service, West Virginia Univ., Ferrum College, and the Univ. of Georgia (Castleberry et al. 2001, 2002a, b, Mengak 2002a, b, Feller unpubl., C. Stihler, West Virginia Dept of Natural Resources pers. comm.). Our survey accounted for all active and historically known colony sites in Maryland regardless of land ownership, whereas efforts in Virginia and West Virginia centered on federally-owned lands (Shenandoah National Park, New River Gorge National River, Blue Ridge Parkway, George Washington Parkway, Harper's Ferry National Historic Site, George Washington-Jefferson National Forest, and the Monongahela National Forest), state lands (state forests and wildlife management areas), and corporate forests, although some records also were obtained from non-industrial private lands. Though highly variable throughout the study area, most of the colony sites in Maryland and Virginia that we examined were known prior to our analyses, and some site records predate the 20th century (Feller unpubl., Mengak unpubl.). Conversely, most of the West Virginia sites were initially recorded no earlier than the 1980s.

Topography of the Blue Ridge/Piedmont subprovince ranges from undulating hills in the Piedmont to rugged mountains in the narrower Blue Ridge portion. Underlying geology is older metamorphic rock with elevations ranging from 100 m in the eastern portions to >1100 m along higher ridges. The Ridge and Valley subprovince is characterized by series of long linear mountains separated by wide valleys. Ridgelines are resistant sandstones whereas the valley floors often exhibit karst formation. Elevations range from 300 to 1300 m. Also of sedimentary origin, the Allegheny Plateau elevation can approach 1500 m. Incised with narrow valleys and steep slopes, summits in the region often are broad and relatively flat (Fenneman 1938). Throughout all subprovinces, Allegheny woodrat colonies occur along clifflines and gorges along watercourses and emergent rock on summits and upper slopes, as well as in large talus breakdown and cave entrances. Emergent rock capable of supporting woodrats is less abundant in the Blue Ridge than in the Ridge and Valley or Allegheny Plateau where numerous ridgeline outcroppings and overhanging cliffs with large, semi-circular interior recesses known regionally as "rockhouses" occur.

Regionally, dominant forest vegetation varies by elevation, aspect, climate, and past disturbance history. Most forests in the drier (≤ 100 cm precipitation annually) Blue Ridge/Piedmont and Ridge and Valley are of the Appalachian oak-chestnut type with abundant hard mast producing oak and hickory *Carya* spp.

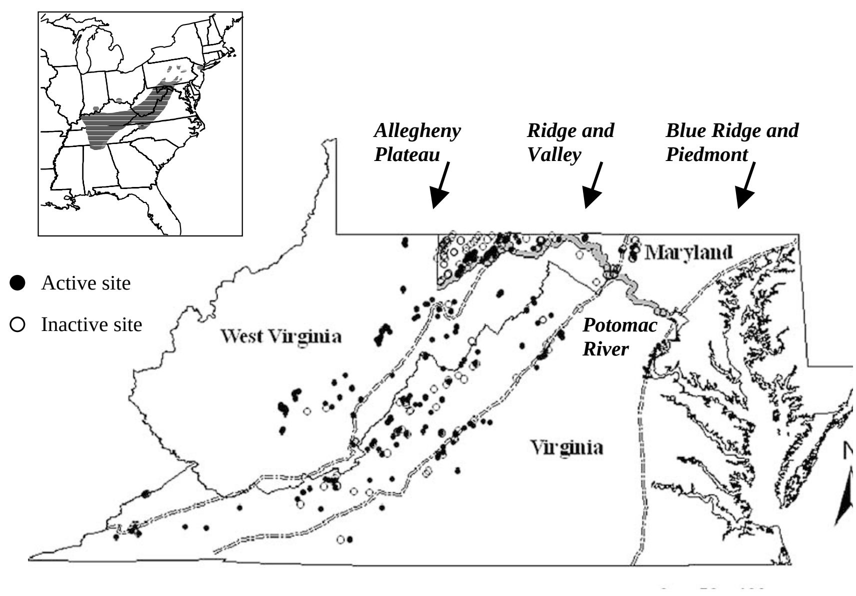

Fig. 1. Locations of active and inactive Allegheny woodrat *Neotoma magister* colony sites across the Blue Ridge/Piedmont, Ridge and Valley and Allegheny Plateau physiographic subprovinces in the mid-Atlantic Highlands of Maryland, Virginia and West Virginia, USA (n = 417). Scale is insufficient to differentiate sites in close proximity. Inset shows the entire distribution of the species in the eastern United States. The Potomac River forms the boundary between Maryland and Virginia and West Virginia to the south.

whereas those in the wetter and cooler ($\geq$130 cm precipitation annually) Allegheny Plateau are of the mixed mesophytic type with a lesser oak component. Also, northern hardwood and montane boreal forests that are somewhat deficient in hard-mast capacity are more widespread in extent ($>$300 000 ha) in the Allegheny Plateau at elevations $\geq$1000 m (Braun 1950, Schuler et al. 2002).

Woodrat survey

We initially assessed whether an Allegheny woodrat colony site was active or inactive based on the presence of middens (collections of sticks and leaves indicative of Allegheny woodrat dens) and communal latrines (Balcom and Yahner 1996, Castleberry et al. 2006) along with live-trapping as described by Castleberry et al. (2001). Absence of middens and latrines combined with 2 to 3 unsuccessful nights of live-trapping reliably indicated woodrat absence at a site to the point that our overall detection probability was near 100% (Mengak 2002b). Most inactive colony sites visited clearly had been active in the past based on visible sign. However, some areas in Virginia were assessed as historically occupied from recorded or anecdotal accounts or inactive but still believed to be "potential" based on rock outcrop characteristics. We visited many sites repeatedly over a decade of monitoring and several colonies disappeared without being recolonized in that time: 8 in Maryland, 9 in Virginia and 2 in West Virginia. Those colonies were designated as inactive in our final analyses. All sites were assigned to their appropriate physiographic subprovince (Blue Ridge/Piedmont, Ridge and Valley, and Allegheny Plateau) based on inherent differences in surficial geology, land use, and variation in forest composition. Moreover, because anthropogenic alteration of the landscape was greater and mountainous regions were lower in elevation and generally less rugged in Maryland and extreme northern West Virginia than the remainder of the study area, all sites were scored as either north of the Potomac River (or 39°12′30″N latitude if west of the Potomac River drainage in West Virginia) or south of the Potomac River.

GIS analyses

We calculated a variety of coarse macrohabitat and landscape variables for all 417 Allegheny woodrat colony sites within ArcMap 8.3® software (ERSI, Redlands, CA, USA) using 7.5′ quadrangle topographic maps, 10 × 10-m resolution elevation models, and 1:100 000 Land-use/Landcover Classification coverages based on 1992 Landsat TM imagery with 30 × 30-m resolution (U.S. Geologic Survey Earth Observation Systems Data Center, Denver, CO, USA; <http://edc.usgs.gov/geodata>; <http://store.usgs.gov/>). Variables generated through GIS for each Allegheny woodrat colony site included: elevation, percent forest cover within 1-km radius, distance to nearest water and its type (bog, stream, river, or lake), presence of a road (primary, heavy-duty, or divided) or railroad within 100 m of colony site, percent area in agriculture or pastoral grazing within 500-m radius, percent area mined within 500-m radius, percent area in residential or development within 500-m radius, and distance to the nearest known active Allegheny woodrat colony site. We measured disturbance variables within a 500-m radius because that represented the upper end of woodrat foraging and non-dispersal movement distances from previous research efforts (Castleberry et al. 2001). Forest cover was assessed within a 1-km radius to provide insights on landscape-level thresholds important to woodrats at a scale that just exceeded an individual woodrat's normal movement patterns (Castleberry et al. 2001), following the habitat scale selection concepts posited by Thomas and Taylor (1990) and used for other mammal species in the central Appalachians (Menzel 2003, Owen 2003, Owen et al. 2003). Variables measured within a 100-m radius represented drastic habitat unsuitability at the scale of the immediate colony site.

Statistical analyses

We compared each continuous macro-habitat or landscape variable obtained between occupied Allegheny woodrat colony sites with those that were inactive using univariate Wilcoxon tests. For categorical or ordinal variables, we used Fisher's exact tests to determine if observed versus expected frequencies differed between occupied or inactive colony sites (Steel and Torrie 1980, Mehta and Patel 1983). We examined the relationship of Allegheny woodrat presence or absence at colony sites with macrohabitat and landscape variables within a series of multiple logistic regression models (Hosmer and Lemeshow 2000). We performed model selection with an information-theoretic approach using Akaike's Information Criterion corrected for small sample size (AIC_c) because overall sample size divided by total parameter units examined was $<$40 (Burnham and Anderson 1998). Accordingly, we constructed a series of a priori models (Wagner and Drickamer 2004, Gibson et al. 2004) to address several potential Allegheny woodrat colony site occupancy questions in the most parsimonious manner. The models we constructed were as follows: 1) NEIGHBOR (distance to nearest occupied colony site in km), 2) ELEVATION (colony site elevation + NEIGHBOR), 3) FOREST (percent forest cover within 1-km radius + NEIGHBOR), 4) DISTURBANCE (road or railroad within 100 m, percent area in agriculture, mined, in residential or developed within 500 m radius + NEIGHBOR), 5) PROVINCE (physiographic subprovince membership [Blue Ridge/Piedmont = 1, Ridge and Valley = 2 and Allegheny Plateau = 3] + NEIGHBOR), 6) POTOMAC (location north [1] or south [2] of the Potomac River + NEIGHBOR), 7) GEOGRAPHIC (physiographic subprovince membership + location north or south of the Potomac River + NEIGHBOR), 8) LANDSCAPE (physiographic subprovince membership + location north or south of the Potomac River + percent forest cover within 1-km radius + NEIGHBOR), and 9) a global model (GLOBAL) containing all parameters. Consistent with an information-theoretic approach, we used our prior knowledge of the species (Castleberry et al. 2006) to construct potentially biologically meaningful models within the constraints of our available data. Thereby, we retained NEIGHBOR in every model because long-term occupancy and genetic viability of a site requires a recolonization source within the relatively limited dispersal distance of the species (Castleberry et al. 2001, 2002b).

Prior to logistic regression analyses, we determined that no continuous variables were highly redundant using Spearman's rank correlation with values of $r_s > 0.7$ and $p < 0.05$ as thresholds. We ranked all candidate models according to their AIC_c scores. We drew primary inference from competing models within 4 units of the lowest AIC_c score ($AIC_{c\text{-}min}$) that are thought to offer empirically-based competing support to the best-approximating model (Burnham and Anderson 1998). To assess a relative measure of model fit of supported models we calculated Nagelkerke's rescaled R^2 (Anon. 1995). We used a jackknife procedure to compute the specificity (percent correct classification of inactive sites) and sensitivity (percent correct classification of currently occupied sites) of both the selected model(s) and the global model (Anon. 1995). For the best approximating model, we examined the Pearson residuals to identify observations not supported by the model (Anon. 1995) and we computed predicted probability values of occupancy for each Allegheny woodrat colony site and plotted those probabilities against observed macro-habitat and landscape variables (Teixeira et al. 2001).

Results

We examined 417 Allegheny woodrat colony sites in the mid-Atlantic Highlands Appalachian Highlands of Maryland, Virginia, and West Virginia; 252 of these were active and 165 were considered inactive by 2001 (Fig. 1). Based on the continuous variables measured, active colony sites were closer to other active colony sites, were located within more completely forested landscapes and less surrounded by agriculture and permanent water than were inactive colony sites (Table 1). Proportionally more Allegheny woodrat colony sites were considered inactive north of the Potomac River (95 of 183) than south of the Potomac River (70 of 234) (Fisher's exact test, $p < 0.0001$). Among physiographic subprovinces, inactive colony sites occurred more than expected in the Blue Ridge/Piedmont (44 of 80) but less than expected in the Ridge and Valley (65 of 156) and Allegheny Plateau (56 of 181) (Fisher's exact test, $p = 0.001$). The proportion of active versus inactive colonies within 100 m of a primary road or a river or lake did not differ (Fisher's exact test, $p = 0.83$ and $p = 0.72$, respectively).

Of the 9 logistic regression models we constructed, the best-approximating model was GEOGRAPHIC, containing the continuous variable of distance to nearest occupied colony site and the 2 ordinal variables scoring physiographic subprovince membership and colony site location north vs south of the Potomac River (Table 2). Although modified by the influence of distance to the nearest occupied colony site, this model indicated that the predicted pattern of extirpation in the mid-Atlantic Highlands seems to increase from the west (Allegheny Plateau) to the east (Blue Ridge/Piedmont) and it appears to be higher and more pronounced north of the Potomac River (Table 3; Fig. 2). Additionally, there was some empirical support for the LANDSCAPE model that was within approximately 2 units of $AIC_{c\text{-}min}$ (Table 2). The LANDSCAPE model added the percent forest area within 1-km radius of an Allegheny woodrat colony site, although its contribution was equivocal within the logistic regression (Table 3) unlike within our univariate analyses (Table 1). The GEOGRAPHIC and LANDSCAPE models had moderate

Table 1. Continuous macro-habitat and landscape variables for active and inactive Allegheny woodrat *Neotoma magister* colony sites in the mid-Atlantic Highlands of Maryland, Virginia and West Virginia, USA (n = 417).

Variable	Active (n = 252)		Inactive (n = 165)		p^a
	Mean	SE	Mean	SE	
nearest neighbor (km)	4.86	0.50	11.11	0.89	<0.0001
percent area forest cover (1 km)	90.57	0.98	87.53	0.15	0.02
percent area agriculture (0.5 km)	3.61	0.75	4.94	1.23	0.06
percent area developed (0.5 km)	1.32	0.45	2.07	0.62	0.17
percent area mined (0.5 km)	1.83	0.48	0.24	0.001	0.22
percent area water (0.5 km)	0.76	0.002	2.01	0.53	0.08

[a]Wilcoxon ranked-sum test $p > Z$.

Table 2. Logistic regression models explaining the influence of macro-habitat and landscape variables on the presence of active Allegheny woodrat *Neotoma magister* colony sites in the mid-Atlantic Highlands of Maryland, Virginia and West Virginia, USA (n = 417). Model rankings were based on Akaike's Information Criterion corrected for small sample size (AIC_c).

Model[a]	K[b]	AIC_c	ΔAIC_c^c	w_i^d	R^{2e}	SEN[f]	SPEC[f]
GEOGRAPHIC	5	481.42	0.00	0.71	0.26	74.3	73.6
LANDSCAPE	6	483.47	2.05	0.26	0.26	74.7	73.2
GLOBAL	13	487.86	6.44	0.03	0.29	69.9	71.1
POTOMAC	3	502.21	20.79	0.00	0.20	77.2	70.5
ELEVATION	3	502.34	20.92	0.00	0.19	67.7	68.5
PROVINCE	4	514.77	33.35	0.00	0.17	65.6	67.9
NEIGHBOR	2	520.99	39.57	0.00	0.13	67.8	67.8
DISTURBANCE	8	522.21	40.79	0.00	0.16	63.0	67.1
FOREST	3	523.01	41.59	0.00	0.13	68.6	67.9

[a]See text for model parameter description.
[b]Number of estimable parameters + 1 in approximating model.
[c]Difference in value between AIC_c of the current model versus the best approximating model (minimum AIC_c).
[d]Akaike weight. Probability that the current model (i) is the best-approximating among those considered.
[e]Nagelkerke's rescaled R^2.
[f] Model specificity (SPEC) and sensitivity (SEN) expressed as %.

performance metrics (i.e. Nagelkerke's rescaled R^2), model specificity, and model sensitivity (Table 2), whereas the 7 remaining models received no strong empirical support based on AIC rankings.

Analysis of Pearson residuals in the GEOGRAPHIC model indicated that the most extreme outliers contributing to poor model performance were observations where Allegheny woodrats were present despite long distances (>35 km) to the nearest known active colony site or conversely were absent despite short distances (<1 km) to the nearest known active colony site across all physiographic subprovinces and location north or south of the Potomac River. A post-hoc analysis of all residuals that deviated from 0 ($n = 111$) showed that inactive colony sites close to active colonies were more common than expected in the Allegheny Plateau physiographic subprovince and less common than expected in the Blue Ridge/Piedmont whereas the opposite was true for active sites that were long distances from other active colonies (Fisher's exact test, $p = 0.006$). Overall mean nearest neighbor distance among the deviant Pearson residuals was 5.56 km (SE = 0.601, n = 83) for inactive colony sites and 15.06 km (SE = 3.28, n = 28) for active colony sites.

Discussion

By virtue of GEOGRAPHIC being the most supported model, our analysis documents a definable spatial pattern of active and inactive Allegheny woodrat colony sites over the distinct physiographic boundaries within the species' distribution in the Appalachian Highlands of the mid-Atlantic region. Similar to other other rodent species with similar habits and environmental affinities (Monty et al. 2003, Walker et al. 2003, Franken and Hik 2004), our previous genetic analyses (Castleberry et al. 2002b) and the importance of proximity to a neighboring active site provides strong additional support for the spatial nature of Allegheny woodrat metapopulation structure as was recently elucidated by LoGiudice (2006). Consistent with anecdotal observations from the region, active colony site persistence appeared to be reduced in the north and to the east across the 3 states surveyed. Inactive colony sites were numerous along the Blue Ridge/Piedmont and Ridge and Valley interface whereas colony inactivity in the Allegheny Plateau was concentrated mainly in extreme NW Maryland to the north of the Potomac River. Although the GEOGRAPHIC model is helpful for quantifying the ob-

Table 3. The best-approximating logistic regression models (GEOGRAPHIC and LANDSCAPE) explaining presence or absence of active Allegheny woodrat *Neotoma magister* colony sites in the mid-Atlantic Highlands of Maryland, Virginia and West Virginia, USA (n = 417). See text for variable definition.

Parameter	Estimate	SE	Wald's χ^2	$p > \chi^2$	Odds ratio
GEOGRAPHIC					
intercept	−2.976	0.648	21.065	<0.0001	–
nearest neighbor	−0.080	0.015	29.138	<0.0001	0.925
physiographic subprovince	0.802	0.168	22.690	<0.0001	2.230
north/south of Potomac R.	1.418	0.251	32.041	<0.0001	4.130
LANDSCAPE					
intercept	−2.910	0.883	10.867	0.001	–
nearest neighbor	−0.080	0.015	28.131	<0.0001	1.000
physiographic subprovince	0.804	0.169	22.491	<0.0001	2.234
north/south of Potomac R.	1.418	0.251	31.901	<0.0001	4.128
% forest area within 1-km	−0.075	0.685	0.012	0.912	0.927

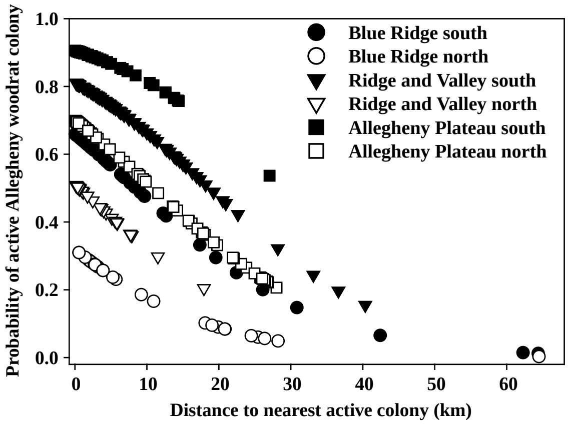

Fig. 2. Predicted probability of active Allegheny woodrat *Neotoma magister* colony sites relative to the distance to the nearest active colony sites across the Blue Ridge/Piedmont, Ridge and Valley and Allegheny Plateau physiographic subprovinces in the mid-Atlantic Highlands of Maryland, Virginia and West Virginia, USA north and south of the Potomac River (n =417).

served landscape patterns, it does not clearly elucidate the reasons for the pattern.

Disturbance

We agree with Balcom and Yahner (1996) that the ultimate causes for declining Allegheny woodrat populations are difficult to address through coarse-filtered macro-habitat or landscape analyses. Their results, as well as ours, often present counter-intuitive findings. Although Allegheny woodrats can behaviorally tolerate some edge or ecotone surrounding their den sites (Castleberry et al. 2001), disturbed forest habitats or edge around rock outcrops can increase den site visibility or serve as corridors into interior forests for potential woodrat predators (Gates 1991). However, our adjacent disturbance hypotheses that included non-forested area and close proximity to permanent edge from road and railroad rights-of-way did not receive support for predicting presence or absence in either study. Nonetheless, there can be a blurring between ultimate and proximate agents operating on a species with regard to landscape or physiographic factors, such that inferences cannot be extended beyond the landscape studied (Gibson et al. 2004). Other researchers have noted links between declining populations and localized extirpation in regions with apparent but unquantifiable levels of human activity, such that a clear cause and effect relationship could not be deduced (Posillico et al. 2004).

The cluster of inactive colony sites in northwestern Maryland corresponds largely to an area where topography has permitted a long history of intensive agriculture that may have limited functional connectivity between colonies. This has been followed over the past 3 decades by substantial recreational and second-home development on the surrounding forested mountainsides where habitable rock outcrops occur. In the mid-Atlantic Highlands, many landscape-level factors that differ between physiographic subprovinces (e.g. location and abundance of suitable emergent rock) can be described broadly but are difficult to adequately measure especially in conjunction with past and current anthropogenic disturbance in that landscape. For example, rock outcrops in the Blue Ridge capable of supporting Allegheny woodrats are less numerous and often display fewer structural features such as deep recesses suitable for midden and den sites than in the other physiographic subprovinces. Therefore habitat changes in that subprovince that contribute to isolation can further exacerbate the likelihood of local extirpation. Conversely, within portions of the Ridge and Valley, long linear forested mountains with long expanses of exposed rock along the summit provide relatively abundant and connected woodrat habitat thereby somewhat mitigating the large areas cleared for agriculture or development in the valley floors.

Change in forest cover

Unlike Balcom and Yahner (1996), we did not find a significant relationship between Allegheny woodrat absence and reduced forest cover in the LANDSCAPE model per se. Rather, we were constrained to note that forest cover differed significantly only between active and inactive sites within our univariate analyses. Although not spatially explicit at a level of resolution comparable to our Allegheny woodrat data, Forest Inventory and Analysis (FIA) data of the USDA Forest Service (<www.fs.fed.us/ne/fia/ >) indicates the overall percent cover on a per county basis throughout the mid-Atlantic Highlands has remained relatively high (>60%) over the period of our data collection. However, from 1992 to 2001, forested areas in the Blue Ridge and the Ridge and Valley north of the Potomac River decreased from 29.3 and 55% to 21.4 and 45.5%, respectively; these changes have had marked impacts on other biological groups (Robbins et al. 1989). Future projections indicate that forest loss to suburban development will continue to increase throughout the entire region (Alig and Butler 2004).

Even where forest cover has not been reduced in extent to create an inhospitable foraging or dispersal habitat matrix, there have been well-documented changes in regional forest composition such as a decline in oak-dominated coverage types that probably have impacted Allegheny woodrats (Balcom and Yahner 1996, Brose et al. 2001, Schuler 2004, LoGiudice 2006). In part, this could explain the strength of the GEOGRAPHIC model over the LANDSCAPE model in that critical aspects of forest cover were tied to composition rather than actual extent at each colony site and were thus embedded in the peculiarities of physiographic subprovinces. During our study, the rate of oak component decrease in the Allegheny Plateau north of the Potomac exceeded 20% whereas the drop in forest cover was only 5%. Thus, current forest conditions might not contribute as appreciably to Allegheny woodrat diets in the spring and summer, and likely do not provide quality cacheable food items for the winter period (Castleberry et al. 2002a). In forest types where oak abundance has always been less, such as in northern hardwood and montane boreal types, management-related changes in forest structure can negatively impact woodrats for a few growing seasons simply from loss of overstory cover (Castleberry et al. 2001, 2002c). Qualitative habitat changes that are largely unnoticed at the landscape-level, especially from dispersed selective timber harvesting or herbivory, can profoundly impact wildlife (Kittredge et al. 2003, Schuler 2004). Our analysis of residual observations counter to the GEOGRAPHIC model would indicate that this could be occurring in that extant Allegheny woodrat colonies in the less managed and more oak-dominated Blue Ridge can persist despite a higher degree of isolation than do some inactive colonies in the more managed, less oak-dominated forests of the Allegheny Plateau where active colony proximity was closer.

Parasitism

Implicated in the drastic Allegheny woodrat population declines in New York and New Jersey (LoGiudice 2003), the status of *B. procyonis* throughout the mid-Atlantic Highlands is uncertain. The parasite has been documented from raccoon feces in extreme northern West Virginia (Schaffer et al. 1981) and much of Maryland, particularly in the Blue Ridge subprovince where occurrences are known from Allegheny woodrat colony sites (Maryland Dept of Natural Resources, unpubl.). Although Owen et al. (2004) failed to document *B. procyonis* on the Allegheny Plateau of east-central West Virginia, they observed several instances of raccoons denning in rock outcrops containing Allegheny woodrats were observed. This demonstrates that the potential transfer mechanism is in place should *B. procyonis* become a common enzootic in the region as may already be occurring north of the Potomac River. Providing evidence for the additive nature of factors possibly implicated in Allegheny woodrat decline, Owen (2003) noted that increased use of emergent rocks as den sites by raccoons probably was correlated with the reduced availability of suitable den trees or snags in surrounding intensively managed or disturbed forests.

Sampling bias

The conservation of Allegheny woodrats in the mid-Atlantic Highlands is a consequence of natural isolation among den sites in rock outcrops that has been aggravated by human-influenced local and landscape habitat changes. Still, our survey data are less than complete in Virginia and West Virginia where observations largely were limited to public lands. Although we are extremely confident that at local landscape scales we surveyed and identified most the of Allegheny woodrat habitat present, it is possible that we missed active colony sites closer to known extant sites, or alternatively that we missed active colony sites around those considered inactive. Underestimation of missing patches can bias modeling efforts such as ours (Moilanen 2002). Also, our use of simple, straight-line distances between colonies across very complex landscapes represented a very imprecise examination of nearest neighbor and potential connectivity (Calabrese and Fagan 2004). Therefore, we note that the relationships between Allegheny woodrat colony site distances reflect negative trends resulting from a loose concept of isolation rather than providing exact or "critical" thresholds values (With and Crist 1995). Calculating inter-colony distance using landscape configurations linked to biologically plausible dispersal habitats (Floyd et al. 2005) would greatly improve our ability to spatially predict woodrat colony status.

Conclusion

With failed recolonization, especially in the Blue Ridge/Piedmont subprovince or for areas north of the Potomac River, naturally occurring stochastic extirpation events at localized and isolated rock outcrops could continue to become permanent spatially-correlated extinction events over the larger landscape (McCarthy and Lindenmayer 2000, Telfer et al. 2001). We do believe that our model can help managers better identify areas for priority conservation where extant populations have high chances of long-term persistence. These include those occupied areas with numerous rock outcrops or cliffs located in a surrounding matrix of unfragmented forest and separated by distances <2.5 km, representing the approximate maximum dispersal distance for Allegheny woodrats in the region (Castleberry et al. 2001, Mengak 2002a). This same rationale could be used for identifying areas for reintroductions to formerly occupied areas, as proposed for a similarly declining subspecies of eastern woodrat *Neotoma floridana illinoensis* (Monty et al. 2003).

Beyond the affinity for emergent rock habitats surrounded by mast-bearing forest communities, our understanding of both the landscape-level variables addressed herein or important micro-habitat variables for Allegheny woodrats is incomplete and requires further research (Castleberry et al. 2002c). Because their rock outcrop habitat is extremely variable in its occurrence, density, and spatial configuration across physiographic subprovinces in the mid-Atlantic Highlands, applying the patchy population concept (Szacki 1999) seems appropriate for managing Allegheny woodrats. Still, enough specifics elude managers trying to make definitive management recommendations to mitigate further declines in Allegheny woodrats in the mid-Atlantic Highlands or elsewhere. Our efforts in Maryland, Virginia, and West Virginia, when combined with the seminal work of Balcom and Yahner (1996) in Pennsylvania, provide evidence that an Allegheny woodrat decline across the larger landscape spanning much of the species' entire distribution is real and ongoing. Coupled with inevitable uncertainties that cannot be adequately addressed in current modeling efforts such as ours (Norris 2004) such as the future forest condition and extent in the mid-Atlantic Highlands or the species' unknown status in much of its range outside of this region, additional range contractions for the species probably will continue unabated.

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References

Alig, R. J. and Butler, J. 2004. Area changes for forest cover types in the United States, 1952 to 1997, with projections to 2050. – USDA Forest Service Gen. Tech. Rep. PNW-GTR-613.

Anderson, G. S. and Danielson, B. J. 1997. The effects of landscape composition and physiognomy on metapopulation size: the role of corridors. – Landscape Ecol. 12: 261–271.

Anon. 1995. Logistic regression examples using the SAS system. – SAS Inst.

Anon. 2006. NatureServe Explorer: an online encyclopedia of life. Ver. 4.7. – NatureServe, Arlington, VA, <http://www.natureserve.org/explorer>.

Balcom, B. J. and Yahner, R. H. 1996. Microhabitat and landscape characteristics associated with the threatened Allegheny woodrat. – Conserv. Biol. 10: 515–525.

Braun, E. L. 1950. Deciduous forests of eastern North America. – Blakiston.

Brose, P. et al. 2001. Bringing fire back: the changing regimes of the Appalachian mixed-oak forests. – J. For. 99: 30–35.

Burnham, R. B. and Anderson, D. R. 1998. Model selection and inference: a practical information-theoretic approach. – Springer.

Calabrese, J. M. and Fagan, W. F. 2004. A comparison-shopper's guide to connectivity metrics. – Frontiers Ecol. Environ. 2: 529–536.

Castleberry, N. L. et al. 2002a. Allegheny woodrat *Neotoma magister* food habits in the central Appalachians. – Am. Midl. Nat. 147: 80–92.

Castleberry, S. B. et al. 2001. Movements of Allegheny woodrats in relation to timber harvesting. – J. Wildl. Manage. 65: 148–156.

Castleberry, S. B. et al. 2002b. Microsatellite DNA analysis of population structure in Allegheny woodrats *Neotoma magister*. – J. Mammal. 83: 1058–1070.

Castleberry, S. B. et al. 2002c. Summer microhabitat selection by foraging Allegheny woodrats (*Neotoma magister*) in a managed forest. – Am. Midl. Nat. 147: 93–101.

Castleberry, S. B. et al. 2006. *Neotoma magister*. – Mammal. Spec. 789: 1–5.

Chamblin, H. D. et al. 2004. Allegheny woodrat (*Neotoma magister*) use of rock drainage channels on reclaimed mines in southern West Virginia. – Am. Midl. Nat. 151: 346–354.

Davidson, W. R. and Nettles, V. F. 1997. Field manual of wildlife diseases in the southeastern United States. – Univ. of Georgia Southeastern Cooperative Wildlife Disease Study.

Dickson, J. G. 2004. Wildlife and upland oak forests. – In: Spetich, M. A. (ed.), Upland oak ecology symposium: history, current conditions, and sustainability. USDA Forest Service Gen. Tech. Rep. SRS-73, pp. 106–115.

Fahrig, L. and Merriam, G. 1985. Habitat patch connectivity and population survival. – Ecology 66: 1762–1768.

Fenneman, N. M. 1938. Physiography of the eastern United States. – McGraw-Hill.

Floyd, C. H. et al. 2005. Marmots on Great Basin mountaintops: using genetics to test a biogeographic paradigm. – Ecology 86: 2145–2153.

Franken, R. J. and Hik, D. S. 2004. Influence of habitat quality, patch size and connectivity on colonization and extinction dynamics of collared pikas *Ochotona collaris*. – J. Anim. Ecol. 83: 889–896.

Gates, J. E. 1991. Powerline corridors, edge effects, and wildlife in forested landscapes of the central Appalachians. – In: Rodiek, J. E. and Bolen, E. G. (eds), Wildlife and habitats in managed landscapes. Island Press, pp. 13–32.

Gibson, L. A. et al. 2004. Landscape characteristics associated with species richness and occurrence of small native mammals inhabiting a coastal heathland: a spatial modeling approach. – Biol. Conserv. 120: 75–89.

Henein, K. and Merriam, G. 1990. The elements of connectivity where corridor quality is variable. – Landscape Ecol. 4: 157–170.

Hosmer, D. W. and Lemeshow, S. 2000. Applied logistic regression. – Wiley.

Kittredge, D. B. et al. 2003. Timber harvesting as ongoing disturbance in a landscape of diverse ownership. – For. Ecol. Manage. 180: 425–442.

Kozakiewicz, M. 1993. Habitat isolation and ecological barriers – the effect on small mammal population and communities. – Acta Theriol. 38: 1–30.

Lawes, M. J. et al. 2000. Patch occupancy and potential metapopulation dynamics of three forest mammals in fragmented afromontane forest in South Africa. – Conserv. Biol. 14: 1088–1098.

LoGiudice, K. 2003. Trophically transmitted parasites and the conservation of small populations: raccoon roundworm and the imperiled Alleghen woodrat. – Conserv. Biol. 17: 258–266.

LoGiudice, K. 2006. Toward a synthetic view of extinction: a history lesson from a North American rodent. – Bioscience 56: 687–693.

Marsh, D. M. and Trenham, P. C. 2001. Metapopulation dynamics and amphibian conservation. – Conserv. Biol. 15: 40–49.

McCarthy, M. A. and Lindemayer, D. B. 2000. Spatially-correlated extinction in a metapopulation model of leadbeater's possum. – Biodiv. Conserv. 9: 47–63.
Mehta, C. R. and Patel, N. R. 1983. A network algorithm for performing Fisher's exact tests in r by c contingency tables. – J. Am. Stat. Assoc. 78: 427–434.
Mengak, M. T. 2002a. Home range and movement of the Allegheny woodrat (*Neotoma magister*) in Virginia. – Banisteria 19: 3–8.
Mengak, M. T. 2002b. Reproduction, juvenile growth and recapture rates of Allegheny woodrats (*Neotoma magister*) in Virginia. – Am. Midl. Nat. 148: 155–162.
Menzel, J. M. 2003. An examination of the habitat requirements of the endangered Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) by assessing nesting sites, habitat use and the development of a habitat model. – Ph.D. thesis, West Virginia Univ.
Moilanen, A. 2002. Implications of empirical data quality to metapopulation model parameter estimation and application. – Oikos 96: 516–530.
Monty, A. et al. 2003. Genetic variation and population assessment of eastern woodrats in southern Illinois. – Southeast. Nat. 2: 243–260.
Norris, K. 2004. Managing threatened species: the ecological toolbox, evolutionary theory and declining population paradigm. – J. Appl. Ecol. 41: 413–426.
Noss, R. F. 2004. Conservation targets and information needs for regional conservation planning. – Nat. Areas J. 24: 223–231.
Owen, S. F. 2003. Ecology and management of raccoons within an intensively managed forest in the central Appalachians. – Ph.D. thesis, West Virginia Univ.
Owen, S. F. et al. 2003. Home-range size and habitat used by the northern myotis (*Myotis septentrionalis*). – Am. Midl. Nat. 150: 352–359.
Owen, S. F. et al. 2004. Raccoon roundworm in raccoons in central West Virginia. – Northeast. Nat. 1: 137–142.
Posillico, M. et al. 2004. A habitat model for brown bear conservation and land use planning in the central Apennines. – Biol. Conserv. 118: 141–150.
Robbins, C. S. et al. 1989. Habitat area requirements of breeding forest birds of the Middle Atlantic states. – Wildl. Monogr. 103: 1–34.
Rodríguez, A. and Andren, H. 1999. A comparison of Eurasian red squirrel distribution in different fragmented landscapes. – J. Appl. Ecol. 36: 649–662.
Schaffer, G. D. et al. 1981. Helminth parasites of translocated raccoons (*Procyon lotor*) in the southeastern United States. – J. Wild. Diseases 17: 217–227.
Schuler, T. M. 2004. Fifty years of partial harvesting in a mixed mesophytic forest: composition and productivity. – Can. J. For. Res. 34: 985–997.
Schuler, T. M. et al. 2002. Successional dynamics and restoration implications of a montane coniferous forest in the central Appalachians, USA. – Nat. Areas J. 22: 88–98.
Steel, R. G. D. and Torrie, J. H. 1980. Principles and procedures of statistics: a biometrical approach. – McGraw-Hill.
Szacki, J. 1999. Spatially structured populations: how much do they match the classic metapopulation concept. – Landscape Ecol. 14: 369–379.
Teixeira, J. et al. 2001. Biogeography of the golden-striped salamander *Chioglossa lusitanica*: a field survey and spatial modeling approach. – Ecography 24: 618–624.
Telfer, S. et al. 2001. Metapopulation processes and persistence in remnant water vole populations. – Oikos 95: 31–42.
Terborgh, J. et al. 2001. Ecological meltdown in predator-free forest fragments. – Science 294: 1923–1926.
Thomas, D. L. and Taylor, E. J. 1990. Study designs and tests for comparing resource use and availability. – J. Wildl. Manage. 54: 322–330.
Van der Ree, R. et al. 2003. Gap-crossing by gliding marsupials: thresholds for use of isolated woodland patches in an agricultural landscape. – Biol. Conserv. 115: 241–249.
Wagner, D. M. and Drickamer, L. C. 2004. Abiotic habitat correlates of Gunnison's prairie dog in Arizona. – J. Wildl. Manage. 68: 188–197.
Walker, R. S. et al. 2003. Effects of patch attributes, barriers and distance between patches on the distribution of a rock-dwelling rodent (*Lagidium viscacia*). – Landscape Ecol. 18: 187–194.
With, K. A. and Crist, T. O. 1995. Critical thresholds in species' responses to landscape structure. – Ecology 76: 2446–2459.

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