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Relationship of ruffed grouse *Bonasa umbellus* to landscape characteristics in southwest Virginia, USA

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We examined ruffed grouse *Bonasa umbellus* selection of landscape characteristics and cover types. Grouse home ranges derived from telemetry data gathered from fall 1996 through fall 1998 were overlaid onto a GIS map of the Clinch Mountain Wildlife Management Area, southwest Virginia, USA, composed of 22 cover types (10,343 ha). We calculated the landscape metrics using FRAGSTATS/ARC. We compared landscape metrics of 23 home ranges to those calculated for the area encompassed by the home range plus a surrounding 300 m buffer, and to metrics calculated for 50 random plots of 33 ha each. We used compositional analysis to test for preferential use of cover types. Ruffed grouse selected areas with high densities of smaller than average patches of uniform size and shape, containing higher than average amounts of high contrast edge ($P < 0.01$). Grouse preferred areas containing a greater diversity of cover types ($P < 0.01$). Regeneration cuts and mesic deciduous stands with a rhododendron *Rhododendron* spp.-laurel *Kalmia latifolia* understory were the most preferred cover types ($P < 0.10$). Creating and maintaining a landscape with high densities of small patches of uniform size and regular shape would provide the highest quality ruffed grouse habitat in this region. These patches should contain early successional cover. Rhododendron and/or laurel thickets may act as supplemental cover in the absence of regeneration cuts, and may also be beneficial as winter cover.

Key words: compositional analysis, habitat, habitat selection, landscape, ruffed grouse, Virginia

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Landscape-level habitat characteristics, such as size, distribution, spatial arrangement and availability of different cover type patches, are important habitat features to species that occupy a variety of habitats during their life (Kareiva 1990, Lamberson, McKelvey, Noon & Voss 1992, McKelvey, Noon & Lamberson 1992, Aberg, Swenson & Andrén 2000). Habitat requirements of ruffed grouse may change with season and grouse behaviour (Bump, Darrow, Edminster & Crissey 1947, Chapman, Bezdek & Dustman 1952, Dorney 1959, Maxson 1978, Thompson & Dessecker 1997). Management recommendations for ruffed grouse suggest the importance of providing and maintaining a mixture of forest age classes and cover types at the landscape scale (Bump et al. 1947, Berner & Gysel 1969, Gullion 1972, Kubisiak, Moulton & McCaffery 1980, Gullion 1989c). The size, configuration and arrangement of cover types in the landscape affect ruffed grouse home range size and movement (Fearer 1999). However, few studies have considered selection by grouse for different characteristics at the landscape scale, such as the size and shape of different patches or landscape-level cover types.

We examined ruffed grouse selection of landscape characteristics, configuration(s) of cover types in the landscape and specific cover types. We tested the hypotheses that the configuration and spatial arrangement of cover types within home ranges do not differ from the landscape in general, and that the relative proportion of cover types within a home range does not differ from those available. Landscape characteristics that differ from those available or disproportionately used cover types may be features that could be managed to enhance grouse habitats.

Methods

Study area

We conducted research from 1996 to 1999 on the Clinch Mountain Wildlife Management Area (CMWMA) located in the counties of Smyth, Washington, Russell and Tazewell, southwestern Virginia, USA. It encompassed 10,343 ha within the Ridge and Valley province (J. Baker, Virginia Department of Game and Inland Fisheries, unpubl. report). The topography is rugged and diverse with elevations ranging within 600-1,400 m a.s.l.. The dominant cover types in the management area were xeric and mesic deciduous stands that included mixed oak *Quercus* spp., mixed hardwood, yellow poplar *Liriodendron tulipifera* and northern hardwoods (J. Baker, Virginia Department of Game and Inland Fisheries, unpubl. report).

Data collection and analysis

From 1996 through 1998 we trapped grouse during fall (September-November) and spring (February-April) using lily-pad style traps with drift fences (Gullion 1965). Sex and age were determined for each bird using standard feather criteria (Servello & Kirkpatrick 1986, Gullion 1989a,b). Each bird was fitted with a 10-11 g necklace-style radio transmitter with a frequency range of 150-151 MHz, a battery life of 12 months and an 8-hour delay mortality sensor (ATS Inc., Isanti, MN). All birds were released at their capture sites.

We estimated the location of each bird by triangulation 2-3 times per week throughout the year. Triangulations consisted of ≥3 azimuths taken within intervals of 30 minutes from telemetry stations with known universal transverse mercator (UTM) coordinates and were taken at all times of the day. We used program LOCATE II (Pacer 1990) to determine the UTM coordinates for each triangulation. When > 3 azimuths were taken, those that best estimated the bird's location were chosen using a Lenth estimator and a goodness-of-fit test (White & Garrott 1990). We calculated the home range size using the adaptive kernel method (Worton 1989) in the animal movement program extension (Hooge & Eichenlaub 1997) designed for ArcView (Environmental Systems Resource Institute 1996, Fearer 1999).

We developed a GIS coverage based on LANDSAT imagery with 22 cover types for CMWMA for our analyses (Fearer 1999). To provide information on habitat structure and species compositions for the GIS cover types, we established 201 stratified random habitat plots with a 20 m radius size in the study area. We chose the plot size to characterize data at a large scale and to approximate the pixel size (30 m) used in the GIS database. We established habitat plots before the GIS database was complete and thus used the following general cover types as strata: deciduous forest, deciduous forest with evergreen understory, mixed forest, riparian zones, open field, shrub/scrub and regeneration cuts (clear cuts 5-20 years old). Habitat data gathered in the plots were based on the methods described by Noon (1981). From the plot centre, we established four transects in the cardinal directions. Using the point intercept method at 4-m intervals along each transect, we recorded canopy cover of deciduous trees, coniferous trees and shrubs as well as percent ground cover of dead woody debris. The height of shrubs to the nearest 0.5 m also was recorded at each 4-m interval. We counted stems (< 8 cm dbh) that intersected a 2-m pole held parallel to and 1.5 m above the ground and perpendicular to the transect while walking the transect. We recorded shrub species within the plot in order of dom-

Table 1. Landscape metrics (see McGarigal & Marks (1995) for detailed descriptions and computational formulas) used to evaluate landscape characteristic selection by ruffed grouse at Clinch Mountain Wildlife Management Area, Virginia, during 1996-1998.

Acronym	Units	Description
NP/ha	#/ha	Number of patches per hectare
LPI	%	Largest patch index; percentage of the home range compared by the largest patch
MPS	ha	Mean patch size
MSI	none	Mean shape index; quantifies patch shape, increases with irregularity in patch shape
TCAI	%	Total core area index; percentage of the home range that is core area. Core area is the interior area of a patch > 50 m from the patch's edge
PSSD	ha	Patch size standard deviation; variation of patch size in the landscape
HRCPR/H	#/ha	Number of cover types per hectare; number of different cover types within a 22-ha circle centered on the kernel centre of the home range
MNN	m	Mean nearest neighbour distance; distance from one patch to another of the same type, averaged across all patches in the landscape
SHDI	none	Shannon's diversity index for cover types
TECI	%	Total edge contrast index; Measure of edge contrast in the landscape, approaches 100% when all edge is maximum contrast (based on preset edge weightings)

inance based on percent cover. We also recorded basal area with an angle gauge and the stand height within the circular plot. We overlaid plot locations onto the GIS database upon its completion and summarized the habitat data by cover types. We determined the dominant tree and shrub species within each cover type based on the percent occurrence of each species across all plots within a cover type as well as the relative abundance within each plot.

We tested for selection of nine landscape characteristics (Table 1) and preferential use of 15 cover types at the home range scale and study area scale (Table 2). For the home range scale analysis, we established a 300 m buffer zone outlining the shape of the 95% contour boundary of each home range to examine what was available to the grouse in their immediate area. We chose 300 m based on the average home range size (33 ha) for the birds analysed in our study. Assuming a circular shape, a 33-ha home range would have a radius of approximately 300 m. Thus, we assumed that an area within 300 m of a home range boundary was readily available to, but not used, by the birds. Using ArcView, we determined cover type coverage within each home range based on the home range's 95% contour boundary, and within the total area encompassed by the home range plus its respective buffer (HR+B) from the GIS database. We used FRAGSTATS/ARC to calculate the landscape metrics for each of these coverages (McGarigal & Marks 1995). We treated home ranges and home ranges plus their buffers as paired samples and tested the hypothesis of no difference in landscape characteristics between the samples using the Wilcoxon signed-rank test (Hollander & Wolfe 1973, Minitab Inc. 1996).

For analysis at the study area scale, we established 50 random 33-ha circular plots across the study area to estimate average landscape characteristics. We determined cover types within random plots and calculated landscape metrics using FRAGSTATS/ARC. We treated the home range and random plot coverages as two independent samples and tested the hypothesis of no difference in landscape characteristics between the samples using the Wilcoxon rank-sum test (Hollander & Wolfe 1973, Minitab Inc. 1996).

Table 2. Mean use (± SE) of cover types by ruffed grouse (N = 23) and mean availability (± SE) of cover types at home range (HR plus 300-m buffer zone) and study area scales in the Clinch Mountain Wildlife Management Area, Virginia, during 1996-1998.

Cover type	Use in home range (%)	Available in HR + 300-m buffer zone (%)	Available at study area scale (%)
Regeneration cut	14.0 (3.3)	5.9 (1.2)	0.5
Mesic coniferous	1.3 (0.3)	1.3 (0.2)	1.5
Mesic deciduous	16.5 (1.7)	17.7 (1.3)	14.4
Mesic deciduous with evergreen understory	10.9 (2.0)	7.4 (1.2)	2.5
Mesic deciduous with mixed understory	4.1 (0.6)	3.2 (0.5)	1.4
Meso-xeric coniferous	0.1 (0.04)	0.2 (0.1)	0.5
Meso-xeric deciduous	5.1 (0.9)	5.0 (0.7)	2.5
Meso-xeric deciduous with evergreen understory	1.0 (0.2)	0.7 (0.1)	0.4
Meso-xeric deciduous with mixed understory	1.0 (0.2)	0.7 (0.1)	0.2
Mesic herbaceous	1.8 (1.4)	0.9 (0.6)	0.2
Xeric coniferous	1.2 (0.3)	1.5 (0.2)	2.5
Xeric deciduous	28.5 (4.0)	40.6 (3.3)	59.1
Xeric deciduous with evergreen understory	8.1 (1.3)	8.1 (0.8)	7.9
Xeric deciduous with mixed understory	5.6 (1.1)	6.1 (0.5)	4.4
Other[a]	0.5 (0.1	0.9 (0.2)	1.9

[a] includes eight cover types each of which had < 0.6% cover on the study area.

Table 3. Mean (±SE) values of random plot habitat data by cover type (in %) in the Clinch Mountain Wildlife Management Area, Virginia, during 1996-1998. Data were collected in 20-m radius circular plots located throughout the study area.

Cover type	N	Deciderous cover %	Coniferous cover %	Dead woody cover %	Shrub cover %	Shrub canopy height (m)	Stems/ ha	Stand height (m)	Basal area (m^2/ha)
Regeneration cut	8	83 (3)	0 (0)	18 (2)	29 (9)	1.2 (0.2)	9439 (1249)	9 (1)	6.1 (0.5)
Open field	8	2 (2)	1 (1)	0 (0)	2 (1)	0.6 (0.4)	136 (65)	0 (0)	0.0 (0.0)
Mesic shrub/scrub	2	10 (0)	3 (3)	5 (5)	28 (3)	1.2 (0.1)	1891 (288)	4 (1)	0.0 (0.0)
Xeric mixed	3	57 (12)	22 (11)	3 (2)	55 (25)	1.9 (0.4)	8098 (4357)	14 (7)	16.0 (6.6)
Mesic deciduous	36	85 (2)	2 (1)	7 (1)	30 (4)	1.8 (0.2)	3403 (333)	20 (1)	13.7 (1.8)
Xeric deciduous	84	85 (1)	1 (0)	9 (1)	21 (2)	1.6 (0.2)	2925 (215)	21 (1)	20.7 (1.0)
Meso-xeric deciduous	4	89 (3)	0 (0)	8 (1)	23 (3)	1.7 (0.3)	4920 (790)	19 (2)	17.2 (3.0)
Mesic deciduous with evergreen understory	14	75 (5)	3 (2)	7 (7)	76 (4)	2.0 (0.1)	4968 (687)	20 (2)	13.2 (2.3)
Mesic deciduous with mixed understory	10	71 (7)	6 (5)	5 (1)	50 (6)	1.7 (0.1)	4413 (565)	17 (2)	16.9 (2.8)
Xeric deciduous with evergreen understory	13	83 (2)	5 (4)	6 (1)	53 (8)	1.7 (0.1)	3521 (390)	21 (2)	21.3 (2.6)
Xeric deciduous with mixed understory	19	82 (3)	1 (4)	7 (2)	56 (5)	1.9 (0.1)	4399 (403)	19 (1)	22.4 (2.9)

We used compositional analysis (Aebischer, Robertson & Kenward 1993) to assess use availability. We determined use and availability of cover types at the home range and study area scales. At the home range scale, used habitat was that located within each bird's home range, and available cover was that located in the home range plus its surrounding 300 m buffer. At the study site scale, used habitat was that located within each bird's home range, and that available was averaged across the entire study area. We determined the percent coverage of each cover type from the ArcView database, and used a SAS algorithm for the compositional analysis calculations (SAS Institute 1989, Ott & Harvey 1997). For compositional analyses, we set $\alpha = 0.10$ to simplify reporting of the data, but report the P-values for the specific relationships we discuss (Johnson 1999). For the remaining analyses, we chose to report P-values rather than setting an α-value (Johnson 1999).

Results

Of the 111 grouse captured between September 1996 and April 1998, 23 had home ranges that were asymptotic given their number of locations. We used these birds in the analyses. We found no difference for any landscape or habitat variable between sex and age classes (ANOVA: $P > 0.06$ for all tests). Additionally, the average movement between the centre of locations in subsequent seasons was 183 m, approximately 25% the diameter of the average 33-ha home range. Therefore, we pooled our data for these analyses.

Habitat data were gathered in 13 of the 22 cover types (Tables 3 and 4), which accounted for 94% of the study site area. Data for all open field plots were similar and were pooled into one open field category. Of the nine cover types not included in the habitat sampling (mesic coniferous, xeric coniferous, meso-xeric coniferous, mesic mixed, meso-xeric mixed, meso-xeric

Table 4. Dominant tree and shrub species by cover type in the Clinch Mountain Wildlife Management Area, Virginia, during 1996-1998.

Cover type	N	Dominant species[a]: Trees	Shrubs
Regeneration cut	8	*Acer rubrum, Magnolia acuminata, Prunus serotina*	*Rubus* spp., *Vaccinium* spp., *Smilax* spp.
Open field	8	N/A	*Rubus* spp.
Mesic shrub/scrub	2	N/A	*Rhododendron* spp., *Vaccinum* spp., *Kalmia latifolia*
Xeric mixed	3	*Quercus rubra, Picea rubens, Betula alleghaniensis*	*Rhododendron* spp., *K. latifolia, Vaccinum* spp.
Mesic deciduous	36	*B. lenta, A. rubrum, Q. rubra*	*Rhododendron* spp., *Hamamelis virginiana, Crataegus* spp.
Xeric deciduous	84	*A. rubrum,Q. rubra, A. saccharum*	*Ilex verticillata, Smilax* spp., *Vaccinum* spp.
Meso-xeric deciduous	4	*A. rubrum, Q. prinus, Q. rubra*	*Vaccinum* spp., *I. verticillata, Smilax* spp.
Mesic deciduous with evergreen understory	14	*A. rubrum, Q. rubra, P. serotina*	*Rhododendron* spp., *H. virginiana, K. latifolia*
Mesic deciduous with mixed understory	10	*A. rubrum, L. tuilpifera, B. alleghaniensis*	*Rhododendron* spp., *K. latifolia, Vaccinum* spp.
Xeric deciduous with evergreen understory	13	*A. rubrum, P. serotina, B. lenta*	*Rhododendron* spp., *K. latifolia, I. verticillata*
Xeric deciduous with mixed understory	19	*A. rubrum, Q. prinus, N. sylvatica*	*Rhododendron* spp., *K. latifolia;H. virginiana*

[a] Tree species data were collected in 10 x 10 m square plots nested in the 20-m radius circular plots used for general habitat data collection. Dominance within cover types was based on presence of a species across plots as well as abundance within each plot.

Table 5. Results of Wilcoxon signed-rank tests of ruffed grouse selection for specific landscape characteristics at the home range scale in the Clinch Mountain Wildlife Management Area, Virginia, during 1996-1998. Paired differences were calculated between 23 home ranges and the home ranges plus their respective 300 m buffers.

Landscape metric	Median				
	Home range	Home range + buffer	Median	Test statistic difference	P
Total core area index (%)	5.59	12.01	-5.69	16.0	<0.01
Patch size standard deviation (ha)	1.07	2.88	-2.05	2.0	<0.01
Mean patch size (ha)	0.44	0.79	-0.29	8.5	<0.01
Mean shape index	1.26	1.29	-0.03	24.0	<0.01
Shannon's diversity index	1.78	1.80	-0.01	129.5	0.61
Mean nearest neighbour distance (m)	102.14	97.42	2.71	119.0	0.71
Number of patches/ha	2.28	0.08	2.10	276.0	<0.01
Largest patch index (%)	25.44	19.54	4.01	188.0	0.07
Total edge contrast index (%)	31.67	26.61	5.68	232.0	<0.01

shrub/scrub, xeric shrub/scrub, meso-xeric deciduous with evergreen understory and meso-xeric deciduous with mixed understory), none had > 6.4% coverage in any individual home range, and seven had < 5% coverage. Also, only two of the nine cover types had > 1% coverage across the study area.

Deciduous cover was relatively high in all cover types except the open field and mesic shrub-scrub types, whereas the xeric mixed type was the only type with > 6% coniferous cover (see Table 3). Shrub cover was highest in the mesic deciduous with evergreen understory cover type, and all cover types with mixed or evergreen understory had > 50% shrub cover (see Table 3). Shrub height was relatively uniform across all cover types. Stem densities were highest in the regeneration cuts and xeric mixed cover type, and were lowest in the open and mesic shrub-scrub types (see Table 3).

The dominant tree species in the mesic deciduous cover types were black birch *Betula lenta*, red oak *Quercus rubra*, red maple *Acer rubrum* and black cherry *Prunus serotina* (see Table 4). The xeric types were typically dominated by red maple, red and chestnut oak *Quercus prinus*, black cherry and yellow poplar. The dominant shrub species in the mesic deciduous cover type was rhododendron, while both rhododendron and mountain laurel were present in the xeric deciduous cover types (see Table 4).

Landscape characteristic selection

Home range scale

The total core area index (TCAI), patch size standard deviation (PSSD), mean shape index (MSI) and mean patch size (MPS) were all smaller ($P \leq 0.01$) in the home ranges than in the HR+B area (Table 5). The number of patches per hectare (NP/ha), the largest patch index (LPI), and the total edge contrast index (TECI) were larger ($P \leq 0.07$) within the home ranges than within the HR+B area (see Table 5). No differences in Shannon's diversity index (SHDI; $P = 0.61$) and mean nearest neighbour distance ($P = 0.71$) were detected between the home ranges and HR+B areas (see Table 5).

Study area scale

All landscape metrics included at the study area scale were different ($P < 0.01$) between home ranges and the random plots in the study area (Table 6). The total core area index, patch size standard deviation, mean shape index, mean patch size and largest patch index were smaller in home ranges than in random plots. Shannon's diversity index, number of patches per hectare, mean nearest neighbour distance, total edge contrast index and patch richness per hectare were greater in home ranges than in random plots (see Table 6).

Table 6. Results of Wilcoxon rank-sum tests of ruffed grouse selection for specific landscape characteristics at the study area scale in the Clinch Mountain Wildlife Management Area, Virginia, during 1996-1998.

Landscape metric	Median			
	Home range (N = 23)	Random plot (N = 50)	Test statistic	P
Total core area index (%)	5.59	11.05	2146.0	<0.01
Patch size standard deviation (ha)	1.07	3.40	2288.5	<0.01
Mean patch size (ha)	0.44	1.11	2286.5	<0.01
Mean shape index	1.26	1.32	2247.0	<0.01
Shannon's diversity index	1.78	1.13	1448.0	<0.01
Number of patches/ha	2.28	0.90	1409.0	<0.01
Largest patch index (%)	25.40	54.60	2229.0	<0.01
Total edge contrast index (%)%)	31.67	21.40	1535.0	<0.01
Patch richness/ha	0.55	0.32	1468.0	<0.01

Preferential use of cover types

Of the above-mentioned cover types, five had < 2% use by ruffed grouse (xeric shrub/scrub, mesic shrub/scrub, xeric mixed, meso-xeric mixed and mesic mixed) and three were not used at all (meso-xeric shrub/scrub, xeric herbaceous and meso-xeric herbaceous). These cover types also had a very low overall coverage in the study area (≤ 0.8% each). Therefore, these cover types were pooled into the category 'Other' for compositional analyses (see Table 2).

Home range scale

Ruffed grouse used cover types disproportionately to their availability at the home range scale ($F_{14,9} = 4.03$, $P = 0.02$). Mesic deciduous with mixed understory (MDMU), mesic deciduous with evergreen understory (MDEU) and regeneration cuts (RC) were ranked first, second and third, respectively; no difference in selection was detected among these three cover types ($P > 0.10$; Table 7). Meso-xeric deciduous with a mixed understory (MXDMU) was ranked fourth at this scale followed by mesic deciduous (MD) and meso-xeric deciduous (MXD). Mesic deciduous was preferred over xeric deciduous (XD) at this scale ($P < 0.02$).

Study area scale

Ruffed grouse used cover types disproportionately to their availability at the study area scale ($F_{14,9} = 16.2$, $P < 0.01$). Regeneration cuts had the highest rank relative to their availability at the study area scale followed by MDMU and MDEU (see Table 7). However, we did not detect differences in selection among these cover types ($P > 0.10$). Meso-xeric deciduous and MD ranked fourth and fifth in preference at the study area scale (see Table 7), and both of these cover types were more preferred than XD ($P < 0.05$).

Discussion

Examining landscape characteristic selection and cover type preference at the study area scale provided a general comparison of what grouse were selecting given the cover types available within the landscape. Conducting the same analyses at the home range level provided a more detailed description of which cover types grouse were selecting at a finer scale. As a result, it allowed us to better address the question of why grouse centered its home range in a particular location.

Landscape characteristic selection

At home range and study area scales, grouse selected areas containing smaller patches, thereby minimizing the core area (> 50 m from the patch edge) within these patches. Grouse home ranges also had high patch densities at both scales, which further illustrates the selection for smaller patches. Grouse were selecting areas where patches were of relatively uniform size and regular (e.g. square) shape and contained more high contrast edge. In fact, the majority of grouse in our study centered their home ranges on these high contrast edges, such as those between regeneration cuts and mature, deciduous stands rather than in the centre of early successional cover.

The majority of the study site was mature, contiguous deciduous forest, and grouse were choosing areas within this landscape that had a greater diversity of cover types. This was reflected by the higher SHDI and number of cover types per hectare in home ranges relative to random plots. Within the areas, however, small-scale differences in cover diversity did not appear to be important.

The study site contained several large, contiguous patches of mature forest that dominated the landscape,

Table 7. Ranked preference of cover types by ruffed grouse based on a compositional analysis for home range and study site scales. Data were collected in the Clinch Mountain Wildlife Management Area, Virginia, during 1996-1998.

	Cover types	
Rank[a]	Home range scale	Study site scale
1	Regeneration cut	Mesic deciduous with mixed understory
2	Mesic deciduous with mixed understory	Mesic deciduous with evergreen understory
3	Mesic deciduous with evergreen understory	Regeneration cut
4	Meso-xeric deciduous	Meso-xeric deciduous with mixed understory
5	Mesic deciduous	Mesic deciduous
6	Meso-xeric deciduous with mixed understory	Meso-xeric deciduous
7	Xeric deciduous with evergreen understory	Xeric deciduous with evergreen understory
8	Xeric deciduous with mixed understory	Meso-xeric deciduous with evergreen understory
9	Meso-xeric deciduous with evergreen understory	Xeric deciduous
10	Xeric deciduous	Mesic herbaceous
11	Mesic coniferous	Xeric deciduous with mixed understory
12	Xeric coniferous	Meso-xeric coniferous
13	Mesic herbaceous	Xeric coniferous
14	Other	Mesic coniferous
15	Meso-xeric coniferous	Other

[a] The lowest rank (1) represents the most preferred habitat. Fearer (1999) provides details of the compositional analysis and all pairwise comparisons.

and this was reflected in the large LPI value for the study site. Grouse home ranges tended to contain several small, less extensive patches, resulting in a smaller LPI value for home ranges relative to the study area. Often, more than half of a grouse's home range contained one or two patches that provided one or several key habitat requirements, such as cover and food. For example, almost 50% of a grouse's home range may have been in a regeneration cut or some other habitat patch that provided cover and some food sources for most of the year. The rest of its home range contained smaller parts of other patches that provided the remainder of its habitat requirements. When the bird's home range and surrounding area are considered (i.e. the home range plus its 300 m buffer), the size of the regeneration cut would not be different from the average size of the neighbouring patches. However, because about half of the bird's home range was in the regeneration cut patch and only relatively smaller parts of the other patches, the LPI value within the bird's home range would be larger than LPI for the home range and buffer area.

Areas containing several small patches of cover types preferred by grouse should provide the habitat diversity that grouse require throughout the year (Bump et al. 1947, Gullion 1972, 1989c). Patches of relatively uniform size and shape can increase the interspersion of different cover types, providing more cover types within a smaller area. The presence of several small patches vs a few large ones also can maximize the amount of edge in the landscape, another important habitat component for ruffed grouse (Bump et al. 1947, Kubisiak et al. 1980, DeStefano & Rusch 1984, Schulz, Bakke & Gulke 1989).

Preferential use of cover types

Cover type preference ranking at the home range scale was similar to that at the study area scale. At both scales, small discrepancies between the ranking of the cover types and differences detected between ranks were the result of variation in selection for cover types by individual birds. Although regeneration cuts were preferred most, relative to availability at the study site scale, the amount of regeneration cuts in the home ranges was variable. This produced a large confidence interval for regeneration cut selection, decreasing the probability of detecting significant differences in selection between this and the other cover types.

Early successional forest structure provided by regeneration cuts is an important habitat component for ruffed grouse (Bump et al. 1947, Thompson & Fritzell 1989, Wiggers, Laubham & Hamilton 1992, Thompson & Dessecker 1997). In the absence of such successional habitats, thick shrub understories in mature stands, such as those provided by rhododendron *Rhododendron* spp. or mountain laurel *Kalmia latifolia*, can provide adequate habitat for ruffed grouse (Bump et al. 1947, Hale, Johnson & Landers 1982, Epperson 1988, McDonald, Storm & Palmer 1998). The mesic deciduous with evergreen and mixed understory cover types were preferred over the meso-xeric deciduous with mixed and evergreen understories and xeric deciduous with mixed and evergreen understories at both scales. Because all these cover types provided the rhododendron/laurel understory cover component, we expected the selection for these cover types to be similar. Differences in habitat structure may provide some additional explanation for differing ranks. The preferred types had higher shrub cover (mesic deciduous with evergreen understory) or higher stem densities (mesic deciduous with mixed understory) than the less preferred types. Given these differences, mixed deciduous cover types probably provided more adequate habitat than xeric deciduous types.

Differences in the habitat structure and composition between mesic deciduous and xeric deciduous cover types likely also contributed to their different ranks, as the mesic types had greater shrub cover and stem densities than the xeric types. Also, the dominant tree species in the mesic types (black birch, red oak and black cherry) provide a nutritional and diverse food source for grouse (Servello & Kirkpatrick 1987, 1989). Thus, the structure and plant species composition of mesic deciduous cover types likely provided better cover and forage than the xeric deciduous cover type.

The preference for regeneration cuts is consistent with the known habitat preferences of ruffed grouse elsewhere within their range. Grouse require a diversity of cover types throughout the year to meet seasonal variations in habitat requirements (Bump et al. 1947, Kubisiak 1978, Gullion 1989c, Thompson & Dessecker 1997). Early successional cover, such as regeneration cuts, or other covers that provide similar understory structures, such as mature forest stands with a thick shrub understory, are the most preferred cover types of ruffed grouse and provide several of the grouse's habitat requirements (Bump et al. 1947, Hale et al. 1982, Epperson 1988, Thompson & Fritzell 1989, Wiggers et al. 1992, Thompson & Dessecker 1997, McDonald et al. 1998). In the eastern and southeastern parts of the ruffed grouse range in North America, rhododendron or laurel can also be important habitat components in winter, as the evergreen leaves of these shrubs provide thermal and escape cover (Bump et al. 1947, Barber 1989). Providing adjacent areas of mature forest that contain several food sources, such as birch catkins, grapes, acorns and cherries, also is important for maintaining a healthy grouse population, especially if rhododendron and/or laurel thickets are the primary source of cover (Norman & Kirkpatrick 1984, Servello & Kirkpatrick 1987,1989, Hewitt & Kirkpatrick 1997).

Based on our results, we recommend creating and maintaining a landscape with high densities of small patches that are of relatively uniform size and shape. Several of these patches should be early successional cover such as regeneration cuts. Regeneration cuts are one of the most preferred cover types, and they also provide an abundance of high contrast edge when interspersed with mature deciduous forest cover. Rhododendron or laurel thickets in moist deciduous forests, also a preferred cover type, may be beneficial as supplemental cover, as they provide thermal cover in winter and a structure similar to early successional forest cover. Mesic stands of mature hardwoods should be well interspersed with these cover types, and the stands should contain several food sources, such as oaks, grapes and birches, to supplement the grouse's diet. There is a multitude of possible landscape configurations that could contain the characteristics and mixtures of cover types we describe (Guthery 1999). Based on the results of our study, we believe creating and maintaining a landscape with these characteristics would provide the highest quality ruffed grouse habitat in the southern Appalachian region.

We believe the approach we have taken here has utility for analysing habitat use by other grouse species in other geographic regions. Comparing habitat within the home range to a buffer surrounding the home range allows determination of relatively small-scale habitat selection. Because the adaptive kernel home range was used rather than individual locations to determine habitat use, the potential effects of telemetry error in determining individual locations, and the associated habitat, was minimized.

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