



FACTORS ASSOCIATED WITH VARIATION IN HOME-RANGE SIZE OF APPALACHIAN RUFFED GROUSE (*BONASA UMBELLUS*)

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ABSTRACT.—From 1996 to 2001, researchers at 10 Appalachian study sites collected radiotracking data sufficient to delineate 1,054 seasonal home ranges of Ruffed Grouse (*Bonasa umbellus*; hereafter “grouse”). Using information-theoretic model selection and paired comparison of home ranges from individual grouse, we evaluated individual, local, and landscape factors hypothesized to affect grouse home-range size. Females and juvenile males occupied home ranges that averaged $>2\times$ larger than those of adult males, and home ranges of females averaged $2.6\times$ larger during successful breeding seasons than during years of reproductive failure. Clearcuts and forest roads are considered high-quality covers, and both were more prevalent in smaller home ranges. Several factors operating at a regional and landscape scale were also important. Previous studies have reported that southern grouse use relatively large home ranges, and we observed a continuous decline in home-range size with increasing latitude across the 710-km range spanned by our study sites. Home-range size of males, particularly juvenile males, was positively related to an index of population density. Given the species' “dispersed lekking” mating system, we interpret this as evidence of competition for preferred display sites. As has been reported for other game birds, all sex and age classes of grouse used smaller home ranges following closure of sites to hunting. Grouse inhabiting oak–hickory forests used larger home ranges than conspecifics in mixed mesophytic forests, and other factors interacted with forest type. In oak–hickory forests, female home-range size was inversely related to use of mesic bottomlands, which support important forage plants, and home ranges of adult grouse increased $2.5\times$ following poor hard-mast crops. By contrast, home ranges of grouse inhabiting mixed mesophytic forests were unrelated to use of bottomlands, and the influence of hard mast was reduced. This is in line with the view that in Appalachian oak–hickory forests, grouse are under strong nutritional constraint. However, this constraint is reduced in mixed mesophytic forests, likely because of the presence of high-quality alternative foods (e.g., cherry [*Prunus* spp.] and birch [*Betula* spp.]).
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Facteurs associés à une variation de la taille du domaine vital de *Bonasa umbellus* dans les Appalaches

RÉSUMÉ.—De 1996 à 2001, des chercheurs postés à 10 sites d'étude dans les Appalaches ont recueillis suffisamment de données télémétriques pour délimiter 1,054 domaines vitaux saisonniers de *Bonasa umbellus* (ci-après gélinotte). En utilisant un modèle de sélection théorique et des comparaisons appariées des domaines vitaux de gélinottes, nous avons évalué les facteurs individuels, locaux et du paysage susceptibles d'influer sur la taille du domaine vital. Les femelles et les mâles juvéniles occupaient des domaines vitaux qui étaient en moyenne plus de 2 fois plus grands que ceux des mâles adultes. Les domaines vitaux des femelles étaient en moyenne 2.6 fois plus grand durant les bonnes années de reproduction par rapport aux mauvaises. Les coupes à blanc et les chemins forestiers sont considérés comme étant des couverts de protection de grande qualité et ils étaient plus répandus dans les domaines vitaux de plus petite taille. Plusieurs facteurs opérant à l'échelle régionale et du paysage étaient aussi importants. Des études ont rapporté que les gélinottes du sud utilisent des domaines vitaux relativement grands. Nous avons observé un déclin continu de la taille du domaine vital à mesure qu'augmentait la latitude sur les 710 km comprenant nos sites d'étude. La taille du domaine vital des mâles, particulièrement des mâles juvéniles, était positivement lié à un indice de la densité de population. Étant donné le système d'appariement de type leks dispersés de l'espèce, nous interprétons ceci comme une preuve de la compétition pour les sites de parade préférés. Comme l'a été rapporté pour d'autres oiseaux gibiers, les deux sexes et toutes les classes d'âge ont utilisé de plus petits domaines vitaux suivant la fermeture des sites pour la chasse. Les gélinottes habitant les forêts de chênes et de noyers ont utilisé des domaines vitaux plus grands que leurs congénères habitant les forêts tempérées mixtes. D'autres facteurs ont aussi interagit avec le type de forêt. Dans les forêts de chênes et de noyers, la taille du domaine vital des femelles était inversement reliée à l'utilisation des terres basses mésiques, lesquelles supportent d'importantes plantes servant à l'alimentation, et les domaines vitaux des gélinottes adultes ont augmenté de 2.5 fois suite à une mauvaise production d'akènes. À l'opposé, les domaines vitaux des gélinottes habitant les forêts tempérées mixtes n'étaient pas associés à l'utilisation des terres basses et l'influence des akènes y était réduite. Ceci converge avec l'idée que dans les forêts de chênes et de noyers des Appalaches, les gélinottes subissent de fortes contraintes nutritionnelles. Néanmoins, ces contraintes sont réduites dans les forêts tempérées mixtes, probablement en raison de la présence de nourritures alternatives de grande qualité (e.g. *Prunus* spp. et *Betula* spp.).

HOME-RANGE SIZE is a fundamental aspect of an animal's behavioral ecology, having implications for energetics, survival, time budgets, movements, and spatial relations with other animals. Larger home ranges may be costly in terms of time and energy allocated to travel, while also increasing encounter rates with predators and competitors (Powell 2000, Yoder et al. 2004). Consequently, it is expected that, under most circumstances, animals should attempt to use

the smallest adequate home range (Badyaev et al. 1996). Further, space use should be positively related to resource needs and inversely related to resource availability, habitat quality, and, ultimately, an individual's fitness. Researchers have reported inverse relations between home-range or territory size and resource availability for a variety of bird species, including wrens, wattlebirds, and hummingbirds (Troglodytidae, Callaeidae, and Trochilidae, respectively; Cody

1985), wood warblers (Parulidae; Morse 1989), woodpeckers (Picidae; Convery 2002), turkey (Meleagrididae; Badyaev et al. 1996), and ptarmigan (Tetraonidae; Miller and Watson 1978). Further, Convery (2002) documented an inverse relation between home-range size and fitness for Red-cockaded Woodpeckers (*Picoides borealis*). However, there are also circumstances under which individuals should expand home-range size beyond that sufficient to meet foraging needs alone—for example, gaining access to mates, acquiring preferred breeding territories or display sites, and displacement by territorial conspecifics. Consequently, knowledge of factors associated with variation in home-range size can help to identify limiting resources and point to differences in habitat ecology and resource needs between demographic groups or populations.

Ruffed Grouse (*Bonasa umbellus*; hereafter “grouse”) inhabit forests across northern North America and, in the east, the species’ range extends south along the Appalachian Mountains to Georgia (Fig. 1). They do not form pair bonds and, with the exception of males in the vicinity of drumming logs (display sites), they are non-territorial and occupy overlapping home ranges (Bergerud and Gratson 1988, Rusch et al. 2000). Researchers have reported that females occupy

larger home ranges than males and that juveniles use larger ranges than adults (Archibald 1975, Thompson 1987, Clark 2000, Fearer and Stauffer 2003). Home-range size is also known to vary among seasons, being largest during fall and winter (Archibald 1975, Maxson 1978, Thompson 1987, Fearer and Stauffer 2003), and also may vary within a breeding season. For example, Maxson (1978) reported that during summer, females with broods made more extensive movements than females without broods. Habitat configuration within home ranges also can affect home-range size. Fearer and Stauffer (2003) reported that home ranges in Virginia were larger when habitat patches were irregularly shaped and as the amount of core habitat (i.e., habitat >50 m from an edge) within patches increased. Conversely, home-range size decreased with increased habitat diversity and density of high-contrast edge (e.g., clearcut or road edge). At a regional scale, it has been reported that home ranges of southern grouse are larger than those of grouse inhabiting central portions of the species’ range (White and Dimmick 1979, Epperson 1988, Thompson and Fritzell 1989, Neher 1993, Fearer and Stauffer 2003). This, combined with low population densities, has led biologists to speculate that quality of grouse habitat is generally inferior in the southern Appalachians.

Our objective was to identify factors associated with variation in grouse home-range size across the southern and central Appalachians and, from this, make inferences about the species’ ecology in the region. Data were collected at 10 Appalachian Cooperative Grouse Research Project (ACGRP) study sites spanning a latitudinal range of 710 km (Fig. 1; see also Norman et al. 2004). We evaluated factors potentially leading to landscape-level variation in home-range size, including latitude, growing-season phenology, forest type, landscape-level habitat availability, interannual variation in hard-mast crops, population density, and hunting activity. We also considered factors acting on individuals, including sex, age, reproductive status, and individual habitat use.

METHODS

Study sites.—Data were collected at 10 sites along the Appalachian extension of the species range (Fig. 1). Study sites ranged in size from 2,000 to 10,000 ha and were located on National

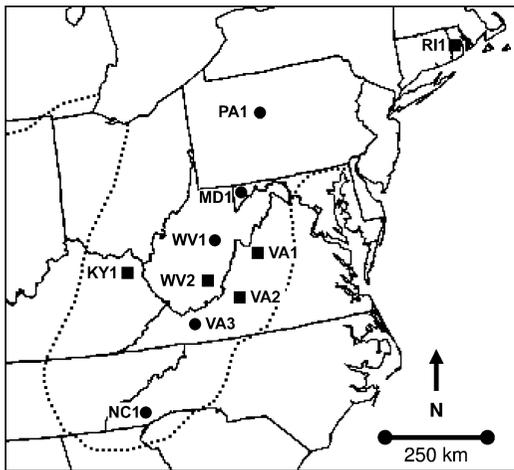


FIG. 1. Locations of Appalachian Cooperative Grouse Research Project study sites, with the southern limit of the geographic range of Ruffed Grouse indicated by the dotted line. Square markers identify study sites with predominantly oak-hickory forests, and circles identify those with mixed mesophytic forests.

Forest lands ($n = 2$), state forest and game management areas ($n = 5$), and industrial forestlands operated by MeadWestvaco Corporation ($n = 3$). Data collection began on the WV1 site in September 1995, and on KY1, MD1, VA2, VA3, and WV2 in September 1996. Monitoring started later on VA1 (September 1997), PA1 (September 1998), and NC1 and RI1 (September 1999). Monitoring ended on all sites in April 2001.

Forest cover on each study site was characterized by one of two general associations. Oak-hickory forests (Braun 1950) dominated cover on the KY1, RI1, VA1, VA2, and WV2 study sites. The most common tree species on these sites was chestnut oak (*Quercus prinus*), and other important species included white, red, scarlet, and black oak (*Q. alba*, *Q. rubra*, *Q. coccinea*, and *Q. velutina*, respectively); shagbark, pignut, bitternut, and mockernut hickory (*Carya ovata*, *C. glabra*, *C. cordiformis*, and *C. tomentosa*, respectively); white, Virginia, pitch, and Table Mountain pine (*Pinus strobus*, *P. virginiana*, *P. rigida*, and *P. pungens*, respectively); eastern hemlock (*Tsuga canadensis*); red and sugar maples (*Acer rubrum* and *A. saccharum*, respectively); and American beech (*Fagus grandifolia*). Where available, buds and catkins of aspen (*Populus* spp.), birch (*Betula* spp.), and cherry (*Prunus* spp.) trees afford grouse a stable supply of high-quality winter food (Servello and Kirkpatrick 1987) but, on average, these species accounted for only ~2% of canopy trees on oak-hickory sites (Whitaker 2003). Hard mast of oaks and beech are also high-quality grouse foods (Servello and Kirkpatrick 1987), and these species represented ~42% of canopy trees on these sites (Whitaker 2003).

Forest cover on the remaining study sites (MD1, NC1, PA1, VA3, and WV1) was dominated by the mixed mesophytic forest association (Braun 1950). The most common canopy-tree species on each of these sites was red maple, and other important species included sugar maple, basswood (*Tilia americana*), sweet and yellow birch (*B. lenta* and *B. alleghaniensis*, respectively), black and pin cherry (*P. serotina* and *P. pensylvanica*, respectively), white ash (*Fraxinus americana*), white pine, American beech, northern red oak, white oak, eastern hemlock, and yellow-poplar (*Liriodendron tulipifera*). Although aspen were rare on most mixed mesophytic study sites, birch and cherry were common, and these three genera accounted for ~22% of canopy trees,

whereas oaks and beech constituted ~23% of canopy trees (Whitaker 2003).

A key goal of the ACRGP was to test the effect of hunting on grouse ecology. For this experiment, monitoring was divided into two phases. During phase I (fall 1996–spring 1999), all study sites were open to fall–winter grouse hunting, whereas during phase II (fall 1999–spring 2001), hunting was closed on three treatment sites (KY1, VA3, WV2) but remained open on all other sites (controls). Hunting seasons typically ran from mid-October through late February, with daily bag limits of 2–4 grouse, though seasons were variable between states. After censoring non-hunting mortalities, mean (\pm SE) annual harvest rates were $16.2 \pm 3.5\%$ of radiomarked grouse on sites open to hunting (Devers et al. 2007).

Home-range estimation.—Lily-pad traps, which passively intercept walking grouse, were used from late August through early November to capture grouse on each study site (Gullion 1965). Sex and age class (juvenile [<15 months] or adult) of captured grouse were assessed based on feather criteria (Kalla and Dimmick 1995). Grouse were equipped with a necklace-style radiotransmitter (10 g, 1.25–2.5% of body mass; Advanced Telemetry Systems, Isanti, Minnesota), released at the site of capture, and given a seven-day conditioning period before being included in the study population.

Detailed methods for collecting and processing radiotracking data are provided in Whitaker (2003). Briefly, roving observers equipped with handheld receiving equipment attempted to locate each bird at least twice weekly. Observers used networks of known-location receiving stations, and azimuths collected from 3–8 stations during <20 min were used to triangulate locations of grouse using Lenth's maximum-likelihood estimator (Lenth 1981, White and Garrott 1990). We conducted a beacon study to quantify mean location error (White and Garrott 1990), and estimated this to be <75 m (Whitaker 2003). Because error increases with distance (Whitaker 2003), we censored observations for which the geometric mean distance from receiving stations to the estimated location exceeded 800 m.

A home range is a repeatedly traversed area where an animal has settled and has a predetermined probability of occurring during a given period (Kenward 2001, Kernohan et al. 2001). Consequently, dispersal should be excluded

when delineating home ranges, because failure to do so will lead to exaggeration of home-range boundaries (Powell 2000, Kenward 2001). Natal dispersal by grouse is rapid, strongly oriented, and typically occurs during fall (September–November) or sometimes spring (March–April) (Small and Rusch 1989, Small et al. 1993, Yoder et al. 2004). We defined dispersal as an extended (>0.5 km) one-way movement through an area that was not revisited, and we identified and removed dispersal events through analyses of sequential movement paths. Dispersal was considered complete when a grouse first entered the repeatedly traversed area.

We estimated spring–summer (1 April–31 August; 153 days) and fall–winter (1 September–31 March; 212 days) home ranges from our location data sets. Season dates were selected to correspond with nest initiation and brood break-up (Haulton 1999, Devers et al. 2007) so that the spring–summer and fall–winter periods would approximate the breeding and nonbreeding seasons, respectively. We used the fixed-kernel method with least-squares cross-validation (LSCV) to estimate home-range boundaries

(Worton 1989), which generally yields the most accurate estimates compared with other contemporary approaches (Seaman and Powell 1996, Powell 2000). Home ranges were estimated using the Animal Movement software extension (Hooge et al. 1999) for ARCVIEW GIS software (ESRI, Redlands, California). As recommended for kernel methods (Seaman et al. 1999), we used a minimum of 30 locations to estimate a home range. This ensured that grouse were followed for ≥ 15 weeks, and we found no association between home-range size and either duration of monitoring or number of locations (Whitaker 2003). Peripheral home-range boundaries can be difficult to delineate accurately, may have reduced biological significance, and are likely only generally perceived by animals, so it is preferable to emphasize central portions in comparisons of home-range area (Seaman et al. 1999, Powell 2000). Consequently, we used 75%-kernel home ranges here, though note that in *post-hoc* tests we obtained similar results using 50% and 95% home ranges (Whitaker 2003).

Explanatory variables.—Several attributes were linked to each home range (Table 1). For individual

TABLE 1. Landscape-level and individual-level variables tested as predictors of home-range size for Appalachian Ruffed Grouse.

Variable	Description
Landscape-level variables	
Forest	Forest association: oak–hickory or mixed mesophytic
Hunt	Whether or not a study area was open to hunting during a given year
L_Acs	Landscape (i.e., study area) density of access routes (roads and trails; m ha^{-1})
L_CC	Landscape availability of clearcuts (percentage of study area)
Mast	Index of hard-mast production by chestnut, red–black, and white oaks and beech
Northing	Mean Northing of a study site divided by 1,000,000 (UTM, NAD 1927 datum)
RPI	Relative phenological index
Trap	Fall trapping success on a study site (captures per 100 trap nights)
Individual-level variables	
Acs	Density of access routes (roads and trails) within a home range (m ha^{-1})
Ag	Agricultural and open lands (percentage of home range)
Age	Hatch-year (juvenile) or after-hatch-year (adult)
Brood	Whether or not the female produced ≥ 1 chick to ≥ 3 weeks posthatch that summer
CC	Clearcuts 0–20 years postharvest (percentage of home range)
CWED	Contrast weighted edge density (m ha^{-1}) ^a
Dist	Urban and other disturbed cover types (percentage of home range)
ED	Edge density within a home range (m ha^{-1}) ^a
Sex	Male or female
TECI	Total edge contrast index within a home range ^a
TED	Total edge density within a home range = CWED + Road (m ha^{-1})
TMI	Topographic moisture index; landforms favoring moist soils (percentage of home range)

^a See McGarigal and Marks (1995) for descriptions of landscape metrics.

grouse, we recorded sex and age (juvenile or adult), and grouse captured as juveniles were graduated to the adult age class on 1 September of their second year (~15 months posthatch). For females, we recorded breeding success during the current or (for fall–winter) subsequent breeding season. Nests were located by homing during incubation, and females were flushed at three weeks posthatch to assess chick survival. Because chick survival was low to three weeks posthatch (17%) but much higher thereafter (78%) (Haulton 1999, Norman et al. 2004, Devers et al. 2007), females were classified as successful breeders if one or more chicks survived to three weeks.

We created digital geographic-information-system (GIS) landcover maps of study sites using ground surveys, Landsat satellite imagery (30 × 30 m pixel resolution), and U.S. Geological Survey digital elevation models (DEMs) (Whitaker 2003). Maps included layers for clearcuts, topography, and access routes (i.e., roads and trails). Using DEMs, we estimated the slope, aspect, and landform of each pixel based on the relative elevation of the adjacent pixels and, from this information, calculated a topographic moisture index (TMI) for the pixel. This TMI was used to classify each pixel as xeric or mesic as compared with the average for the landscape. Maps of mesic habitats closely reflected the distribution of hollows, valley bottoms, and riparian zones, and are referred to hereafter as “mesic bottomlands.” Revised maps including newly created clearcuts and roads, as well as updated ages for existing clearcuts, were generated for each year of data collection. Habitat information for each grouse home range was extracted from GIS maps using FRAGSTATS/ARC software (McGarigal and Marks 1995). We used our own experience, tests for spurious associations with polygon area, and a literature review to select a subset of landscape metrics we considered potentially important to grouse (Table 1; see also Fearer and Stauffer 2003).

A number of landscape-scale (i.e., study-area) attributes were also evaluated (Table 1). These included the dominant forest association on each study area, the mean universal transverse mercator (UTM) northing for each study area divided by 1,000,000 (i.e., the distance from the equator to the study area, measured in thousands of kilometers), and whether or not a study area was open to hunting in a given fall–winter. To test whether home-range size was related to

growing-season phenology, we estimated a mean relative phenological index (RPI) for each site. The RPI predicts the expected delay in spring phenology for each study site, in relation to a common reference site, based on the site’s mean latitude, longitude, and elevation (Hopkins 1938, McCombs 1997, Devers et al. 2007). Our grouse traps were passive, and we used mean capture rate as an index of population density on each site each fall (range: 0.33–7.01 captures per 100 trap nights). Mast of red–black, white, and chestnut oaks, and beech are all high-quality grouse foods (Servello and Kirkpatrick 1987, Servello et al. 1987), and we ranked mast production by each species on a 0–3 scale for each site each fall (0 = no mast, 1 = light, 2 = moderate, 3 = heavy). We took the sum of the rankings for these four tree species as an index of hard-mast production for each site each fall (observed range: 1–11). Finally, we used the distribution of radiomarked grouse to delineate the effective boundary of each study area each season by placing an 800-m buffer around any grouse location collected that season. We recorded the percentage of cover of clearcuts and mean density of access routes (m ha^{-1}) within these seasonal study-area boundaries as estimates of landscape-level availability of these habitats (Whitaker et al. 2006).

Data analyses.—We performed logistic regression using fall–winter home-range size as a predictor of whether a grouse would attempt to nest and, for those grouse that hatched eggs, whether they still had one or more chick alive after three weeks (JMP statistical software, version 4.0.3; SAS Institute, Cary, North Carolina). We included female age as a covariate in these tests. For these and all other hypothesis tests, the level of significance was set at $\alpha = 0.05$.

For many individual grouse, we were able to estimate spring–summer or fall–winter home ranges during more than one year. This allowed pairwise comparisons of an individual’s home-range size under different circumstances. If an individual was a juvenile when the first home range was estimated, we tested the effect of age (juvenile vs. adult) on home-range size. When an adult grouse was followed during more than one fall–winter, we compared home-range size from the year with the higher mast index with that of the year with the lower mast index. Because other analyses suggested that the importance of hard mast differed between oak–hickory and mixed mesophytic forests,

this comparison was subdivided by forest type (Whitaker et al. 2006). Finally, when a female raised one or more chicks to three weeks of age in one spring–summer but failed to do so in another, we compared home-range size between successful and unsuccessful breeding seasons. All comparisons were made via paired *t*-tests, with the null hypothesis that mean difference in size for each home-range pair did not differ from zero (Sokal and Rohlf 1995).

Next, we undertook a series of model-building exercises to identify factors associated with variation in home-range size. Our goal was to develop global models that incorporated all observed landscape-level (i.e., study-area) and individual-level relations with grouse home-range size, which allowed us to identify any interactions between factors and to generate parameter estimates in a multivariate context. Our first model-building exercise investigated variation in fall–winter home-range size across all grouse sex and age classes. We then undertook similar model-building exercises for spring–summer home ranges. However, because we had no estimate of reproductive success for male grouse, separate model-building exercises had to be done for male and female grouse during spring–summer.

For each model-building exercise, we used the 75% fixed-kernel home-range area (in square meters) as the response variable (*Y*) and fit data to linear models using JMP. To avoid heterogeneous variance of residuals, home-range area was natural-log-transformed before model-fitting. To avoid pseudoreplication (Hurlbert 1984), we restricted our model-building data sets to one home range per individual. We then performed a preliminary evaluation of each explanatory variable listed in Table 1 by adding it to a base model including Sex and Age (fall–winter home ranges) or Age (spring–summer home ranges). The influence of each explanatory variable was assessed via Δ_i , the change in Akaike's Information Criterion adjusted for sample size (AIC_c) resulting from the addition of that term to the model. Reductions in $AIC_c > 2$ indicate a substantial improvement in model fit (Burnham and Anderson 2002). We then developed multivariate models based on results of these tests of individual variables, existing knowledge of grouse habitat ecology, and hypothesized interactions between variables. For each model set, we assessed the fit of the global or most complex

model through inspection of residual plots and a goodness-of-fit test. Multivariate models were compared using AIC_c , AIC_c differences (Δ_i), and R^2_{adj} . We report the set of "best" models (i.e., any models having $\Delta_i \leq 2.0$ in relation to the model with the lowest AIC_c); for reference, we also report the null model for each data set (i.e., a model including the intercept alone).

RESULTS

Our final data set included 647 fall–winter home ranges from 575 individual grouse and 407 spring–summer home ranges from 379 grouse. Home ranges of females were typically 2–3 \times larger than those of adult males, and home ranges of juvenile males were larger during fall–winter than during spring–summer (Fig. 2). Although fall–winter home-range size was unrelated to subsequent brood success, female grouse that did not nest had typically used larger home ranges during the preceding fall–winter than those that nested (Table 2).

Comparing pairs of home ranges identified causes of variation in home-range size for individual grouse between years (Table 3). During both fall–winter and spring–summer, individual juvenile males used ranges that were $\sim 2\times$ larger than those of adult males. By contrast, home-range size of females did not differ by age during either season. However, individual females had larger home ranges during spring–summers in which they successfully raised broods than during those seasons when they experienced reproductive failure. On sites with oak–hickory forests, adult grouse of both sexes expanded their fall–winter home ranges $> 2.5\times$ following poor fall hard-mast crops. No such response was detected for grouse on study sites with mixed mesophytic forests.

Our best multivariate model indicated that, for grouse, fall–winter home-range size was related to a diverse range of factors, including several operating at the landscape scale (i.e., study-site level) (Table 4). There was a latitudinal gradient in home-range size, home ranges typically being smaller on more northerly study sites ($\beta_{\text{Northing}} = -0.77 \pm 0.33$; note that parameter estimates are for natural-log-transformed home-range sizes, measured in square meters). Home ranges of grouse inhabiting mixed mesophytic forest sites were typically smaller ($\text{Forest}_{\text{[MMJ]}} = 11.78 \pm 0.07$) than those of grouse inhabiting oak–hickory

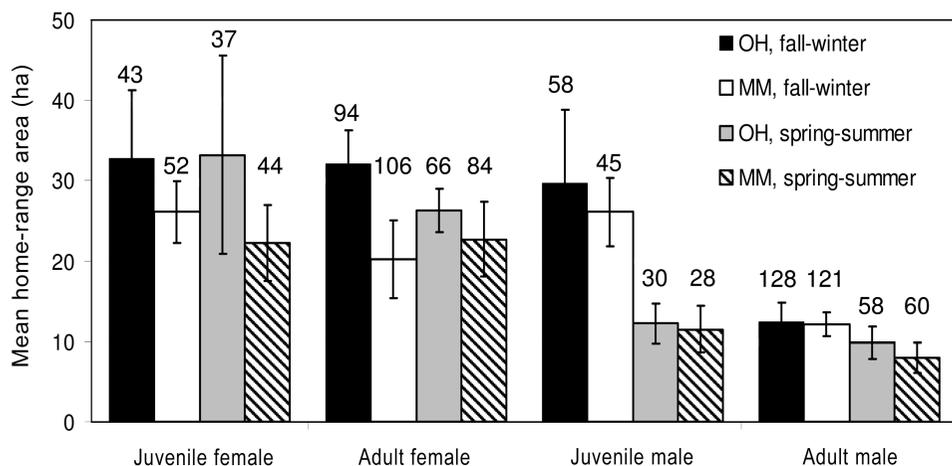


FIG. 2. Mean (\pm SE) size of 75% fixed-kernel home range occupied by Ruffed Grouse during non-breeding (fall–winter) and breeding seasons (spring–summer) at 10 study sites across the central and southern Appalachians, 1996–2001. Values were averaged by forest type, with five study sites characterized as having oak–hickory forests (OH) and five having mixed mesophytic forests (MM). Total numbers of home ranges are indicated above the error bars, but note that means from each study site were used to calculate the overall mean by forest type.

TABLE 2. Tests of fall–winter home-range size (ha) as a predictor of whether female Appalachian Ruffed Grouse attempted to nest or successfully reared ≥ 1 chick to three weeks of age (1996–2001). Comparisons were made via logistic regression, with age included as a control variable.

	n	Fall–winter home range size (ha)			Age (juvenile or adult)	
		Mean \pm SE	Wald χ^2	P	Wald χ^2	P
Attempted to nest						
Did not nest	13	36.6 \pm 5.7	4.86	0.0274	1.73	0.1887
Nested	146	25.9 \pm 1.9				
3-week brood success						
Lost entire brood	24	20.0 \pm 2.7	1.03	0.3113	0.83	0.3615
≥ 1 chick alive	53	26.5 \pm 2.8				

forest sites ($\text{Forest}_{[\text{OH}]} = 11.97 \pm 0.06$) (i.e., 13.1 ha vs. 15.8 ha; see also Fig. 2). Home-range size was inversely related to the annual hard-mast crop on a study site ($\beta_{\text{Mast}} = -0.047 \pm 0.014$). There was an interaction between sex and fall trapping success, which resulted from the much stronger positive relation between trapping success and home-range size for males ($\beta_{\text{Trap}} = 0.171 \pm 0.025$) than for females ($\beta_{\text{Trap}} = 0.068 \pm 0.031$). However the only competing model ($\Delta_i = 2.0$) suggested a three-way interaction between sex, age, and trapping success, where this relation was strongest for juvenile males ($\beta_{\text{Trap}} = 0.273 \pm 0.053$), intermediate for adult males ($\beta_{\text{Trap}} = 0.134 \pm$

0.029), weaker for adult females ($\beta_{\text{Trap}} = 0.085 \pm 0.041$), and negligible for juvenile females ($\beta_{\text{Trap}} = 0.050 \pm 0.049$). Finally, grouse home ranges typically were smaller when a study site was closed to hunting ($\text{Hunt}_{[\text{open}]} = 12.13 \pm 0.04$; $\text{Hunt}_{[\text{closed}]} = 11.61 \pm 0.10$) (i.e., 18.5 ha vs. 11.0 ha).

Four individual-level factors also were related to the size of fall–winter home range used by grouse (Table 4). Home ranges differed between sexes and ages (Sex*Age), being smallest for adult males (11.37 \pm 0.07; 8.7 ha), intermediate for juvenile males (12.01 \pm 0.09; 16.4 ha) and adult females (12.03 \pm 0.08; 16.8 ha), and largest for juvenile females (12.11 \pm 0.10; 18.2 ha). Size of

TABLE 3. Influence of age, mast crop, and presence or absence of a brood on 75% fixed-kernel home-range area (ha) of individual Appalachian Ruffed Grouse (1996–2001). Paired *t*-tests were used to compare pairs of home ranges for individual Ruffed Grouse followed in different years.

Class	Condition 1		Condition 2		<i>n</i>	<i>t</i>	<i>P</i>
	Feature	Mean ± SE	Feature	Mean ± SE			
Fall–winter home ranges							
Males	Juvenile	38.6 ± 8.2	Adult	19.0 ± 2.7	37	3.00	0.005
Females	Juvenile	29.9 ± 5.8	Adult	17.4 ± 3.5	17	1.89	0.076
Adult males, MM ^{a,b}	Low mast	10.0 ± 1.1	High mast	11.6 ± 1.6	23	1.08	0.290
Adult males, OH ^{a,b}	Low mast	22.3 ± 6.7	High mast	7.3 ± 1.4	17	2.15	0.047
Adult females, MM ^{a,b}	Low mast	22.5 ± 3.0	High mast	23.7 ± 3.9	21	0.32	0.750
Adult females, OH ^{a,b}	Low mast	51.6 ± 11.7	High mast	19.7 ± 1.7	16	2.56	0.022
Spring–summer home ranges							
Males	Juvenile	22.4 ± 3.2	Adult	11.8 ± 1.8	15	2.96	0.010
Females	Juvenile	27.9 ± 6.3	Adult	49.1 ± 14.2	13	1.44	0.180
Females ^c	Failed	14.8 ± 4.3	Successful	39.2 ± 11.2	12	2.39	0.036

^aMM = mixed mesophytic forest sites (MD1, NCl, PA1, VA3, WV1); OH = oak–hickory forest sites (RI1, WV2, VA1, VA2, KY1).

^bMean differences in mast index between low and high mast years were as follows: MM males = 3.15, OH males = 4.09, MM females = 3.83, and OH females = 4.19.

^cFemales were considered successful if they raised ≥1 chick to ≥3 weeks of age.

an individual’s home range was inversely related to the density of access routes it contained ($\beta_{\text{ACS}} = -0.0037 \pm 0.0014$). Finally, there was an interaction between sex and use of clearcuts by individuals (Sex*CC): for females, home-range size was unrelated to use of clearcuts ($\beta_{\text{CC}} = -0.0013 \pm 0.0023$); but for males, home-range size was inversely related to the proportional coverage of clearcuts ($\beta_{\text{CC}} = -0.0104 \pm 0.0017$).

As with fall–winter, our best models of spring–summer home-range size for female grouse indicated that individuals on mixed mesophytic forest sites typically used smaller home ranges (Forest_[MM] = 12.01 ± 0.10; 16.4 ha) than those on oak–hickory forest sites (Forest_[OH] = 12.54 ± 0.16; 27.9 ha) (Table 4 and Fig. 2). Home ranges of females also continued to be inversely related to fall hard-mast crops during spring–summer ($\beta_{\text{Mast}} = -0.057 \pm 0.026$). As in our paired tests (Table 3), female grouse in mixed mesophytic forests used smaller spring–summer home ranges if they failed to successfully rear a brood (Brood_[failed] = 11.71 ± 0.13; Brood_[successful] = 12.31 ± 0.14) (i.e., 12.2 ha vs. 22.2 ha). However, there was an interaction with forest type, and no difference between unsuccessful and successful hens was observed in oak–hickory forests (Brood_[failed] = 12.61 ± 0.19; Brood_[successful] = 12.48 ± 0.18) (i.e., 30.0 ha vs. 26.3 ha). Best models also included a negative relation between home-range size and

the density of access routes within home ranges ($\beta_{\text{ACS}} = -0.0049 \pm 0.0028$). Unlike our fall–winter models, one of our three best models indicated that during spring–summer, size of home range for female grouse was inversely related to proportional coverage of clearcuts, though the parameter estimate was not strongly supported ($\beta_{\text{CC}} = -0.0037 \pm 0.0024$). Finally, two of the three best models included an interaction between forest type and the influence of mesic bottomlands. This resulted from the inverse relation between percentage of cover of mesic bottomlands and home-range size in oak–hickory forests ($\beta_{\text{TMI}} = -0.0164 \pm 0.0074$), compared with the lack of any such relation on sites having mixed mesophytic forests ($\beta_{\text{TMI}} = -0.0027 \pm 0.0047$).

No landscape-level variables were included in any of our “best” models for spring–summer home-range size of male grouse, and models in this set had lower explanatory power than those for the other two data sets (Table 4). These models indicated that, though they used smaller home ranges than they had used during fall–winter, juvenile males continued to use larger home ranges (Age_[juvenile] = 11.54 ± 0.10; 10.3 ha) than adult males (Age_[adult] = 11.29 ± 0.08; 8.0 ha). The only other factor that consistently appeared in best models of spring–summer home-range size of male grouse was percentage of cover of clearcuts within home ranges ($\beta_{\text{CC}} =$

TABLE 4. Best multivariate models (i.e., models having $\Delta_i \leq 2.0$) to explain variation in fall–winter and spring–summer home-range size for Appalachian Ruffed Grouse (1996–2001). The response variable in all models was the natural log-transformed size of the 75% fixed-kernel home range (m²). Null models are included for reference.

Model	n	SSE	K	AIC _c	Δ_i	r ²	r ² _{adj}
Fall–winter home ranges, male and female:							
Y = 15.48 + Northing + Forest + Hunt + Sex + Age + (Sex*Age) + CC + Acs + Mast + Trap + (Sex*CC) + (Sex*Trap) + ε	502	289.0	14	-248.3	0.0	29.5	27.7
Y = 15.46 + Northing + Forest + Hunt + Sex + Age + (Sex*Age) + CC + Acs + Mast + Trap + (Sex*CC) + (Sex*Trap) + (Age*Trap) + (Sex*Age*Trap) + ε	502	287.7	16	-246.3	2.0	29.8	27.7
Y = 11.96 + ε (null model)	502	409.7	2	-98.0	150.3	–	–
Spring–summer home ranges, female:							
Y = 13.23 + Forest + CC + Acs + TMI + Mast + Brood + (Forest*Brood) + (Forest*TMI) + ε	180	121.0	10	-50.2	0.0	20.4	16.7
Y = 13.19 + Forest + Acs + TMI + Mast + Brood + (Forest*Brood) + (Forest*TMI) + ε	180	122.7	9	-49.9	0.3	19.3	16.0
Y = 12.90 + Forest + Acs + Mast + Brood + (Forest*Brood) + ε	180	125.9	7	-49.7	0.5	17.2	14.8
Y = 12.15 + ε (null model)	180	152.0	2	-26.3	23.9	–	–
Spring–summer home ranges, male:							
Y = 11.53 + Age + CC + ε	142	72.3	4	-87.6	0.0	5.6	4.2
Y = 11.61 + Age + CC + Acs + ε	142	71.5	5	-87.0	0.6	6.7	4.7
Y = 11.62 + Age + CC + Acs + (CC*Age) + (Acs*Age) + ε	142	70.0	7	-85.6	2.0	8.6	5.3
Y = 11.39 + ε (null model)	142	76.6	2	-83.5	29.7	–	–

-0.0041 ± 0.0020). However, one model included an age difference in the influence of clearcuts on home-range size, indicating an inverse relation for adult males ($\beta_{CC[adult]} = -0.0054 \pm 0.0025$) and no relation for juvenile males ($\beta_{CC[juvenile]} = -0.0010 \pm 0.0038$). Density of access routes also was included in two models in the best-model set, and again there was evidence of an age effect. However, in this case, the interaction suggested an inverse relation for juvenile males ($\beta_{Acs[juvenile]} = -0.0063 \pm 0.0035$) and none for adult males ($\beta_{Acs[adult]} = -0.0006 \pm 0.0025$).

DISCUSSION

We found that, compared with those that nested, female grouse that did not attempt to nest typically had occupied $\sim 1.4\times$ larger home ranges during the preceding fall–winter (Table 2; see also Mack and Clark 2006). For female Appalachian grouse and other tetraonids, pre-breeding nutrition affects reproductive success (Moss et al. 1975, Servello and Kirkpatrick 1988, Norman et al. 2004, Devers et al. 2007), and we suspect that the larger prebreeding home ranges of non-nesters was a reflection of low availability of high-quality foods. Our study design was unsuited to an assessment of any relation between home-range size and survival, though other researchers have reported higher survival for grouse occupying smaller home ranges (Thompson and Fritzell 1989, Clark 2000). Tirpak (2000) also reported that, on our ACGRP study sites, chick survival was higher for broods that remained closer to nest sites. These connections to reproduction and survival support our supposition that home-range size is an important feature of grouse behavior with ties to individual fitness.

We observed relations between grouse home-range size and both individual traits and habitat available within the home range. As has been reported previously, juvenile male grouse used larger home ranges than adult males, and females occupied larger ranges than males (Fig. 2) (Archibald 1975, Thompson 1987, Clark 2000, Fearer and Stauffer 2003). However, we did not detect a reduction in home-range size between juvenile and adult females. During spring–summer, females with broods had relatively large home ranges, at times exceeding 100 ha, whereas those without broods reduced their home-range size by 45–60%. These were the

smallest home ranges we observed for females at any time, and this was the only circumstance in which female home ranges were comparable in size to those of adult males (Table 3; see also Maxson 1978). However, this reduction in home-range size for unsuccessful females was more strongly expressed in mixed mesophytic forests than oak–hickory forests.

Other factors operating at the individual level were also related to the size of a grouse's home range. These related specifically to the prevalence of three important habitat features within an individual's home range—clearcuts, access routes, and mesic bottomlands. Relations between habitat use and space use have been widely documented for birds (Smith and Shugart 1987), and we see two related mechanisms leading to increased representation of a habitat feature in smaller home ranges. First, if the habitat feature is rare and animals preferentially center their home ranges on it, small home ranges will inevitably encompass a lesser proportion of background (matrix) habitat. In line with this reasoning, the three habitat features we tested were all selected by grouse on our study sites (Whitaker et al. 2006), and use of each was related inversely to home-range size. Second, the feature may represent high-quality habitat that allows an individual to meet its resource needs within a smaller area. If, as one might predict and as research suggests (Whitaker et al. 2006), habitats that grouse select are in fact of high quality, then both of these reasons would hold true.

An increase in proportional cover of clearcuts in smaller home ranges was observed for males year-round and females during spring–summer. It is well known that grouse select dense early-successional stands such as clearcuts, and it is generally assumed that these serve primarily as escape cover (Bump et al. 1947, Rusch et al. 2000). Supporting this notion, recent research has found that survival was higher for grouse whose home ranges contained more early-successional cover (Clark 2000). There was also evidence that home-range size was inversely related to density of forest access routes (roads and trails) for all sex and age classes throughout the year. Correlation between the proportion of clearcuts and density of access routes within home ranges was low ($r = 0.18$, Pearson's correlation; Sokal and Rohlf 1995), so we do not believe that the relation between road density

and home-range area resulted simply from an association between forest roads and clearcuts. Edges along access routes are a preferred habitat for grouse in the Appalachian Mountains, providing thick cover, abundant herbaceous plant and invertebrate foods, and grit for digestion (Hollifield and Dimmick 1995, Rusch et al. 2000, Schumacher 2002, Whitaker et al. 2006). However, it has also been suggested that forest edges, such as those created by roadways, act as secondary habitat and are used more extensively when large early-successional stands are unavailable (Bump et al. 1947, Gullion 1984, Whitaker 2003). This would account for the fact that home ranges of adult males appeared to be more strongly influenced by clearcuts, whereas juvenile males responded more strongly to access routes, because territorial adult males may exclude juveniles from higher-quality early-successional habitats (Small 1985).

Relations between home-range size and habitat use differed between male and female grouse. Although always showing a strong association for males, our multivariate models suggested that there was no association between home-range size and use of clearcuts for females during fall–winter. Other studies indicate that this is a period of nutritional stress for Appalachian grouse (Norman and Kirkpatrick 1984, Servello and Kirkpatrick 1988) and that females make a trade-off between use of clearcuts and more favorable foraging habitats (Whitaker et al. 2006). For example, acorns are a key high-quality food (Servello and Kirkpatrick 1987) that typically is not produced in clearcuts and therefore must be sought elsewhere.

Although not evident for males in either forest type or for females on mixed mesophytic sites, smaller spring–summer home ranges of female grouse inhabiting oak–hickory forests were associated with a greater prevalence of mesic bottomlands. The lack of relation for male grouse is not surprising, given that they typically select display sites along ridges (Thompson et al. 1987, Fettinger 2002). Greater importance of bottomlands as brood habitat in the Appalachians, particularly in oak–hickory forests, has been suggested previously (Stewart 1956, Whitaker et al. 2006). On our study sites, females with broods selected stands with well-developed herbaceous groundcover and high insect biomass (Haulton et al. 2003, Fettinger 2002), which together constitute the majority

of the diet of grouse chicks (Rusch et al. 2000). Upland soils in oak–hickory forests are typically xeric and support relatively little herbaceous understory vegetation, which suggests a reason for the selection of bottomlands by brood-rearing females. By contrast, uplands in mixed mesophytic forests typically have moist soils that support abundant herbaceous vegetation (Braun 1950), presumably relaxing this constraint. Similarly, Smith and Shugart (1987) reported that habitat use by Ovenbirds (*Seiurus aurocapilla*) differed between forest types and that in each forest type the habitat supporting the greatest density of food was preferred. Further, availability of these habitats was the proximate cue controlling space use by Ovenbirds. These observations indicate that habitat use and space use are interdependent and highly plastic in birds, being adjusted to suit local conditions experienced by individuals (Jones 2001, Whitaker et al. 2006).

Regional and landscape-level relations.—Previously, researchers have reported that grouse in the southern Appalachians have larger home ranges than conspecifics in northern forests (White and Dimmick 1979, Epperson 1988, Thompson and Fritzell 1989, Neher 1993, Fearer and Stauffer 2003). Our observation of a continuous decrease in fall–winter home-range size with increasing latitude over a range of 710 km indicates that this dichotomy represents points along a cline, and not simply a punctuated shift occurring at some ecological threshold. However, our observation of a general difference in home-range size between oak–hickory and mixed mesophytic forests indicates that transitions between forest types are also important. Thus, both punctuated shifts and a continual trend in space use interact to generate differences in grouse home-range size between northern and southern forests. We did not investigate potential causes of the latitudinal trend in home-range size, though it may be related to grouse foods becoming more dispersed and of generally lower quality at lower latitudes (e.g., Servello and Kirkpatrick 1987, Hewitt and Kirkpatrick 1997a). Climatic conditions may also be less favorable at lower latitudes. For example, during winter, grouse often burrow into the snow to roost and, while snow-roosting, experience reduced heat loss and are well concealed from predators. However, accumulations of snow deep enough for snow

roosting are rare and transient in the southern Appalachians (Whitaker and Stauffer 2003).

Grouse also modified home-range size in response to factors operating at the local landscape scale (i.e., study sites). As mentioned above, there was a general difference in fall–winter home-range size between the two dominant forest types in the region, whereby grouse inhabiting oak–hickory forests typically used home ranges 1.2× larger than those of grouse in mixed mesophytic forests (Fig. 2). Although this indicates that grouse are sensitive to landscape-level forest conditions, we did not detect a response to landscape-level availability of two key habitats—clearcuts and access routes. We presume that this difference occurred because a change in forest type has implications for the quality of all habitats in a landscape, whereas availability of a particular habitat type is only important within the area used by an individual. However, this does not mean that other landscape-level factors relating to individual habitat types, such as patch distribution, size, and shape, are unimportant to grouse. For example, some passerines move more extensively in fragmented forests (Norris and Stutchbury 2001, Fraser and Stutchbury 2004), and we presume that habitat configuration is also important to grouse (e.g., Fearer and Stauffer 2003).

Our comparison of home ranges used by individuals in different years indicated that grouse inhabiting oak–hickory forests increased the size of their fall–winter home ranges >2.5-fold during years when hard-mast crops were poor, whereas grouse in mixed mesophytic forests were unresponsive to mast crops (Table 3). A general influence of mast crops on fall–winter home ranges was also evident in our multivariate models (Table 4), and we tested for a difference between forest types by adding the appropriate interaction term to our best model (i.e., Age*For*Mast). Although this interaction term was statistically significant ($P = 0.0372$) and also suggested that the relation was restricted to adult grouse inhabiting oak–hickory forests ($\beta_{\text{Mast}[\text{OH}]} = -0.057 \pm 0.019$ vs. $\beta_{\text{Mast}[\text{MM}]} = 0.023 \pm 0.030$), the added complexity of the expanded model meant that it was not included in our best-models set ($\Delta_i = 2.9$). Effects of both forest association and hard-mast crops were also evident during spring–summer for female grouse, though male grouse appeared to be

insensitive to any landscape-level factors during the breeding season. These findings indicate that the availability of this high-quality food had an important effect on space use by grouse and, though not strongly supported in all tests, suggest that grouse inhabiting oak–hickory forests were more sensitive to availability of this resource.

Though they are largely solitary and have overlapping home ranges, grouse do not occupy their environment independently of one another. We observed a positive relation between fall–winter home-range size and fall trapping success, which suggests that space use by grouse was positively correlated with population density. Competition for display sites was likely a key factor driving this relation, given that it was strongest for male grouse in general and juvenile males in particular. On average, the lowest and highest fall capture rates we observed on each ACGRP study site were 1.25 and 3.31 grouse per 100 trap nights. When incorporated into the appropriate model (Table 4), these values yield home-range estimates for juvenile males of 12.1 ha during years when populations were low and 21.8 ha when populations were high. Although females are nonterritorial, male grouse aggressively defend drumming logs, and established adults occupy a preferred subset of these display sites (Gullion and Marshall 1968). Juvenile males compete for available sites and, when populations increase, are more often nonterritorial and likely have to range farther and monitor a greater number of occupied sites in hopes of acquiring a preferred display site (Marshall 1965, Archibald 1976, Gullion 1981). Anecdotal behavioral observations support this view—juvenile males often abandon a territory and relocate within 24 h of the death of an established neighboring male, and aggressive contests for ownership of the neighbor's territory often ensue (Marshall 1965, Rusch and Keith 1971; ACGRP unpubl. data).

Our observation of a positive relation between home-range size and population density seems at odds with findings for socially monogamous passerines, where territory size typically is inversely correlated with population density (e.g., Krebs 1971, Morse 1989). However, home ranges are not directly comparable with defended territories, and home-range sizes have rarely been reported for passerines. However, recent radiotracking studies make it clear that

even strongly territorial, socially monogamous passerines make extensive daily extraterritorial forays (e.g., Smiseth and Amundsen 1995, Norris and Stutchbury 2001, Fraser and Stutchbury 2004). Consequently, both grouse and passerines could conceivably have territories constrained by population density yet still respond to increased competition by making more extensive extraterritorial movements. Key to resolving relations between population size and space use is an understanding of the behavioral motivations compelling birds to make extraterritorial movements. For example, extra-pair mating is seen as an important motive for extraterritorial forays in socially monogamous species (e.g., Norris and Stutchbury 2001), but, given the species' polygynous "dispersed lekking" mating system, this would seem unimportant to grouse (Bergerud and Gratson 1988).

To maximize fitness, most animals reduce risk under increased predator pressure by reducing movements and increasing refuging behavior (Lima 1998). By contrast, we observed a typical reduction in home-range size from 18.5 ha to 11.6 ha after study sites were closed to hunting, which suggests that hunting pressure, in fact, led to a substantial increase in space use. In an observational study in Michigan, Clark (2000) reported a similar response to hunting by grouse, and increased movement in response to hunting pressure has also been reported for Wild Turkey (*Meleagris gallopavo*) and American Black Duck (*Anas rubripes*; Hoffman 1991, Clugston et al. 1994). This contrast between the response of game birds to hunting and the typical response of animals to predation risk is curious. We hypothesize that hunters, who typically focus their efforts on preferred habitats of their quarry (Kilgo et al. 1998, Lyon and Burcham 1998, Brøseth and Pedersen 2000), may compel game to abandon these areas in favor of lower-quality covers and thereby interfere with normal refuging behavior. In line with this suggestion, other analyses showed that grouse on our study sites made greater use of preferred habitats following closure of hunting (Whitaker et al. 2006). Also, if hunters flush animals repeatedly, they may cause a net increase in movements and home-range size, even if animals are attempting to reduce their activity levels. Under either scenario, an increase in space use could lead to indirect negative effects of hunting on grouse, including reduced

condition and increased predation rates, potentially exacerbating consequences of hunting for populations. However, we detected no change in predation rate or reproductive success following closure of grouse hunting on our study sites (Devers et al. 2007).

Oak-hickory and mixed mesophytic forests.—Several of our observations suggest pronounced differences in spatial ecology between grouse inhabiting oak-hickory forests and those in mixed mesophytic forests. Previous studies suggested that Appalachian grouse are under strong nutritional constraint, and availability of sufficient hard-mast foods may be important both for maintenance of body condition through winter and subsequent reproductive success (Norman and Kirkpatrick 1984, Servello and Kirkpatrick 1988). In line with this, home ranges of grouse inhabiting oak-hickory forests were >2× larger during years when mast crops were poor. By contrast, fall-winter home-range size of grouse inhabiting mixed mesophytic forests were less clearly affected by hard-mast crops, and home ranges of these individuals were comparable in size to those used by grouse in oak-hickory forests during years when hard-mast production was high. Thus, although these observations support the view that hard mast is a key limiting resource for Appalachian grouse in some circumstances, they also suggest important differences in the nutritional ecology of the species between forest types. Other research conducted through ACGRP has supported this observation, showing that in oak-hickory forests, hard-mast crops affected habitat use, female condition during the prenesting period, and reproductive success (Norman et al. 2004, Whitaker et al. 2006, Devers et al. 2007). An increase in home-range size following poor hard-mast crops also suggests that availability of this resource could affect survival of grouse, though this was not observed on our study sites (Devers et al. 2007).

The continued influence of fall hard-mast crops on spring-summer home-range size for female grouse was surprising, and the fact that females in both forest types responded equally suggests that this resource is of general importance to females during the breeding season. The expectation that a large proportion of hard mast has been consumed or buried in surface litter by late spring led us to speculate that the influence of mast crops occurred early in spring in

the form of reduced prenesting movements, or that females were able to maintain higher body-fat reserves well into the breeding season, or both (Servello and Kirkpatrick 1988). However, acorns of red and black oak do not germinate until spring, and their emergence may lead to increased availability at that time (F. Servello pers. comm.). This explanation is supported by the observation that, on our study sites, acorns were regularly found in crops of female grouse during spring, and their consumption was positively correlated with both prebreeding condition of females and local mast crops during the previous fall (Norman et al. 2004).

Given the strong association between hard-mast crops and home ranges in oak-hickory forests, it is interesting that home ranges of grouse in mixed mesophytic forests appeared to be less affected by variation in production of this resource. Habitat use and reproductive success of grouse in mixed mesophytic forests were also unaffected by mast crops (Whitaker et al. 2006, Devers et al. 2007). This leads us to believe that grouse in mixed mesophytic forests do not endure the same degree of nutritional constraint experienced by conspecifics in oak-hickory forests. In northern forests at the core of the species range, grouse feed heavily on buds and catkins of aspen, birch, and cherries during winter, and these trees provide a reliable and accessible source of high-quality food (Servello and Kirkpatrick 1987). Ten-fold-higher abundance of these trees in mixed mesophytic forests (Braun 1950, Whitaker 2003) may buffer any response by grouse to changing mast crops by providing a reliable supply of high-quality alternative food during winter (see also Servello and Kirkpatrick 1987). Also, a diverse range of understory shrubs and herbaceous plants that are important grouse foods are more widely available in mixed mesophytic forests (Braun 1950, Stewart 1956, Servello and Kirkpatrick 1987). By contrast, alternative winter foods in oak-hickory forests consist largely of low-quality evergreen leaves high in toxic secondary metabolites (Servello and Kirkpatrick 1987, Hewitt and Kirkpatrick 1997b). Consequently, grouse in oak-hickory forests are more sensitive to both annual variation in mast production and the distribution of sites such as riparian zones and bottomlands, which can afford a stable supply of alternative foods. These observations suggest that habitat-management prescriptions for Appalachian

grouse should be tailored by forest type and, in particular, should be aimed at stabilizing or increasing grouse foods in oak-hickory forests.

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