FACTORS AFFECTING HOME RANGE SIZE OF APPALACHIAN RUFFED GROUSE

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ABSTRACT

Home range size is often considered to relate inversely to habitat quality, and, regardless of the veracity of this relationship, is a fundamental aspect of a species' habitat ecology. Researchers at 10 Appalachian Cooperative Grouse Research Project (ACGRP) study sites collected 647 fall-winter and 407 spring-summer home ranges from ruffed grouse (*Bonasa umbellus*). We conducted analyses investigating the influence of individual traits, demographics, resource availability, habitat, and hunting pressure on home range size. Juveniles occupied 2× larger winter home ranges than adults, and females >2× larger winter and summer home ranges than males. Female home ranges were 260% larger during summers when they successfully raised broods than following reproductive failure. Fall-winter home range size of juvenile males increased as population density increased, suggesting that they are in close competition with conspecifics for displaying sites. Percent cover of clearcuts and density of access routes both were typically greater in smaller home ranges. Hard mast crop had a large effect of on fall-winter home range size for adult grouse in oak-hickory forests, with individuals increasing home range size 250% during poor mast years. In contrast, home ranges of grouse inhabiting mixed mesophytic forests were unaffected by mast crops. This supports the view that grouse in many Appalachian forests are food-limited, though more dependable alternate foods (e.g., cherry [*Prunus* spp.] and birch [*Betula* spp.] buds) may relieve this constraint in mixed mesophytic forests. Also, smaller home ranges of females contained a greater proportion of bottomlands in oak-hickory forests. Several of our findings supported the notion that individual grouse attempt to minimize home range size in the face of conflicting pressures. Further, we found some evidence that female grouse occupying smaller fall-winter home ranges experienced higher reproductive success the following summer, suggesting that home ranges size may be inversely correlated with habitat quality. However, contrary to expectations grouse increased home range size under hunting pressure.

INTRODUCTION

Home range size is a fundamental aspect of an animal’s habitat ecology, having important 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. Consequently it is expected that in most circumstances animals should attempt to use the smallest adequate home range, and that home range size will be positively correlated with resource needs for particular demographic groups. At the same time home range size should typically be inversely related to resource availability, habitat quality, and, ultimately, to an individual’s fitness. Researchers have reported inverse relationships between home range size and resource availability in a variety of bird species including wood warblers, wrens, wattlebirds, hummingbirds, woodpeckers, and ptarmigan (Cody 1985, Convery 2002). Despite this connection to resource availability, relationships with habitat quality can only be demonstrated by considering demographics (Van Horne 1983). In one of the few studies able to adequately test this, Convery (2002) documented an inverse relationship between home range size and fitness for red-cockaded woodpeckers (*Picoides borealis*). However there are also circumstances under which individuals should expand home ranges beyond that needed to meet their resource needs. These might include locating high quality territories and mates.

Ruffed grouse (*Bonasa umbellus*) are a popular gamebird inhabiting boreal and temperate forests of North America. They are resident throughout the year, have precocial young, and, with the exception of males in the immediate vicinity of drumming (display) sites, are largely non-territorial (Rusch et al. 2000). While most common in more northerly forests, in eastern North America the species range extends south along the Appalachian Mountains to Georgia (Figure 1). In northern forests ruffed grouse are most abundant in early-successional trembling aspen (*Populus tremuloides*) forests, which provide thick escape cover and high quality foods, particularly aspen buds and catkins. In contrast aspen are rare or absent from most Appalachian forests, and forbs, evergreen leaves and hard and soft mast form the majority of grouse diets (Servello and Kirkpatrick 1987). Unlike those in more northerly forests, grouse populations in Appalachian forests are non-cyclic.

Individual, local, and regional factors are known to affect ruffed grouse home range size. Researchers have reported that females have larger home ranges than males (Archibald 1975, Clark 2000, Fearer and Stauffer 2003) and that juveniles use larger ranges than adults (Thompson 1987, Clark 2000, Fearer and Stauffer 2003). Home range sizes are also known to vary between seasons, being relatively large during fall and winter, small during spring displaying, laying and incubation, and intermediate during summer (Archibald 1975, Maxson 1978, Thompson 1987, Fearer and Stauffer 2003). Maxson (1978) reported that females with broods make more extensive movements than females without broods. Habitat within home ranges also can affect home range size. Fearer and Stauffer (2003) reported that in Virginia home range size increased when habitat patches were irregularly shaped and as the amount of core habitat within patches increased. Conversely, home range size decreased with increased habitat diversity and availability of high contrast edge (e.g., clearcut or road edge; Fearer and Stauffer 2003). At a regional scale, it has been repeatedly found that home ranges of southern grouse are typically larger than those of grouse inhabiting the Great Lake States (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 ruffed grouse habitat is inferior in the southern Appalachians.

Here we present an analysis of factors affecting home range size of ruffed grouse at 10 study sites in the Appalachian Mountains. In addition to the factors described above, we investigated the influence of reproductive success, interannual variation in hard mast, population demographics, hunting pressure, and habitat composition of landscapes. Identifying factors affecting home range size can help identify limiting resources, and point to differences in habitat ecology and resource needs between demographic groups or populations. Knowledge of such factors can be useful in habitat management planning.

STUDY AREAS

Data were collected at 10 sites along the Appalachian spur of the ruffed grouse species range (Figure 1). Radiotracking data were collected on most sites from September 1996 through April 2001 (55 months). However pilot data collection began on WV1 in September 1995, while monitoring started later on VA1 (September 1997), PA1 (September 1998), and NC1 and RI1 (September 1999).

Forest cover on study sites represented two general associations. Oak-hickory forests dominated cover on the KY1, RI1, VA1, VA2 and WV2 study sites (Braun 1950). Important tree species on these sites include white, chestnut, red, scarlet, and black oak (*Quercus alba*, *Q. prinus*, *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 beech (*Fagus grandifolia*). In the understory great rhododendron (*Rhododendron maximum*) and mountain laurel (*Kalmia latifolia*) often form dense evergreen thickets. Prior to the virtual elimination of American chestnut (*Castanea dentata*) as a canopy tree shortly after 1900, forests on these sites likely represented the oak-chestnut forest association (Braun 1950).

Forest cover on the remaining study sites (MD1, NC1, PA1, VA3, and WV1) was representative of the mixed mesophytic forest association (Braun 1950). Important canopy tree species on these sites include sugar maple, basswood (*Tilia americana*), sweet and yellow birch (*Betula lenta*, and *B. alleghaniensis*, respectively), black cherry (*Prunus serotina*), white ash (*Fraxinus americana*), white pine, American beech, northern red oak, eastern hemlock, and yellow poplar (*Liriodendron tulipifera*; Braun 1950). A relative phonologic index, which estimates differences in growing season based on latitude, longitude, and elevation, indicated that in spite of their geographic interspersion (Figure 1), climates were more northerly on all mixed mesophytic sites (P. Devers and S. Klopfer, personal communication).

A key goal of the ACGRP was to experimentally test effects of hunting on grouse ecology. During phase I (fall 1996-spring 1999) all study sites were open to fall-winter grouse hunting. During phase II (fall 1999-spring 2001) hunting was closed on three sites (KY1, VA3, WV2), but remained open on all other sites.

METHODS

Home Range Estimation

Lily-pad traps, which passively intercept moving grouse, were used from late August through early November to trap grouse on each study site (Gullion 1965). Captured grouse were sexed and aged based on feather criteria (juvenile [< 1 year old] or adult; Kalla and Dimmick 1995), and fitted with a necklace-style radio-transmitter (10 g, 1.25-2.5% of body mass; Advanced Telemetry Systems, Isanti, MN). Grouse were released at the site of capture, and, before being entered into the study population, given a one week conditioning period to allow them to acclimate to the collar and recover from the stress of capture. Thereafter roving observers equipped with handheld receiving equipment attempted to locate each bird at least twice weekly. A network of telemetry receiving stations was established on each study site, and the UTM coordinates of each obtained using a global positioning system (GPS) corrected against a base station (accurate to < 5 m). To obtain location estimates for each bird, sets of azimuths were collected from 3-8 stations during a period of < 20 minutes (White and Garrott 1990). Signal mode (constant, varying or mortality) and strength were recorded for each azimuth. Azimuths typically were collected between dawn and dusk, so reflect diurnal habitat use.

Grouse location estimates were calculated from sets of telemetry azimuths using Lenth's maximum likelihood estimator (Lenth 1981) calculated using a modified a SAS program presented by White and Garrott (1990). We conducted a beacon study as outlined by White and Garrot (1990), from which we determined that the mean bearing error in our azimuth data was approximately 7° (Chapter 1/Whitaker 2003). We used this value when calculating the extent of 95% confidence ellipses for each location estimate. Prior to inclusion in the data set presented here, we screened telemetry locations to eliminate unreliable observations. Location estimates were considered unreliable if the 95% confidence ellipse exceeded 10 ha or the Geometric Mean Distance (GMD) between receiving stations and the location estimate exceeded 800m. This approach placed more emphasis on proximity of the observer to the location estimate than on confidence ellipse size, as proximity was a far better predictor of error in our telemetry data (Chapter 1/Whitaker 2003). Following these criteria, mean error for the *worst* locations considered acceptable should be < 160m, while overall mean location error will be considerably less than this. Prior to inclusion in tests of factors influencing home range size, both raw and cleaned location datasets for each grouse were plotted and visually compared to ensure that portions of home ranges were not being excluded because they extended beyond 800m from the telemetry station network.

Fall-winter (September 1 – March 31; 212 days) and spring-summer (April 1 – August 31; 153 days) home ranges were estimated for each grouse. These changeover dates were selected to approximately correspond with nest initiation and brood break up, so the fall-winter and spring-summer time periods approximate the non-breeding and breeding seasons, respectively. We used the fixed kernel method with least squares cross validation (Worton 1989), which generally yields the least biased estimates of home range boundaries compared to other contemporary approaches (Seaman and Powell 1996). Home ranges boundaries were delineated using the animal movement software extension (Hooge et al. 1999) for ArcView GIS software (Environmental Systems Research Institute, Inc., Redlands, CA). As recommended by Seaman et al. (1999) for kernel methods, we used a minimum of 30 locations to estimate home ranges.

Because data are sparse, home range estimators often perform poorly near the periphery of the home range and can generate erratic estimates of home range extent. Further, peripheral portions of home ranges may have reduced biological significance, and it is often difficult to obtain accurate estimates of an animal's location for distant portions of its home range. Consequently it is preferable to use estimates that emphasize central portions of home ranges for comparisons of home range area (Seaman et al. 1999), and we used 75% fixed kernel home ranges. These typically were about half as extensive as the corresponding 95% fixed kernel home ranges.

A home range has been defined as the area where an animal has a predetermined probability of occurrence during a given time period (Kerhonan et al. 2001), or as an area repeatedly traversed by an animal (Kenward 2001). An assumption of these definitions is that the animal has settled and is restricting its movements to that locality, and areas no longer traversed have been excluded. Consequently efforts should be made to exclude dispersal movements when delineating home range boundaries (Kenward 2001). This was critical in our analyses, as fixed kernel home ranges become dramatically exaggerated when location data sets include excursive movements. Consequently, once subsets of seasonal locations had been delineated we identified and removed obvious extended dispersal events through visual analyses of sequential movement paths. Dispersal movements, which for ruffed grouse typically occur either during early fall (September-November) or early spring (March-April; Small et al. 1993), were identified as extended (1-25 km) one-way movements through an area that was not revisited later. Such movements are generally easily recognized, as ruffed grouse dispersal is rapid and strongly oriented (Small and Rusch 1989, Small et al. 1993). We considered dispersal movements to include all locations up until the grouse first entered the repeatedly traversed home range. This >

1 km distance criteria corresponds to the diameter of a circle having an area > 78 ha. In contrast >95% of our home ranges were < 78 ha.

Explanatory Variables

A number of variables were obtained from the ACGRP database as well as from digital habitat maps of each study site (Table 1). For each grouse we recorded sex, age, and, for females, breeding success during the current, previous and subsequent year. Females were classified as successful nesters if they had ≥ 1 chick alive at 3 weeks post-hatch. At the study site level, we used trapping success (captures/100 trap nights) as an index of population density each fall. We used the ratio of juveniles to adult females in these captures as an index of the age structure of the grouse population. Surveys of displaying males were conducted on a fixed block exceeding 150 ha on each site each April, and were used as an index of the density of the spring breeding population (drumming males/100 ha). Finally, fall hard mast crops (i.e. nuts and acorns) may be a critical food resource for Appalachian ruffed grouse (Servello and Kirkpatrick 1987, 1988). Mast production was evaluated on each site each fall by ranking production by red/black, white, and chestnut oaks and beech on a 0-3 scale (0 = no mast, 1 = light, 2 = moderate, 3 = heavy). We took the sum of the mast indices for these four tree species as an index of hard mast production on that site that year. When a mast species was not found on a site we assigned it a value of zero in all years, in effect penalizing sites having a lower diversity of hard mast producing trees.

The Conservation Management Institute at Virginia Tech (Blacksburg, VA) created digital Geographic Information System (GIS) habitat maps for each study site using available remote sensing data. To make habitat classes comparable across all 10 sites our habitat classification scheme was necessarily coarse. GIS maps included raster-based layers for landcover and topographic moisture (30×30m pixel), and a vector-based layer for access routes (i.e. roads and trails). Landcover was classified as coniferous forest, mixed forest with or without an evergreen understory, deciduous forest with or without an evergreen understory, 0-10 year old clearcut, 10-20 year old clearcut, water, agricultural and open land, and disturbed and developed sites. A Topographic Moisture Index (TMI) was calculated from the slope, aspect, and landform at and around each pixel, and was used to classify each pixel as xeric or mesic relative to the average for the landscape. Maps of 'mesic' habitats closely reflected the distribution of concave landforms in the landscape (e.g., hollows, valley bottoms and riparian zones). Access routes were classified as paved, dirt, or vegetated roads or trails. When the habitat on a site changed during the course of a year, usually due to the creation of a new clearcut or road, an updated map layer was created and used for all grouse location data collected from that point forward.

Map accuracy is essential for generating reliable inferences when overlaying animal locations on habitat maps. Accuracy of some map classifications used here will be near 100%. These include anthropogenic features which are visually obvious on imagery or whose locations were measured using GPS, such as clearcuts, agricultural land, and roads. Also, TMI, which was determined from USGS Digital Elevation Models (DEMs), should also be relatively accurate. Other features are often more difficult to map accurately, particularly vegetation cover types. One way of reducing errors is to use a coarser classification scheme, so we classified forest cover (conifer, mixed, or deciduous) and understory (evergreen or no evergreen) separately. With this approach additive effects of classification errors in either the canopy or understory are avoided. We conducted accuracy assessments on each site using standard map evaluation procedures (Campbell 1996). Reference data were obtained from 400 m^2 vegetation survey plots sampled on each site (J. Tirpack, unpublished data). Each reference point was classified as having a deciduous (< 20% conifer), mixed (20-80% conifer), or coniferous forest canopy (> 80% conifer canopy cover). Also, understories at each point were classified as evergreen (> 10% evergreen shrub cover) or non-evergreen (< 10% evergreen shrub cover).

Habitat information for each home range was extracted from GIS maps using FRAGSTATS/ARC software (McGarigal and Marks 1995). In addition to landcover composition, this program will calculate many landscape metrics from digital habitat maps (see McGarigal and Marks 1995). However rather than test all possible habitat metrics in a "fishing trip", we used our own "expert" opinion plus a literature review to select an a priori list of landscape metrics that are likely important to ruffed grouse (Table 1; see also Fearer and Stauffer 2003). A risk when comparing landscape metrics to polygon (i.e. home range) size is that these may be geometrically (rather than biologically) related to polygon size. These types of relationships often result from edge-area ratio effects or when a variable (e.g. patch richness) quickly reaches the maximum value as polygon size increases. To avoid spurious findings of this nature we created a test set of 100 randomly placed circular "home ranges" ranging in size from 0.5-200 ha on the GIS map of the VA1 study site. We then extracted all of the same habitat variables for each circle as we had extracted for each home range and ran linear and quadratic regressions of each habitat variable against circle area. Significant relationships were identified for mean patch size, mean shape index, mean nearest neighbor distance, total core area index, largest patch index, patch richness density, and patch density (see McGarigal and Marks [1995] for definitions), so these variable were dropped from further consideration.

At the landscape scale, we defined an area of "available" habitat based on the distribution of radioed grouse each season. We did this by placing an 800m buffer around any telemetry station falling within 800m of a grouse location from that season. This approach ensured that any habitat considered "available" was in the vicinity of a current grouse home range. It also ensured that portions of study areas where locations would be considered unreliable and consequently censored (i.e. areas > 800m from the telemetry station network) were not considered available. Habitat variables were then extracted from this area of available habitat following the same methods as used for individual home ranges.

Data Analyses

For many individual grouse we were able to estimate summer or winter home ranges in more than one year. This allowed direct pairwise comparisons of home range size under different circumstances while controlling for many individual sources of variability (e.g., local habitat). If an individual was a juvenile when the first home range was estimated, we compared size between juvenile and the subsequent adult home range. When an individual adult was followed during > 1 winter we tested for an effect of hard mast crop by designating each member of the pair of home ranges as either the high mast or low mast year based on fall mast indices for that site during those years. When an adult was tracked for > 2 winters we used the pair of home ranges having the greatest difference in mast index. Finally, when a female was successful in raising ≥ 1 chick to 5 weeks of age in one summer but failed to raise any chicks to 5 weeks in another summer we compared home range size between successful and unsuccessful breeding attempts. All comparisons were evaluated using paired *t*-tests with the difference in size of the 75% fixed kernel home ranges as the response variable (Sokal and Rolf 1995).

To test for a relationship between home range size and each explanatory variable we fit data to a linear model (JMPin statistical software v. 4.0.3, SAS Institute, Cary, NC). We used the 75% kernel home range area as the response variable (Y), which was natural log-transformed prior to model-fitting to avoid heterogeneous variance of residuals. Because effects of site, sex, or age might mask relationships with individual variables, we first fit each of these variables and, if they explained a measurable proportion of the variance in home range size, included them as control variables in tests of other variables. We also ran an expanded models including a SEX×AGE interaction term. If significant we removed this interaction by combining the two traits into a single 4-class variable, SexAge (juvenile male, adult male, juvenile female, or adult female). Each additional explanatory variable was then fit to the appropriate base model, and its influence 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, as well as by $\Delta R^2_{\mathrm{adj}}$, the change in overall model fit (Burnham and Anderson 1998). Reductions in $\mathrm{AIC}_c > 2$ suggest a substantial improvement in model fit (Burnham and Anderson 1998). Residuals were inspected for homogeneity of variances and non-random patterns (e.g. a bowl shape). If residuals suggested a poor model fit we attempted to remedy the problem by fitting a higher order model (e.g. adding a quadratic term). Finally, we tested each variable for interactions with cohort (Sex, Age, or SexAge) and site. When we detected an interaction with cohort we fit the model to each cohort separately to identify the cause of the interaction. When we detected a site interaction we refit the model to oak-hickory and mixed mesophytic forest sites separately. If this failed to account for the site interaction we fit the model to each site individually.

When the value of the response variable is likely to remain fixed across years for an individual, inclusion of multiple home ranges for that individual may constitute pseudoreplication (Hurlbert 1984). To avoid this we restricted our data set to one home range per individual for all habitat variables. However when the level or value of the explanatory variable is likely to change each year inclusion of replicate observations from individuals is acceptable or even desirable, as differences in response to changing conditions for an individual should give a reliable estimate of its influence. Consequently, for explanatory variables that were determined on an annual basis, such as mast crop or reproductive success, we included multiple home ranges from individuals in our analyses.

The preceding tests were designed to test individual explanatory variables as if they acted in isolation. However habitat selection is a multivariate process not a univariate pattern. To quantify relationships between factors affecting home range size we developed sets of multivariate linear models for different cohorts of grouse in summer and winter. We considered these as sets of *a priori* models, and compared them via information-theoretic model selection procedures (Burnham and Anderson 1998). Development of models was based both on the results of the preceding tests for individual variables, on the scientific literature of grouse habitat ecology, and on expected logical relationships between variables. Prior to building these model sets we tested candidate variables for correlations, as multicollinearity can lead to model overfitting. We computed Pearson's product-moment correlation coefficient for all pairs of continuous variables (Sokal and Rolf 1995), and censored one member of each pair having a correlation > 0.6. In all model sets the fit of the global models was examined through inspection of residual plots. Models within each set were compared using Akaike's Information Criterion adjusted for sample size (AIC_c), AIC_c differences (Δ_i), R^2_{adj}, and Akaike weights (ω_i) (Burnham and Anderson 1998). To increase comparability, when individuals in a cohort were modeled separately by forest type we tested the same set of candidate models in both forest types. The set of 'best' candidate models (*sensu* Burnham and Anderson 1998) was defined as all models having Akaike weights > 0.05. To estimate the influence of individual variables in these best model sets we report a Relative Importance Value (RIV) for each variable. These RIVs were calculated as the sum of the Akaike weights for all models in the subset of 'best' models that included that variable (Burnham and Anderson 1998).

Because hunting treatments were applied using an experimental design we employed a hypothesis testing approach to assess any affect on grouse home range size (Sokal and Rolf 1995). We tested the null hypothesis that hunting did not affect home range size using a repeated measures mixed linear model (Bennington and Thayne 1994; PROC MIXED, SAS Institute, Cary, NC). To avoid pseudoreplication we took the mean of the natural log-transformed fall-winter home range sizes for each sex and age cohort on each site each year as the response variable. Subjects of repeated measures were sites, which were nested within treatments. Treatment (experimental or control), phase (1 = pre-treatment, 2 = hunting closed on experimental sites), mast index, and SexAge were included as fixed effects, while year (nested within phase) was included as a random effect. A PHASE×TREATMENT interaction term was used to test for any effect of hunting on home range size, and a three-way interaction (PHASE×TREATMENT×SEXAGE) tested for a differential response by cohorts to hunting closure.

A common assumption is that animals will use smaller home ranges in higher quality habitat. This assumption can only be tested by comparing the fitness of individuals on home ranges of different size, which requires estimates of both survival probability and reproductive success. We were unable to address this relationship directly, as we could not estimate home range size for individuals that did not survive and because females may increase their movements while raising a brood (Maxson 1978). However we did test to see if female reproductive success during spring-summer was related to home range size during the preceding fall-winter. To test this we carried out a logistic regression analysis using winter home range area for female grouse as the explanatory variable and nesting success the following summer as the response variable (successful = raising ≥ 1 chick to 3 weeks post-hatch, unsuccessful = failed to nest successfully or lost all chicks by 3 weeks post-hatch). We tested for a univariate relationship, then expanded the model to include terms for site, mast index, and a home range size by mast index interaction.

Finally, we were interested in influence of habitat composition at the landscape scale on home range size. At this scale statistical analyses were not possible, as our sample size was reduced to one observation for each of the ten study sites. However we conducted an exploratory analysis for relationships by plotting the mean extent of each habitat variable on each study site against the mean home range size for each cohort of grouse on that study site during fall-winter and spring summer.

RESULTS

Our final data set included 647 fall-winter home ranges from 575 individual grouse and 407 spring-summer home ranges from 379 individuals. In fall-winter 75% fixed kernel home ranges for adult females averaged 30.6 ± 2.0 ha (mean ± SE; n = 200), while juvenile females averaged 34.8 ± 4.0 ha (n = 95), adult males averaged 14.4 ± 0.9 ha (n = 249), and juvenile males averaged 33.5 ± 4.0 ha (n = 103). In spring-summer adult female home ranges averaged 28.3 ± 2.6 ha (n = 150), while juvenile females averaged 29.8 ± 5.2 ha (n = 81), adult males averaged 10.0 ± 0.8 ha (n = 118), and juvenile males averaged 15.1 ± 1.9 ha (n = 58). We found no relationship between number of telemetry locations and home range size for any grouse sex or age class during either spring-summer or fall-winter (range = 30-75 locations). The same was true in tests comparing the time interval between the first and last location to home range size. Consequently neither number of locations nor duration of monitoring was included as a covariate in subsequent analyses.

Our evaluation of user's accuracy for forest cover on our GIS maps yielded mixed results. Overall, overstory was classified correctly for 85% of vegetation points, while understory was classified correctly on 80% of points (n = 1354). Accuracy was highest for deciduous forest canopy (DECID; 93%) and stands without evergreen shrubs in the understory (NEU; 85%). However these two cover classes form the landscape matrix, with 89% and 79% of our reference vegetation plots being classed as DECID and NEU, respectively. Thus relatively high accuracy might be expected due largely to chance. User's accuracy for the remaining rare cover classes was lower. Mixed canopy forests (MIX) represented 8% of reference points and were classified correctly 23% of the time, while 3% of reference points had coniferous canopy cover (CONIF), and 50% were classified correctly. In the understory, 21% of reference points had Evergreen shrub cover (EU), and user's accuracy was 53% for these points on our GIS maps.

Comparing pairs of home ranges for individual grouse revealed a number of changes in home range size resulting from changes in conditions grouse were experiencing (Table 2). Males used smaller home ranges as adults than they had used as juveniles during both fall-winter and spring-summer (Table 2). Though often reported in the literature, we did not find a comparable reduction in fall-winter home range sizes for females as they graduated from the juvenile to adult age class. Spring-summer home range sizes also did not differ for females as juveniles and then adults. Following poor fall hard mast crops both female and male adult grouse on sites having oak-hickory forests expanded their fall-winter home ranges by > 250%. No such difference was detected for males or females on study sites having mixed mesophytic forests (Table 2). Finally, individual females had larger home ranges during summers in which they successfully raised broods than during summers when they experienced reproductive failure (Table 2).

In our test of the influence of individual variables study site (SITE) was found to have a strong association with home range area in both spring-summer and fall-winter, and so was included as a control variable in all other tests of individual factors (Tables 3 and 4). Sex was also found to have an important influence on fall-winter home range size, and so was included in all models applied to datasets including both male and female grouse. Grouse age influenced the size of fall-winter home ranges. However there was an interaction between sex and age resulting from the fact that juvenile male home ranges typically were intermediate in size between those of juvenile and adult females. To avoid this interaction we combined sex and age into a single 4-level control variable (SEXAGE) in subsequent tests of fall-winter home range size (Table 3). Sex was also found to influence summer home range size, though age was not. Consequently we only included SITE and SEX as control variables in tests of factors influencing summer home range size (Table 4).

We detected relationships between home range size and all population parameters we tested, though none of these relationships applied to all sexes and ages of grouse. In our test of fall-winter home ranges we observed an interaction between trapping success (TRAP) and SEXAGE, which led us to test this relationship separately for each cohort. These tests revealed a strong positive relationship between trapping success and fall-winter home range size for juvenile males. Interactions between SEXAGE and the ratio of juveniles per adult female in fall trapping (J:AF) as well as between site and J:AF led us to test this relationship for each SEXAGE cohort in each forest type separately. These tests revealed a negative relationship between the proportion of juveniles in the fall population and home range size of adult grouse on sites having oak-hickory forest types (Table 3). During summer we found a curvilinear relationship between densities of drumming males (DRUM) and the home range size of male grouse, where home ranges were smallest at intermediate densities of displaying males. However this relationship was only evident if SITE was not included as a control variable in our models. As with the paired tests reported above, females raising broods had larger home ranges than unsuccessful breeders.

There was a strong inverse relationship between our hard mast index (MAST) and fall-winter home range size for adult grouse on study sites having oak-hickory forest types. However, as with our paired tests (above) we found no relationship for grouse on sites having mixed mesophytic forests. During spring-summer there was an inverse relationship between female home range size and the hard mast index from the preceding fall in oak-hickory forests.

We found relationships between several habitat variables and fall-winter home range size (Table 3). Clearcuts comprised an increasing proportion of home range area as home ranges became smaller. Conversely, we observed a general increase in the proportion of home ranges represented by forests having evergreen understories (EU) as fall-winter home range size increased. For male grouse we observed an increase in the proportion of deciduous forests (DECID) with increasing home range size, while for females the proportion of coniferous forest (CONIF) increased in larger home ranges. Several variables relating to road density showed an inverse relationship with fall-winter home range size. Of these, the combined density of all roads plus trails (ACCSS) showed the strongest relationship (Table 3).

We also observed a number of relationships between spring-summer home range size and habitat composition (Table 4). Once again there was a general increase in the proportion of home ranges occupied by clearcuts as home range size decreased. Conversely, the proportion of deciduous forests (DECID) and forests without an evergreen understory (NEU) was positively correlated with home range size for both males and females. As in winter, a number of variables relating to the density of access routes were inversely related to home range size and again the strongest of these relationships was for ACCSS. Finally, proportion of mesic bottomlands (TMI) showed a strong inverse relationship with spring-summer home range size for females on sites having oak-hickory forests.

Prior to specification of our multivariate models we eliminated a number of candidate variables having high correlations with other variables. Young clearcut (YCC) and old clearcut (OCC) were dropped in favor of all clearcuts combined (CC), while total edge density (TED) and other variables related to roads (ROAD, UNPVD_RD, DRT_RD, and ALL_CLSD) were dropped in favor of all access (ACCSS). Finally, there was a strong inverse correlation between the proportion of clearcut in home ranges and that of both of deciduous forests (DECID) and forests without evergreen understories (NEU). Since DECID and NEU could both be considered the landscape matrix and increased to near background levels as home range size increased, we assumed that the correlations we observed were an indirect consequence of grouse selecting less abundant cover types such as clearcuts, and so dropped them.

While our univariate tests indicated that clearcuts were important to all grouse in both spring-summer and fall-winter, our multivariate modeling indicated that this habitat type was not equally influential in all cases (Tables 5, 6, and 7). While being strongly selected in all ‘best’ model sets for males in fall-winter, clearcut was less often represented in ‘best’ models of male spring-summer home range size. For females the opposite was true; clearcuts had limited influence on fall-winter home range size, but were typically specified in the ‘best’ models of spring-summer home range size (Tables 5 and 6).

In our set of models for juvenile females during fall-winter density of access routes (ACCSS) was the only cover feature to emerge as a predictor of home range size. This led us to hypothesize that the importance of access routes to these individuals resulted primarily from the edge habitat they afford, in which case total edge density (TED) would be a better predictor of home range size. To test this we did a *post-hoc* substitution of TED for ACCSS in the 'best' model, yielding a substantial improvement in model fit (Table 5).

Though there was no characteristic difference in home range size between oak-hickory and mixed mesophytic forests 'best' model sets differed considerably by forest type (Tables 5 and 6). While mast and mesic sites (TMI) were the most important variables for females on oak-hickory sites during spring-summer, clearcuts and association with a brood were most important for females on sites having mixed mesophytic forests. Mast was also specified in the best models of fall-winter home range size for juvenile females, but models lacking a forest type by mast interaction had a very low AIC weight, again pointing to the difference in relative importance of this resource between the two forest types. Hard mast production was specified in all of the best models for adult fall-winter home range size in oak-hickory forests, but had less influence in models for adults in mixed mesophytic forests.

Our test of the effect of hunting on home range size indicated that grouse home range changed significantly following closure of hunting on treatment sites (Table 8), being on average ≈ 32% smaller. This response was consistent across sites and sex and age classes, regardless of hard mast crop.

Though the relationship was weak, logistic regression indicated that females having smaller winter home ranges were more likely to raise broods to at least 3 weeks post-hatch the following summer (n = 159, $\Delta_i = 2.61$, Wald $\chi^2 = 4.43$, $P = 0.035$, Concordance = 59.6%).

Expanded models incorporating site, age, and mast index were tested but yielded no appreciable change in interpretation of the relationship between home range size and reproductive success.

Finally, we carried out exploratory analyses for relationships between mean home range size in both spring-summer and fall-winter and the mean extent of CC, EU, TMI, and ACCSS on each study site. There was no clear relationship between the extent of these habitat features on each landscape and mean home range size for any cohort in either season.

DISCUSSION

Habitat selection is a process not a pattern (Jones 2001), and our findings make it clear that, in terms ruffed grouse home range size, it is a complex multivariate process. Factors we identified as being associated with home rage size included individual traits, resource availability, population parameters, habitat structure, and hunting pressure. Further, the suite of factors that were important differed by forest type, season, and the sex and age of an individual grouse.

Individual traits played an important role in determining home range size for grouse. As has been reported previously, juvenile grouse had larger winter home ranges that adults, and females occupied larger ranges than males (Archibald 1975, Thompson 1987, Clark 2000, Fearer and Stauffer 2003). This age relationship was maintained through summer for males, but for females was no longer evident during the breeding season. While females with broods had large home ranges, loss of a brood allowed them to restricted their movements to the smallest home ranges we observed for females at any time; this was the only circumstance where female home range sizes were comparable to those of adult males (Table 2; see also Maxson 1978).

Hard mast crops had a strong negative influence on home range size for grouse in oak-hickory forests. In contrast, hard mast crop showed little influence on home range size in mixed mesophytic forests (Tables 2, 3, and 4). This suggests important differences in the nutritional ecology of the species by forest type, and that mast is likely a key resource in oak-hickory forests (see also *Oak-hickory and Mixed Mesophytic Forests*, below). The continued influence of fall hard mast crops on summer home range size for female grouse on oak-hickory sites was surprising. Presumably all hard mast from the preceding fall has either been consumer or germinated by late spring, leading us to speculate that females are able to carry some benefit of good mast crops, such as higher body condition, into the breeding season.

Though largely solitary, ruffed grouse do not occupy their environment independently of one another. Juvenile males greatly increased the size of their home ranges during falls when populations densities were high (as indicated by trapping success), suggesting that they are in direct competition with conspecifics for territories. In line with this, Gullion (1981) reported that the proportion of non-territorial males (primarily juveniles) was positively correlated with population size. No other cohort adjusted its home range size in response to population density.

In oak-hickory forests adult grouse of both sexes occupied smaller fall-winter home ranges when the proportion of juveniles our fall captures increased. *One interpretation of this finding is that adults reduce home range size when the proportion of unestablished individuals in the population increases. For example, males may increase defense of their display sites from prospecting juvenile males.* However, we find a more mundane explanation more plausible. Adult grouse in oak-hickory forests occupy smaller fall-winter home ranges when mast crops are heavy (Tables 2, and 3), which likely reduces their vulnerability to the passive drift fence trapping technique we employed. In contrast, juvenile grouse did not show a pronounced change in home range size in response to mast crop size, so vulnerability to trapping should be unaffected. Under these circumstances one would expect an increase in the proportion of juveniles in the captured population during poor mast years even if the age structure of the overall population remained constant. This explanation is supported by the fact that multivariate models were not improved by including both MAST and J:AF (i.e. effects were not additive; Table 5), and would explain the absence of a similar relationship in mixed mesophytic forests.

We observed a curvilinear relationship between the density of drumming (displaying) males in spring and the spring-summer home range size of male grouse. In this male home range size was smallest at moderate drummer densities. Since this relationship was only evident when site was excluded from our statistical models there is presumably a relatively characteristic density of drumming males on each site, which may relate to the number of perennial drumming logs in the survey area on each site (see Gullion and Marshall 1968). Consequently the observed relationship may simply be the result of drumming male density acting as a surrogate for site in the model. However, an alternative interpretation is that social interactions such as this account for much of the site level effect we observed. If this is the case then the curvilinear form of this relationship suggests that different social processes become important at different densities of displaying males. It is known that males often use multiple display sites (Rusch et al. 2000), and it may be that this is more common when densities of displaying males are low. However this would not account for the inflexion of this relationship back towards larger home ranges as numbers of drumming males went from moderate to high densities. Proportions of non-territorial males increase as populations increase (Gullion 1981, Rusch et al. 2000), and it may be that these floaters occupy larger home ranges or increase their movements as the density of displaying males increases.

Prevalence of some habitat types was inversely associated with home range size. There are two possible non-exclusive explanations for increased representation of a habitat type in smaller home ranges. First, the feature may represent high quality habitat that allows an individual to meet its resource needs within a smaller area. Second, if the habitat is rare and animals preferentially center home ranges on it, small home ranges will inevitably encompass a lower proportion of background (matrix) habitat. If, as one might expect, habitat types that grouse select are in fact of high quality, then both of these reasons would hold true. Smaller female spring-summer home ranges in oak-hickory forests contained a greater proportion of mesic bottomlands. Bottomlands have been identified as preferred brood habitat in studies conducted in southern portion of the species range, and associated understory vegetation may afford broods with foraging and escape cover not found on more xeric uplands (Stewart 1956, Thompson et al. 1987, Fettinger 2002). For all cohorts we observed an increase in proportional cover of clearcuts in smaller home ranges, as well as increased densities of access routes (roads and trails). It is well known that ruffed grouse preferentially select high-stem density early successional stands, and has been suggested that these serve 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). Correlation between the proportion of clearcuts and density of access routes within home ranges was low ($R = 0.18$), so we do not feel that the relationship between road density and home range area resulted from association of forest roads with clearcuts. Schumacher (2002) identified edges along access routes as preferred grouse habitat in North Carolina, citing them as sources of herbaceous groundcover and invertebrate foods, as well as grit for digestion (see also Rusch et al. 2000). For juvenile females during fall-winter total edge density (TED), which incorporated densities of both access routes and (contrast-weighted) edges between forest stands, was a much better predictor of home range size than the density of access routes alone (Table 5). This suggests that some more fundamental aspect of edges was also important to juvenile females. *During fall-winter juvenile females had the largest home ranges we observed, and are more likely to disperse than any other cohort (personal observation; Small and Rusch 1989). Thus this increased association with edges may result from using them as travel corridors.*

In contrast some habitat features were more prevalent in larger home ranges. During fall-winter deciduous forests (DECID), evergreen understory forests (EU), and, for females, coniferous forest (CONIF), were more prevalent on large home ranges. During summer deciduous forest, and forests lacking an evergreen understory (NEU) were more prevalent in large home ranges. Cover types that are proportionately more common in larger home ranges likely represent low quality or non-preferred habitat, and this increase occurs as proportions approach background levels in larger, less selective home ranges. This was almost certainly the case with deciduous forests and forests lacking evergreen understories, which, representing > 80% of canopy and understory cover on our study sites, could be considered as matrix habitat. Proportions of this cover type showed a strong inverse correlation with proportion of clearcuts, and thus became more prevalent as the proportional representation of (preferred) clearcuts declined in larger home ranges.

An alternative explanation for increased representation of a cover type in large home ranges is that size increased due to a change in habitat selection in response to unfavorable conditions. During winters following poor hard mast crops grouse home ranges increased in size on sites having oak-hickory forests (Table 5), and in the absence of hard mast grouse consume large amounts of mountain laurel leaves during winter (Servello and Kirkpatrick 1987). Thus the *increase in proportions of evergreen understory forests in larger home ranges may have resulted from a dietary shift following mast failure. We included a MAST×EU interaction in some of our multivariate models to test for this relationship, but found little evidence to support it (Tables 5 and 7).*

Even after inclusion of the above-mentioned variables, site level effects still typically had a large effect on home range size. Some of this may undoubtedly relate to site-level errors in estimation of home range size (e.g., topography affecting telemetry error). However some variables seemed to account for some of the site-level variation in our data, as their importance was reduced multivariate models including SITE. These include densities of drumming males (see above), the proportion of evergreen understory in home ranges, and density of access routes. However, the fact that the overall extent of a particular habitat type in a landscape did not show a clear relationship with mean home range size suggests that habitat available within a grouse's immediate surroundings is more important than availability of that feature at the landscape level. Perhaps this should be expected; animals do not settle at random across landscapes, but rather are seeking out localities affording favorable conditions. Thus the extent of an important habitat feature in a landscape might be better correlated with the ratio of use to availability of that feature or the density of individuals the landscape supports, rather than the home range size of individuals within the landscape. Put another way, animals adjust their home range size to suit their immediate surroundings rather than average conditions across the landscape.

In an effort to maximize their fitness most animals reduce risk under increased predation pressure by reducing movements and increasing refuging behavior (Lima 1998). In contrast, our test of the effect of hunting on home range size indicated that grouse reduced their home ranges ≈ 32 % when hunting pressure was removed (Table 8). In a correlative test Clark (2000) reported a similar response by ruffed grouse in Michigan, and increased movement under hunting pressure has also been reported in wild turkey (*Meleagris gallopavo*) and black ducks (*Anas rubiripes*; Hoffman 1991, Clugston et al. 1994). This contrast between the response of game species to hunting pressure and the typical response of animals to predators is striking. Hunters, who typically focus their efforts on preferred habitat patches, may be causing animals to abandon these cover types in favor of lower quality cover types and thereby interrupting normal refuging behavior. Alternatively, if hunters flush animals often enough they may cause a net increase in movements and home range size even if animals are attempting to reduce their activity levels. In either case this response could lead to non-lethal negative effects of hunting on grouse, including reduced condition and increased predation rates, both of which would exacerbate the effect of hunting on populations. *(does this paragraph belong in the next section?)*

Selective Pressures Affecting Home Range Size

A central issue in studies of home ranges is the relationship between range size and Darwinian fitness, which is maximized both through increased survival rates and through high reproductive success. It seems logical to think that individuals occupying smaller areas will experience reduced encounter rates with predators and competitors, be more familiar with escape cover, and expend less energy and time in transit. However stationary individuals may also forgo opportunities to locate and occupy higher quality alternate home ranges and have lower encounter rates with potential mates. Consequently we may expect the factors affecting the size of an individual’s home range to change depending on the individual’s immediate resource needs, its social status, and its experience level. We could not test the effect of home range size on survival rate, though some evidence suggests survival is higher for grouse occupying smaller home ranges (Thompson and Fritzell 1989, Clark 2000). However our results did indicate that females occupying smaller home ranges during fall and winter were more likely to reproduce successfully during the following summer. Thus the general premise that individuals occupying smaller home ranges have increased fitness may hold for ruffed grouse.

In keeping with the idea that grouse should occupy the smallest adequate home range, our analyses indicate that adult grouse actively try and minimize home range size. Hard mast is a high quality food resource, and adult grouse in oak-hickory forests reduced the size of their fall-winter home ranges ≈ 60% following good hard mast crops (Tables 2 and 3). Females use larger home ranges when rearing broods, presumably due to the increased resource needs of the brood. However females with broods still used relatively smaller home ranges in summers following abundant hard mast crops, and reduced home range size 60% if a brood was lost (Table 2). Resource needs are likely lowest for males in summer, and these individuals occupied the smallest home ranges. Further, our multivariate models suggested that male home ranges were relatively unaffected by environmental variation during summer (Tables 5 and 6).

Social pressures and the need to identify and occupy a high-quality home range suggest that, as observed, juvenile grouse should range widely compared to adults. While this was true, our observations suggest that even with these pressures juveniles attempt to minimize home range size. Juvenile females in oak-hickory forests occupied smaller home ranges as hard mast became more abundant (Table 5). Males aggressively defend displaying sites, and established adults occupy a preferred subset of these these sites (Gullion and Marshall 1968). Consequently when population densities are high juvenile males likely have to range farther and monitor more occupied sites in order to obtain a preferred drumming site. The strong positive relationship we observed between fall trapping success and fall-winter home range size of juvenile males suggests that this is indeed the case (Tables 3 and 5). *Anecdotal behavioral observations also* *support the view that juvenile males are continually monitoring their neighbors and prospecting for available high-quality drumming sites (see also Rusch and Keith 1971). On two occasions when established adult males we were monitoring were killed during fall, neighboring radioed juvenile males abandoned their current drumming sites and relocated to the vacant display site within 24 h (ACGRP, unpublished data). In one instance 2 males were observed fighting at the vacant drumming site (S. Freidhof, personal communication). In the other case the newly established juvenile was killed later that fall and a third male occupied the site, again within 24h of the death of the resident male (DMW, personal observation).*

Oak-hickory and Mixed Mesophytic Forests

One of our most striking findings is the difference in habitat ecology of ruffed grouse inhabiting oak-hickory forests compared to those inhabiting mixed mesophytic forests. The ecological importance of this distinction is made more convincing by the geographic interspersion of study sites representing these two forest associations. Further, segregating analyses by forest type removed all site interactions, supporting the ecological relevance of this dichotomy. This said, we found no characteristic difference in home range size between these two forest types.

Previous authors have suggested that ruffed grouse in Appalachian forests are under strong nutritional constraint, where availability of sufficient hard mast foods may be important for maintenance of body condition through the winter and subsequent reproductive success (Norman and Kirkpatrick 1984, Servello and Kirkpatrick 1988). The relationship we observed between hard mast crop and home range size, which was stronger than other any environmental variable we identified for grouse in oak-hickory forests (Tables 2, 3, 5, and 7), provides strong evidence that hard mast is a key limiting resource. This increase in home range size following poor hard mast crops also suggests that availability of this resource has important consequences for predation risk. This combined with possible effects of condition on reproductive success support the hypothesis that fall hard mast crops may regulate grouse populations in Appalachian oak-hickory forests. Given the strength of the relationship between mast crops and home range size in oak-hickory forests, it is interesting that grouse home ranges in mixed mesophytic sites were relatively unaffected by availability of this resource. In northern forests at the core of the species range grouse feed heavily on buds of aspen, cherries and birch during winter, and these provide a reliable and accessible source of high-quality food. This leads us to speculate that the higher abundance of these tree species in mixed mesophytic forest types, particularly birches and cherries, damps any response by grouse to changing mast crops by providing a stable and easily accessed supply of high-quality food during winter (see also Servello and Kirkpatrick 1987). In contrast alternate foods in oak-hickory forests consist largely of low-quality evergreen leaves (Servello and Kirkpatrick 1987, Hewitt and Kirkpatrick 1997).

The negative relationship between TMI and female home range size in spring-summer suggests that bottomlands provide preferred brood-rearing habitat in oak-hickory forests, and other researchers have reported that grouse broods in southern portions of the species range select lower slope positions and riparian zones (Stewart 1956, Thompson et al. 1987, Fettinger 2002). On some of these same ACGRP study sites researchers found that females with broods selected stands having well developed understories and relatively high insect biomass (Haulton 1999, Fettinger 2002). Groundcover vegetation, soft mast, and insects associated with understory plants constitute the majority of the diet of grouse chicks (Rusch et al 2000). Uplands in oak-hickory forests are typically xeric and support little understory vegetation, suggesting a mechanism for the association of smaller female home ranges with bottomlands. In contrast, uplands in mixed mesophytic forests typically have mesic soils and support well developed understory vegetation, likely relaxing this constraint.

These findings suggest that habitat management for ruffed grouse in Appalachian forests should be tailored to the forest type in the management area. In oak-hickory forests harvesting strategies that promote or maintain mast production within or adjacent to high stem density escape cover should provide the high quality habitats (see also Thompson and Dessecker 1997). This might be best achieved by retaining good mast producing trees in the overstory of management units, either through group selection cutting, heavy thinning, or seed tree cuts. Thinning has been shown to increase masting by residual canopy trees, so may afford the combined benefit of providing high-quality food in association with escape cover (Thompson and Dessecker 1997, Healy 2002). Further, the importance of clearcuts and mesic soils for females during summer suggest that creation of early successional habitats in bottomlands may provide the highest quality brood habitat in oak-hickory forests. In contrast, our observation suggest that more traditional ruffed grouse habitat management focusing on creation of even-aged early successional habitats, edges, and vegetated roadsides may be sufficient in mixed mesophytic forests in the region.

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Table 1. Variables tested as predictors of 75% home ranges size for ruffed grouse on ACGRP study sites.

Variable	Description
ACCSS	Density of access routes (ROAD + TRAIL; m/ha)
AG	Agricultural and open lands (% of home range)
AGE	Hatch-year (juvenile) or after-hatch-year (adult)
BROOD	Whether or not the female produced ≥ 1 chick to ≥ 3weeks post-hatch that summer
CC	All Clearcuts (YCC + OCC; % of home range)
CONIF	Coniferous forests (% of home range)
CWED	Contrast Weighted Edge Density (m/ha)[a]
DECID	Deciduous forests (% of home range)
DIST	Urban and other disturbed habitat types (% of home range)
DRT_RD	Density of dirt roads (m/ha)
DRUM	Density of drumming males in spring (drummers/100 ha)
ED	Edge Density (m/ha)[a]
EU	Forests having evergreen understories (% of home range)
FOREST	Oak-hickory or Mixed Mesophytic
J:AF	Ratio of juveniles per adult female in fall captures
MAST	Index of hard mast production by chestnut, red/blac, and white oaks and beech
MIX	Mixed coniferous-deciduous forests (% of home range)
NEU	Forest without evergreen understories (% of home range)
OCC	Old clearcuts (10-20 years post-harvest; % of home range)
PVD_RD	Density of paved roads (m/ha)
ROAD	Density of all road classes combined (m/ha)
SEX	Male or female
SEXAGE	Sex and age classes combined to create four cohorts (AM, AF, JM, JF)
SITE	ACGRP study site (n = 10)
TECI	Total Edge Contrast Index[a]
TED	Total Edge Density = CWED + ROAD (m/ha)
TMI	Topographic Moisture Index; landforms favoring moist soils (% of home range)
TRAIL	Density of trails (m/ha)
TRAP	Fall trapping success (captures/100 trap nights)
UNPVD_RD	Density of all unpaved roads (DRT_RD + VEG_RD; m/ha)
VEG_RD	Density of seeded roads (m/ha)
YCC	Young clearcuts (< 10 years post harvest; % of home range)

[a] See McGarigal and Marks (1995) for a detailed description of landscape metrics.

Table 2. Change in home range area for individual grouse between years. Difference in size between pairs of 75% fixed kernel home ranges coming from the same individual in different years were used to test the null hypothesis that the mean difference in home range area did not differ from zero (paired T test). Units for all home range sizes are hectares.

	Condition 1		Condition 2					
Cohort	Feature	Mean ± SE	Feature	Mean ± SE	n	Diff. ± SE	*t*	*P*
Winter Home Ranges								
Males	Juvenile	38.6 ± 8.2	Adult	19.0 ± 2.7	37	19.6 ± 6.5	3.00	0.005
Females	Juvenile	29.9 ± 5.8	Adult	17.4 ± 3.5	17	12.5 ± 6.6	1.89	0.076
Adult males, MM[a]	Low mast	10.0 ± 1.1	High Mast	11.6 ± 1.6	23	-1.6 ± 1.5	1.08	0.290
Adult males, O-H[a]	Low mast	22.3 ± 6.7	High Mast	7.3 ± 1.4	17	15.0 ± 7.0	2.15	0.047
Adult females, MM[a]	Low mast	22.5 ± 3.0	High Mast	23.7 ± 3.9	21	-1.2 ± 3.6	0.32	0.750
Adult females, O-H[a]	Low mast	51.6 ± 11.7	High Mast	19.7 ± 1.7	16	31.9 ± 12.5	2.56	0.022
Summer Home Ranges								
Males	Juvenile	22.4 ± 3.2	Adult	11.8 ± 1.8	15	10.6 ± 3.6	2.96	0.010
Females	Juvenile	27.9 ± 6.3	Adult	49.1 ± 14.2	13	-21.1 ± 14.7	1.44	0.180
Females[b]	Failed	14.8 ± 4.3	Successful	39.2 ± 11.2	12	-24.4 ± 10.2	2.39	0.036

[a] MM = study sites having Mixed Mesophytic forests (MD1, NC1, PA1, VA3, WV1); O-H = sites having Oak-hickory forests (RI1, WV2, VA1, VA2, KY1).

[b] Females were considered successful if they raised ≥ 1 chick to at least 5 weeks of age.

Table 3. Results of tests of the influence of individual variables on fall-winter home range size of ruffed grouse on ACGRP study sites. Variables not found to influence home range size are not reported (see Table 1 for a full list of variables tested). The response variable in all models was the natural log-transformed size of the 75% home range.

Model[a]	Sites[b]	Cohort[c]	n	SSE	K	AIC$_c$	Δ_i	R^2	R^2_{adj}	$\Delta\ R^2_{\mathrm{adj}}$	Coefficient ± SE[d]
Y = β_0 + *SITE*	All	All	556	436.5	11	-112.1	-39.4	0.099	0.084	0.084	-
Y = β_0 + Site + *SEXAGE*	All	All	556	375.8	14	-189.1	-77.0	0.224	0.207	0.123	-
Y = β_0 + Site + Age + *DECID*	All	M	296	160.0	12	-157.1	-31.3	0.293	0.265	0.079	0.0117 ± 0.0021
Y = β_0 + Site + Sex + *MAST*	O-H	A	222	130.1	8	-101.9	-21.6	0.323	0.304	0.075	-0.0909 ± 0.0184
Y = β_0 + Site + SexAge + *CC*	All	All	541	327.9	15	-240.0	-20.3	0.262	0.244	0.031	-0.0079 ± 0.0017
Y = β_0 + Site + SexAge + *EU*	All	All	541	330.5	15	-235.7	-16.0	0.256	0.238	0.025	0.0168 ± 0.0040
Y = β_0 + Site + Sex + *J:AF*	O-H	A	222	135.6	8	-92.8	-12.5	0.294	0.275	0.046	-0.0725 ± 0.0189
Y = β_0 + Site + SexAge + *YCC*	All	All	541	335.2	15	-228.1	-8.5	0.245	0.227	0.017	-0.0086 ± 0.0027
Y = β_0 + Site + *TRAP*	All	JM	95	69.6	11	-4.3	-7.9	0.237	0.156	0.088	0.3384 ± 0.1074
Y = β_0 + Site + SexAge + *OCC*	All	All	541	336.3	15	-226.3	-6.7	0.243	0.224	0.011	-0.0056 ± 0.0019
Y = β_0 + Site + Age + *CONIF*	All	F	245	147.8	13	-96.2	-5.8	0.189	0.151	0.025	0.0232 ± 0.0084
Y = β_0 + Site + SexAge + *ACCSS*	All	All	535	335.1	15	-219.4	-5.7	0.236	0.217	0.012	-0.0042 ± 0.0015
Y = β_0 + Site + SexAge + *TED*	All	All	535	335.4	15	-218.9	-5.2	0.235	0.216	0.011	-0.0023 ± 0.0009
Y = β_0 + Site + SexAge + *ROAD*	All	All	535	336.6	15	-216.9	-3.3	0.232	0.213	0.008	-0.0036 ± 0.0016
Y = β_0 + Site + SexAge + *UNPVD_RD*	All	All	535	336.7	15	-216.9	-3.2	0.232	0.213	0.008	-0.0037 ± 0.0016
Y = β_0 + Site + *TRAP*	All	AF	188	108.2	12	-78.2	-2.2	0.162	0.114	0.015	0.1088 ± 0.0528

[a] The variable of interest in each model is indicated by italicized capital letters. Δ_i and Δ- R^2_{adj} values for these models were calculated as the improvement in the model fit to that same data set resulting from the inclusion of the variable of interest.

[b] Study sites to which the model applies; All = all sites; O-H = only sites having oak-hickory forest types (RI1, WV2, VA1, VA2, KY1).

[c] Cohorts to which the model applies; A = Adults (after-hatch-year); AF = Adult Females; F = Females; JM = Juvenile Males (hatch year).

[d] Coefficient for the variable of interest in each model; only reported for continuous variables.

Table 4. Results of tests of the influence of individual variables on spring-summer home range size of ruffed grouse on ACGRP study sites. Variables not found to influence home range size are not reported (see Table 1 for a full list of variables tested). The response variable in all models was the natural log-transformed size of the 75% home range.

Model[a]	Sites[b]	Cohort[c]	n	SSE	K	AIC$_c$	Δ_i	R^2	R^2_{adj}	ΔR^2_{adj}	Coefficient ± SE[d]
$Y = \beta_0 + \mathit{SITE}$	All	All	360	273.3	11	-76.4	-25.7	0.116	0.093	0.093	-
$Y = \beta_0 + \text{Site} + \mathit{SEX}$	All	All	360	231.2	12	-134.5	-58.1	0.252	0.231	0.138	-
$Y = \beta_0 + \mathit{DRUM} + \mathit{DRUM}^2$	All	M	148	69.9	4	-102.7	-21.8	0.161	0.150	0.100	0.0340 ± 0.0080
$Y = \beta_0 + \text{Site} + \text{Sex} + \mathit{DECID}$	All	All	372	225.3	13	-159.5	-16.4	0.279	0.257	0.036	0.0087 ± 0.0020
$Y = \beta_0 + \text{Site} + \text{Sex} + \mathit{CC}$	All	All	372	226.3	13	-157.9	-14.8	0.276	0.254	0.033	-0.0082 ± 0.0020
$Y = \beta_0 + \text{Site} + \mathit{TMI}$	O-H	F	90	50.9	7	-35.9	-12.9	0.188	0.140	0.146	-0.2560 ± 0.0065
$Y = \beta_0 + \text{Site} + \text{Sex} + \mathit{NEU}$	All	All	372	227.6	13	-155.7	-12.6	0.272	0.250	0.029	0.0079 ± 0.0021
$Y = \beta_0 + \text{Site} + \text{Sex} + \mathit{ACCSS}$	All	All	371	225.8	13	-157.3	-10.2	0.274	0.252	0.023	-0.0060 ± 0.0017
$Y = \beta_0 + \text{Site} + \text{Sex} + \mathit{ROAD}$	All	All	371	226.4	13	-156.2	-9.1	0.272	0.250	0.021	-0.0059 ± 0.0018
$Y = \beta_0 + \text{Site} + \text{Sex} + \mathit{UNPVD\_RD}$	All	All	371	227.7	13	-154.2	-7.1	0.268	0.245	0.016	-0.0053 ± 0.0018
$Y = \beta_0 + \text{Site} + \text{Sex} + \mathit{TED}$	All	All	371	227.8	13	-153.9	-6.8	0.267	0.245	0.016	-0.0031 ± 0.0010
$Y = \beta_0 + \text{Site} + \text{Sex} + \mathit{DRT\_RD}$	All	All	371	228.3	13	-153.2	-6.1	0.266	0.243	0.014	-0.0055 ± 0.0019
$Y = \beta_0 + \text{Site} + \text{Sex} + \mathit{YCC}$	All	All	372	231.7	13	-149.1	-6.0	0.259	0.236	0.015	-0.0092 ± 0.0033
$Y = \beta_0 + \text{Site} + \text{Sex} + \mathit{OCC}$	All	All	372	232.4	13	-147.9	-4.8	0.257	0.234	0.013	-0.0060 ± 0.0023
$Y = \beta_0 + \text{Site} + \mathit{MAST}$	O-H	F	103	68.0	7	-27.5	-3.7	0.085	0.038	0.038	-0.0788 ± 0.0327
$Y = \beta_0 + \text{Site} + \mathit{BROOD}$	All	F	198	142.1	13	-37.6	-1.7	0.124	0.077	0.025	-

[a] The variable of interest in each model is indicated by italicized capital letters. Δ_i and Δ- R^2_{adj} values for these models were calculated as the improvement in the model fit to that same data set resulting from the inclusion of the variable of interest.

[b] Study sites to which the model applies; All = all sites; O-H = only sites having oak-hickory forest types (RI1, WV2, VA1, VA2, KY1).

[c] Cohorts to which the model applies; F = Females; M = Males.

[d] Coefficient for the variable of interest in each model; only reported for continuous variables.

Table 5. Multivariate models explaining variation in fall-winter home range size. All models with Akaike weights (ω_I) > 0.05 are presented.

Model	n	SSE	K	AIC	AIC$_c$	Δ_i	R^2	R^2_{adj}	ω_i
Adult females – Oak-hickory forests									
Y = β_0 + MAST + CONIF + TMI	94	55.45	5	-39.6	-38.9	3.1	0.190	0.163	0.06
Y = β_0 + MAST + TMI	94	56.12	4	-40.5	-40.0	2.0	0.181	0.163	0.11
Y = β_0 + MAST + J:AF	94	55.95	4	-40.8	-40.3	1.7	0.183	0.165	0.13
Y = β_0 + MAST + CONIF	94	55.46	4	-41.6	-41.1	0.9	0.190	0.172	0.19
Y = β_0 + MAST	94	56.23	3	-42.3	-42.0	0.0	0.179	0.170	0.29
Adult females - Mixed Mesophytic forests									
Y = β_0 + SITE + CC + TRAP	90	43.36	7	-51.7	-50.4	3.0	0.244	0.199	0.06
Y = β_0 + SITE + CC	90	44.09	6	-52.2	-51.2	2.1	0.231	0.195	0.09
Y = β_0 + SITE + MAST	90	44.04	6	-52.3	-51.3	2.0	0.232	0.196	0.09
Y = β_0 + SITE + TRAP	90	43.45	6	-53.5	-52.5	0.8	0.243	0.207	0.17
Y = β_0 + SITE	90	44.17	5	-54.1	-53.3	0.0	0.230	0.203	0.25
All juvenile females									
Y = β_0 + MAST	83	58.48	3	-23.1	-22.8	6.0	0.041	0.029	0.04
Y = β_0 + ACCSS + MAST + FOREST + MAST×FOREST	83	50.15	6	-29.8	-28.7	0.0	0.177	0.135	0.78
Y = β_0 + TED + MAST + FOREST + MAST×FOREST [a]	83	47.77	6	-33.9	-32.7	-4.0	0.216	0.176	NA
Adult males – Oak-hickory Forests									
Y = β_0 + SITE + CC + MAST + J:AF + EU	125	54.65	10	-83.4	-81.5	3.1	0.286	0.237	0.06
Y = β_0 + SITE + CC + MAST + ACCSS + EU	125	54.65	10	-83.4	-81.5	3.1	0.286	0.237	0.06
Y = β_0 + SITE + CC + MAST + J:AF	125	55.33	9	-83.9	-82.3	2.3	0.277	0.234	0.09
Y = β_0 + SITE + CC + MAST + ACCSS	125	55.33	9	-83.9	-82.3	2.3	0.277	0.234	0.09
Y = β_0 + SITE + CC + MAST + EU + MAST×EU	125	54.01	10	-84.9	-83.0	1.7	0.295	0.246	0.13
Y = β_0 + SITE + CC + MAST + EU	125	54.65	9	-85.4	-83.9	0.8	0.286	0.243	0.20
Y = β_0 + SITE + CC + MAST	125	55.33	8	-85.9	-84.6	0.0	0.277	0.241	0.30
Adult males - Mixed Mesophytic forests									
Y = β_0 + SITE + CC + ACCSS + MAST + J:AF + EU	118	48.93	10	-83.9	-81.8	4.0	0.277	0.224	0.05
Y = β_0 + SITE + CC + ACCSS + EU	118	50.29	8	-84.6	-83.3	2.5	0.257	0.217	0.10
Y = β_0 + SITE + CC + ACCSS + MAST + EU	118	49.19	9	-85.2	-83.6	2.2	0.273	0.227	0.12
Y = β_0 + SITE + CC + ACCSS	118	50.35	7	-86.5	-85.5	0.3	0.256	0.223	0.31
Y = β_0 + SITE + CC + ACCSS + MAST	118	49.25	8	-87.1	-85.8	0.0	0.272	0.233	0.36
All juvenile males									
Y = β_0 + CC + TRAP + ACCSS + EU + MAST	88	54.33	7	-28.4	-27.0	2.2	0.270	0.226	0.07
Y = β_0 + CC + TRAP + MAST	88	56.97	5	-28.3	-27.5	1.7	0.235	0.207	0.10
Y = β_0 + CC + TRAP + ACCSS + EU	88	54.70	6	-29.8	-28.8	0.5	0.265	0.230	0.18
Y = β_0 + CC + TRAP + EU	88	56.15	5	-29.5	-28.8	0.5	0.246	0.219	0.18
Y = β_0 + CC + TRAP + ACCSS	88	56.05	5	-29.7	-29.0	0.3	0.247	0.220	0.19
Y = β_0 + CC + TRAP	88	57.30	4	-29.8	-29.3	0.0	0.230	0.212	0.23

[a] Model developed *post hoc*.

Table 6. Multivariate models explaining variation in spring-summer home range size. Only models having Akaike weights (ω_I) > 0.05 are presented.

Model	n	SSE	K	AIC	AIC_c	Δ_i	R^2	R^2_{adj}	ω_i
Females – Oak-hickory forests									
Y = β_0 + SITE + TMI + CC	79	42.99	8	-32.1	-30.0	3.9	0.274	0.213	0.05
Y = β_0 + TMI + MAST + ACCSS	79	46.85	5	-31.3	-30.5	3.4	0.208	0.177	0.06
Y = β_0 + SITE + TMI + MAST + CC + BROOD + BROOD×MAST	79	38.59	11	-34.6	-30.7	3.2	0.348	0.263	0.06
Y = β_0 + SITE + TMI + MAST	79	42.56	8	-32.9	-30.8	3.1	0.281	0.221	0.07
Y = β_0 + SITE + TMI + MAST + CC + ACCSS	79	39.29	10	-35.2	-31.9	1.9	0.336	0.260	0.12
Y = β_0 + SITE + TMI + MAST + CC	79	39.63	9	-36.5	-33.9	0.0	0.330	0.264	0.32
Females - Mixed Mesophytic forests									
Y = β_0 + SITE + CC + BROOD + ACCSS + TMI + MAST	114	74.81	9	-30.0	-28.3	1.2	0.240	0.190	0.15
Y = β_0 + SITE + CC + BROOD + TMI	114	76.24	8	-29.9	-28.5	1.0	0.226	0.182	0.17
Y = β_0 + SITE + CC + BROOD + ACCSS	114	75.54	8	-30.9	-29.5	0.0	0.233	0.190	0.28
Y = β_0 + SITE + CC + BROOD	114	77.10	7	-30.6	-29.5	0.0	0.217	0.181	0.28
Males – Oak-hickory Forests									
Y = β_0 + SITE + CC + ACCSS + MAST	87	31.93	9	-69.2	-66.9	1.7	0.368	0.312	0.05
Y = β_0 + SITE + TMI	87	33.74	7	-68.4	-67.0	1.6	0.332	0.291	0.06
Y = β_0 + SITE + CC + TMI + MAST	87	31.85	9	-69.4	-67.1	1.5	0.369	0.314	0.06
Y = β_0 + SITE + AGE	87	33.70	7	-68.5	-67.1	1.5	0.333	0.292	0.06
Y = β_0 + SITE + AGE + CC	87	32.71	8	-69.1	-67.3	1.3	0.352	0.304	0.06
Y = β_0 + SITE + CC + MAST	87	32.60	8	-69.4	-67.6	1.0	0.355	0.306	0.07
Y = β_0 + SITE + MAST	87	33.51	7	-69.0	-67.6	1.0	0.337	0.296	0.07
Y = β_0 + SITE + CC + TMI	87	32.57	8	-69.5	-67.6	0.9	0.355	0.307	0.08
Y = β_0 + SITE + CC + ACCSS	87	32.55	8	-69.5	-67.7	0.9	0.356	0.307	0.08
Y = β_0 + SITE	87	34.25	6	-69.1	-68.1	0.5	0.322	0.289	0.09
Y = β_0 + SITE + ACCSS	87	33.23	7	-69.7	-68.3	0.2	0.342	0.302	0.11
Y = β_0 + SITE + CC	87	33.14	7	-70.0	-68.6	0.0	0.344	0.303	0.12
Males - Mixed Mesophytic forests									
Y = β_0 + AGE + DRUM + DRUM^2	58	17.51	5	-59.5	-58.3	1.3	0.290	0.251	0.12
Y = β_0 + AGE + CC+ DRUM + DRUM^2	58	16.45	6	-61.1	-59.4	0.2	0.333	0.283	0.21
Y = β_0 + SITE + CC + AGE	58	15.70	7	-61.8	-59.6	0.1	0.364	0.302	0.22
Y = β_0 + SITE + AGE	58	16.39	6	-61.3	-59.7	0.0	0.336	0.286	0.23

Table 7. Relative Importance Values (RIV) for explanatory variables included in the best model sets presented in tables 4 and 5. The combined Akaike weight for all models in each set of best models is provided in the column $\Sigma\ \omega_i$.

Model set	$\Sigma\ \omega_i$	Accss	Age	Brood	CC	Conif	Drum^2	EU	Forest	J:AF	Mast	Site	TMI	Trap	Mast × Brood	Mast × EU	Mast × Forest
Fall-winter																	
Adult females – O-H	0.78	0.00	-	-	0.00	0.25	-	0.00	-	0.13	0.78	0.00	0.17	0.00	-	0.00	-
Adult females – MM	0.66	0.00	-	-	0.15	0.00	-	0.00	-	0.00	0.09	0.66	0.00	0.23	-	0.00	-
All juvenile females	0.82	0.78	-	-	0.00	0.00	-	0.00	0.78	0.00	0.82	0.00	-	-	-	-	0.78
Adult males – O-H	0.93	0.15	-	-	0.93	-	-	0.45	-	0.15	0.93	0.93	-	-	-	0.13	-
Adult males – MM	0.94	0.94	-	-	0.94	-	-	0.27	-	0.05	0.53	0.94	-	-	-	0.00	-
All juvenile males	0.95	0.44	-	-	0.95	-	-	0.43	0.00	-	0.17	0.00	-	0.95	-	-	0.00
Spring-summer																	
Females – O-H	0.68	0.18	0.00	0.06	0.55	-	-	-	-	-	0.63	0.62	0.68	-	0.06	-	-
Females – MM	0.88	0.43	0.00	0.88	0.88	-	-	-	-	-	0.15	0.88	0.32	-	0.00	-	-
Males – O-H	0.93	0.24	0.12	-	0.52	-	0.00	0.00	-	-	0.25	0.91	0.20	-	-	-	-
Males – MM	0.78	0.00	0.78	-	0.43	-	0.33	0.00	-	-	0.00	0.45	0.00	-	-	-	-

Table 8. Test of the effect of hunting on fall-winter home range size of Appalachian ruffed grouse. Data were analyzed using a repeated measures mixed linear model with year included as a random effect (n = 127). Models were fit using restricted maximum likelihood (REML) estimation.

Source	Numerator df	Denominator df	*F* (Type III)	*P*
PHASE	1	40.3	2.17	0.1481
TREATMENT	1	45.7	0.15	0.7021
SEXAGE	3	82.3	10.26	<0.0001
MAST	1	46.6	6.57	0.0137
MAST×SITE	8	35.1	3.38	0.0056
PHASE×TREATMENT	1	40.3	5.54	0.0235
SEXAGE ×TREATMENT	3	82.3	0.49	0.6877
SEXAGE ×PHASE	3	83.9	0.49	0.6933
SEXAGE ×PHASE×TREATMENT	3	83.9	0.87	0.4600

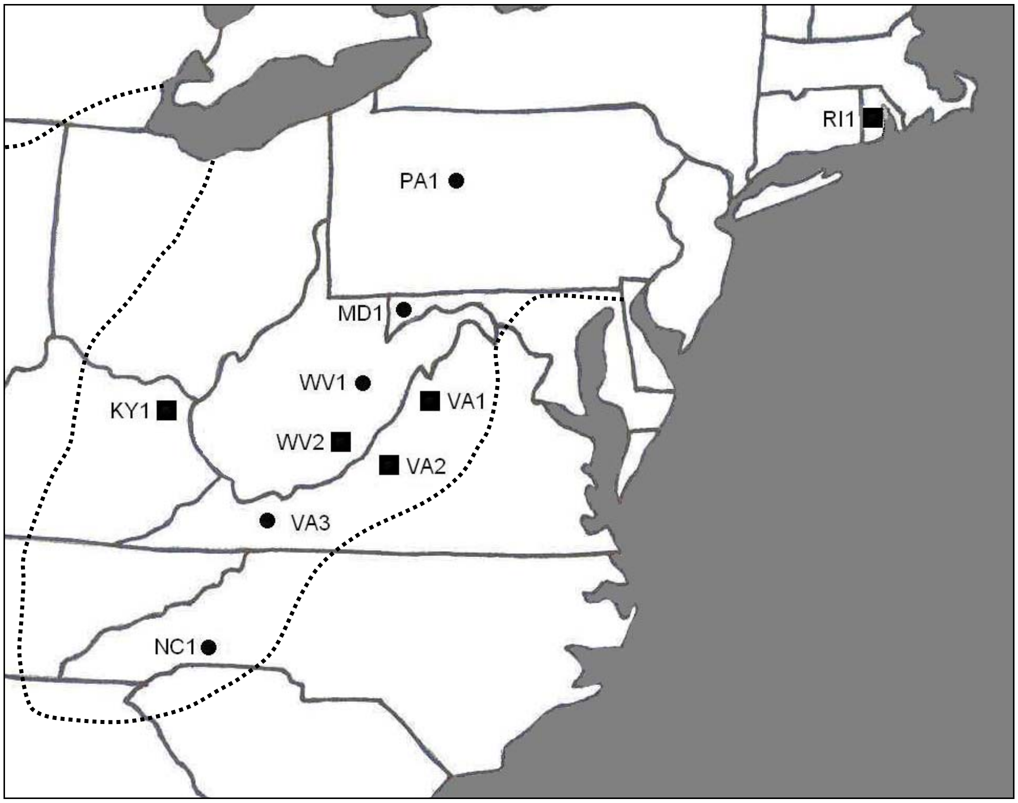

Figure 1. Locations of ACGRP study sites, with the southern limit of the geographic range of ruffed grouse indicated by the dotted line. Study sites having Oak-Hickory forests are identified by square markers, while those having Mixed Mesophytic forests are identified with circles.