Integrating Grouse Habitat and Forestry: An Example Using The Ruffed Grouse Bonasa umbellus in Minnesota

Authors: Zimmerman, Guthrie S., Gilmore, Daniel W., and Gutiérrez, R. J.

Source: Wildlife Biology, 13(sp1) : 51-58

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/0909-6396(2007)13[51:IGHAFA]2.0.CO;2

Integrating grouse habitat and forestry: an example using the ruffed grouse *Bonasa umbellus* in Minnesota

Guthrie S. Zimmerman, Daniel W. Gilmore & R.J. Gutiérrez

Zimmerman, G.S., Gilmore, D.W. & Gutiérrez, R.J. 2007: Integrating grouse habitat and forestry: an example using the ruffed grouse *Bonasa umbellus* in Minnesota. - Wildl. Biol. 13 (Suppl. 1): 51-58.

We quantified forest stand attributes at ruffed grouse *Bonasa umbellus* drumming display sites to develop tree stocking guides as a tool for guiding ruffed grouse management. We estimated tree density and basal area surrounding grouse drumming sites and compared these with unused sites. We used model selection to assess predictions about whether tree density and basal area surrounding drumming sites varied by site classification (primary drumming site, alternate site, unused site) or forest type. We plotted the predicted values from the best model on tree stocking guides, which are tools commonly used by forest managers. Tree density and basal area varied by site classification and by forest type. Our results show that stem density was higher and basal area lower at both primary and alternate drumming sites compared to unused sites in all forest types. We also found that grouse sites in aspen stands had a greater stem density and lower basal area than grouse sites in pine and spruce/fir stands. Incorporating these results into a tree stocking guide suggested that management for grouse in aspen stands should attempt to maintain stands with average stem density and basal area for this species. In contrast, foresters who are managing for conifers and also wish to maintain some grouse habitat should favour wider spacing of trees in stands. Wider spacing will encourage the development of dense understory vegetation favoured by grouse as well as enhance the growth of quality saw-logs. Our study describes a method for incorporating habitat data on ruffed grouse and other wildlife into tree stocking charts, which are commonly used to facilitate management of forest stands.

Key words: basal area, Bonasa umbellus, drumming habitat, forest management, ruffed grouse, tree density, tree stocking guides

Guthrie S. Zimmerman & R.J. Gutiérrez, University of Minnesota, Department of Fisheries, Wildlife, and Conservation Biology, and the Cloquet Forestry Center, 200 Hodson Hall, St. Paul, Minnesota 55108, USA - e-mail addresses: Guthrie.Zimmerman@fws.gov (Guthrie S. Zimmerman); gutie012@umn.edu (R.J. Gutiérrez)*
*Daniel W. Gilmore**, University of Minnesota, Department of Forest Resources, 1861 Highway 169 East, Grand Rapids, Minnesota 55744, USA - e-mail: dgilmore@umn.edu*

Present addresses:
**U.S. Fish and Wildlife Service, Division of Migratory Bird Management, 11510 American Holly Drive, Laurel, Maryland 20708, USA*
***Residents' Committee to Protect the Adirondacks, PO Box 27, 7 Ordway Lane, North Creek, New York 12853, USA*

Corresponding author: Guthrie S. Zimmerman

The ruffed grouse *Bonasa umbellus* is an important game bird whose populations are responsive to forest management (Gullion & Alm 1983). Consequently, there have been many studies of its ecology, population trends and habitat use (e.g. Bump et al. 1947, Rusch & Keith 1971, Gullion 1984, Rusch et al. 2000). The ruffed grouse is a forest-dependent species that often exhibits population fluctuations of approximately 10-year duration (Gullion 1984). Male ruffed grouse have a unique breeding display called 'drumming', where a male produces a low-pitched sound by rapidly beating his wings back and forth. Air rushing to fill the vacuum created as the wings are pulled back generates a miniature sonic boom (Rusch et al. 2000). This display allows the bird to be detected in forests that are usually very dense. Most male ruffed grouse drum from an elevated display stage, usually a log, and this log marks the centre of their territory (Archibald 1975). In contrast to males, females are not easily detected. However, while they nest in a variety of forest types, the young, dense forests typically used by drumming males year-round are also believed to provide ideal habitat for non-breeding females, and for those rearing broods (Gullion & Alm 1983, Rusch et al. 2000). Therefore, the absence of early seral stage forests appears to limit populations of this species (Rusch et al. 2000, Dessecker & McAuley 2001).

Although young seral stage forests are important habitats for ruffed grouse, forest stands used by ruffed grouse differ with respect to tree-species composition across their range. Conifer forests are important to the ruffed grouse in the eastern portion of its range, whereas aspen and mixed hardwood stands are more important throughout much of the rest of its range (Gullion & Alm 1983, Thompson & Fritzell 1988, Barber 1989, Wiggers et al. 1992). These range-wide differences in habitat use may be related to regional availability of snow roosts and alternative cover during the winter (Thompson & Fritzell 1988). Gullion (1984) showed that different age classes of aspen stands, particularly quaking *Populus tremuloides* and bigtooth *P. grandidentata*, are used by grouse for different purposes in Minnesota (Gullion & Alm 1983). Therefore, Gullion (1984) advocated managing for grouse by interspersing small (~ 4 ha) patches of aspen at various age classes across the landscape. However, Gullion (1990:183) later hypothesized that ruffed grouse could attain relatively high densities in "…association with pine plantations" in northern Minnesota if aspen comprised at least 10% of these plantations. However, he did not provide specific information on the structure (i.e. basal area and tree density) of non-aspen stands that were used by ruffed grouse. In addition, we could find only one study occurring in the southern portion of the ruffed grouse's range (Wiggers et al. 1992) that quantified forest structure using stand attributes and could be easily incorporated directly into silvicultural prescriptions. To provide easily interpretable management guidelines for ruffed grouse, we quantified specific forest characteristics (e.g. tree density and basal area) associated with ruffed grouse drumming display locations in aspen, pine (red pine *Pinus resinosa*, jack pine *P. banksiana* and white pine *P. strobes*), and white spruce *Picea glauca*/balsam fir *Abies balsamea* forest stands using tree stocking guides (hereafter TSGs). TSGs are tools commonly used by foresters for developing and maintaining stand silvicultural prescriptions (Gingrich 1967, Ernst & Knapp 1985).

Study area

We conducted our research on the Cloquet Forestry Center (CFC) in northeastern Minnesota, USA (46°31'N, 92°30'E), which encompassed 1,352 ha. The climate was warm and humid during the summer, and cold and dry during the winter (Tester 1997). Average annual precipitation was 800 mm during 1972-2002, with most (64%) precipitation falling during the growing season (May-September). The average daily low temperature during January between 1972 and 2002 was -18°C and the average daily high temperature in July was 27°C. CFC had little topographic relief, with elevations ranging within 374-394 m a.s.l.

CFC was characterized by a complex mosaic of forest-types, age classes, stand structures and other vegetation types (e.g. open fields and wetlands). Approximately 70% of CFC was upland forests and clearings, whereas 30% was lowland habitat (e.g. bogs and forested wetlands). Pine (mostly red and jack pine) and aspen were the dominant forest types, covering 28 and 16% of CFC, respectively. White spruce, balsam fir, red maple *Acer rubrum*, paper birch *Betula papyrifera*, tamarack *Larix laricina*, and red oak *Quercus rubra* were also common tree species throughout the forest. Beaked hazel *Corylus cornuta* was the dominant shrub cover in closed-canopy forests. Other common shrubs included Juneberry *Amelanchier* spp., pin cherry *Prunus pennsylvanica*, chokecherry *P. virginiana*, and alder *Alnus* spp. Ruffed grouse inhabited most forest zones, particularly aspen, where they used all age classes and stem densities.

Methods

Ruffed grouse display by drumming from a structure such as a log or a rock (Bump et al. 1947, Rusch et al. 2000). These drumming display sites (structures) represent activity centres, and males confine much of their activity to within 2.5 ha of a primary and one or more alternate drumming structures throughout the breeding season (Archibald 1975). Primary drumming structures represent the site used most consistently throughout the spring, whereas alternate sites are used only occasionally (Gullion 1967). We conducted drumming surveys to locate display sites that were occupied by ruffed grouse during the spring breeding season (April-early June). Male and female ruffed grouse share the same habitats during the winter and early spring breeding periods. Thus, the area surrounding the drumming log represents habitat for both sexes during the physiologically stressful winter and early spring seasons (Gullion & Alm 1983). Radio-telemetry studies indicate that survival rates of ruffed grouse are lowest and predation rates highest during these seasons (Lauten 1995). Thus, providing habitat for drumming male ruffed grouse benefits the entire population. Our sampling units for this study were all the grouse activity centres (N = 110) on CFC.

We conducted drumming surveys along nine permanent transects that provided complete survey coverage of the study area. We conducted 15 surveys along each transect between 1 April and 13 June, 2002-2005. We divided the 15 surveys into three short-duration (i.e. 5-day) periods based on the robust design, which allowed confidence that we sampled most of the population (Zimmerman & Gutiérrez in press). Surveys consisted of walking along transects while listening for drumming males. We alternated the direction travelled along each transect between successive surveys. We located and mapped all drumming birds and their display structures using binoculars, a compass and GPS. If the grouse flushed before being located, we searched for accumulations of faecal droppings that indicated heavy use of a drumming structure (Gullion & Marshall 1968).

We estimated tree density and basal area at every drumming structure and within every upland forest stand not used by grouse on CFC using a variable plot procedure with a wedge prism (Husch et al. 2003). The variable plot procedure entails sampling trees based on their diameter and distance from the plot centre. This technique allows estimation of tree density and basal area on a per hectare basis for each sample point (Husch et al. 2003). At each sample site we measured: 1) basal area of all woody vegetation ≥ 5 cm diameter at a height of 1.37 m, 2) diameter at 1.37 m of each tallied tree, and 3) several additional variables quantifying shrub density and drumming structure characteristics.

Tree stocking guides (TSG)

Common objectives of forest management are timber production, wildlife habitat and recreational activities. Maximizing management returns could include maximizing species numbers, hunting opportunities or financial gains from timber sales. Forest managers attempt to maximize these returns by encouraging aspects of natural stand development that meet management objectives. TSGs are common tools used by forest managers in North America and Europe because they illustrate two important measures of stand density: tree density (stems/ha) and basal area (m^2/ha; Ernst & Knapp 1985). TSGs are plots of basal area against tree density for different diameter size classes (Fig. 1). The different diameter classes are often used as a surrogate for age class because older trees usually have greater diameters. Absolute tree density is not useful for management because density is known to vary by stand age and species composition. Thus, reference stocking levels are needed to chart stand growth, given stand age and species composition (Ernst & Knapp 1985). The two most common frames of reference used in TSGs are called the A- and B-lines. The A-line (see Fig. 1) represents the zone of maximum tree density where self-thinning occurs for a given diameter class and species. Stands that are above the A-line are considered to be 'overstocked' and tree density is sufficiently high so that natural mortality and competition can lead to a net negative growth rate of the stand. The B-line represents the zone where full site occupancy and complete canopy closure occurs for a given diameter class. Densities below the B-line result in open spaces within the canopy. Foresters thin stands to maintain them between the A- and B-lines. The relative position of the stand, based on basal area and tree density, within the A- and B-lines depends on management objectives. We recreated a published stocking guide for aspen, pine and spruce/fir forests. We constructed the A-line using data on red pine (Benzie 1977), spruce/fir (Frank & Bjorkbom 1973) and aspen (Perala 1986). We constructed the B-lines for red pine, balsam fir, white spruce and aspen using equations for the crown dimensions of trees grown in open areas free from competition (Ek 1974). Spruce and fir are of-

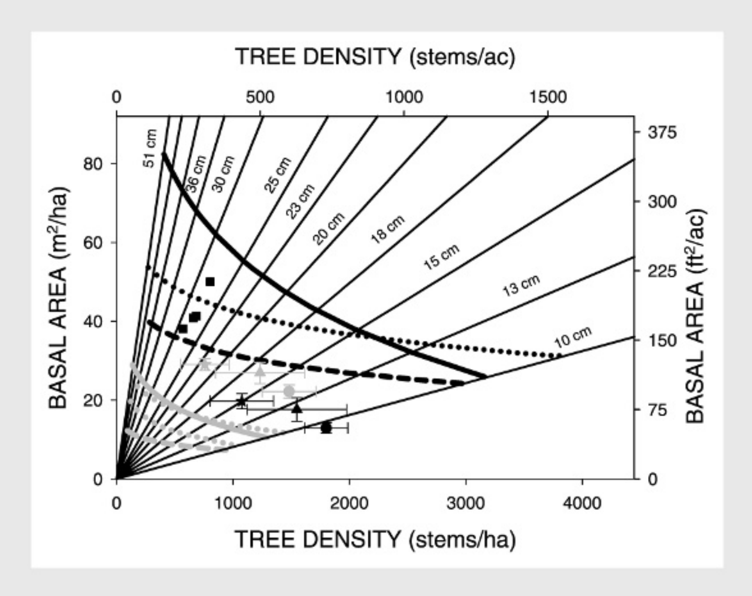

Figure 1. Tree stocking guide for aspen (dashed lines), spruce/fir (dotted lines), and pine (solid lines) with grouse data. Black lines represent A-lines and gray lines represent B-lines (see text for explanation). Black circle, triangle and star represent stand characteristics around used sites in aspen, spruce/fir and pine forests, respectively. Gray circle, triangle and star represent predicted stand characteristics around unused sites in aspen, spruce/fir and pine forests, respectively, based on best model. Error bars represent 95% confidence intervals for predicted stand characteristics. We included North American equivalents to metric units for density (i.e. stems per acre; stems/ac) and basal area (square feet per acre; ft^2/ac) to facilitate their use by American foresters. Black squares represent goshawk foraging locations as obtained from Boal et al. (2005).

ten managed together, and we could find no published A-line that considered these species separately. However, the crown dimensions for these two species are different, which would affect the equations used to estimate the B-line. Thus, we estimated a single A-line for the spruce/fir category and separate B-lines for spruce and fir tree species. We constructed these lines to project ruffed grouse habitat characteristics onto these charts (see below) to provide easily interpretable management guidelines for this species. Although we used a hardwood stand class (mix of birch, maple and aspen) in the analyses below, we did not include hardwoods in our TSG, because these are not actively managed at CFC.

Statistical analyses

We estimated characteristics of grouse habitat that would be useful for grouse management by: 1) specifying *a priori* hypotheses (models) to assess whether tree density and basal area differed by site use category (i.e. primary drumming structure, alternate drumming structure or unused site) or forest type (pine, aspen, spruce/fir or northern hardwood; Table 1), 2) then we estimated the parameters of the models using multiple linear regression (PROC GENMOD in SAS), 3) ranked the models using a small sample adjustment of Akaikes's Information Criterion (AIC_c; Burnham & Anderson 2002), and 4) retained the highest-ranked (lowest AIC_c) model to estimate tree density and basal area to add to the ruffed grouse TSG. Once we calculated tree density and basal area from the best model, we plotted these estimates on the TSG to indicate the management zone for ruffed grouse. Because goshawks *Accipiter gentilis* commonly prey upon ruffed grouse in our study area (Gullion 1981b), we also plotted tree density and basal area measured at goshawk foraging locations using data collected by Boal et al. (2005).

A priori models

We identified five *a priori* hypotheses; each of these hypotheses was evaluated using tree density as the response variable and each was also evaluated using tree basal area as the response variable (i.e. we conducted two sets of modelling). Because our objective was to plot tree density and basal area of ruffed grouse locations directly onto a TSG, we used our modelling to derive estimates of tree density and basal area. That is, our response variables were tree density and basal area (i.e. X and Y variables on the TSG). Thus, our approach differed from a modelling study where the

Table 1. Percent of unused locations (N = 301) and used grouse drumming structures (N = 220) in six different forest types at the Cloquet Forestry Center, Minnesota, USA, during 2002-2005.

Forest type	Percent of points	
	Unused	Used
Aspen	24	67
Forested wetland	12	5
Mix	7	1
Northern hardwood	8	5
Pine	38	18
Spruce/fir	11	4

Table 2. Results of model selection for assessing the difference in tree density around structure types and within different forest types at the Cloquet Forestry Center during 2002-2005. Forest types include aspen, pine, spruce/fir, northern hardwood, mixed hardwood/conifer, and forested wetlands. Primary and alternate drumming logs are indicated as 1° and 2°, respectively.

Model no	Model	Sample size	Number of parameters	AIC_c	ΔAIC_c	AIC_c weight
4	Used vs unused + Forest type	521	7	7994.40	0.00	0.68
5	1° vs 2° vs unused + Forest type	521	8	7996.43	2.03	0.24
3	Forest type	521	6	7998.77	4.37	0.08
1	Used vs unused	521	2	8017.44	23.04	0.00
2	1° vs 2° vs unused	521	3	8019.46	25.06	0.00

objective is to differentiate between used and unused (or available) sites (i.e. a binary (0/1) response variable). Although we included 'used' versus 'unused' as a categorical predictor variable rather than a response variable, the confidence interval for the predictor variable still provided insight into whether we could distinguish between used and used sites. For example, if the 95% confidence interval for the parameter representing site classification (e.g. whether a site was used or unused) excluded zero, then we concluded that the response variable (basal area or tree density) differed among the site classification categories. We specified two models that predicted that tree density and basal area varied by site use classification (models #1 and #2; Tables 2 and 3). Model #3 (see Tables 2 and 3) predicted that tree density and basal area varied by forest type (i.e. aspen, pine, spruce/fir, northern hardwood, mixed hardwood/conifer and forested wetlands), but not by site use classification. Models #4 and #5 predicted that the response variables varied by site use classification and forest type. All predictor variables in the models were 0 or 1 indicator variables. For example, in model #4, sites were assigned a 1 if they were used by grouse, and a 0 if they were unused locations. For each of the forest type variables, we assigned a 1 for the forest type containing the location and a 0 otherwise. We included unused aspen sites as a reference for all habitat models. Thus, for model #4, we included an intercept, one variable for use and five indicator variables for six forest types. Because our sampling units were the activity centres, primary and alternate logs within an activity centre were not independent units (i.e. a unique grouse selected one primary and ≥1 alternate structure). To assess whether this dependency affected our results, we estimated each model using the full set (all primary and alternate logs) and then estimated all models using a reduced data set (a single primary log from each activity centre).

Results

We located 220 ruffed grouse drumming sites from 2002 through 2005. We sampled vegetation at 301 unused locations in upland forest stands, which represented the complete stand inventory on the CFC. Most of the 220 drumming locations occurred in aspen stands, whereas most of the unused locations occurred in pine stands (see Table 1). Model selection results and assessment of parameters within the AIC_c selected models were identical using the full (primary and alternate drumming logs) and reduced (a single primary log from each activity centre) data sets. Therefore, we concluded that the dependence among some of the logs did not bias our conclusions. We present all results based on the full data set because we were interested in assessing whether forest characteristics surrounding primary structures differed from characteristics surrounding alternate structures in ad-

Table 3. Results of model selection for assessing the difference in tree basal area around structure types and within different forest types at the Cloquet Forestry Center during 2002-2005. Forest types include aspen, pine, spruce/fir, northern hardwood, mixed hardwood/conifer, and forested wetlands. Primary and alternate drumming logs are indicated as 1° and 2°, respectively.

Model no	Model	Sample size	Number of parameters	AIC_c	ΔAIC_c	AIC_c weight
4	Used vs unused + forest type	521	7	5318.17	0.00	0.60
5	1° vs 2° vs unused + forest type	521	8	5319.09	0.81	0.40
1	Used vs unused	521	2	5365.66	47.39	0.00
2	1° vs 2° vs unused	521	3	5366.07	47.80	0.00
3	Forest type	521	6	5415.38	97.11	0.00

Table 4. Parameter estimates from AIC_c selected regression model for estimating tree density for ruffed grouse management at the Cloquet Forestry Center during 2002-2005. Forest type is a categorical predictor variable and the aspen category was used as the reference level (i.e. predicted values for aspen are estimated by assigning all other forest types a zero).

Parameter	Parameter estimate	SE	95% CI Lower	95% CI Upper
Intercept	600.44	48.32	505.74	695.14
Used	128.52	50.54	29.46	227.57
Mix	-369.99	118.28	-601.82	-138.16
Pine	-293.49	57.60	-406.38	-180.60
Forested wetland	-311.84	85.24	-478.90	-144.78
Hardwood	-104.36	97.45	-295.35	86.64
Spruce/fir	-101.71	88.56	-275.28	71.86

Table 5. Parameter estimates from AIC_c selected regression model for estimating tree basal area for ruffed grouse management at the Cloquet Forestry Center during 2002-2005. Forest type is a categorical predictor variable and the aspen category was used as the reference level (i.e. predicted values for aspen are estimated by assigning all other forest types a zero).

Parameter	Parameter estimate	SE	95% CI Lower	95% CI Upper
Intercept	96.68	3.71	89.42	103.94
Used	-40.50	3.88	-48.09	-32.90
Mix	-1.81	9.07	-19.59	15.96
Pine	29.83	4.42	21.17	38.48
Forested wetland	-4.84	6.54	-17.65	7.97
Hardwood	11.44	7.47	-3.20	29.09
Spruce/fir	20.52	6.79	7.21	33.83

dition to assessing whether forest characteristics differed between used (i.e. primary and alternate sites pooled) and unused sites.

Both tree density (see Table 2) and basal area (see Table 3) varied between used and unused sites, and amongst forest types. The best model (with the lowest AIC_c) for tree density indicated that used sites had greater tree densities than unused sites and that aspen stands had greater tree densities than other forest types with the exception of the spruce/fir type (95% confidence interval = -275.28, +71.86; Table 4). AIC_c weights indicated strong support for this model because it was 2.8 times more likely than the second ranked model. The best model for basal area indicated that used sites had less basal area than unused sites, and that pine and spruce/fir stands had greater basal area than aspen stands (Table 5). Model selection also indicated some support for differences in basal area between primary, alternate and unused locations (see Table 3).

The plots of the predicted tree density and basal area illustrated that grouse locations were characterized by greater stem densities and less basal area than unused sites in the three forest types (see Fig. 1). However, the 95% confidence intervals indicated that there was great overlap in tree density between the used and unused sites. Grouse locations were characterized by greater tree density and less basal area in aspen stands than in pine stands used by grouse. Tree densities and basal area surrounding grouse locations within spruce/fir stands were highly variable and overlapped those measured at grouse locations within aspen and pine (see Fig. 1). The TSG indicated that grouse used younger aspen stands, which were in the middle of the 'target' management zone for aspen stands. Similarly, grouse locations in pine and spruce/fir were also in younger stands, but close to the B-line. In contrast, goshawks tended to forage in 'fully stocked' or 'overstocked' stands, which had larger diameter trees than was typical of trees in ruffed grouse habitat.

Discussion

Many researchers have studied ruffed grouse habitat (Rusch et al. 2000). A unifying theme from ruffed grouse habitat studies is that stands characterized by high stem density are important for grouse drumming and breeding habitat (Dessecker & McAuley 2001). However, most studies do not provide managers with guidelines for managing specific stand attributes to encourage ruffed grouse. Moreover, most published quantitative data from the upper Midwestern United States are based on data from aspen-dominated stands, which does not guide foresters who are managing conifer forests for other uses (e.g. timber production), but are also interested in providing some grouse habitat. We used ruffed grouse to demonstrate one technique that can be used to apply the results of wildlife research to management, and we present recommendations for grouse management in non-aspen forests. Our inferences apply directly to drumming and non-breeding habitat. Nesting females or females with broods may require different stand attributes (Rusch et al. 2000). Nonetheless, ruffed grouse survival rates are the lowest during the winter and spring seasons (Lauten 1995) when both sexes use similar habitats (Gullion & Alm 1983). Thus, managing for drumming grouse habitat is important to ruffed grouse populations.

Our data show that different management strategies should be applied to different forest types to encourage development of ruffed grouse habitat. The major effects of forest type occurred between the pine and aspen categories. Sites occupied by grouse within pine stands were characterized by a lower tree density and greater tree basal area than sites occupied by grouse in aspen stands. This difference is likely due to differences in the natural structure of pine and aspen trees (Thompson & Fritzell 1988). Pine stands with lower density and higher basal area often have open canopies, which allow the development of a shrub component and small inclusions of aspen. A shrub component may provide cover requirements for ruffed grouse, and small inclusions of aspen may provide habitable microsite characteristics as hypothesized by Gullion (1990). Consequently, grouse sites in pine and spruce/fir stands at CFC have stem densities and tree basal areas that are closer to the B-line, whereas aspen stands used by ruffed grouse occur in the middle of the aspen management zone (i.e. directly between the A-line and B-line). In contrast, data collected by Boal et al. (2005) indicate that goshawks commonly forage in older conifer stands that were fully stocked or overstocked (i.e. closer to the A-line). Generally, forest managers manipulate stands to be closer to the B-line when they are interested in faster growth of high-quality saw-logs and timber. Such manipulations entail various thinning techniques to reduce tree density, which: 1) allow harvest of some merchantable wood that would have been lost to mortality and 2) increase the resources available to subsequent diameter growth of the remaining trees (Smith et al. 1997). Different thinning techniques include low thinning, crown thinning, row thinning or free thinning (Smith et al. 1997). Low thinning removes trees from the lower crown class, which may be important cover for ruffed grouse (Boag 1976). Row thinning removes trees in distinct rows, which could provide flight corridors to goshawks (Gullion 1981a). Thus, we recommend that those interested in encouraging ruffed grouse in conifer stands use crown thinning or free thinning prescriptions. Free thinning, which removes trees to encourage individual crop trees, could be used as a tool to encourage the inclusion of dense understory vegetation necessary for drumming cover if small patches of conifers are removed in the process. We do not imply that our management recommendations for conifer stands would result in grouse densities similar to densities attained in aspen, but we do hypothesize that our proposed management strategies for conifer stands would result in higher grouse densities than would be possible under other strategies for conifer stands.

Wildlife research can greatly improve the quality of conservation programmes if the results of studies could be efficiently incorporated into management (Noss 1990, Åberg et al. 2003). We demonstrate in our analyses that wildlife (in this case ruffed grouse) habitat data can be incorporated directly into forest management plans by using traditional forest silviculture tools such as tree stocking charts. We encourage wildlife researchers to exercise considerable thought not only about collecting data that are ecologically interesting, but also collecting data that are easily interpretable by forest, range or other land managers.

Acknowledgements - we thank our dedicated field assistants N. Bygd, R. Heinen, S. Kyle, K. Oelhafen, T. Radtke, W. Ruhman, D. Stangle and D. Vincent. D. Grandmaison provided valuable logistical and field support and B. Loeffelholz helped edit the GIS map. D. Andersen, J. Nichols, M. Seamans, W. Thogmartin, S. Banerjee, J. Zimmerman, M. Larson, J. Fieberg and G. Giudice provided helpful design and analysis suggestions. Comments from L. Ellison and two anonymous reviewers greatly improved the quality of the manuscript. The University of Minnesota (Department of Fisheries, Wildlife and Conservation Biology, Graduate School Fellowship to Guthrie S. Zimmerman, and Huempfner Ruffed Grouse Fund), D.H. Rusch Scholarship to Guthrie S. Zimmerman, Cloquet Forestry Center, Leigh Perkins Fellowship to Guthrie S. Zimmerman, Minnesota Agriculture and Experiment Station Project MIN-41-036 to R.J. Gutiérrez, Orvis Foundation, and The American Museum of Natural History provided financial support.

References

Åberg, J., Swenson, J.E. & Angelstam, P. 2003: The habitat requirements of hazel grouse (Bonasa bonasia) in managed boreal forest and applicability of forest stand descriptions as a tool to identify suitable patches. - Forest Ecology and Management 175: 437-444.

Archibald, H.L. 1975: Temporal patterns of spring space use by ruffed grouse. - Journal of Wildlife Management 39: 472-481.

Barber, H.L. 1989: Evergreen controversy. - In: Atwater, S. & Schnell, J. (Eds.); Ruffed Grouse. Stackpole Books, Harrisburg, Pennsylvania, USA, pp. 328-329.

Benzie, J.W. 1977: Red pine in the north-central states. - USDA Forest Service General Technical Report NC-33, St. Paul, MN, USA, 22 pp.

Boag, D.A. 1976: The effect of shrub removal on occupancy of ruffed grouse drumming sites. - Journal of Wildlife Management 40: 105-110.

Boal, C.W., Andersen, D.E. & Kennedy, P.L. 2005: Breeding season foraging habitat of breeding male northern goshawks in the Laurentian Mixed Forest Province, Minnesota. - Journal of Wildlife Management 69: 1516-1527.

Bump, G., Darrow, R.W., Edminster, F.C. & Crissey, W.F. 1947: The ruffed grouse: life history, propagation, management. - New York State Department of Environmental Conservation, Albany, New York, 915 pp.

Burnham, K.P. & Anderson, D.R. 2002: Model selection and multimodel inference. A practical information-theoretic approach. 2nd edition. - Springer Science and Media, Inc., New York, New York, 488 pp.

Dessecker, D.R. & McAuley, D.G. 2001: Importance of early successional habitat to ruffed grouse and American woodcock. - Wildlife Society Bulletin 29: 456-465.

Ek, A.R. 1974: Size-age relationships for open grown red pine. - University of Wisconsin-Madison, Forest Research Notes 156: 1-2.

Ernst, R.L. & Knapp, W.H. 1985: Forest stand density and stocking: concepts, terms, and the use of stocking guides. - USDA Forest Service General Technical Report WO-44, Washington, DC, 8 pp.

Frank, R.M. & Bjorkbom, J.C. 1973: A silvicultural guide for spruce-fir in the northeast. - USDA Forest Service General Technical Report NE-6, Upper Darby, PA, 29 pp.

Gingrich, S.F. 1967: Measuring and evaluating stocking and stand density in upland hardwood forests in the Central States. - Forest Science 13: 38-53.

Gullion, G.W. 1967: Selection and use of drumming sites by male ruffed grouse. - The Auk 84: 87-112.

Gullion, G.W. 1981a: A quarter century of goshawk nesting at Cloquet. - The Loon 53: 3-5.

Gullion, G.W. 1981b: The impact of goshawk predation upon ruffed grouse. - The Loon 53: 82-84.

Gullion, G.W. 1984: Grouse of the north shore. -Willow Creek Press, Oshkosh, Wisconsin, 144 pp.

Gullion, G.W. 1990: Ruffed grouse use of conifer plantations. - Wildlife Society Bulletin 18: 183-187.

Gullion, G.W. & Alm, A.A. 1983: Forest management and ruffed grouse populations in a Minnesota coniferous forest. - Journal of Forestry 81: 529-536.

Gullion, G.W. & Marshall, W.H. 1968: Survival of ruffed grouse in a boreal forest. - The Living Bird 7: 117-167.

Husch, B., Beers, T.W. & Kershaw, J.A. Jr. 2003: Forest Mensuration. 4th edition. - John Wiley and Sons, Inc., Hoboken, New Jersey, USA, 443 pp.

Lauten, D.J. 1995: Survival, demography, and behavior of ruffed grouse of different color phase during a cyclic decline in northwestern Wisconsin. - M.Sc. thesis, University of Wisconsin, Madison, Wisconsin, USA, 65 pp.

Noss, R.F. 1990: Indicators for monitoring biodiversity: A hierarchical approach. - Conservation Biology 4: 355-364.

Perala, D.A. 1986: Aspen management. - In: North Central Experiment Station Staff (Ed.); Proceedings of the Integrated Pest Management Symposium for Northern Forests, Madison, Wisconsin. University of Wisconsin Cooperative Extension Service Publication, Madison, Wisconsin, USA, pp. 87-97.

Rusch, D.H. & Keith, L.B. 1971: Ruffed grouse-vegetation relationships in central Alberta. - Journal of Wildlife Management 35: 417-429.

Rusch, D.H., DeStefano, S., Reynolds, M.C. & Lauten, D. 2000: Ruffed Grouse (Bonasa umbellus). - In: Poole, A. & Gill, F. (Eds.); The Birds of North America, No. 515. The Birds of North America, Inc., Philadelphia, Pennsylvania, USA, 28 pp.

Smith, D.M., Larson, B.C., Kelty, M.J. & Ashton, P.M.S. 1997: The practice of silviculture: Applied Forest Ecology. 9th edition. - John Wiley & Sons, Inc., New York, New York, USA, 537 pp.

Tester, J.R. 1997: Minnesota's Natural Heritage. An Ecological Perspective. - University of Minnesota Press, Minneapolis, Minnesota, USA, 332 pp.

Thompson, F.R. III & Fritzell, E.K. 1988: Ruffed grouse winter roost site preference and influence on energy demands. - Journal of Wildlife Management 52: 454-460.

Wiggers, E.P., Laubhan, H.K. & Hamilton, D.A. 1992: Forest structure associated with ruffed grouse abundance. - Forest Ecology and Management 49: 211-218.

Zimmerman, G.S. & Gutiérrez, R.J. in press: The influence of ecological factors on detecting drumming ruffed grouse. - Journal of Wildlife Management.