AN ABSTRACT OF THE THESIS OF

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Abstract approved:

John A. Crawford

Fall and winter movements, habitat associations, and survivorship were compared

among adult and immature, female and male blue grouse (Dendragapus obscurus) during

3 years in northeastern Oregon. Fall movement distances were similar among groups;

however, immature grouse ranged over larger areas in winter than adults (P = 0.01).

Habitat use and selection were similar between adult females and adult males, which

selected large trees in dense clumps within parklands (areas of $\geq$ 900 m^2 with < 10%

canopy cover and < 30 m between trees) and avoided forested stands (areas of $\geq$ 900 m^2

with >10% canopy cover). Immature males also selected large trees within parklands,

whereas immature females failed to show selection for large trees and selected forested

stands as well as parklands. Immature males additionally selected Douglas-firs

(Pseudotsuga menziesii) infested with dwarf mistletoe (Arceuthobium douglasii)(P =

0.04), and immature females used these trees to a greater degree than all other groups (P

= 0.01). Crop contents of collected birds revealed grouse ate Douglas-fir and ponderosa

pine (Pinus ponderosa) needles during winter. Blue grouse were located on the ground

increasingly throughout winter; forbs occurred in crops as snow melted during spring. Adult females, adult males, and immature birds exhibited similar survivorship through fall (77%); adult female survivorship was higher than immature survivorship in winter ($P = 0.04$). No relationship existed between fall movement distance and survivorship; blue grouse that lived through winters occupied sites with higher tree densities than those that died ($P = 0.04$).

Blue Grouse Winter Ecology in Northeastern Oregon

by

Eric C. Pelren

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Eric C. Pelren, Author

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INTRODUCTION

Intraspecific variation in life-history strategies may allow resource partitioning among individuals or groups. This strategy may be especially effective in times or areas of relatively poor resource availability or quality. Blue grouse (Dendragapus obscurus) use areas with relatively harsh climatological conditions and low-quality forage during winter (Marshall 1946, Hoffmann 1961, Bendell and Elliott 1967, Johnsgard 1983). Relationships between winter habitats and blue grouse populations are poorly understood. Although forested habitats typically used by blue grouse in winter may be plentiful, resource exploitation by humans, such as timber harvest, may decrease quantity or quality of such habitats. Past studies detected partial differences between adult and immature, and female and male winter life-history characteristics. Further comparison among groups of movements to and within winter ranges and habitat associations on these ranges may refine the perception of differential winter life-history strategies in blue grouse. Comparison of fall and winter survivorship among groups may aid in interpretation of effectiveness of different strategies.

Female and male blue grouse differ in weight by as much as 30% (Boag 1965) and, consequently, may exhibit different strategies for maximizing fitness, particularly during winter when energy demands are high and food resources are of relatively low quality. Immature birds are smaller and less experienced than adults; therefore, age also may influence behavioral strategies. Management for this species may be enhanced by

better comprehension of the degree to which age and sex groups of blue grouse exhibit differential strategies for optimization of survival in winter.

Many studies of blue grouse during winter dealt with diets, which consisted almost entirely of conifer needles (Beer 1943, Stewart 1944, Marshall 1946, Zwickel and Bendell 1986, Remington 1990). Hoffmann (1961) speculated that quantity of conifer needles during winter compensated for their low nutritional quality to blue grouse; however, studies have not adequately addressed differential use or selection of winter food resources by different age or sex groups or the effects of these differences on habitat associations.

Other winter studies dealt with migration, home-range characteristics, and habitat associations. Females migrated shorter distances (range = 0.1 to 4.2 km) than males (range = 1.0 to 29.5 km) in Colorado (Cade 1985); no differences in migration distances were detected between sexes in British Columbia, but immature birds moved farther (range = 0 to 15.0 km) than adults (range = 0 to 5.4 km)(Hines 1986). Cade (1985) examined blue grouse winter habitat associations in Colorado and found no differences in winter habitat use among sex or age classes. Stauffer and Peterson (1985) examined habitat selection in southeastern Idaho but failed to contrast females and males or adult and immature birds. Hines (1986) observed differences in elevations and, possibly, stand density of winter habitats used by female and male blue grouse in British Columbia. He found no difference in survivorship between immature females and males; adults were not included in the analysis. Pekins (1988b) examined winter ecological energetics of blue grouse in Utah but did not compare sexes or ages. These studies provided evidence that

winter life-history characteristics may differ among adult and immature female and male blue grouse, and they demonstrated a need to better understand these differences.

The Oregon Department of Fish and Wildlife began collection of wings and tails from hunter-harvested grouse in 1980 as an index of annual harvest rates and age and sex ratios and to better understand the status of the species in the state. These data failed to clarify the status of blue grouse in Oregon because of large annual fluctuations in number of wings collected and proportion of young in the harvest. Further, there was a lack of understanding of the effects of timber harvest and other ongoing land-management practices on the species. Increased understanding of movements, habitat associations, and survivorship may increase effectiveness of management decisions regarding such factors as hunting seasons and bag limits, road closures, location of breeding and winter habitats, and impacts of land management activities. Additionally, clarification of the range of tolerances exhibited by blue grouse may provide greater ability to effect management positive for the species.

The premise of this study was the observation that adult and immature female and male blue grouse exhibit size dimorphism and occupy relatively harsh winter habitats, which may result in different survival-optimization strategies. I hypothesized that age and sex groups would differ in their movement and habitat selection strategies and that groups would exhibit unequal winter survivorship. The goal of the project was to better understand variation in winter life-history characteristics among age and sex groups. Specifically, the objectives were to measure movements from summer to winter ranges and within winter ranges, determine habitat relationships on these ranges, estimate fall and

winter survivorship, and compare movement, habitat associations, and survivorship among age and sex groups. Secondary objectives were to examine philopatry, relationships between weather and habitat use, diet, and grouping to ascertain the potential of these factors as influences on winter life-history strategies, and to relate movement characteristics and habitat associations between birds that survived through winter to those that died for each age and sex group to ascertain possible effectiveness of different strategies.

STUDY AREA

The study area was located on the Wallowa Ranger District of the Wallowa-Whitman National Forest (WWNF), which lies within the Northeastern Highland Climatic Region of Oregon (Loy et al. 1976). The area was approximately 30 km north of Enterprise, Wallowa County, Oregon (Fig. 1). Miller Ridge, located in the Joseph Creek drainage, was the prominent geological feature and constituted most of the area. Blue grouse were trapped on an area of Miller Ridge composing approximately 10 km^2. Elevation ranged from approximately 950 to 1,500 m.

North-facing slopes on the area were characterized by timber stands dominated by Douglas-fir (Pseudotsuga menziesii) and ponderosa pine (Pinus ponderosa). Western larch (Larix decidua) also was present, and lodgepole pine (Pinus contorta), true firs (Abies spp.), and junipers (Juniperus spp.) occurred at low densities. South-slope bunchgrass meadows were dominated by Idaho fescue (Festuca idahoensis) and bluebunch wheatgrass (Agropyron spicatum). Common understory and transition-zone shrubs included hawthorns (Crataegus spp.), snowberry (Symphoricarpos albus), and mallow ninebark (Physocarpus malvaceus). Drainages and valley bottoms contained few aspens (Populus spp.) and mixed conifers.

Based on wings of harvested birds submitted by hunters to state biologists, blue grouse were abundant on the area in relation to the rest of the state (V. L. Coggins, Ore. Dep. Fish and Wildl., unpubl. data), which was open to hunting in September and October during the study. Road density ranged from 0 to approximately 5 km of
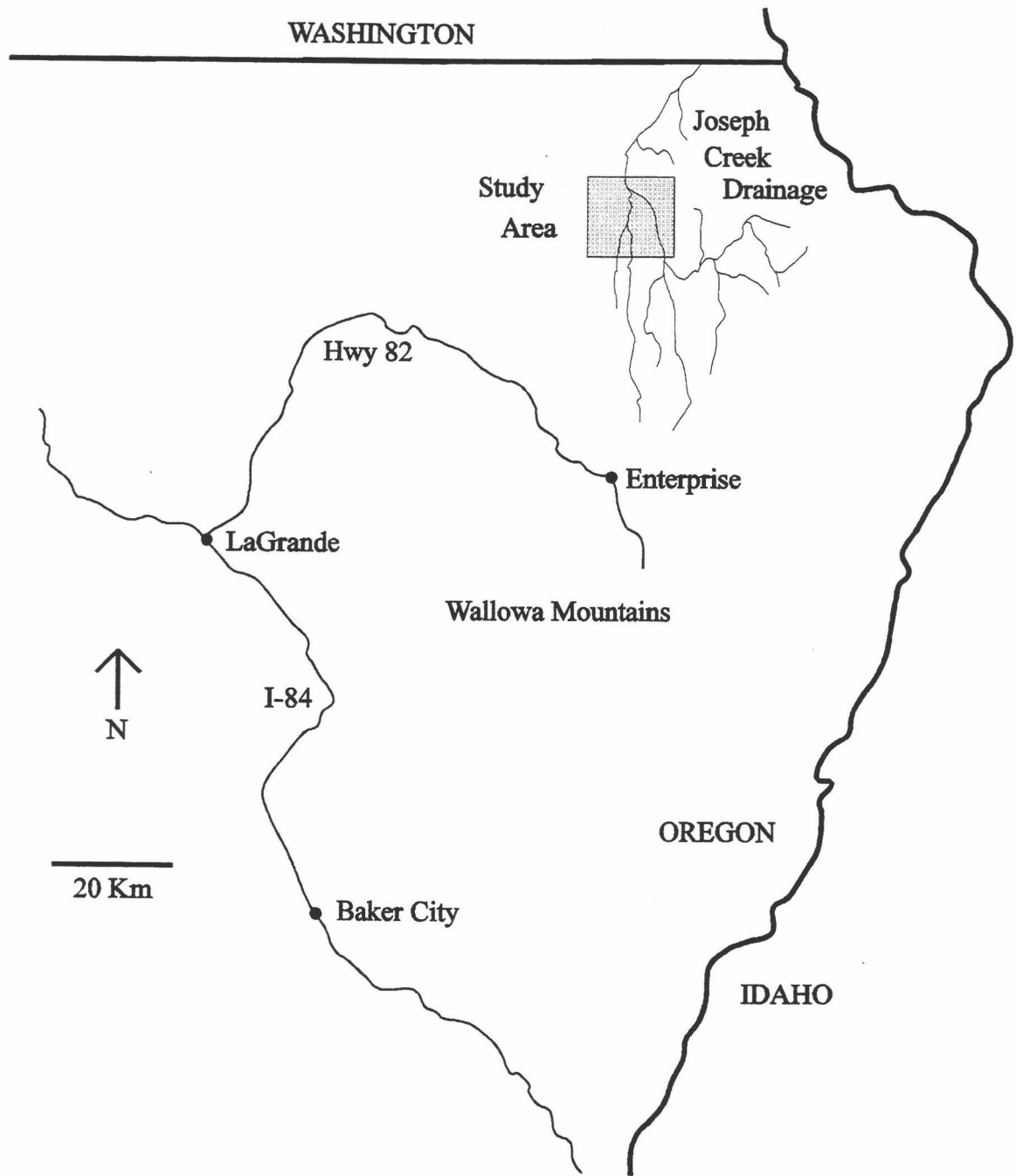
Fig. 1. Blue grouse winter ecology study area, Wallowa County, Oregon.

roads/km^2. Timber harvest occurred on the area before and during the study. Ground- and helicopter-based systems were used to remove trees with even- and uneven-aged management approaches. Approximately 5,000 ha of the Joseph Creek drainage were cut between 1989 and 1994; 97% of these cuts were partial cuts and 3% were clearcuts (U.S. Dep. Agric. 1994). Timber management practices included burning, thinning, and removal of trees infested with Douglas-fir dwarf mistletoe (Arceuthobium douglasii). Fires periodically burned portions of the area; the most recent fire occurred in 1986. Miller Ridge was part of a 12,000-ha grazing allotment, of which approximately 10,000 ha were grazed by cattle between mid-April and late October at a density of 0.62 animal unit months/ha (U.S. Dep. Agric. 1994).

Regional topographic and elevational factors contributed to highly variable temperatures and precipitation (Johnson and Simon 1987). Winter temperatures averaged -10 to 1^0 C in the region surrounding the study area. Precipitation averaged 20 cm at 950 m elevation with an increase of approximately 12.5 cm/300 m increase in elevation (Johnson and Simon 1987). The heaviest precipitation was in winter; 50% occurred during months when temperatures were $\leq 0°$ C (Johnson and Simon 1987).

METHODS

CAPTURE, INSTRUMENTATION, AND RADIO-TELEMETRY

Blue grouse were captured and equipped with radio transmitters from June

through August 1991 through 1993. Capture devices were primarily interception-style

walk-in traps (Pelren and Crawford 1995, Appendix A) but also included noose poles

(Zwickel and Bendell 1967), net guns (Coda Enterprises, Mesa, Ariz.), and fish landing

nets. Grouse were captured primarily where they were found at relatively high densities;

these areas were mainly on ridgetops during summer 1991, but included mid and lower

slopes during the next 2 summers as trappers became more familiar with areas of grouse

concentrations. Bird handling procedures followed guidelines set forth by Oring et al.

(1988). Captured birds were weighed to the nearest 10 g with Pesola spring scales; age

(immature or adult, with yearlings classified as adults) and sex were determined by visual

examination of wing plumage characteristics and primary feather replacement (Braun

1971, Hoffman 1985). A numbered aluminum band was attached to a leg for visual

identification. Battery-operated transmitters, weighing approximately 15 g (Advanced

Telemetry Systems, Inc., Isanti, Minn.) or 18 g (Telemetry Systems, Inc., Mequon, Wis.)

and operating in the 150-151 MHZ range, were placed on captured grouse with necklace

(Markström et al. 1989) or poncho mounts (Armstrup 1980) modified by a vertical slit at

the base of the poncho hole to prevent esophageal obstruction (Pekins 1988a).

Transmitters had life-expectancies of 12 to 20 months and were equipped with motion

sensors. Hines and Zwickel (1985) were unable to detect that 25- to 31-g radio packages

impacted survival of immature blue grouse >6 weeks old. The instrumented birds in their study were 50-75% of adult weight; harness design was the backpack mount described by Brander (1968). To minimize potential bias from transmitter effects in my study, immature birds with masses <500 g, which represents approximately 50% of adult weight (Boag 1965), were not equipped with transmitters. Radio monitoring of each grouse began immediately after capture in summer and continued until September. Birds were located weekly by approach and visual observation to ascertain survival or death, and Universal Transverse Mercator (UTM) coordinates were noted for later use in determination of fall movement distances.

Winter monitoring began in late November. Initial winter telemetry was conducted aerially to locate birds that moved substantial distances from summer ranges; a scanning receiver (Advanced Telemetry Systems, Isanti, Minn.) was used with a 3-element hand-held antenna (AF Antronics, Inc., White Heath, Ill.) to approach birds on foot. I located radio-equipped grouse randomly, by approach and visual observation, during daylight hours until late March.

HABITAT SAMPLING

Habitat characteristics were measured at sites where radio-equipped grouse were observed. UTM grid coordinates were recorded at each site for later determination of cover-type with the USFS Geographic Information System (GIS) ArcInfo and USGS topographic maps and aerial photographs. Three primary cover-types were identified. Areas of ≥ 900 m^2 with $\geq 10\%$ canopy cover were termed "forests". "Parklands" were

defined as areas of $\geq$ 900 m^2 with <10% canopy cover and <30 m between trees. Areas with $\geq$30 m between trees were termed "grasslands".

Several other site characteristics were quantified, including distance to the nearest forest edge and species of tree in which grouse were located (use-tree). A diameter tape was used to measure diameter-at-breast-height (dbh); use-tree height was estimated with a clinometer and age determined from a core sample. A spherical crown densiometer was used to determine percent canopy cover by trees. Dwarf mistletoe was detectable in Douglas-fir trees by presence of dense clusters of stems and needles, or witches' brooms, grown as a response by the tree to the parasite. Presence or absence of mistletoe in the tree was noted. Tree density was determined with the point-centered quarter method (Cottam and Curtis 1956) with use-tree as the center of the sample site, which was divided into the 4 cardinal directions. The distance from use-tree to the nearest tree >10 cm dbh, the minimum dbh used by grouse in a winter study in Colorado (Cade 1985) and from that tree to its nearest neighbor in a direction >90^0 away from the use-tree was measured to obtain an index of horizontal heterogeneity or "patchiness" of trees (Besag and Gleaves 1973, Diggle et al. 1976). A patchiness value of -1 represented even tree distribution, 0 represented random tree distribution, and +1 indicated clumped tree distribution. Temperature was measured with a thermometer and wind speed was estimated, both at the bases of use-trees when birds were located. Presence of other blue grouse in each use-tree was noted. Eleven percent of use-trees were used by >1 radio-equipped grouse, or in >1 instance by individual grouse. Grouse locations in these trees

were treated independently to maximize sample size and to weigh these observations to account for potential importance of these trees to grouse.

Habitat characteristics were measured at 1 randomly-selected tree within 100 m of each winter use site to determine individual-level habitat availability. This area of availability was chosen to represent a distance that blue grouse might typically be required to fly to reach a neighboring tree. Measurements at random sites were identical to those taken at use-trees. Additionally, a minimum convex polygon was configured around bird use sites, and ArcInfo and USGS aerial photographs were used to calculate percent of each cover-type within the polygon for an estimate of population-level cover-type availability (Fig. 2). I excluded the 2 winter locations of a hen that migrated 12 km from this polygon; these locations added 29 km^2 (30%) of area to the polygon that was unused by all other radio-equipped grouse.

DATA ANALYSIS

The minimum, straight-line distance from the last August radio location to the first location in December was measured for each bird to determine fall movement distance and elevational shift. Mean distances moved and shifts in elevation were compared among age and sex groups with general linear models provided by the computer program SAS. Movement distance and elevational shift served as response variables in separate models, and sex, age, and a sex*age interaction were included as explanatory variables. I also included year as a variable in the models to account for spatially expanded trapping efforts in 1992 and 1993. Cade (1985) observed that blue grouse movement to winter

↑
N

1 km

Fig. 2. Forest (black, 19%), parkland (gray, 11%), and grassland (70%) habitat available within polygon encompassing blue grouse radio-locations, Wallowa County, Oregon, 1991-1994.

ranges began as early as July in Colorado, so I used a paired t-test to compare movement to winter range from late summer with movements of the same birds from locations before 15 July to ascertain whether measurement of movements from last summer locations to first December locations accurately reflected movement from breeding to winter ranges.

Number of locations/grouse (mean = 7, range = 1 to 24) prohibited estimation of winter home range sizes. Minimum convex polygons (Mohr 1947) were constructed, with the computer program Calhome, from 7 randomly selected winter locations of each grouse that was located >7 times during a winter. These polygons served as indices to winter movement. A general linear model was used to compare range sizes among age and sex classes. Polygon size served as the response variable in the model; explanatory variables were age, sex, and age*sex interaction. To better understand philopatry to winter ranges, I measured distance between the 2 nearest locations between winters for each of 3 blue grouse monitored ≥ 2 winters, and presented these data summarily.

Johnson (1980) developed an intuitively appealing conceptual model in which organisms select habitat at various hierarchical spatial scales. Because selection by individuals, sexes or age classes, populations, metapopulations, subspecies, and species all may differ, description of habitat selection should include consideration of the spatial scale at which selection occurs and the characteristics of the group that is selecting habitat.

I examined use and selection of cover-types, and of habitat variables within these cover-types, by radio-equipped adult and immature female and male blue grouse, and I

compared this use and selection among age and sex groups. Differences in use of cover-types were examined by comparison of percent forest, parkland, and grassland habitats used among adult and immature females and males with a Pearson Chi-square contingency table. Cover-type selection was examined by comparison of use with availability within the minimum convex polygon that contained radio-equipped bird use sites. All locations from grouse in each age and sex group were combined for this analysis. Chi-square rank-ordering was used to determine selection of each cover-type by each group; differences in selection were compared among groups with Bonferroni 90% simultaneous confidence intervals (Neu et al. 1974).

All measures of habitat availability are arbitrary in that they are relative. To ascertain differences in habitat associations not observed with cover-type selection analysis, I compared differences in specific habitat variables at sites used among the 4 age and sex groups with a Chi-square analysis designed for estimated availability (Marcum and Loftsgaarden 1980) for categorical variables and with general linear models for continuous variables. Each general linear model included a habitat variable as the response, and age, sex, and an age*sex interaction as explanatory variables. Habitat variables included distance to forest edge; use-tree species, dbh, height, and age; presence or absence of mistletoe in the use-tree; percent canopy cover; forest density at the site; and an index of horizontal heterogeneity or patchiness.

Habitat variables measured at use-trees were compared with those at random locations within 100 m of use sites for each age and sex group with logistic regression to ascertain selection for these habitat variables and differences in selection among age and

sex groups. All habitat variables and their interactions were individually compared between use sites and random sites with logistic regression analysis at significance level P ≤ 0.15. Significant variables were included in logistic regression models with a stepwise selection procedure and significance level $P \leq 0.10$. A separate model was constructed for each age and sex group. The models included site (use or random) as the binary response variables, and habitat variables and their interactions as explanatory variables. Although tree species other than Douglas-fir and ponderosa pine were present on the study area, they were not included in the analysis because of lack of use by grouse and low availability. Larches were present in measurable quantities but were excluded from analysis because they are deciduous. Tree dbh was correlated with tree height ($r = 0.65$, $P < 0.01$) and tree age ($r = 0.58$, $P < 0.01$); therefore, the single variable dbh was used in analysis to represent tree size. Observations of birds on the ground were not included in habitat selection analysis but were described separately.

Habitat variables observed at each grouse use site were compared to temperature and wind speed at the time of observation with general linear models. The habitat characteristics served as response variables in the models, and temperature, wind speed, and their interaction were explanatory variables. Observed relationships between weather conditions and habitat use may reflect partial cause for habitat selection.

Fifteen birds were collected in a spatially and temporally random fashion from Douglas-firs, ponderosa pines, and the ground during winter 1993-1994 for analysis of crop contents, to determine whether diet corresponded with habitat use. I determined percent dry weight of crop contents of each bird in each of 3 categories: Douglas-fir

needles, stems or buds; ponderosa pine needles or buds; and forbs. I noted primary crop content based on these weights. I also noted habitat from which each bird was collected (Douglas-fir, ponderosa pine, or ground) and compared habitats to primary crop contents to determine if grouse obtained food from all habitats used.

Sexes and ages of associated radio-equipped blue grouse were summarily examined. These data provided inferences on the potential of agonistic behavior as a mechanism influencing habitat associations in some age or sex groups.

Fall (September through November) survivorship and 90% confidence intervals were estimated with binomial distribution analysis and compared among age and sex groups with Chi-square analysis (White and Garrott 1990). Winter (December through March) survivorship and 90% confidence intervals were estimated and compared among age and sex groups with the Kaplan-Meier product limit estimator (Kaplan and Meier 1958) and a log-rank test (Cox and Oakes 1984) provided by Proc Lifetest in the SAS computer software program. The Kaplan-Meier product limit estimator was chosen primarily because of its insensitivity to temporally variable survival, which may have occurred as weather conditions and food availability changed in late winter. Immature female and male birds were combined for this analysis because of low sample sizes. Although during winter immature birds were nearer in size to adult birds of the same sex than to immature birds of the opposite sex, I combined both sexes of immature birds because they shared lack of experience at winter habitat selection.

Fall movement distances and habitat use were compared with logistic regression analysis, for each age and sex group, between birds that survived throughout winter and

birds that died. Survival served as the binary response variable in the model, and the movement and habitat characteristics served as explanatory variables. This analysis allowed determination of possible effects of fall movement and winter habitat use on survivorship for each group.

All data were tested for normality with the computer program SAS. Highly skewed distributions were transformed with logarithms or logistic multipliers. Confidence limits for all statistical tests were established a priori at $P = 0.10$. SAS was used to plot residuals for verification of uniform distributions; potential bias evidenced by non-uniform distributions was reported in the results.

RESULTS

One-hundred and twenty-four blue grouse were captured and equipped with radio transmitters during the summers 1991 through 1993 (Table 1). Sixty-three percent of these birds were alive at the onset of winter following trapping, and these birds were located 536 times ($\bar{x}$ = 7 locations/grouse) during the 3 winters of the study.

MOVEMENTS

Fall Movement Distances

No differences were detected in linear distances moved by individuals between late August and December ($\bar{x}$ = 1,633 m, range = 36 to 11,949 m) or between early July and December ($\bar{x}$ = 1,782 m, range = 18 to 12,281 m). Therefore, to maximize sample sizes, measures of August to December movement distances and elevational shifts were used for analysis of fall movement characteristics.

The longest fall movement was 12 km; the next longest was 6 km. I was unable to relocate 9 grouse during winter (1 adult female, 5 adult males, and 3 immature females). Three of these birds were relocated during the following summer (1 adult female and 2 immature females). These birds may have moved >12 km; however, I conducted aerial telemetry searches throughout winter within approximately 40 km of spring ranges of missing birds without success. The longest documented blue grouse movement between spring and winter ranges was 50 km (Zwickel et al. 1968). At least 2 known radio failures during winter provided evidence that loss of some radio signals may

Table 1. Blue grouse capture and location sample sizes, Wallowa County, Oregon, 1991-1994.

	No. radio-equipped	No. present after autumn	No. winter locations
Adult female	38	22	160
Adult male	39	27	224
Immature female	22	16	66
Immature male	25	13	86
Overall	124	78	536

have resulted from transmitter failure.

Fall movement distances ranged from 36 m to 11,949 m ($\bar{x}$ = 1,633). No differences were detected in movement distance between ages or sexes, or among years; however, some adults remained on spring range throughout winter, whereas all immature birds moved >350 m in fall. Fall elevational shifts were different (P < 0.01) in 1991 than in following years, likely as a product of concentrated trapping efforts on ridgetops during that year, which minimized the possibility of moving upward without traveling relatively long distances. Analysis of age and sex relationships with elevational shifts was conducted separately for 1991. Elevational shifts were not different for different sexes or ages in 1991 ($\bar{x}$ = -112 m, range = -308 to 97 m). During the next 2 years, however, immature birds made greater upward elevational shifts in fall ($\bar{x}$ = 96 m, range = -308 to 403 m) than did adults ($\bar{x}$ = 23 m, range = -244 to 286 m)(P = 0.06). No difference in elevational shifts was detected between sexes during these 2 years.

Winter Range Sizes

Minimum convex polygons constructed to compare winter movement among groups were based on 7 randomly-chosen locations/grouse. Although these polygons did not represent home range sizes, they provided inferences about relative extent of winter movements. Polygons of immature grouse ($\bar{x}$ = 67 ha, range = 17 to 211 ha) were larger than those of adults ($\bar{x}$ = 28 ha, range = 2 to 90 ha)(r = 0.40, P = 0.02); no differences were detected between polygon sizes of male and female grouse (Table 2).

Table 2. Winter ranges of blue grouse based on minimum convex polygons, Wallowa County, Oregon, 1991-1992 through 1993-1994.

Age, sex	n	Minimum convex polygon (ha)		
		$\bar{x}$	Minimum	Maximum
Adult female	7	34	2	90
Adult male	12	24	4	82
Immature female	6	70	22	167
Immature male	7	66	17	211

Philopatry

Three birds were monitored for 2 consecutive winters: 1 adult female, 1 adult male, and 1 immature male. All of these birds returned to winter locations within 200 m of locations occupied during the previous winter. The adult male and female exhibited movement along similar routes during both winters. The immature male remained within 1 km of his 25 August capture site until March 1993, whereupon he moved approximately 3 km. He remained in this area until June, when he returned to the area in which he was trapped and wintered. He remained in this area until his radio failed in February 1994. Although limited in sample size, these data revealed that these birds exhibited philopatry to winter ranges.

HABITAT ASSOCIATIONS

Cover-Type Associations

Forests composed 17% of sites used by blue grouse, 70% were in parklands, and 13% were in grasslands. Comparison of differences in use of these cover-types among age and sex groups revealed greater use of forested habitat by immature females than by any other age and sex group ($x^2 = 21$, 3 df, $P < 0.01$). No other differences in use of forested habitat were detected among age or sex groups.

Cover-types available to blue grouse consisted of 19% forest, 11% parkland, and 70% grassland. Chi-square analysis revealed selection for parklands and avoidance of forests and grasslands by adult birds during winter. Immature males selected parklands,

avoided grasslands, and used forests in relation to availability. Immature females selectively used forests and parklands and avoided grasslands (Table 3).

Use-Tree Associations

Comparison of habitat use among age and sex groups revealed different levels of use of several habitat components by groups. Immature females used mistletoe-infested Douglas-fir trees to a proportionally greater degree than other age and sex groups ($\bar{x} = 16\%$ of trees used)($P = 0.01$). Additionally, immature birds used less densely forested sites ($\bar{x} = 45$ trees/ha, range = 3 to 872 trees/ha)($P < 0.01$) and smaller trees ($\bar{x} = 42$ cm dbh, range = 13 to 114 cm dbh)($P < 0.01$) than adult birds ($\bar{x} = 84$ trees/ha, range = 4 to 624 trees/ha, and $\bar{x} = 51$ cm dbh, range = 12 to 215 cm dbh, respectively). Adult females used trees with more clumped distribution than did immatures ($\bar{x} = 0.07$ patchiness index, range = -0.28 to 0.30 patchiness index)($P < 0.01$), and adult males used trees with more clumped distribution than observed in immature males ($P < 0.01$).

Comparison of habitat use with habitat available (Table 4) to each age and sex group revealed differential selection among groups (Table 5). All groups except immature females selected trees with larger dbh than available ($P < 0.01$). Immature females selected trees of sizes similar to those available. Females selected trees in areas of lower density than available ($P = 0.01$), whereas I could not detect selection by males for areas of higher or lower density. Although immature females used mistletoe-infested Douglas-fir trees to a greater degree than other age and sex groups, these trees

Table 3. Selection[a] of forest (19%), parkland (11%) and grassland (70%) cover-types by adult and immature, female and male blue grouse during winter, Wallowa County, Oregon, 1991-1992 through 1993-1994.

Category (n[b])	No. observations	% Use	Range of 90% CI	Use
Adult female (22)				
Forest	20	13	7 - 18	avoidance
Parkland	112	70	62 - 78	selection
Grassland	28	17	11 - 24	avoidance
Adult male (27)				
Forest	27	12	7 - 17	avoidance
Parkland	169	75	69 - 82	selection
Grassland	28	13	8 - 17	avoidance
Immature female (16)				
Forest	26	39	27 - 52	selection
Parkland	36	55	42 - 68	avoidance
Grassland	4	6	0 - 12	avoidance
Immature male (13)				
Forest	16	19	10 - 28	proportional
Parkland	59	68	58 - 79	selection
Grassland	11	13	5 - 20	avoidance

[a] Estimated with chi-square goodness-of-fit analysis (Neu et. al 1974).
[b] Number of individuals.

Table 4. Habitat characteristics at adult and immature, female and male blue grouse use-trees and random trees within 100 m of use-trees, Wallowa County, Oregon, winters 1991-1992 through 1993-1994.

Age, sex	Site	n[a]	Variable	x̄	SE	Minimum	Maximum
Adult female	Random	160	Edge[b]	21	3.27	0	350
			Douglas-fir[c]	55	3.99		
			Dbh[d]	46	2.00	10	150
			Mistletoe[e]	14	2.79		
			Canopy Cover[f]	82	1.44	25	100
			Density[g]	105	7.50	6	389
			Patchiness[h]	0.18	0.02	-0.30	0.54
	Use-tree	104	Edge	29	4.83	0	250
			Douglas-fir	59	4.83		
			Dbh	50	2.96	12	215
			Mistletoe	11	3.05		
			Canopy Cover	81	1.97	10	100
			Density	82	10.64	4	624
			Patchiness	0.14	0.01	-0.16	0.44

Table 4 continued.

Table 4. Continued.

Age, sex	Site	n	Variable	$\bar{x}$	SE	Minimum	Maximum
Adult male	Random	224	Edge	10	1.30	0	120
			Douglas-fir	57	3.41		
			Dbh	41	1.50	12	128
			Mistletoe	19	2.73		
			Canopy Cover	84	1.16	19	100
			Density	81	4.84	5	439
			Patchiness	0.23	0.02	-0.24	0.88
	Use-tree	163	Edge	41	4.40	0	350
			Douglas-fir	48	3.93		
			Dbh	52	1.73	16	122
			Mistletoe	12	2.59		
			Canopy Cover	76	1.65	13	100
			Density	86	8.33	4	624
			Patchiness	0.12	0.01	-0.32	0.44

Table 4 continued.

Table 4. Continued.

Age, sex	Site	n	Variable	x̄	SE	Minimum	Maximum
Immature female	Random	66	Edge	10	2.47	0	90
			Douglas-fir	59	6.87		
			Dbh	44	3.30	12	97
			Mistletoe	19	5.36		
			Canopy Cover	85	2.33	21	100
			Density	77	14.01	5	562
			Patchiness	0.29	0.03	-0.21	0.57
	Use-tree	45	Edge	64	12.21	0	400
			Douglas-fir	80	6.03		
			Dbh	40	2.86	13	97
			Mistletoe	38	7.39		
			Canopy Cover	77	3.47	15	100
			Density	37	6.03	4	244
			Patchiness	0.08	0.02	-0.15	0.30

Table 4. Continued.

Age, sex	Site	n	Variable	x̄	SE	Minimum	Maximum
Immature male	Random	86	Edge	11	2.24	0	100
			Douglas-fir	56	5.89		
			Dbh	40	2.83	11	117
			Mistletoe	11	3.65		
			Canopy Cover	84	2.12	20	100
			Density	61	7.66	9	382
			Patchiness	0.27	0.03	-0.17	0.70
	Use-tree	55	Edge	53	8.57	0	200
			Douglas-fir	71	6.26		
			Dbh	44	2.86	13	114
			Mistletoe	24	5.85		
			Canopy Cover	81	3.13	12	100
			Density	53	16.19	3	872
			Patchiness	0.05	0.02	-0.28	0.30

[a] Represents combined observations of all individuals; random locations include trees within 100 m of grouse located on ground. Sample size of individual grouse provided in Table 1.

[b] Edge = distance (m) to nearest forest edge, when forest is area $\geq 30m^2$ with $\geq 10\%$ canopy cover.

[c] Douglas-fir = % of locations in Douglas-fir trees. All other tree locations were in ponderosa pines.

[d] Dbh measured in cm with diameter tape.

[e] Mistletoe = % of locations in mistletoe-infested Douglas-fir trees.

[f] % Canopy cover averaged from 4 cardinal directions at base of use-tree.

[g] Density = trees / ha.

[h] Patchiness = an index of tree horizontal heterogeneity, with -1 = even, 0 = random, and 1 = clumped distribution.

Table 5. Blue grouse selection of habitat components during winter based on logistic regression models, Wallowa County, Oregon, 1991-1992 through 1993-1994.

Age, sex	n[a]	Parameter	Coefficient	SE	P
Adult female	104	dbh	+1.04	0.30	< 0.01
		density	-0.59	0.15	< 0.01
		spacing	-1.60	0.76	0.04
Adult male	163	edge	+0.50	0.07	< 0.01
		dbh	+1.50	0.28	< 0.01
		canopy	-0.24	0.08	< 0.01
		spacing	-2.53	0.56	< 0.01
Immature female	45	edge	+0.67	0.19	< 0.01
		canopy	-0.49	0.23	0.03
		density	-1.26	0.46	0.01
		spacing	-9.66	2.16	< 0.01
Immature male	55	edge	+0.68	0.15	< 0.01
		tree species	+1.63	0.59	0.01
		mistletoe	+10.44	4.99	0.04
		dbh	+1.68	0.57	< 0.01
		spacing	-5.81	1.27	< 0.01
		mistletoe*dbh[b]	-2.75	1.37	0.05

[a] Represents combined observations of all individuals. Sample size of individual grouse provided in Table 1.
[b] Mistletoe*dbh = interaction between these 2 variables.

were readily available to immature females, which resulted in lack of selection for these trees among trees within 100 m of use-trees. Although immature males used Douglas-fir trees and mistletoe-infested Douglas-fir trees proportionately less than immature females, they nevertheless selected Douglas-fir trees to a greater degree than available ($P = 0.01$) and, more particularly, mistletoe-infested Douglas-fir trees ($P = 0.04$). No other groups showed selection for or avoidance of Douglas-firs or mistletoe-infested trees.

Use of Ground Cover

Blue grouse were located on the ground in 169 instances (32% of winter locations). Percentage of radio-equipped birds observed on the ground in December, January, February, and March was 8, 13, 27, and 57, respectively. No snow roosts were detected; birds on the ground were primarily in areas without snow, although tracks indicated grouse traversed >100 m over snow. Cover-types of ground locations followed trends similar among age and sex groups to those observed in cover-types of grouse use-trees (Table 6), although ground locations frequently (35%) were in grasslands.

Weather Relationships

Temperature at grouse use sites during the 3 winters of the study averaged 5^0C (range = -15 to 29^0C). Wind speed typically was 0 to 8 kph, but increased to as much as 80 kph. Trends observed in relationships between habitat use and these weather variables were weak. Grouse used increasingly denser forest stands as wind speed increased ($r = 0.17$, $P < 0.01$). Decreasing temperatures corresponded with increased use of

Table 6. Blue grouse locations on ground in 3 cover-types during winter, Wallowa County, Oregon, 1991-1992 through 1993-1994.

Age, sex	n[a]	Locations (%)		
		Forest	Parkland	Grassland
Adult female	56	7	50	43
Adult male	61	3	53	34
Immature female	21	29	52	19
Immature male	31	13	55	32
Total	169	13	52	35

[a] Represents combined observations of all individuals. Sample size of individual grouse provided in Table 1.

ponderosa pines (r = 0.20, P < 0.01), increased canopy cover at use sites (r = 0.14, P < 0.01), and increased use of randomly-distributed trees rather than clumped distribution (r = 0.17, P < 0.01).

Crop Content Analysis

To ascertain whether trees used by blue grouse were associated with foods consumed at those sites, 15 blue grouse were collected during winter 1993-1994 and their crop contents were identified (Appendix B). Some materials may bypass the crop (D. A. Boag, pers. comm.); therefore, crop contents may not precisely reflect diet. Results, nevertheless, confirmed that grouse used both Douglas-fir and ponderosa pine as food resources. Seven crops (47%) contained Douglas-fir needles, stems, or buds, and 6 crops (40%) contained ponderosa pine needles or buds. Crops of all grouse located in pines contained pine needles or buds, and crops of 5 grouse located in Douglas-fir trees contained Douglas-fir needles, stems, or buds. One grouse located in a Douglas-fir tree had an empty crop, and the crop of another grouse collected from a Douglas-fir contained pine needles. Additionally, 2 birds collected from the ground in March had consumed several species of ground-layer forbs (Appendix B). Because Douglas-fir and ponderosa pine were the only tree species used by grouse, and both were used as food resources, birds did not seem to require different tree species for roosting cover than they used for food resources during the time period monitored.

Grouping

Radio-equipped grouse were located in trees with other blue grouse in 57% of winter observations (42, 49, 65, and 66% of locations in December through March, respectively). Mean group size was 3 in December and 2 from January through March. Maximum group size was 30. Ages or sexes of grouse without transmitters were not identified; however, location of ≥2 radio-equipped grouse in the same tree on 11 occasions revealed association among all sex and age groups, with the following exceptions: immature males were not located together, and adult females were not located with adult males.

SURVIVORSHIP

Six missing birds were censored from fall survivorship analysis. No differences in survivorship were detected among age or sex groups with Chi-square analysis (Table 7), so sexes and ages were grouped and re-analyzed. Overall fall (September through November) survivorship was 0.77 (90% CI = 0.70 to 0.84). Hunting, which occurred during September and October, accounted for 5% of fall mortality of radio-equipped birds during the 3 years of the study.

Comparison of winter survivorship among adult females, adult males, and immature birds (Table 7) revealed greater survivorship by adult females than by immature grouse ($x^2 = 6.35$, 2 df, $P = 0.04$). Adult males did not survive differently than other groups. Overall winter survivorship was 0.84 (90% CI = 0.78 - 0.90).

Table 7. Blue grouse fall and winter survivorship, Wallowa County, Oregon, 1991-1994.

	n	Survivorship	Range of 90% CI
Fall[a]			
Adult female	27	0.78	0.65 - 0.91
Adult male	32	0.84	0.74 - 0.95
Immature	42	0.71	0.59 - 0.82
Winter[b]			
Adult female	22	0.95	0.88 - 1.00
Adult male	27	0.89	0.79 - 0.98
Immature	29	0.71	0.60 - 0.83

[a] Binomial distribution analysis (White and Garrott 1990).

[b] Staggered entry modification (Pollock et al. 1989) of the Kaplan-Meier (1958) product limit estimator.

SURVIVAL-MOVEMENT AND SURVIVAL-HABITAT RELATIONSHIPS

No differences were detected in fall movement distances between birds that lived throughout winter ($\bar{x}$ = 1,757 m, range = 36 to 11,949 m) and those that died ($\bar{x}$ = 1,719 m, range = 172 to 4,379); therefore, no evidence was found that fall movement distance was associated with survivorship. Analysis of relationships between survivorship and habitat use revealed that birds that survived through winter used sites with higher tree densities than birds that died (r = 0.26, P = 0.04). This relationship was weak and corresponded with adult use of higher-density sites ($\bar{x}$ = 84.0 trees/ha, range = 4 to 624 trees/ha) than immatures ($\bar{x}$ = 45.0 trees/ha, range = 4 to 872 trees/ha) and greater number of adults surviving through winter (92%) than immatures (71%); therefore, survivorship may have been more a function of age than use of sites with high tree densities. No other relationships were observed between survivorship and habitat use.

SCOPE AND INFERENCES

Multiple locations of individuals are seldom independent in space and time. The use of radio-telemetry data to quantify movement and habitat associations can violate assumptions of independent observations of sampling units, which results in pseudoreplication; however, quantification of movements and habitat associations would not have been possible without these data, and results remain valid among individuals sampled.

The observational experimental design limits the inferential power of this study. Because treatments (sex and age) could not be assigned randomly to experimental units (individual grouse), I was unable to determine whether relationships were causal. Therefore, inference extended beyond the spatial and temporal scope of this study is conjectural, and likely is more applicable to areas of climatological, geographical, and vegetative conditions similar to those present on the study area, than to other areas.

DISCUSSION

MOVEMENTS

I observed a greater upward elevational shift by immature birds than by adults in

1992 and 1993, but this difference probably was because of greater horizontal movement

distances by immature birds. Although birds wintered at a wide array of elevations on the

study area (range 950 to 1,500 m), areas greater than 1,800 m elevation were within 5

km, and areas >2,500 m elevation were within 40 km, which was within the potential fall

movement distance of blue grouse. Blue grouse typically move upward in fall (Anthony

1903, Marshal 1946, Wing 1947, Caswell 1954, Bendell 1955, Cade and Hoffman 1993).

However, some birds move downward (Rogers 1968) or are sedentary (Hoffmann 1956).

Zwickel and Bendell (1972) suggested altitudinal migration likely occurred because of

differences in elevation of suitable breeding and winter habitats. Cade and Hoffman

(1993) observed altitudinal migration on an area where conifer stands occurred in bands

situated in particular elevational zones and suitable breeding habitat was lower in

elevation. My study area was composed of timbered north-facing slopes that occurred

throughout the range of elevations with breeding habitat located at the edges of these

stands. Cade (1985) suggested fall movement may be a response to desiccation of

ground-level vegetation and that grouse may move upward to find less senescent

vegetation for food and cover. Altitudinal movement may not have occurred on my study

area because of lack of adjacent suitable habitat at sufficiently higher altitude to provide

more vital vegetative resources. Timing of movement may nevertheless have been in

response to desiccation. Cade (1985) noted initiation of movements to winter ranges as early as late June. Mean blue grouse hatching date in Wallowa County from 1981 through 1995 was 1 June, and 85 % of chicks were hatched by 12 June (J. A. Crawford, pers. commun.). Males and broodless females captured in mid-June or later may have been in transition to winter ranges. Females with broods also may have been in this transition, although early movement likely was limited by chicks. Nevertheless, I was unable to detect a difference between July to December movement and late August to December movement, probably because of short movement distances.

Greenwood (1980) stated that among species that used sites consistently, one sex is generally more philopatric than the other and, in birds, females generally make longer seasonal movements than males. Differential seasonal movement distances of the sexes was widely reported for tetraonids among which females generally moved greater distances than males (Seiskari 1962, Hoffman and Braun 1975, Herzog and Keppie 1980, Schroeder 1985, Schroeder and Braun 1993). However, studies of blue grouse fall movements in Colorado (Cade and Hoffman 1993) and British Columbia (Hines 1986) revealed greater movements by males than by females. Hines (1986) also found greater movement by immature blue grouse than by adults. Seasonal movement distances commonly are different among age groups for many wildlife species (Baker 1978). Among philopatric species, this difference may be attributed to the difference between nonphilopatric juvenile dispersal from the natal area, and philopatric seasonal movement of adults between winter and breeding areas, which is conventionally termed migration.

Grouse in my study moved shorter mean distances than observed in other studies (Hines 1986, Cade and Hoffman 1993), which may have accounted for my observations of similar fall movement distances among age and sex groups. Cade (1985) suggested differential migration distances in blue grouse may represent mixed evolutionarily stable strategies among individuals. Such mixed strategies might occur when relative fitness is equivalent for long- and short-distance migrants. However, areas of highly interspersed winter and spring resources may allow minimal fall movements. Differential movement of age and sex groups has been attributed to factors including avoidance of competition for resources or mates (Dobson and Jones 1985). I observed differential habitat selection, which may lower incidence of competition for structural components of habitat as effectively as spatial separation through differential movements without potentially associated risks. However, habitats selected by all ages were well-distributed throughout the study area, and I observed no indication of territoriality in winter and frequently saw adult and immature grouse of both sexes in flocks. Although average fall movements were similar for immature blue grouse and adults, minimum fall movement distances were different between the 2 age groups. Some adults remained on spring range throughout winter, whereas all immature birds moved >350 m in fall. Linear distances moved between breeding and winter range may be a less useful description of differences in movements than range sizes, which, during winter, revealed marked differences between age groups in this study.

Immature blue grouse had larger mean winter ranges than adults in my study, likely as a result of greater minimum winter range sizes by immature grouse than by

adults; maximum winter range sizes were similar for both age groups. The relatively extensive winter movements of immature grouse in this study provided evidence that immature dispersal continued through winter. The typical pattern of dispersal in young blue grouse likely began with a movement in search of suitable habitat in fall and continued through winter. Young blue grouse may continue to move until an undefended breeding territory is found in spring. Movement of some immature and adult grouse to breeding territories may have occurred in late winter; several grouse exhibited elevated movements during early March. Grouse on the study area were philopatric to previously-used winter ranges and to successful breeding territories. Philopatry to winter ranges also was observed by Cade (1985) and Hines (1986); Zwickel (1992) reviewed multiple studies noting philopatry to spring ranges. Schroeder and Braun (1993) suggested migratory movements may reflect dispersal of birds from their first winter area to their first breeding area. My observations of greater minimum fall movement by immature birds than by adults, and philopatry to breeding and winter ranges, lent support to this hypothesis.

HABITAT ASSOCIATIONS

Beer (1943) suggested blue grouse distribution may be limited to that of Douglas-fir and true firs. Zwickel and Bendell (1986) contested this assertion and noted that pines and other tree species may be more heavily used for food by blue grouse in winter than Douglas-firs or true firs. This conjecture was supported by their results and those of Boag (1958) and Harju (1974). The occurrence of Douglas-fir and ponderosa pine on my

study area provided opportunity to further test this hypothesis. Based on availability sampling, 57% of trees within 100 m of sites used by grouse in winter were Douglas-fir and 43% were ponderosa pine. Although immature males selected Douglas-firs, I did not detect selection for either tree species among adults or immature females. Additionally, no selective use was obvious for either tree species as food resources; crop contents contained needles from both species.

Blue grouse selection of habitat may be based more on structural components than on species composition. Birds in Colorado (Cade and Hoffman 1990), Idaho (Stauffer and Peterson 1986), Utah (Pekins et al. 1989), and in my study used larger trees on average than those available. Blue grouse frequently were observed in "wolf trees" (Caswell 1954, Cade 1985, Pekins 1988b), which are typically short, large-diameter trees that were stressed by lightning, mistletoe, insect infestations, or disease. Cade and Hoffman (1990) suggested selection of large conifers was related to food requirements rather than thermoregulatory or concealment value. Hoffmann (1961) noted differences in crude protein content between white fir (Abies concolor) needles located in high and low parts of canopies in trees used by blue grouse. Such variation may contribute to differential selection not only of forest structure, but also of micro-habitat features. Selection for forest structure was exemplified by the 12 km fall movement of a hen from parkland habitat through forested true fir habitat to another parkland area typified by Douglas-fir and ponderosa pine. Caswell (1954), King (1971), and Stauffer (1983) observed blue grouse winter selection of either large conifers or dense clumps of conifers within open habitat and concluded selection may be based more on forest structure than

species composition. My observations supported this hypothesis. Some birds on the Miller Ridge study area selected large diameter evenly-distributed trees in open habitats, whereas other birds were observed in smaller trees in more heavily-forested stands.

Analysis of differences among age and sex groups further elucidated differential use and selection. Adults and immature males selected large trees in parkland conditions and avoided forested habitats; immature males additionally selected mistletoe-infested Douglas-firs within these cover-types. Immature females selected both parklands and forested habitats and within these cover-types used mistletoe-infested Douglas-fir trees to a greater degree than other groups. These results implied that different age and sex groups may use different forest structure and micro-habitats. King (1971) found adult male blue grouse on Vancouver Island, British Columbia wintered in open stands of mountain hemlock (Tsuga mertensiana), away from immature birds and females. This segregation was attributed to use of different elevational zones by age and sex groups and was supported by similar findings by Hines (1987). Hines (1987) further suggested that females and males used stands of different ages during winter. Zwickel and Bendell (1986) noted that the typically open structure of ponderosa pine forest provided poor winter cover. Clumped pines in open habitat were plentiful and apparently adequate habitat for adult birds in my study area. However, this habitat may lack a sufficient degree of cover or food abundance needed by immature males and females, which selected mistletoe-infested Douglas-firs in open conditions and in heavily forested stands, respectively. Differential food selection was observed among age and sex groups on my study area during fall (Crawford et al. 1986). Adult males used western larch to a greater

degree than other age and sex groups, and immature birds ate grasshoppers more than adults. These dichotomies may further exemplify the need for different, perhaps higher-quality, resources by smaller birds (i.e., females and immature birds). An alternative explanation for differential habitat associations may be antagonistic behavioral interactions among age or sex groups. However, the flocking observed provided evidence that such interactions likely did not occur during winter.

Grouse fed in both of the tree species in which they were located, which indicated that tree species used for thermal cover also provided food resources. This contradicted findings of Pekins et al. (1991), who observed differential winter feeding and roosting habitat use by blue grouse in Utah. Birds primarily used large Douglas-fir trees for feeding; roosts were mostly in subalpine firs (Abies lasiocarpa), which provided cover superior to Douglas-firs. Thermal requirements likely were met by tree structure rather than by tree species. Although roosts examined by Pekins et al. (1991) were nocturnal sites, the cover provided by subalpine firs in their study might have been equally provided by mistletoe-infested Douglas-firs on my study area, as evidenced by copious amounts of droppings under many mistletoe-infested trees on the study area. Furthermore, Pekins et al. (1991) frequently observed mistletoe at blue grouse roost sites.

Although I did not observe snow-roosting, birds were located on the ground increasingly as winter progressed. Presence of forbs in crops of birds collected from the ground where snow had melted indicated that birds may have been on the ground to forage for emerging vegetation. Bergerud and Gratson (1988) suggested fall movement of forest grouse from ground-level habitat to arboreal habitat may occur partially to decrease

conspicuousness following snowfall. Similarly, movement to ground in spring following snowmelt may have allowed exploitation of relatively high-quality forbs for food, without the risk of high visibility to predators which grouse may incur when the ground is covered with snow. However, blue grouse in my study moved into trees before snowfall in the fall, and, in coastal areas with little or no snow, they begin using ground-layer food resources immediately upon emergence of these resources in spring (Zwickel 1992). Likely, shifts to trees in the fall and to the ground in the spring is primarily in response to availability of ground-level food resources. Breeding behavior also may have influenced use of ground by grouse; males were observed displaying on the ground during March and, in 1992, during February. During summer, grouse were located on the ground in 99% of 614 observations during daytime and in 100% of 69 nocturnal observations on the study area, possibly to maximize exposure to food resources (Popper et al. 1996). Blue grouse in coastal areas use trees throughout the year (Zwickel 1992); use of ground-layer resources in spring and summer may reflect adaptations to environmental conditions not present where grouse stay in trees throughout the year.

Winter habitats likely were selected for food, predator-avoidance cover, and thermal cover. The degree of each of these influences on habitat selection likely differed among and within groups (flocks, age and sex classes, populations, subspecies, etc.) and among spatial and temporal scales. Pekins et al. (1991) suggested that nocturnal habitat selection is driven primarily by thermal considerations. Although I noted relationships between diurnal habitat use and temperature and wind speed, these relationships were weak. Diurnal weather may not have been harsh enough to prompt strong selection of

habitat based on thermal considerations. Cade (1985) conjectured that blue grouse remained at sites as long as food was available, after which they sought sites with adequate food resources. I submit that larger birds obtain adequate nutrition and cover in generally large conifers in open habitat, whereas smaller birds must go through a more rigorous selection process to acquire sufficient dietary and thermal resources. These resources frequently are in different places, which requires greater movement by these smaller birds and a concomitant risk of higher mortality.

SURVIVORSHIP

Immature grouse may be vulnerable in fall, when they move to new areas, break brood associations, form new flocks, and change diets to conifer needles, stems, and buds. This vulnerability may continue through winter if the birds do not settle on a concentrated range, but rather continue to range widely. An additional disadvantage to immature birds is their relatively small size. Resource competition is unlikely to occur among blue grouse during winter (Bergerud 1988). Although partial or complete separation of sexes was reported for blue grouse in winter (Marshall 1946, King 1971, Hines 1986), I observed most age and sex groups in association during this time, as did Cade and Hoffmann (1990). However, young birds ranged more widely during winter perhaps because of inability to find or recognize suitable habitat; these movements may have contributed directly or indirectly to increased mortality.

Birds monitored for 2 winters in my study showed philopatry for areas occupied during winter, which supported Cade (1985) and Hines (1986). The resulting familiarity

with the winter habitat among adults, along with their shorter fall movements and smaller winter range sizes, likely contributed to lower mortality than that exhibited by immature birds.

Hines (1987) observed higher immature mortality in fall than in winter. Bergerud (1988b) suggested that from the perspective of food and nutrition, winter should not be a time of population bottleneck for the species, and Redfield (1973) found blue grouse gained weight in winter. Mortality was not significantly greater during fall than during winter in my study, despite loss of 5% of radio-equipped birds to hunters in September and October. Fall and winter may not be particularly detrimental periods for blue grouse populations. Females and males exhibited similar survivorship despite size differences.

SURVIVAL-MOVEMENT AND SURVIVAL-HABITAT RELATIONSHIPS

Although seasonal movement distances were similar among birds that survived through winter and those that died, greater winter movements by immature grouse than by adults and lower winter survivorship by immature grouse than by adult females provided evidence that winter movement may have partially impacted survivorship. Immature dispersal began in fall and continued through winter in the form of greater movement than exhibited by adults. Birds were philopatric to their first winter and breeding ranges.

Age and sex groups used habitat differently. Adult blue grouse selected large ponderosa pines and Douglas-firs in parkland conditions equally for roosts and food. Immature females selected parkland conditions and more heavily-forested stands but did

not select larger trees from among those available. Immature males selected large trees in parkland conditions as did adults, and they heavily used mistletoe-infested Douglas-firs within these stands. Birds that survived through winter occupied sites with higher tree density than birds that died. These sites were more frequently occupied by adult birds than by immatures, and more adults lived through winter than immatures, which may have accounted for the observed relationship between density and survival. Forested sites occupied by immature females contained lower tree density than parkland sites selected by all age and sex groups. Perhaps the relatively dense tree structure or a related habitat feature provided by parkland habitats was limited for grouse in the study area. No evidence existed that survivorship was correlated with association of any other habitat variables.

Differential use of resources among age and sex groups occurred during winter in my study. Similarities in habitat associations among age and sex groups, and frequent observation of individuals from different age and sex groups in flocks, indicated that this differential use was not complete. Additionally, dissimilar survivorship exhibited among groups suggested that habitat needs possibly were not being met equally among groups. Lower survivorship among birds that occupied sites of lower tree density may reflect habitat deficiencies for all sex and age groups. Birds subjected to altered winter habitat conditions (i.e., lowered tree density caused by fires or timber harvest) may not move to more favorable locations because of their apparent philopatry to winter ranges. Regardless, the differential movements exhibited between the blue grouse age groups, and the resource partitioning exhibited among adults, immature females, and immature males,

exemplify the need to consider differences among group life-history strategies when making wildlife management decisions.

MANAGEMENT IMPLICATIONS

FOREST MANAGEMENT

Terrain occupied by blue grouse historically was frequently unsuitable for timber harvest; however, economic demand for timber in northeastern Oregon and advances in silvicultural technology have made logging feasible and commonplace in blue grouse winter habitat in this region. Regeneration systems such as clearcutting and thinning may destroy winter habitat for adults and immature male blue grouse by temporarily creating young stands with even tree distributions. Fire suppression may further detriment blue grouse populations by causing increased fuel loads, which result in relatively high-intensity fires that destroy entire forest stands rather than creating parkland conditions selected by blue grouse, which typically was the result of historical fires in ponderosa pine habitats (Agee 1994).

Grouse on the study area occupied habitat containing more parkland and less forest than on adjacent habitat unused by radio-equipped birds. Even-aged forest patterns historically occurred at the stand or group scale and uneven-aged forest patterns occurred at the landscape scale in such ponderosa pine habitats (Agee 1994). Management of timber for blue grouse in this habitat should be directed toward increasing parklands, which provide winter and breeding habitat for all age and sex groups. Additionally, fire suppression may be decreased or discontinued to diminish fuel loads and subsequently lessen intensity of fires that occur and the likelihood of occurrence of stand-replacement fires. Parklands should be interspersed with patches of forested conditions for the benefit

of immature females. Such patches may occur naturally; interspersing parklands with forest patches of 1 to 2 ha in size should provide adequate winter habitat for immature females. Grasslands additionally should be maintained. Although grasslands were avoided by blue grouse in winter, these areas were used by grouse during spring and summer (Popper et al. 1996). Because trees were largely limited to north slopes on the study area, north aspects should be managed for forests or parklands as much as possible to maximize winter habitat of blue grouse.

Spatial arrangement of cover-types may be a critical aspect of within-range habitat requirements, of movement between winter and spring ranges, and of immature dispersal in fall and winter to new ranges. Blue grouse may be limited by lack of parkland habitat; therefore, this cover-type should be maintained throughout the desired range of the population. Most seasonal movements on the study area were <6 km, and birds were capable of traveling this distance in single flights; therefore, connectivity of winter and breeding ranges is currently not a concern on the study area. However, extensive areas of forest or grassland habitat may limit longer migrations or juvenile dispersal. Forests that occur between more suitable parkland habitat should be managed to promote patches of parkland conditions within the forest landscape. Grasslands frequently are on south-facing slopes where trees do not easily grow. Drainages and areas with north aspects that occur in grasslands should be managed to provide patches of trees for migrating or dispersing grouse.

Cover-types should be managed dynamically as well as spatially, with prompt action to account for temporal changes in the landscape. Because trees grow primarily on

north aspects and south slopes are dominated by bunchgrass communities in this area, parkland cover-types should be maintained, where possible, indefinitely as shifting steady states of mature or old-growth trees with interspersed patches of varying ages to replace old trees lost to harvest or natural processes. Fire may be a useful thinning mechanism in this process; return intervals in Pacific Northwest ponderosa pine ecosystems ranged from 7 to 38 years (Agee 1994). Management of blue grouse habitat should be adaptive, with active monitoring of changes in cover types and stand structural conditions to allow managers to compensate for forest stand deaths caused by natural factors such as insect or disease outbreaks and drought.

Habitat within cover-types may be maximized by retention of the largest trees within parklands. Large mistletoe-infested Douglas-firs should be retained within parklands for immatures, and within forested stands for immature females. Although mistletoe decreased growth rates of Douglas-fir trees in the WWNF (Filip et al. 1993), it may be controlled in several ways. Clumps of mistletoe-infested trees may be separated from non-infected trees by distances of $\geq$12 m, which represents the average maximum distance of seed dispersal (Knutson and Tinnin 1980). Maintenance of trees in clumps additionally provides sites of high tree density favorable for blue grouse survivorship. Additionally, rate of mistletoe dispersal within thinned stands was 1.5 times greater than in un-thinned stands in British Columbia (Knutson and Tinnin 1980); therefore, maintenance of trees in clumps may slow the rate of mistletoe dispersal. Mistletoe is more difficult to control in forested conditions. However, grouse readily used lower canopies, from which mistletoe rate of dispersal is slower; therefore, retention of trees

with mistletoe low in the canopies would provide the resource while limiting rate of dispersal. Upward dispersal of mistletoe within trees was <0.6 m/year (Knutson and Tinnin 1980), and trees with mistletoe located low in the crowns frequently grew at a greater rate than the upward spread of the parasite. Trees additionally may be pruned above mistletoe-infested branches to discourage upward, and eventually outward, dispersal.

Many blue grouse winter habitat associations observed likely represented more complex interactions between birds and their environments that remain poorly understood. As historically-existent habitat conditions are better understood, such conditions should be promoted in areas of historical blue grouse occupancy. This action would maximize the possibility that habitat needs are being met for all age and sex groups.

HUNTING

Five percent of radio-equipped blue grouse were harvested during the study. This harvest occurred during September and October, when birds frequently were on the ground. The hunting season was closed on the study area in late October. No evidence exists that radio-equipped grouse and other grouse were harvested at unequal rates; therefore, 5% may represent a close approximation of the percent of the total population harvested. Hunting mortality represented 22% of total fall mortality, and 0% of winter mortality. Blue grouse near roads may have experienced higher fall hunting mortality than other birds. All radio-equipped grouse harvested on the study area were within

approximately 1 km of open roads. Road closures may be an effective tool to minimize

hunting pressure where roads pass through areas of high blue grouse density during fall.

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APPENDICES

Appendix A. A trap for blue grouse

Numerous techniques have been developed to capture blue grouse (Dendragapus

obscurus) for scientific purposes, but efficacy differs among methods and is influenced by

terrain, habitat conditions, and wariness of birds. Zwickel and Bendell (1967) captured

over 1,200 blue grouse in British Columbia between 1950 and 1967 with a "noosing

pole." Zwickel estimated that 10,000 to 15,000 blue grouse have been captured with

nooses in parts of their range from Alaska to California and from Alberta to Colorado

(pers. comm.). However, noosing poles and other approach-based techniques may not be

effective for capturing blue grouse in areas where birds do not permit close approach by

humans, where baiting is ineffective, or where topographic or habitat conditions preclude

use of drive traps. Consequently, additional methods are needed to supplement existing

techniques.

Henderson (1960), Standing (1960), and Bauer (1962) used walk-in traps to

capture over 520 blue grouse in northcentral Washington from 1956 to 1961. We

developed a similar trap for spring and summer capture of adult and juvenile blue grouse

in northeastern Oregon where the wary nature of the birds made noosing poles and other

approach-based capture techniques ineffective. Our objective is to describe the design

and success rate of a walk-in trap for blue grouse and to present this method as a viable

alternative when approach-based capture methods are ineffective.

We used a walk-in style trapset designed to intercept the movement of birds

through the trapping area and guide these individuals along wire fences into funnels

connected to trap boxes (Gullion 1966). Our trapsets usually consisted of three open-bottomed boxes (range 1-7) connected by fences (Fig. 1) and required 1-3 h for placement. Trap boxes were constructed in approximately 45 min from plastic or metal wire or netting. A primary concern in choosing trap material is that birds may injure themselves on the traps. Fish netting and/or vegetation on the top of the box reduces the possibility of injury (Henderson 1960, Standing 1960, Bauer 1962). Size and placement of entrance funnels is critical. We fitted 5-cm hexagonal-weave chicken wire funnels to the entrance holes; funnels had inner-opening dimensions of 6 cm width x 10 cm height if the trap was intended primarily for immatures and 8 cm width x 12 cm height if the trap was intended primarily for adult birds.

Successful traps were constructed where birds had been located repeatedly within a 5- to 10-m² area. Fences between boxes were shorter where grouse were more highly localized to increase the concentration of trap boxes in those areas.

We captured 140 grouse in 2,327 trap(set)-days during summers 1991, 1992, and 1993 at rates of 23, 19, and 12 trap-days/capture, respectively (Table 1). Increased trapping efficiency in 1992 and 1993 was likely a product of refined trapping techniques, experience of trappers, and knowledge of bird movements. Henderson (1960) achieved capture rates of 7 and 8 trap-days/capture in 1958 and 1959, respectively. Variations in capture success rates may be influenced by grouse population density and distribution. Habitats in which grouse are evenly distributed are more difficult to trap than areas in which grouse congregate in dense clumps.

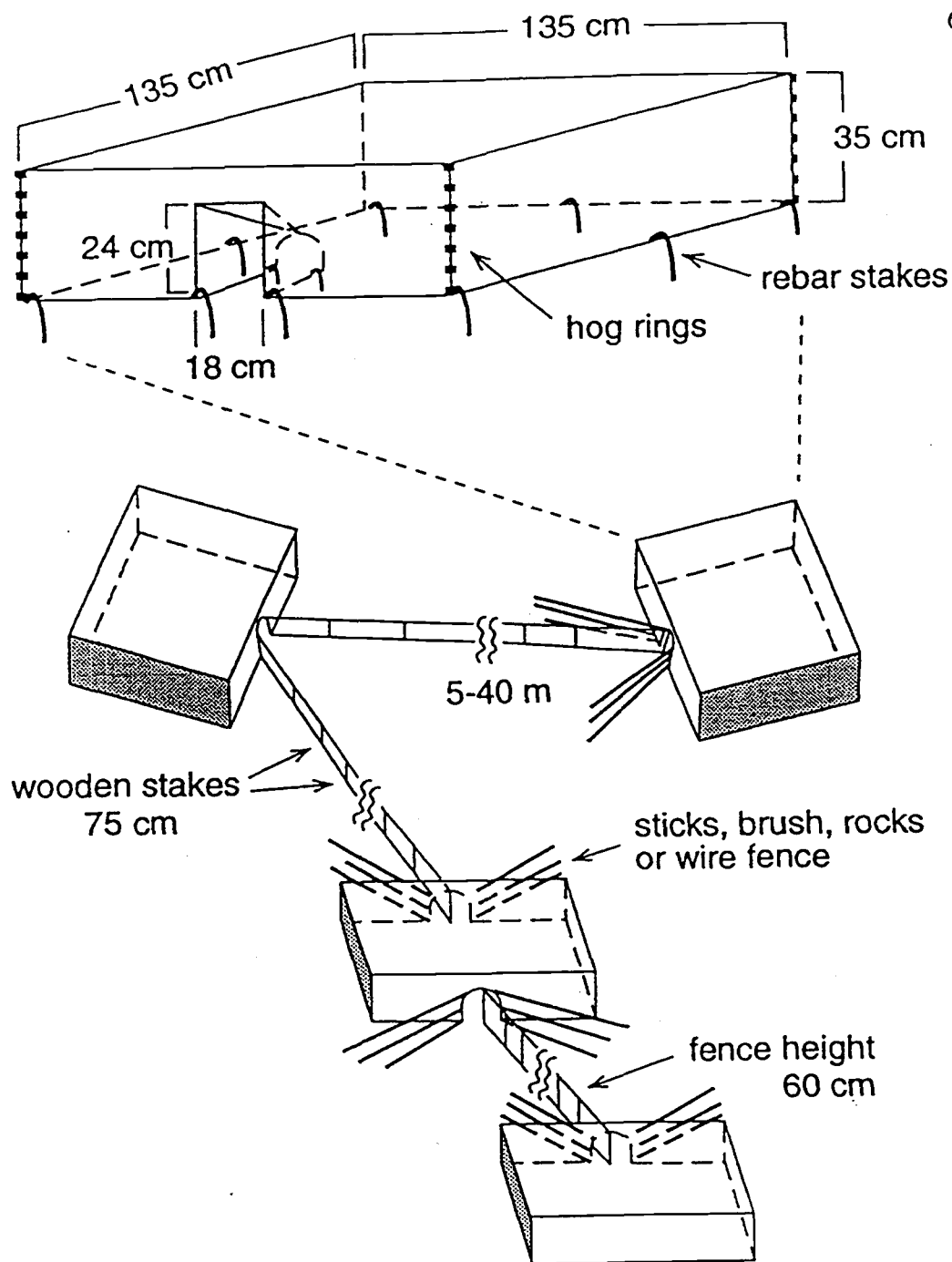Many variations in design, material, construction, and placement of walk-in traps

Fig. 1. Interception trap design incorporating V-shaped and linear arrangement for capturing blue grouse.

Table 1. Blue grouse interception trap capture statistics, June through August 1991, 1992, and 1993, in Wallowa County, Oregon.

	Year			
	1991	1992	1993	Total
Number of birds captured	27	50	63	140
Trap-days	618	941	768	2327
Trap-days/capture	23	19	12	17

exist. Flexibility, creativity, and an understanding of the system in which trapping efforts take place are critical for successful application of this trap to specific conditions.

The noosing pole is an effective method for capturing blue grouse in much of its range. This technique requires significantly less time, manpower, and money than traps; however, in areas where birds are too wary to be approached and captured by noosing pole, interception traps may provide a viable alternative capture technique for blue grouse.

ACKNOWLEDGMENTS

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Appendix B. Crop contents of 15 blue grouse collected during winter, Miller Ridge, Wallowa County, Oregon, 1993-1994.

Age and sex	Date collected	Bird wt (g)	Habitat	Content dry wt (g)	Contents
Immature male	14 Dec	1150	Douglas-fir	2	fir needles
Immature male	16 Dec	1125	ponderosa pine	12	pine needles
Immature male	6 Jan	1275	ponderosa pine	4	pine needles
Immature male	19 Jan	1175	Douglas-fir	<1	empty
Immature male	25 Jan	1200	ponderosa pine	12	pine needles, buds
Adult female	2 Feb	975	Douglas-fir	6	fir stem tips, needles
Adult female	16 Feb	975	Douglas-fir	3	fir stem tips, buds, needles
Immature male	16 Feb	1150	ground	7	pine needles
Adult female	18 Feb	990	Douglas-fir	9	fir needles, buds, rock
Immature female	14 Mar	900	Douglas-fir	<1	fir needles
Immature male	14 Mar	900	ground	2	fir stem tips, buds, needles
Immature male	14 Mar	900	ground	<1	empty
Immature male	14 Mar	1300	Douglas-fir	1	pine needles
Adult male	15 Mar	1360	ponderosa pine	12	95% pine needles, 5% forbs[a]
Immature male	16 Mar	1200	ground	3	60% fir needles, 40% forbs[b]

[a] prairie star (Lithophragma spp.), strawberry (Fragaria vesca), yarrow (Achillea millefolium), and dandelion (Taraxacum officinale).
[b] sage buttercup (Ranunculus glaberrimus), yarrow, mustard.