

*Dendragapus
obscurus*

FRENCH:
Tétras sombre
SPANISH:
Gallo azul

Blue Grouse

Blue Grouse, endemic to mountainous regions of western North America, have a restricted geographic range. Nevertheless, they occupy a wide range of breeding habitats from maritime to continental in climate, from sea level to 3,600+ m in elevation, and from northwestern coast rainforest to shrub/steppe high desert and subalpine/alpine tundra. Virtually all populations winter in conifer forest, where conifer needles comprise the main winter food. Their distribution appears to be partly determined by the proximity of suitable breeding areas to montane forest acceptable for use in winter. As a species, they share physical and behavioral attributes with both "forest" and "prairie" grouse in the subfamily *Tetraoninae*. Eight subspecies separate into two clear groups, interior and coastal.

Blue Grouse can attain high population densities and are still distributed throughout most of their historic range. Occupation of relatively inaccessible montane forests during much of the year contributes to a healthy current status in most areas.

**The
Birds of
North
America**
Life Histories for
the 21st Century

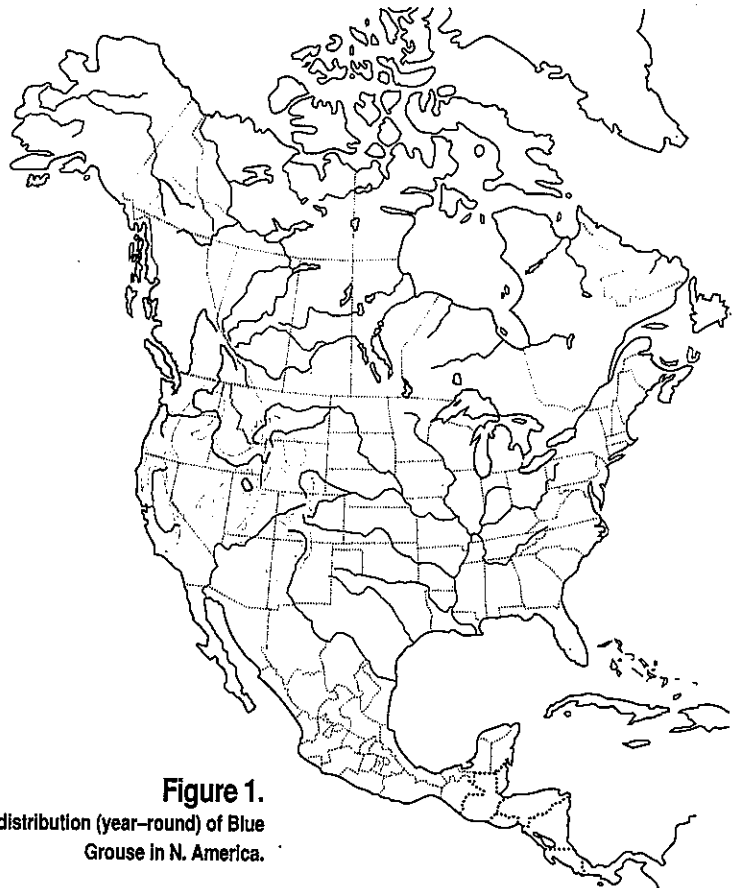
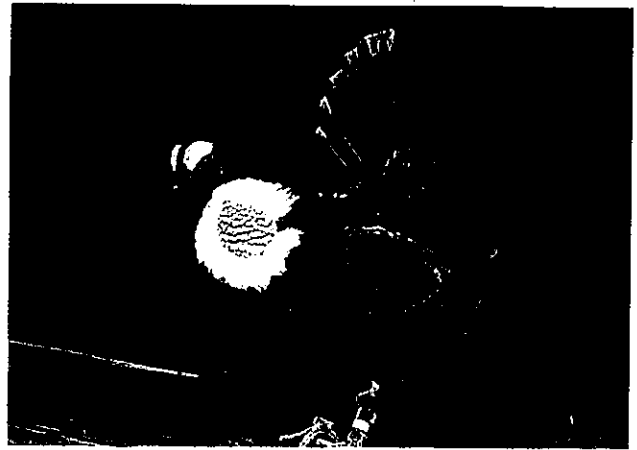


Figure 1.
The distribution (year-round) of Blue
Grouse in N. America.



DISTINGUISHING CHARACTERISTICS

Second largest among nine North American tetraonines, fourth largest among all tetraonines. Body length of adult males (coastal British Columbia (BC)) averages 50.1 cm, females 44.8 cm; mass 1,273 g (males, spring-summer), 839 g (females, summer). Males and females dimorphic in color—males bluish to blackish gray, females brownish gray to brown—and size. Females about 75% as heavy as males in autumn, about 80% in spring, and about 65% at end of incubation (FCZ). A heavy-bodied grouse with moderately long, rounded wings and 10 primaries; moderately long, unspecialized tail. Fourteen secondaries and 4 tertials appear usual. Rectrices 15 to 22: about 80% of four coastal subspecies and *D. o. obscurus* have 18, about 70% to 80% of *D. o. pallidus* and *D. o. richardsonii* have 20; not clear for *D. o. oreinus* (Zwickel et al. 1991). Male with highly specialized cervical apteria (bare neck patch) that are exposed during display. The only grouse in which supraorbital apteria (skin above eyes) of males change basic color, yellow to red, during courtship. Legs feathered to base of toes, with short feathers on small webs between toes 2 and 4.

In the field, females can be confused with those of Spruce Grouse (*Dendragapus canadensis*) and Ruffed Grouse (*Bonasa umbellus*), but are larger than either, with markings on underparts less distinct; generally lack strong tail pattern of Ruffed Grouse.

DISTRIBUTION

AOU CHECK-LIST REGION

Breeding and winter range. Found in all major cordilleras of w. North America, about 33° to 63°N and about 105° to 138°W, and often as disjunct populations in isolated outlier ranges that were likely once ecologically continuous with main cordilleras (Fig. 1). Also found on many coastal islands, some with little topographic relief. Most populations are locally migratory. Successful introductions onto Mt. Taylor, NM (J. Herring pers. comm.); San Francisco Peak, AZ (Brown 1977); Texada (Sugden and Mitchell 1951), Moresby (Bergerud and Hemus 1975), and Lasqueti (FCZ) islands, BC; and, perhaps, the White Mountains, NM (J. Herring pers. comm.). Unsuccessful introductions into Ontario (Speirs 1985), the Black Hills, SD (Kranz 1976), Kodiak Island, AK (Burris and McKnight 1973), Sidney and Portland islands, BC (Bergerud and Hemus 1975), and Orcas (C.F. Martinsen pers. comm.) and Stuart (Bergerud and Hemus 1975) islands, WA.

FOSSIL HISTORY

Two extinct species of Blue Grouse, *D. lucasi* and *D. gilli*, are described from late Pleistocene deposits not more than 29,000 years old at Fossil Lake, OR (Jehl 1969). *D. gilli* also reported from northern California. Jehl considers *D. lucasi* the most likely ancestor of *D. obscurus*. No other fossil localities.

SYSTEMATICS

Four interior subspecies, *D. o. obscurus*, *oreinus*, *pallidus*, and *richardsonii*, are separated from four coastal subspecies, *D. o. howardi*, *sierrae*, *fuliginosus*, and *sitkensis*, most clearly by characteristics of the male (Ridgway and Friedman 1946). Apparent hybrids between interior and coastal subspecies have been reported (Munro and Cowan 1947, Zwickel et al. 1991). Interior and coastal groups were once considered as separate species, *D. obscurus* and *D. fuliginosus*, respectively. Taxonomic relationship of interior to coastal subspecies is still moot.

Blue Grouse have hybridized with Sage Grouse (*Centrocercus urophasianus*; Rensel and White 1988), Sharp-tailed Grouse (*Tympanuchus phasianellus*; Brooks 1907), Spruce Grouse (Jollie 1955), Ruffed Grouse (Batterson 1957), and Ring-necked Pheasant (*Phasianus colchicus*; Hudson 1955). Contrary to present convention (AOU 1983), Blue Grouse may have evolved from a prairie grouse ancestor and may be more closely related to Sage than Spruce Grouse (Bendell and Zwickel 1984).

MIGRATION

NATURE OF MIGRATION

Autumn migration is usually from relatively open breeding areas to denser conifer forest (Anthony 1903, Wing 1947). Most birds move from low elevation breeding areas to montane forests at upper elevations; less commonly from alpine/subalpine breeding areas to subalpine or lower coniferous forests. Interior subspecies north of about 54°N are largely confined to the alpine/subalpine zone in breeding season. Their autumn migration is presumably downward to montane forest or into conifers of the subalpine. On the northwest coast, breeding is common at sea level and some individuals winter at or near this elevation. Some populations or individuals may not migrate (Hoffmann 1956, Rogers 1968), but the reason for differences among or within populations is not known; probably related in part to proximity of winter habitat to breeding habitat.

TIMING AND ROUTES OF MIGRATION

Timing. Movement to breeding range is rapid (Wing 1947). On lowland Vancouver Is., BC, adult males arrive late Mar to early Apr, followed shortly (mid-Apr) by yearling males and adult females; yearling females about one week later (Zwickel 1977), with some overlap among sex/age classes (see Fig. 4). Return to winter range is more protracted (Anthony 1903, Wing 1947). Males leave breeding range before hens with broods (Bent 1932, Bendell 1955b). On Vancouver Is., 11 radio-marked yearling males initiated return to winter range 3–27 Jun (mean = 18 Jun); 11 broodless females, 14 Jun–22 Aug (mean = 19 Jul), about four weeks after loss of nests or broods (Sopuck 1979). Most adult males leave breeding range by 31 Jul (Bendell 1955a, Zwickel 1972a), but few brood females before 1 Sep (Bendell and Elliott 1967). On Hardwicke Island, BC, first of 9 radio-marked adult males abandoned breeding territory on 17 or 18 Jun; 8 of 9 by 20 Jul, and the last 11 Aug (Lewis 1985b). Pattern for Vancouver (Fig. 4) and Hardwicke islands seems general, but dates may vary among areas and years. Most birds in most areas have abandoned breeding range by Oct (Anthony 1903, Wing 1947, Mussehl 1960, Standing 1960, Zwickel 1972a).

Routes. Routes reflect mainly the juxtaposition of breeding to wintering areas, not particular compass orientations (Bendell and Elliott 1967, Sopuck 1979, Mussehl 1960, Zwickel et al. 1968).

Distances moved, altitude changes. Most records based on hunter recoveries of birds banded on breeding range. Some may not have reached winter sites when killed and some movements may be dispersive wandering of juveniles rather than migration. Longest direct recovery was for a juvenile female in ne. Washington, killed 50 km from where banded. Here, of five yearling/adult females, one was killed 35 km, two 29 km, one 18 km, and one 8 km from where banded. Winter range could have been reached within 2 km in all cases (Zwickel et al. 1968). Fifty percent of 30 recoveries here were more than 8 km and 30% more than 16 km from where birds were banded. Recovered birds were spread over an area about 25 times larger than that in which banded. Most were banded at less than 915 m elevation but killed above that elevation, some at 1,525 m. Blue Grouse show roughly similar trends in other regions, although most move shorter distances (Mussehl 1960, Boag 1966, Sopuck 1979). Median distances moved by males ($n = 11$) and females ($n = 19$) in Colorado were 10.6 and 1.2 km, and median gains in elevation 450 m and 120 m, respectively, both significantly different between sexes (Cade 1985).

MIGRATORY BEHAVIOR

In ne. Oregon, birds moving to breeding range walked to the tops of ridges and "sailed until the rising ground brought them to the surface of the snow on the south side of the creek" (Anthony 1903: p. 25). They then climbed on foot to tops of those ridges, repeating the performance downward toward breeding range. Movements were by singles, pairs, or small flocks and flights were at about sunrise or sunset. Anthony reported that the return migration is similar but Lance (1970), on Vancouver Is., followed a radio-marked brood about 10.5 km toward winter range for 6 days and the birds did not fly, up or down slope. Travel was by day only and unidirectional, heading, on day 6, within 2° of the direction on day 1. Migration toward winter range begins abruptly with a long, directional move from a restricted summer home range (Lance 1970, Sopuck 1979). Sopuck documented rates of travel of five radio-marked yearling/adult hens as 1.0, 1.2, 1.7, 1.8, and 1.8 km/d.

No direct studies on control and physiology of migration but gonadal development is under way in yearling/adult males and adult females at time of arrival on breeding range (Hannon et al. 1979). Thus, spring migration is likely hormonally mediated, although gonads of yearling females develop after arrival on breeding range. Return to winter range of males and broodless females coincides with gonadal regression; here too, hormones are likely involved. Brood hens leave breeding range about when parent/offspring bonds are weakening and broods disbanding (Zwickel et al. 1968, Hines 1986b), suggesting that physiological influences may initiate the movement. Timing may be modified by availability of food or desiccation of vegetation (Mussehl 1960, Bendell and Elliott 1967).

HABITAT**BREEDING RANGE**

Interior subspecies. May occur in shrub/steppe and grassland communities out to 2+ km from forest edge; in or along edge of virtually all montane forest communities with relatively open tree canopies; and in alpine/subalpine ecotones. From south to north, they may occupy some of the hottest and most xeric to some of the coldest (but dry) montane habitats in North America. Shrub/steppe habitats most used are dominated by big sagebrush (*Artemisia tridentata*) and/or bitterbrush (*Purshia tridentata*), with various mixtures of bunchgrasses and xeric herbs; forest habitats by

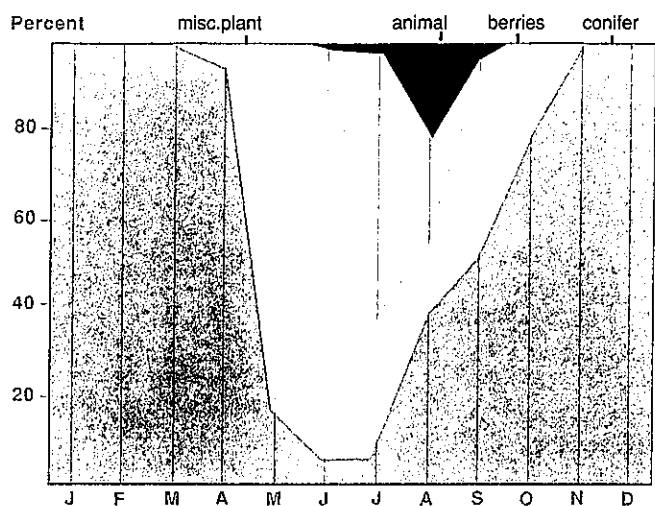


Figure 2.
Foods of adult
Blue Grouse in
different months of
the year (redrawn
from Beer 1943).

ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), and true firs (*Abies* spp.), alone or in combination. Shrub/steppe and forest habitats often are mixed with varying amounts of quaking aspen (*Populus tremuloides*).

Coastal subspecies. Subspecies *howardi* and *sierrae* do not reach the coast and occupy relatively open montane forest from lower tree line to the alpine/subalpine. Forest communities are structurally and climatically similar to those of interior subspecies but shrub/steppe communities seem little used. Subspecies *fuliginosus* and *sitkensis* breed in forest habitats from sea level to alpine/subalpine. Climate is generally maritime, with moderate temperatures; in the north, very mesic. Lowland forest is a principal habitat; in the south it is most often dominated by Douglas-fir and north of about 50°N, by western hemlock (*Tsuga heterophylla*), with various mixtures of western red cedar (*Thuja plicata*), and Sitka spruce (*Picea sitkensis*). Old-growth forest and early forest serres following logging and/or fire are both occupied (Zwickel and Bendell 1972, Doerr et al. 1984, Niederleitner 1987). A key component of breeding range appears to be a well developed herb/grass/shrub stratum (Zwickel and Bendell 1985). Birds may pass through various vegetation zones in moving between breeding and winter ranges.

WINTER RANGE

Almost exclusively montane conifer forest though some birds in Colorado may remain year-round on "brush range" up to 16 km from conifers (Rogers 1968). May winter in coastal forest near sea level to coastal and interior montane forest, including subalpine forest (King 1971); in stands dominated by any of the following conifers, alone or in combination: white fir (*Abies concolor*; Hoffmann 1956), spruce (*Picea engelmannii*)/

subalpine fir (*Abies lasiocarpa*; Cade and Hoffman 1990), Douglas-fir (Beer 1943), lodgepole pine (*Pinus contorta*; Cade and Hoffman 1990), limber pine (*Pinus flexilis*; Zwickel and Bendell 1986), western hemlock (Hines 1987), mountain hemlock (*Tsuga mertensiana*; King 1971), and perhaps, pinyon pine (*Pinus edulis*; Pekins et al. 1989). Many birds winter at high elevations: on Vancouver Is. > 1,220 m (King 1971), in Idaho > 1,800 m (Marshall 1946) and > 2,285 m (Stauffer and Peterson 1985), in Colorado > 2,530 m (Cade and Hoffman 1990). See Schroeder (1984) for more detailed review of habitat use.

FOOD HABITS

FEEDING

Main foods taken. Mainly vegetable matter throughout year (Fig. 2) but heavy use of invertebrates by small juveniles. In some areas, grasshoppers (Orthoptera) may be taken heavily by older grouse in mid- to late summer.

Microhabitat for foraging. On breeding range, territorial males feed mainly within confines of their territories. Those with arboreal songposts tend to feed within trees from which they sing. In spring, hens may be attracted to clearings for foraging (Bendell and Elliott 1967). Hens with young broods often select open areas (Wing et al. 1944, Armleder 1980), often mesic sites with lush vegetation (Mussehl 1963, Bendell and Elliott 1967), perhaps due to insect abundance (Wing 1947). In mid- to late summer, broods may move to more mesic sites (Marshall 1946, Zwickel 1973) or those with greater canopy cover (Wing et al. 1944, Armleder 1980) as vegetation in open areas dries. Whether related to microclimate or foraging is not clear.

Food capture and consumption. Feeding diurnal, with strong bouts in crepuscular hours. In spring/summer, feed mainly from the ground, except males with arboreal songposts; territorial males break for short feeding sessions between bouts of singing. In early spring, may fly into deciduous trees for newly emerging leaves; mid- to late summer may fly into tall shrubs for berries. Conifer needles may be taken whole, or more often, distal end clipped off. Conifer buds may be taken alone or with portions of twigs. A well-developed crop allows storage of up to 45 g (Beer 1943), or more, of food. Incubating females feed voraciously when off the nest. In winter, birds may spend several days in a small group of feeding trees. Small stones or hard seeds (grit) are used for grinding foods in a well-developed muscular ventriculus (Beer and Tidyman 1942). Grit may

contribute some nutrients (King and Bendell 1982) and, in areas with deep snow, may be retained throughout winter (Marshall 1946).

DIET

Major food items. *SPRING/SUMMER:* leaves and flowers of herbs; leaves, flowers, and berries of shrubs; conifer needles (especially coastal populations); and invertebrates (especially young juveniles). Diet includes a broad spectrum of plant species that vary locally, change seasonally, and may be eaten only when phenologically appropriate, e.g., fruits when ripe. Food plants recorded by Beer (1943) from Oregon, Washington, and Idaho include: hawthorn (*Crataegus* sp.), currants (*Ribes* spp.), serviceberry (*Amelanchier* spp.), strawberry (*Fragaria* spp.), rose (*Rosa* spp.), fruits of *Rubus* spp., bearberry (*Arctostaphylos uva-ursi*), huckleberries (*Vaccinium* spp.), salal (*Gaultheria shallon*), and small amounts of *Agoseris* sp., *Arnica* sp., *Balsamorhiza* sp., *Erigeron* sp., and *Taraxacum* sp.; principal invertebrates were ants (Formicidae), beetles (Coleoptera), and grasshoppers. Other common summer foods in some areas: buffalo berry (*Shepherdia canadensis*), cherry (*Prunus* sp.), buckwheat (*Eriogonum* spp.), and vetch (*Vicia* spp.; Stewart 1944). Major plant foods on Vancouver Is.: Douglas-fir, willow (*Salix* spp.), bracken fern (*Pteridium aquilinum*), salal, clover (*Trifolium repens*), red huckleberry (*V. parvifolium*), cat's ear (*Hypochaeris radicata*), and blackberry (*Rubus ursinus*), with ants and spittle bugs (Cercopidae) the main animal foods (King and Bendell 1982). In subalpine Vancouver Is., the most important summer foods were three species of *Vaccinium* (King 1973). Western larch (*Larix occidentalis*) may be used heavily in late summer/autumn (Beer 1943).

WINTER: conifer needles are staple items, late autumn to early spring; also smaller amounts of conifer buds, twigs, and staminate cones. Douglas-fir (Beer 1943, Stewart 1944) and true firs (especially *Abies grandis* and *A. nobilis* (Beer 1943) and *A. concolor* (Hoffmann 1956) provide the major winter diet for some populations. Some pines (*Pinus* spp.), especially lodgepole and limber, provide principal foods in other areas (Zwicker and Bendell 1986). Western hemlock (Beer 1943, Hines 1987) and mountain hemlock (King 1971) may provide most of the winter diet for north coastal and some high altitude populations, respectively. Blue Grouse subsist on a variety of different conifers, alone or in combination (Zwicker and Bendell 1986, Pekins et al. 1989, Cade and Hoffman 1990).

Quantitative analysis. Year-round food habits of adults are heavily oriented toward conifer needles except in spring/summer (Fig. 2), but

with variation among areas. Proportions of different food items used may vary among sex/age classes; e.g., juveniles eat mainly animal matter in first 3 to 4 weeks of life, and coastal males may feed mainly on conifer needles, even on breeding range (Beer 1943, King and Bendell 1982). Amount of conifer in winter diet is usually > 90%, but the main genera may vary among areas, e.g., *Pseudotsuga* and/or *Pinus* for interior birds; *Abies*, *Pseudotsuga*, and/or *Tsuga* for coastal birds (Beer 1943, Stewart 1944, King 1973, Zwicker and Bendell 1986, Hines 1987).

NUTRITION AND ENERGETICS

Juveniles. No empirical information on gross daily consumption. Mean daily food requirements of 1 to 4 week-old juveniles estimated as 15.5, 32.4, 61.1, and 130.1 g per day, each week, respectively; metabolizable energy (ME) requirements as 14.1, 27.5, 53.1, and 91.1 kcal per day, respectively (Stiven 1961). Animal foods during this period were calculated as yielding 0.91 kcal/g (wet weight), plant foods, 0.57 kcal/g. Seven invertebrate groups averaged 69.3% crude protein; seven plant foods 13.3% crude protein (% dry weight). Compared to plants, invertebrates eaten by juveniles are lower in CHO, ash, and Ca, but higher in N, P, and Na (King and Bendell 1982).

Adults. No information on gross daily consumption or requirements of wild birds. In captivity, mean daily dry matter consumptions of Douglas-fir needles in winter by two males, and two females, were 93.8 ± 0.97 g/bird (wet mass = 187.7 ± 1.85 g [2 mean errors = SE throughout account]) and 79.4 ± 1.21 g/bird (wet mass = 151.3 ± 2.31 g), respectively (calculated from Remington 1990).

Composition of plants eaten by adult females in May and June on Vancouver Is.: 70% CHO, 10% fat, 6% ash, 2.6% N, 0.3% P, 1% K, 0.6% Ca, 0.2% Mg, % dry weight (King and Bendell 1982). White fir needles, the principal winter food at one site in California, had a crude protein content of about 4% to 7% (Hoffmann 1961). Lodgepole pine needles, a principal winter food in se. Alberta, a crude protein content of 4.52% and a caloric content of 4.97 kcal/g (Boag and Kiceniuk 1968). No seasonal differences in protein levels at either area. Based on trials with captive birds (Remington 1990), ME of four potential winter foods ranked as follows: Douglas-fir (1.75 kcal/g dry matter) = lodgepole pine (1.69 kcal/g) > subalpine fir (1.51 kcal/g) > Engelmann spruce (1.12 kcal/g). Metabolizable nitrogen (MN) followed the same rank order. ME and MN tended to decline as age of needles increased. Birds maintained body mass on a diet of Douglas-fir but not with the other

species. Pekins (1988) reported the mean caloric equivalent of the winter field metabolic rate (FMR) of seven wild males as 157 kcal per day, within 2% of that provided by an average daily diet of Douglas-fir, 153 kcal. Digestibility by captive Blue Grouse of neutral detergent fiber in needles of Engelmann spruce, Douglas-fir, lodgepole pine, and subalpine fir averaged 13%, range = 7.5%–17.3% among species (Remington 1989). Among tetraonines, Blue Grouse have relatively short ceca but a high-fiber diet (Remington 1989).

METABOLISM AND TEMPERATURE REGULATION

Mean body temperature of yearlings and adults on Vancouver Is. = $42.1 \pm 0.05^\circ\text{C}$, range = 40.1°C – 43.3°C , $n = 120$ (FCZ). Standard metabolic rate (SMR) of *D. o. obscurus* in Utah = $0.812 \text{ LO}_2/\text{kg}^{0.734}/\text{h}^{-1}$ in winter (Pekins et al. 1992), $0.751 \text{ LO}_2/\text{kg}^{0.734}/\text{h}^{-1}$ in summer (P. Pekins pers. comm.). Lower critical temperature occurs between -5° and -10°C in winter, lower than reported for Ruffed Grouse, Rock Ptarmigan (*Lagopus mutus*), and Black Grouse (*Lyrurus tetrrix*; P. Pekins pers. comm.). Winter FMR averaged $1.4 \times \text{SMR}$ as measured with doubly-labeled water. Thus energetic constraints on Blue Grouse occupying suitable habitat during winter appear to be minimal (Pekins 1988).

DRINKING AND DEFECACTION

Free water is used on breeding range (Beer 1943, Wing et al. 1944) but may not be required if succulent foods are available (Beer 1943). On dry commercial food, Blue Grouse drank only about half as much water per mass as Ruffed Grouse (Bendell and Elliott 1966).

Three principal kinds of droppings are produced by Blue Grouse: intestinal, cecal, and clocker. Intestinal droppings are cylindrical, generally low moisture excreta that have bypassed the ceca, although moisture content may vary with succulence of the diet. Winter intestinal droppings are most consistent, mainly fibrous remnants of conifer needles. Individual winter feeding trees may have accumulations of intestinal droppings up to 2.5 cm deep (Marshall 1946), ≥ 1 bushel beneath them (Beer 1943). Overnight snow roosts contain 18 to 24 intestinal droppings (King 1971). Cecal droppings are dark greenish, amorphous, and very moist. They are likely evacuated from the ceca once each day, at termination of night roosting. Clocker droppings are composed of intestinal droppings that accumulate to form a large spiral-like mass in incubating hens; appearance suggests a high content of uric acid. After a bout of incubation, this dropping is usually evacuated at some distance from the nest, though hens may leave it in or near

nest at time of final departure. Clocker-like droppings may be produced by hens after overnight brooding of very young juveniles (Zwickel 1967a).

FOOD SELECTION

Preferences may vary among age classes and season (Beer 1943). On Vancouver Is. in spring, the birds select leaves of willow, bracken fern, and huckleberry, and needles of Douglas-fir (King and Bendell 1982); in mid- to late summer, select leaves and flowers of clover, flowers of cat's ear, and berries of salal, huckleberry, and blackberry. Many common plants, or parts thereof, avoided, e.g., fireweed (*Epilobium angustifolium*), grass (Gramineae), bracken fern, and leaves of cat's ear. Flowers of cat's ear selected; higher in fat, ash, N, P, K, Mg, and Na than those of rarely eaten salal. Summer juveniles take most invertebrates as available, but avoid flies (Diptera), spiders (Arachnida), and Lepidoptera larvae. Adults take invertebrates less frequently than available. No relationship found between selection and chemical composition of fruits or groups of invertebrates (King and Bendell 1982). In winter, needles of Douglas-fir, some pines (especially lodgepole), and some true firs selected; those of spruces and subalpine fir avoided (Beer 1943, Pekins et al. 1989, Cade and Hoffman 1990, Remington 1990). Within species, particular trees may be selected for feeding, e.g., dwarf or stunted trees near timberline or larger trees within a stand (Wing 1947), larger trees within parkland (King 1971), Douglas-firs with atypical or stressed growth patterns (Remington 1990, Pekins et al. 1991). In winter, in Colorado, birds fed mainly in the mid- to upper canopy of older Douglas-firs, on 1- to 2-yr-old needles. No consistent relationship between species of trees selected, or needles selected within a species, and the content of N, neutral detergent fiber, acid detergent fiber, lignin, or monoterpenes (Remington 1990). The basis for selection was often not always clear, but the net effect was that ME and/or MN was maximized.

SOUNDS

VOCALIZATIONS

Basic vocalizations similar throughout range. Some variation between songs of interior and coastal males. Males have a repertoire of 1 song and 2 calls (perhaps 3 calls, or 1 with 2 variants); females have about 11 calls (Albright 1985).

Vocal development. Soft clicking heard within egg about one day before pipping and during hatching. Small juveniles may "peep" during brooding, and while feeding. Peeping seems to

signify contentment and may help maintain contact between hen and juveniles. Juveniles that seem to lose contact with the hen "wail," causing her to respond. Wailing becomes louder with age, perhaps carrying as much as 400 m under favorable weather and topographic conditions (Zwicker 1967a). At about 3–4 weeks of age, wailing takes on a vibrato and seems to decrease in pitch; peeping ends but birds may give short chirps when disturbed. At about 5–6 weeks, juveniles may give short hen-like clucks. Yearling females seem to have full array of adult vocalizations. Yearling males may sing, perhaps more softly than adults (McNicholl 1978), but may not "whoot" (Jamieson 1985).

Vocal array. MALES: the song of interior males, the "hoot," usually has five syllables, that of coastal males six (Johnsgard 1983); syllables per song may vary from 1 to 5 at start-up of singing (McNicholl 1978). Fundamental frequencies of the hoot of interior and coastal males differ. Hjorth (1970) reports 50–100 Hz for interior males, 110–150 Hz for coastal males; Degner (1988) reports 100–110 Hz for *pallidus*, 110–175 Hz for 4 populations of *fuliginosus*, the mean tending to increase from south to north. Song of interior males is soft, often inaudible beyond 30 m (Rogers 1968) to 40 m (Hjorth 1970); that of coastal males is loud, often audible beyond 300 m (Stirling and Bendell 1970), up to 500 m (Hjorth 1970). Loudness can be varied by the individual (McNicholl 1978). Males often sing in small groups (Bendell and Elliott 1967), likely countersinging (Lewis 1985a), and individuals discriminate between songs of neighbors and strangers (Falls and McNicholl 1979). A precopulatory call, the whoot (Stirling and Bendell 1970), or single hoot (Hjorth 1970), is given at termination of a courtship rush toward a female (Stirling and Bendell 1970). Fundamental frequency is higher than that of the hoot, 200–300 Hz (Hjorth 1970, Degner 1988), with no clear distinction between interior and coastal subspecies. Males produce a "growl" (Stirling and Bendell 1970), the "harsh staccato cantus" of Hjorth (1970), in what appear to be agonistic situations. There are two variants of this call, a relatively soft *gugugug...* given at the approach of a human, and a more harsh *ca-ca-ca...* given to intruding males (perhaps different calls). See sonograms in Hjorth (1970), Stirling and Bendell (1970), and Degner (1988).

Vocal array. FEMALES: Stirling and Bendell (1970) describe two reproductive calls, the "whinny" and the "quaver cry," and one aggressive call, the "hard cluck." Albright (1985), lists 11 possible calls, some with two variants: "cluck," a chicken-like cluck, with prenesting ("hard cluck" of Stirling

and Bendell) and brood hen variants (perhaps different calls), seems to express alarm or concern at times of disturbance and can vary in intensity, length, and loudness. "Cackle" (quaver cry of Stirling and Bendell 1970), peaks at time of breeding and may have a spacing or aggressive function (Hannon 1980). "Whinny," peaks at time of breeding, a precopulatory call that stimulates courtship behavior in males (Stirling and Bendell 1970), a variant (perhaps a different call) is given by brood hens. "Liquid cluck," given by incubating hens near time of hatch or on return to a nest at which a dummy female has been placed (J. Kristensen pers. comm.), appears to be agonistic. "Hiss," given by incubating and brood hens, an aggressive reaction to disturbance. A soft *cu-cu-cu* that may initiate brooding (brood call of Zwicker 1967a) or reassemble juveniles after disturbance (Kristensen 1973), often follows wailing by dispersed juveniles. A softer *cu-cu-cu* (contact call of Zwicker 1967a), similar to the latter call (perhaps a variant), but lower in pitch and nearly inaudible, appears to help maintain contact between hen and juveniles when not disturbed. *Coo*, a very soft, almost inaudible, cooing sound given by incubating hens during late incubation and hatching, sometimes by brood hens with very small juveniles, appears to express contentment. *Kweer-kweer*, a high-pitched cry given by hens returning to a brood after prolonged disturbance, often stimulated by wailing of juveniles, seems to express concern about juveniles under duress. *Kwa-kwa*, a high-pitched call given when a brood is disturbed and the hen "...appeared more solicitous of the brood than usual" (Zwicker 1967a: p. 3), often stimulates juveniles to wail. *Skree*, a high-pitched scream by a brooding hen when disturbed by an intruder, most often given as the hen breaks from brooding. The cluck, cackle, whinny, liquid cluck, hiss, brood call, contact call, and coo are documented on tape, but the others are not.

Fundamental frequencies about 200 to 2000+ Hz, much higher, on average, than those of males. See Stirling and Bendell (1970) and Albright (1985) for sonograms. More work needed on vocalizations of females, including comparisons among subspecies. Presumed functions may be tenuous and some calls, or variants thereof, are likely yet to be described.

Chronology and daily pattern. MALES: singing begins with arrival of first females on breeding range, late Mar to early Apr in many populations. Singing by territorial males more or less continuous throughout day at peak breeding, with short breaks for feeding; wanes during full daylight as the peak is passed. Crepuscular and sporadic daytime

singing may continue by some males as long as they remain on territory (Bendell 1954). Around peak breeding, some males may sing in complete darkness; e.g., coastal BC: 01:20 h ($n = 1$); 03:15–04:35 h ($n = 12+$); 20:30 h ($n = 1$); 23:20 h ($n = 2$; FCZ). In se. Alaska, singing began 58 to 95 min before sunrise ($n = 5$ d) and ended 19 to 65 min after sunset ($n = 7$ d; Stewart 1967). The whoot occurs when males court females. It is most frequent at time of peak breeding and wanes during incubation, with a small surge after hatch when males court brood hens.

FEMALES: Cackles first heard Apr, most frequent in period of peak copulation and egg laying; rarely beyond late May on Vancouver Is. (Hannon 1980). Whinnies follow a similar pattern but may be heard to late June (Stirling and Bendell 1970). Those in June may be the brood hen variant. Clucking and hissing of brood hens most intense if with juveniles up to 4 wk old (Kristensen 1973). Most female calls are chronologically related to particular stages of the breeding/rearing cycle, as described above.

Places of vocalizing. Coastal males usually sing from trees, interior males from the ground (Bent 1932, Johnsgard 1983). Samples from various coastal areas (clear-cuts excluded) showed 94% of 156 males singing from trees; from interior areas, 95% of 199 singing from the ground (FCZ). In se. Alaska, all singing males in old growth forest ($n = 140$) were in trees and 8 of 9 on clear-cuts were in live, residual trees; one was on ground (Doerr et al. 1984). On larger clear-cuts from Oregon to southern British Columbia, coastal males readily adapt to terrestrial songposts. On one clear-cut, 80% of singing males were on ground, 8% on logs, and 12% on stumps ($n = 208$); elevated songposts, knolls, logs, or stumps, are used more at dawn and dusk than during day (FCZ). When disturbed, brood females often fly to elevated posts such as trees or stumps where they may cluck loudly.

NONVOCAL SOUNDS

Array of sounds. **MALES:** Territorial males "flutter-flight:" about 1–m flight with wings fluttering loudly (a ripping sound), a small, circular, twisting flight with one wing apparently beating faster than the other, and a return to, or near, the spot from which the flight began. May be initiated by flutter-flights of other males, by other grouse flying nearby, by approach of females, or by playbacks of some female calls. Most frequent at dawn and dusk during peak breeding period (Wing 1946); may be performed as often as once per minute at peak periods (Harju 1974). Flutter-flight of coastal males less complex, a short, straight flight with wings fluttering loudly; perhaps less frequent than that of interior males. May fly from

ground or from branch to branch in a tree; some variations due to situation and local terrain. Territorial males that are flushed often land with exaggerated wingbeats (McNicholl 1978), "landing on loudwing," especially if they land within the confines of their territory or are reacting to vocalizations or flights of females. This differs from flutter-flights in that fluttering occurs only at termination of flight. Blackford's (1958) "wingclap" has not been verified by other workers. **FEMALES.** No ritualized flutter-flight but may land on loudwing (Bendell and Elliott 1967, Harju 1974).

BEHAVIOR

LOCOMOTION

Walking, hopping, climbing, etc. Generally walk upright but may creep away or run with body almost horizontal to ground when disturbed; disturbed brood hens often run with body in this posture (Kristensen 1973). Tend to crouch and fly from intruders in open areas, but may run in areas with good ground cover. In trees, may hop from branch to branch, spiraling around trunk to gain height. Well adapted to walking along branches for feeding and to gripping branches for roosting. Mainly arboreal in winter (Marshall 1946), but may come to ground, perhaps more often than suggested (Wing 1947, Pekins 1988). Pectinations on toes short (≤ 2 mm) relative to those of the smaller Ruffed Grouse and Sharp-tailed Grouse (FCZ). Adult males carry about 80 g mass/cm² of foot surface, more than twice that of Ruffed Grouse (King 1971), thus probably not well adapted for walking on snow.

Flight. Except for coastal males, generally ground oriented on breeding range. Strong flyer with rapid wingbeats over short distances; good maneuverability in forested areas. Seldom fly voluntarily, mostly to or from trees or shrubs for foraging or roosting, or during courtship, e.g., flutter flights. Can outdistance some large raptors in level flight (FCZ). Not found on most islands more than about 2 km from a source population, so this may be beyond their limit of level flight. Flushed from a high point they may glide, or glide and flap, 2 km or more, but tend to lose altitude. Usually fly downslope or along the contour when flushed but can fly upslope over short distances. May climb steeply from ground into a tall tree.

SELF-MAINTENANCE

Preening, bathing, etc. Dustbathing common on summer range; in finer dry soils, woody debris from well-rotted logs, occasionally in anthills. Whole broods, including hen, may dustbathe

synchronously. Feathers much fluffed in dust-bathing; vigorous shaking. Preening may follow. On breeding range, often appear to sunbathe. In hot weather, often gular flutter, seek shade for loafing. In winter, 71% of 163 grouse observed on sunny days were classified as sunbathing (Pekins 1988). No waterbathing observed.

Roosting. In spring/summer, on shrub/steppe breeding ranges or where forests were clear-cut, most birds roost on the ground, under cover or in open. May fly into nearby trees to roost, if available. On forested breeding ranges, often roost in trees at night. Prior to full thermoregulatory capabilities, small juveniles are brooded on ground; later may roost in trees. In winter, most roosts in trees. Subalpine firs and certain growth forms of Douglas-fir may be used selectively for night roosts to minimize energy costs imposed by weather (Pekins et al. 1991). Snow roosting appears to be less common than in other northern tetraonines (Pekins 1988).

Daily time budget. Few quantitative data available. In spring and summer, almost strictly diurnal or crepuscular. Bursts of courtship activity in morning and evening crepuscular periods, especially at peak of breeding; bursts of feeding activity in same periods. Evening activity rises rapidly, starting at about 4 foot-candles and extending beyond the ability to measure light on a GE exposure meter; peaks at about 2 foot-candles. Morning activity begins before a reading on the meter is possible and declines at 2 to 4 foot-candles (Bendell 1954). Yearling males spend about one-third of time feeding; relatively inactive through most of day, with bursts of activity at dusk (Jamieson 1985). Broods feed throughout much of day. In winter, birds may spend eight weeks or more in a small group of trees, presumably quite inactive except for feeding; may spend entire night, or more, in a snow roost (King 1971).

AGONISTIC BEHAVIOR

Physical and communicative interactions. Most adult males on breeding range defend territories against intruding males, using threat postures, vocalizations (the growl), and physical attack (Bendell and Elliott 1967, Stirling and Bendell 1970, Jamieson 1985). Female/female aggression has been observed in the field in spring (Lewis 1984a, Bergerud and Butler 1985, FCZ); females may peck at their mirror images or kill other females in captivity (Stirling and Bendell 1970). Some nest hens may hiss, fluff feathers, and peck at a hand or other object extended toward them (FCZ). Hens returning from a feeding bout may liquid cluck and attack a dummy female at their nest (Hannon 1978). Hens with small juveniles



Figure 3.
Male courtship display: the "feather spread."
By D. Olte.

may fluff body feathers, droop wings, fan tails, cluck loudly, hiss, and fly at and strike an intruder, or attempt to lead the intruder away (so-called distraction display). Intruders so attacked include a black bear (*Ursus americanus*; Sullivan 1979), a wolf (*Canis lupus*; J. Hines pers. comm.), humans, and dogs. Though common in captivity, no intersibling aggression was noted in wild juveniles to 12 d of age (Zwickel 1967a).

Spacing. Breeding territories of males are mostly exclusive of other males (Boag 1966, Bendell and Elliott 1967, McNicholl 1978); tend to be uniformly spaced (Bendell and Elliott 1967, Martinka 1972, Lewis and Zwickel 1981). A tendency toward clumping, likely related to dispersion of thickets, is reported for one population (Lewis 1985a). Distance between territories may vary with population density and dispersion of habitat. Females may be spaced on breeding range in early spring (Zwickel 1972a, 1980, Hannon and Zwickel 1979, Bergerud and Butler 1985); may be dynamic (related to individual distance) and not related to exclusive home ranges (Hines 1986a). Hens with small juveniles may be dispersed, those without, clumped (Zwickel 1973). No evidence for winter territories, except perhaps adult males (King 1971), but more work is needed.

SEXUAL BEHAVIOR

Mating system and sex ratio. Males are promiscuous (likely polygynous) on dispersed territories (Wiley 1974), but whether females mate with more than one male is not known. Males may court any female with which they come in contact (Bendell 1955a). Communal display (lek behavior) has been suggested, e.g., Blackford (1963), but evidence for this interpretation is weak (Lewis 1985a). Sex ratio is usually, but not always, balanced (Zwickel et al. 1988).

Pair bond. Blackford (1963) suggests season-long pair bonding but the weight of evidence

suggests that on breeding range male and female come together for copulation only (Lance 1970, FCZ). In courtship and copulatory displays, males sing and may perform flutter-flights; both presumably have advertising functions (Bendell and Elliott 1967, Stirling and Bendell 1970). On hearing a female cackle or whinny, or seeing a female at a distance, male may begin phase I of the courtship display, the feather spread (Fig. 3). If female is in view, or advances toward male, he may rush and whoot (phase II), followed by head bobbing (phase III). If ready to mate, the female squats, and may whinny. Male mounts her back, grasps feathers of her nape in his beak, drops his wings over her sides, and treads on her back as he settles his vent to her cloaca. Cloacal contact lasts 2 to 5 sec, after which male dismounts and both birds ruffle their feathers for about 30 sec. Male may resume singing. Courtship and copulatory descriptions as per Stirling and Bendell (1970); also see Hjorth (1970).

SOCIAL AND INTERSPECIFIC BEHAVIOR

Sociality. In general, not social. **SUMMER:** in one sample from Vancouver Is. (Apr to Aug), 97% of 715 males were alone (> 10 m from any other bird), 10 were with another male, and 14 were with a female; 90% of 220 broodless females were alone, 8 were with another female, and 14 were with a male; 154 brood hens were associated only with juveniles. In seven cases, males flew in and courted brood females that clucked in response to disturbance (FCZ). Broods may form loose flocks in late summer, at times without hens. A flock of 45 to 50 birds has been reported in late Jul (Caswell 1954). Pattern of habitat dispersion may produce aggregations (Zwicker 1973).

WINTER: adult males return to winter range alone (Caswell 1954) or in groups of 3 to 6, broodless females alone or in groups of 2 to 3 (Wing et al. 1944). In subalpine habitat on Vancouver Is., adult males were found only alone (King 1971). At lower elevations in coastal BC, all sex/age classes were found both singly, $n = 462$, and in flocks; mean flock size = 2.9 ± 0.1 birds, range = 2–15, $n = 210$ flocks. Grouse associated most often with birds of their own sex/age class (Hines 1986b). Caswell (1954) reported frequent flocks of 6 to 10 birds and, on occasion, loosely associated flocks of up to 20; Cade (1985) most often found birds alone or in flocks of 2 to 6, but occasionally 12 to 20.

Play. Juveniles may perform a "spread tail running act" in late summer (Caswell 1954); this may, or may not, involve other juveniles and whether play or aggression is not known. Also occurs in captivity (FCZ).

Table 1. Geographic variation in time of peak hatch for Blue Grouse.

AREA	LATITUDE	PEAK HATCH	SOURCES ¹
Green Mt, CO	39° 52'	22 Jun–5 Jul	1
Centennial, WY	41° 18'	15–28 Jun	2
Enterprise, OR	44° 38'	22 May–4 Jun	3
Vancouver Is., BC ²	49° 42'	11–24 Jun	4
Vancouver Is., BC ³	49° 43'	1–14 Jul	5
Sheep River, AB	50° 20'	15–28 Jun	6

¹1, Hoffman (1981); 2, Harju (1974); 3, Crawford et al. (1986); 4, FCZ; 5, King (1971); 6, Boag (1966)

²Lowland population

³Subalpine population

Interspecific interactions. Have been closely associated with Gray Partridge (*Perdix perdix*; Caswell 1954). Broods also have intermingled with young Ruffed Grouse (Wing et al. 1944) and Chukar Partridge (*Alectoris chukar*; FCZ). Sympatric with Ruffed Grouse and Spruce Grouse in much of range but tend to separate locally based on different use of plant communities. Brood ranges may overlap with those of Ruffed and Spruce Grouse in forest habitats and of Sage and Sharp-tailed Grouse in shrub/steppe habitats.

PREDATION

Most nest failures result from predation (Zwicker et al. 1988). In one sample, 88% of 34 destroyed nests were terminated by mammals, the remainder by birds (FCZ). Raptors were responsible for 75%, mammals for 25% of 155 kills of yearlings/adults in coastal BC; raptors for 35%, mammals for 65% of 20 kills of juveniles, as determined from remains (FCZ). Data for juveniles may be biased due to total consumption of small individuals. Northern Goshawk (*Accipiter gentilis*), Red-tailed Hawk (*Buteo jamaicensis*), Golden Eagle (*Aquila chrysaetos*), Prairie Falcon (*Falco mexicanus*), Great Horned Owl (*Bubo virginianus*), and Canada lynx (*Lynx canadensis*) are known predators of adults. Circumstantial evidence implicates Bald Eagle (*Haliaeetus leucocephalus*), coyote (*Canis latrans*), wolf, red fox (*Vulpes vulpes*), black bear, badger (*Taxidea taxus*), mountain lion (*Felis concolor*), bobcat (*Lynx rufus*), and either short-

tailed weasel (*Mustela erminea*) or marten (*Martes americana*). Goshawk, Sharp-shinned Hawk (*Accipiter striatus*), Cooper's Hawk (*A. cooperii*), Red-tailed Hawk, Merlin (*Falco columbarius*), Prairie Falcon, and red fox are known predators of juveniles. Where found, Northern Goshawks appear to be the most important predators on birds themselves; 74% of 19 witnessed successful attacks in coastal BC were by this species (FCZ).

BREEDING

CHRONOLOGY

Pair formation. Males court females any time they are encountered on breeding range, beginning late Mar to early Apr on Vancouver Is.; first copulations by adult females late Apr, peak first week of May (lowland areas). Yearling females about one week later. Copulations, including those for renesting, span a period of about 10 wk thereafter. Geographic and local variation in start of breeding depends on climate, as does annual variation at each locale (Zwicker 1977).

Breeding chronology. Fig. 4. First eggs lowland Vancouver Is. late Apr; peak first half of May (Zwicker 1977). Hatch about 40 d after copulation, with about 60% in a two-week period (Zwicker 1977). Breeding chronology (illustrated by peak hatch) varies among areas (Table 1), apparently related to local phenology, the latter partly dependent on altitude. One brood per season; second nest may be initiated 14 to 15 d after destruction of first nest, even late in incubation (Zwicker and Lance 1965, Sopuck and Zwicker 1983). Renesting may be absent in populations with late breeding seasons, e.g., Colorado (Table 1).

NEST SITE

Selection process. By female only. Nests are almost always outside male territories (FCZ), perhaps to avoid repeated courtship advances. Nests are rarely within about 50 m of another nest, suggesting spacing, but on Vancouver Is. two active nests were under the same shrub, about 2 m apart. Both hatched (FCZ).

Site characteristics. Extremely variable but almost always on ground; 2/605 on stumps. May be on recent burns with virtually no cover (Zwicker and Bendell 1972) and in virtually all community types occupied in breeding season. Most nests have overhead cover (Caswell 1954), but single dead twig will suffice. Among 605 nests, <1% had no overhead cover (FCZ). In young coastal forest serres, most nests are under small conifers (62%) or logs or stumps (27%), $n = 488$; in interior forests,

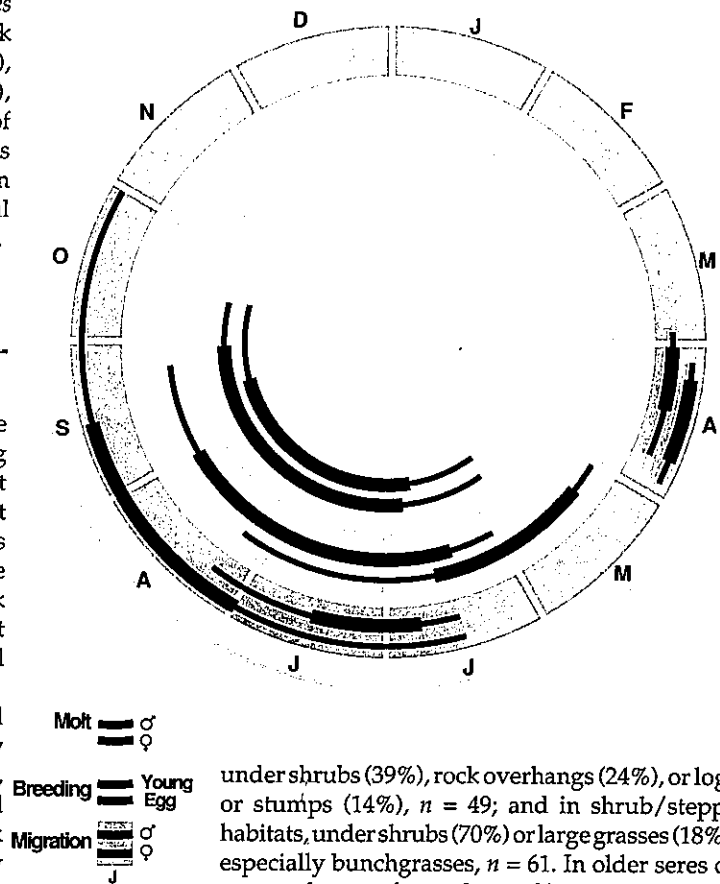


Figure 4. Annual cycles of breeding, molt, and migration for Blue Grouse of lowland Vancouver Is., BC.

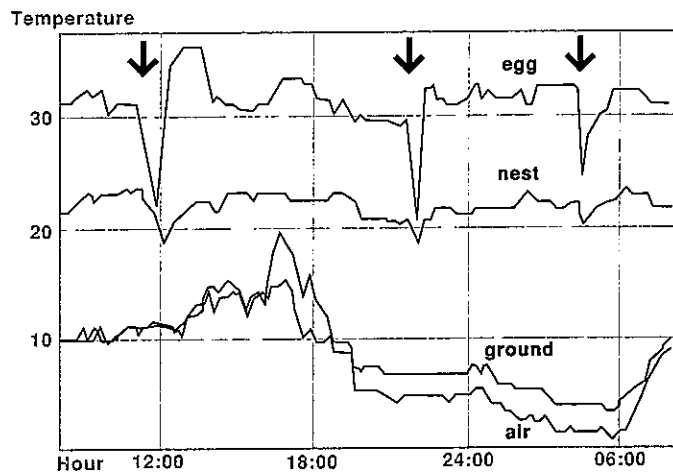
Thick lines equal peak activity, thin lines off peak activity.

under shrubs (39%), rock overhangs (24%), or logs or stumps (14%), $n = 49$; and in shrub/steppe habitats, under shrubs (70%) or large grasses (18%), especially bunchgrasses, $n = 61$. In older serres or mature forest, often at base of large tree with no immediate cover except trunk (FCZ). Subalpine nests often under krummholz subalpine fir (M. Degner pers. comm.).

Nests (hens or eggs) may be in full view or hidden, e.g., under dense, overhanging limbs of small conifers. Nest site may change with growth of vegetation, from barren at time of laying to lush and well concealed at hatch. In young coastal forest, median distance of 435 nests from free-water was 50 m, range = <1–550 m; on an interior shrub/steppe range in Washington, median distance of 24 nests from free-water was 150 m, range = 10–800 m (FCZ).

NEST

Dimensions, construction. A shallow scrape in the ground about 17 cm in diameter, 4–5 cm deep (Caswell 1954). On Vancouver Is., 18 nests averaged 22 ± 0.4 cm in diameter and 8 ± 0.6 cm deep (ranges = 17.8–22.9 cm and 1.3–12.5 cm, respectively; FCZ). Nest bowls often poorly lined, mainly with dead vegetation (leaves, twigs, needles, moss, bark, rotted wood), apparently within reach of hen on nest; usually contain a few contour feathers, perhaps from brood patch.



Microclimate. Probably variable, but little direct study; sites range from coastal old-growth forest (humid sites) to xeric shrub/steppe (hot, dry sites), to subalpine habitats (cold sites). Some sites completely concealed and shaded, others with little cover from sun or rain. At one nest on Vancouver Is., mean temperatures of egg surface and nest bottom thermistors when hen was on the nest were $32.2 \pm 0.16^\circ\text{C}$ and $22.5 \pm 0.09^\circ\text{C}$, respectively (Fig. 5).

Maintenance or reuse of nests, alternate nests. No nest sites are known to have been reused and alternate nests are not known. Median within year distance between first and second nests (renests) of 10 banded hens was 162 m, range = 45–531 m (Sopuck and Zwickel 1983; FCZ). Median distance between nest sites of 26 hens whose nests were found in more than one year was 174 m (9–1,956 m), not significantly different than for renests (FCZ).

EGGS

Shape. Short subelliptical; occasionally more subelliptical.

Size. Coastal BC: mean lengths \times diameters, volumes, and fresh mass of 88 eggs from 32 clutches of yearling hens = $5.2 \pm 0.02 \times 3.6 \pm 0.01$ cm, 33.7 ± 0.33 ml, and 34.9 ± 0.35 g, respectively; were significantly smaller in all measures than 144 eggs from 45 clutches of adult hens = $5.3 \pm 0.02 \times 3.7 \pm 0.01$ cm, 36.3 ± 0.30 ml, and 37.6 ± 0.31 g, respectively; volume and mass calculated as per Hoyt (1979; FCZ). Composite samples by subspecies, length \times diameter (from Bent 1932): *obscurus* = 5.0×3.5 cm, $n = 54$; *richardsonii* = 4.8×3.3 cm, $n = 32$; *sierrae* = 4.9×3.5 cm, $n = 23$; *howardi* = 5.0×3.7 cm, $n = 5$; *fuliginosus* = 4.9×3.5 cm, $n = 92$. Mean fresh mass (calculated as per Hoyt) of eggs of adult females: e. Nevada = 32.6 ± 0.41 g, $n = 15$;

nw. California = 29.5 ± 0.41 g, $n = 16$; Montana = 28.8 ± 0.39 g, $n = 26$; all significantly less than for coastal British Columbia, above; nw. California and Montana less than e. Nevada (FCZ).

Mean mass of single yearling and adult eggs = 3.8% and 3.7% of mean May body masses of yearling/adult females, respectively. Mean mass of clutches of yearling and adult eggs = 20.7% and 25.9% of mean May body masses of yearling/adult females, respectively. If a yearling renests, total mean mass of eggs produced = 37.6% of mean May body mass of yearling females, that of an adult = 46.8% of adult females (FCZ).

Eggshell thickness. Means: coastal British Columbia, 1969–1984 = 0.23 ± 0.001 mm, $n = 104$ eggs from 32 clutches; Montana and ne. Washington, 1986, 1968, $n = 17$ eggs, 4 clutches (all *pallidus*) = 0.23 ± 0.003 mm; nw. California, 1985 = 0.24 ± 0.002 mm, $n = 7$ eggs, 1 clutch (FCZ).

Surface texture and color. Smooth. Background buffy, ranging from near pale horn (#92, Smithe 1975) to beige (#219D). Normally more-or-less speckled, or lightly spotted, with darker browns such as Brussels brown (#121B) or mikado brown (#121C); rarely, unmarked.

Egg laying. Laying interval reported as 1 egg per 1.5 d (Caswell 1954, Standing 1960). Data from Vancouver Is. suggest 1 per 2–2.5 d (FCZ), but evidence equivocal; needs better documentation. Rarely, eggs of two different shapes or colors may be in one nest, suggesting dumping.

INCUBATION

Incubation patch. One large patch, female only. Incipient near start of laying, complete near (Bendell 1955a) or just after (FCZ) start of incubation. Reforeathering begins first week after hatch; completed mid- to late Aug on Vancouver Is. (FCZ).

Onset of broodiness and incubation period. Incubation by female only; begins with laying of last egg. Incubation period = 26 ± 1 d; range = 25–28 d; evidence for wider range (e.g. Bent 1932) equivocal (McKinnon and Zwickel 1988).

Parental behavior. Females leave nest for about 10–60 min feeding bouts, usually 2–3 times/24 h at dawn, dusk, and often midday. May defend nest vigorously. Many leave nest only if approached to within ≤ 1 m; some leave only when touched.

HATCHING

Preliminary events and vocalizations. Female “coos” to embryos/juveniles prior to first pipping and during hatching. May encourage juveniles to pip, or create bonding between hen and juveniles.

Shell breaking and emergence. Pipping of first egg until hatch of entire clutch lasts about 24–48 h.

Figure 5. Sample 24 hr record of temperatures ($^\circ\text{C}$) during incubation, Vancouver Is.: surface of one egg, bottom of nest, ground near nest, and ambient near nest; 96 observations/thermistor at 15 min intervals (FCZ). Arrows indicate departures of female from nest for feeding.



Hatching more-or-less synchronous within clutch, all juveniles usually hatch within ≤ 24 h (FCZ). Parental assistance not known. Eggshells remain in nest more or less intact when brood departs.

YOUNG BIRDS

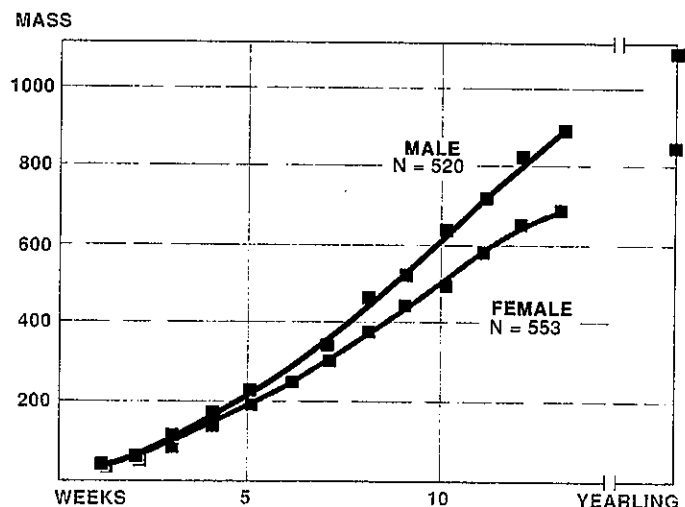
Condition at hatching. Precocial and nidifugous. Down-covered and wet at hatch, dry several hours later. Mean mass at hatch: Vancouver Is. = 25.8 ± 0.14 g, $n = 321$; Montana = 19.4 ± 0.26 g, $n = 43$; e. Nevada = 22.7 ± 0.29 g, $n = 13$ (FCZ). Brood usually leaves nest at 12–24 h posthatch, usually in morning of day following completion of hatch (FCZ). Does not normally return to nest. Egg tooth falls off first day out of nest.

Growth and development. Grow rapidly (Fig. 7); mass of males begins to noticeably diverge from females at about 3 wk. At 13 wk, chicks are about 80% of early spring mass of yearlings. Very rapid growth of foot, wing, and intestinal tract. Foot attains adult length at about 10 wk; small intestine, ceca, and colon at 10–11 wk. Wing approaches about 95% of yearling length at about 13 wk. Increases in masses of heart, liver, and ventriculus parallel that of total mass. Major breast muscles, pectoralis major and pectoralis minor, account for about 2% of total mass at 1–2 d of age, 15–20% at 9–10 wk (FCZ).

Juvenal primaries 1–7 present as pinfeathers at hatch; first shed at 16–17 d of age (Zwicker and Lance 1966, Redfield and Zwicker 1976), initiating development of postjuvenal plumage. Juvenal rectrices first appear in second week (Bendell 1955b, Smith and Buss 1963). Juvenal plumage predominates at 4 wk, terminated at about 10 wk. First postjuvenal rectrices emerge at 5–6 wk (Bendell 1955b, Smith and Buss 1963). Postjuvenal plumage complete at about 17 wk.

Figure 6. Chicks, newly hatched. By D. Otte.

Figure 7. Mean weekly masses (g) of juvenile Blue Grouse, Vancouver Is., BC. Mean masses of yearling males and females (9–10 months old) are on right vertical axis (FCZ).



Control of body temperature. Little information, but see Parental Care, below.

Behavior/locomotion. Move clumsily within nest shortly after hatch. Walk and run somewhat clumsily on first day out of nest. Make short "hop flights" at 6–7 d of age; fly 10–15 m at 8–9 d, 30–60 m at 2 wk (Zwicker 1967a); usually make 1 flight only at < 2 wk of age. Normally "freeze" when disturbed at ≤ 4 d of age, but may first run or crawl under vegetation, logs, or other objects. Often freeze in place at 6–7 d of age, but may follow that with short flush; readily flush at 10–28 d of age, sometimes after an initial freeze. Usually wail and search for female within 10–60 min after disturbance (Caswell 1954, Zwicker 1967a). In absence of female, reassemble as a unit on their own. A brood of day old juveniles traveled about 80 m in 6 h; the next day, about 510 m in 9 h; tended to stay within 5 m of hen. A brood of 5–6 day-old juveniles traveled about 170 m in 7 h and 200 m in 5 h; ranged out to 15 m from hen (Zwicker 1967b). Median distance between brooding locations, data of above broods combined, was 18 m, range = 1–61 m, $n = 40$. Movements may be ≥ 1 km in first week posthatch (Sopuck 1979). Seven yearling females with brood were a mean distance of 543 ± 225 m from their nests at end of first week posthatch; 14 adult females, 214 ± 43 m (Armleder 1980). Broods may aggregate in and near thickets in mid- to late summer, perhaps because of desiccation of vegetation (Caswell 1954, Zwicker 1973).

PARENTAL CARE

Brooding. By female only, usually on bare ground; juveniles brooded on nest till dry, up to 24 h after last chick emerges from egg. May be initiated or terminated by either female or juveniles. Most non-brooding time spent feeding, with near-

continuous peeping. Among 97 sightings of hens brooding juveniles during the day, coastal British Columbia, 58% of the broods were 1–4 d of age, 33% 5–8 d; 5% 9–12 d; 3% 13–16 d; 1% > 16 d (FCZ). Circumstantial evidence indicates very young juveniles are brooded throughout night; those 9 d or older may be brooded more often at night than indicated above. Two families of juveniles, 1–2 d and 5–7 d of age, were brooded 88% and 77% of observation time on “cold” days and 50% and 51% on “warm” days, respectively. Feeding bouts increased, brooding bouts decreased, in duration on warm vs. cold days (Zwikel 1967b).

Feeding. Juveniles feed on their own from time nest is abandoned, at about one day old. In first days, juveniles often peck at undersides or tips of leaves for insects and appear to be testing different plant and animal foods. By three days of age, >80% of residual yolk present on day 1 has been used (FCZ). Female likely determines travel routes but does not feed juveniles or direct them to specific items of food. Small juveniles feed to about 5–15 m from female; wail and return to female beyond that distance (Zwikel 1967a). Distance increases with age. If not feeding themselves, females may act as sentinels by perching on shrubs, stumps or logs as juveniles feed on ground around them. Juveniles may hop off ground to obtain items out of reach or fly into berry producing shrubs to feed.

COOPERATIVE BREEDING

Not known to occur. Rare instances of two females with one brood of small juveniles are likely coincidences of simultaneous use of area. Mixing of two broods by disturbance usually results in return of juveniles to proper mothers. Occasional mixing of broods at young ages may result from death of one hen, but no clearly documented cases. Marked juveniles of removed hens have joined other broods (FCZ).

FLEDGLING STAGE

See Young birds, above.

IMMATURE STAGE

Brood organization disintegrates late summer to autumn. Some females desert their broods, which may form small bands that wander on breeding range prior to migration (Wing et al. 1944, Zwikel et al. 1968). Juveniles may (Bendell and Elliott 1967, Lance 1970, Sopuck 1979), or may not (Wing 1947, Zwikel et al. 1968, Hines 1986b), move to winter range with their mothers. Hines found no marked siblings together after 1 Oct; most juveniles had separated from their mothers by this time. From 1 Oct till spring movements began, 57% of 170 juvenile males and 55% of 267

Table 2. Clutch sizes and % frequency distributions of clutch sizes of Blue Grouse from Vancouver Island, sw. Alberta, ne. Washington, and w. Montana.¹

	V. I.	AB	WA	MT
No. of clutches	201	20	25	15
Mean clutch ± SE	6.3 ± 0.1	6.5 ± 0.4	6.9 ± 0.3	7.5 ± 0.4
CLUTCH SIZE (# EGGS)	PERCENT FREQUENCY			
2	–	5	–	–
3	2	–	–	–
4	5	–	8	–
5	23	15	12	–
6	23	35	20	27
7	27	15	24	33
8	18	25	16	20
9	2	5	20	7
10	–	–	–	13

¹Data from Alberta (D. Boag pers. comm.); other data FCZ.

juvenile females were in groups, most often composed of their own sex and age class.

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY

Age at first breeding. Few yearling males breed (Bendell and Elliott 1967), even though they are physiologically able to do so (Standing 1960, Hannon et al. 1979). Some may take territories created by removal of adults (Bendell et al. 1972, Zwikel 1972a), others may not (Lewis and Zwikel 1980). Many yearling females breed (Zwikel and Bendell 1967) but circumstantial evidence from reproductive tracts (Standing 1960, Hannon and Zwikel 1979) and removal studies (Bendell et al. 1972, Zwikel 1972a, 1980) indicates that some do not. Proportion breeding may vary among years (Zwikel 1972a) or populations. In se. Alberta, only 14% of 106 banded yearlings are thought to have bred (Boag 1964); in coastal British Columbia, 82%–87% (Sopuck 1979, Hines 1986a). During recent studies in Nevada, California, Montana, and British Columbia, nesting was confirmed for 13 of 13 radio-marked adults, but for only 3 of 10 radio-marked yearlings (FCZ).

Clutch. 1–12 eggs. Reported clutches > 12 (e.g., Jewett et al. 1953) likely from 2 females (Bent 1932). Clutch size on Vancouver Is. significantly smaller than in w. Montana and ne. Washington, but not se. Alberta (Table 2). Those from Montana,

Washington, Alberta do not differ, but samples are small. Mean clutch of yearling females, Vancouver Is. = 5.56 ± 0.21 , range = 4–7, $n = 20$, significantly smaller than that of adults, 6.93 ± 0.16 , 4–9, $n = 55$ (Zwickel 1975). Mean clutch of first nests larger than renests (Zwickel 1975, Sopuck and Zwickel 1983) by about 1–1.5 eggs (FCZ).

Nest success, egg fertility, hatchability. Nest success (% of all nests that hatch) and fertility and hatchability of eggs appear constant among years and the same in yearlings and adults (Zwickel et al. 1988). Nest success: Vancouver Is., 58% (156 nests); Hardwicke Island, 82% of 108 (Zwickel et al. 1988); se. Alberta, 81% of 21 (D. Boag pers. comm.); ne. Washington, 64% of 14 (FCZ); north-central Colorado, 80% of 10 (Hoffman 1981); w. Montana, 71% of 14 (FCZ). Data for Vancouver and Hardwicke islands, corrected for bias (Mayfield 1961), indicate true nesting success is about 10% lower than indicated above.

On Vancouver Is., egg fertility as follows: 98% of 322 eggs (55 clutches; Zwickel 1975); composite sample from interior populations, 90%, $n = 224$ eggs, 38 clutches (FCZ). Egg hatchability (fertile eggs only): Vancouver Is., 97%, $n = 370$ eggs, 66 clutches; composite sample from interior populations, 97%, $n = 194$ eggs, 36 clutches (FCZ).

Brood production. Mean late-summer brood size varies among areas, generally higher in interior than in coastal populations (Table 3). In a Vancouver Is. population, 60% of females estimated to have produced broods (Bendell 1955c); in another 50%+ (Zwickel and Bendell 1967). Yearling females significantly less productive than adults; 53% of 289 banded yearlings and 84% of 462 banded adults produced broods on Vancouver Is.; on nearby Hardwicke Island, 73% of 323 yearlings and 88% of 727 adults (FCZ). Yearlings differed between areas; adults did not (FCZ). Latter data serve only as indexes. They exaggerate the percentage of hens with brood as those with juveniles are more easily captured or identified than those without.

Annual and lifetime reproductive success. Late-summer brood size varies significantly among years. Mean for a Vancouver Is. population = 3.3 ± 0.17 juveniles/female with brood, range = 2.3–3.9, $n = 9$ yr (see also Table 3). Percentage of all banded females with brood also differed among years: mean = 72%, 61%–84%, $n = 9$ yr (latter data serve as index only; see above; FCZ).

Lifetime. Virtually all males 2 yr or older take territories (Bendell 1954) and presumably attempt to breed, but a few do not (Lewis and Zwickel 1980, Lewis 1984b). Once attained, a territory is usually held for life (Bendell and Elliott 1967), but breeding may be skewed toward certain males,

Table 3. Late-summer brood sizes for selected coastal and interior populations of Blue Grouse. Years of data are in parentheses.

AREA	SIZE OF BROOD		SOURCES ²
	MEAN ¹	RANGE	
<i>COASTAL POPULATIONS</i>			
Lower Quinsam, BC	2.4 (5)	1.7–3.3	1,2
Middle Quinsam, BC	2.7 (5)	2.2–3.7	3,4
Comox Burn, BC	3.3 (9)	2.3–3.9	5
Hardwicke Island, BC	2.2 (6)	1.3–2.9	5
<i>INTERIOR POPULATIONS</i>			
Gorge Creek, AB	3.7 (8)	2.9–4.4	6
Brownlee, ID	4.3 (3)	3.6–4.9	7,8
Frazier Creek, WA	3.4 (7)	1.7–4.7	5,9,10,11
Skalkaho, MT	3.9 (6)	3.0–4.9	5,12
Green Mt., CO	3.2 (4)	2.5–3.7	13

¹Calculated from annual means, not from total numbers of broods and chicks.

²1, Fowle (1960); 2, Bendell (1955c); 3, Zwickel and Bendell (1967); 4, Ash (1979); 5, FCZ; 6, Boag (1966); 7, Caswell (1954); 8, Heebner (1956); 9, Standing (1960); 10, Henderson (1960); 11, Bauer (1962); 12, Schladweiler (1968); 13, Hoffman (1981).

for territories can vary in quality (Lewis and Zwickel 1980).

Sixty females banded as yearlings on Vancouver Is. (2 cohorts, each monitored for 9+ yr, with no female alive beyond 8 yr) produced an estimated 283 chicks to late summer over their lifetimes, 4.7/female (range = 0–19, FCZ). This estimate is minimal because reproductive success of females known to be alive was not determined in 16 of 66 adult bird years.

LIFE SPAN AND SURVIVORSHIP

First-year survival low. In spring, as few as 10% of previous year's hatchlings recruited; highest mortality is in first 2 wk of life (Zwickel and Bendell 1967). At least 40% of 99 Vancouver Is. juveniles banded at 9–10 wk of age survived to yearling age (Zwickel 1983). Minimum overwinter survival of juveniles radio-marked in late summer ranged between 21%–28% for males, 28%–35% for females, Hardwicke Island (Hines 1986a).

Despite relatively high first-year mortality, Blue Grouse are long-lived among the tetraonines. Maximum known longevity for males ≥ 14 yr, for females 11 yr (Zwickel et al. 1989). Annual survivorship constant (66%–75%) in males two or more years of age (Bendell 1955c, Bendell and Elliott 1967, Zwickel and Bendell 1967, Schladweiler 1968, Redfield 1975); in se. Alberta, 52% (Boag 1966). Mean life expectancy for males on

Vancouver Is.: 3.1, 2.6, 2.3, 2.1, 2.0, 1.9, 1.1, 0.9, 0.5 yr, each year of age from 2–10, respectively (Lewis and Zwickel 1982). Within populations, survivorship appears constant among females one or more years of age, but variation may occur among populations (40%–71%; Redfield 1975, Zwickel et al. 1983, Boag 1966).

MORTALITY AND DISEASE

Disease. WILD BIRDS. Low grade papillary carcinomata (cancerous tumors) identified from birds on Vancouver Is. (Cowan 1940), later correctly identified as fowl pox, *Epithelioma contagiosum* (Cowan 1942). A bird found dead in Idaho had a severe case of *Aspergillus fumigatus* (Caswell 1954). Bendell (1955c) found 10 cases of bacterial infections, presumably associated with injuries, among 60 juveniles. Among almost 11,000 birds captured for marking in British Columbia, 7 with tumor-like growths, 3 with wart-like growths, 2 with mole-like growths, and 5 with scale-like skin growths were noted; body mass was recorded for 16 of these birds and 14 were within normal ranges for their sex/age class; 2 were subnormal (FCZ).

CAPTIVE BIRDS. Ulcerative enteritis killed 10 birds brought into captivity (Buss et al. 1958). *Aspergillus*, gizzard erosion, and enteritis were principal causes of death in birds from coastal British Columbia. Other diseases were ulcerative gizzard and proventriculitis; except *Aspergillus*, pathogens were not identified (Stirling 1965). Pathologies in 178 juveniles from Vancouver Is. included one case of uremia and several cases of ascites, excess urate deposits in kidneys and ureters, hardened corelike cecal deposits, and excess yolk retention (the latter may reflect incubator problems); 57% had inflamed intestines. Attempts to isolate pathogens were all negative (Zwickel and Bendell 1967). Among 45 wild juveniles collected for comparison, 4 had inflamed intestines, 1 exhibited yolk retention, and 1 had cecal cores.

Parasites. ECTOPARASITES. *Degeeriella perplexa*, *Lagopoecus lyrurus*, *Ornithomyia anchineuria* identified by Beer (1944); *Goniodes merriamanus*, by Emerson (1951); *Ixodes auritulus*, *Ceratophyllus diffinus*, *Lagopoecus obscurus*, and *Ornithomyia fringillina* by Bendell (1955c). Others listed in review by Wheeler and Threlfall (1989).

ENDOPARASITES. Reviewed by Braun and Willers (1967); see also White and Bennett (1979), Stabler and Kitzmiller (1976). Incidences of infection and/or pathologies of various ecto- and endoparasites are considered by Beer (1944), Fowle (1946), Bendell (1955c), Jensen (1962), Casperson (1963), Holmes and Boag (1965), Williams et al. (1980), and Mahrt et al. (1991). No clear evidence of serious effects

from disease or parasites on population level. A report that parasites might limit populations (Bendell 1955c) not supported by subsequent study (Zwickel and Bendell 1967).

RANGE

Dispersal from natal site. Medians and ranges of natal dispersal distances for banded juveniles on Vancouver Is.: males = 1.1 km, range = 0.04–9.1 km, $n = 49$; females = 2.0 km, 0.1–10.0 km, $n = 50$ (Jamieson and Zwickel 1983). On Hardwicke Island, medians and ranges of natal dispersal distances for radio-marked juveniles were: males = 0.9 km, 0.2–2.6 km, $n = 24$; females = 1.4 km, 0.3–11.0 km, $n = 42$ (Hines 1986b). In both studies, females settled as yearlings/adults at significantly greater distances from where banded (as juveniles) than did males.

Fidelity to breeding site and winter home range. Territorial males, usually ≥ 2 yr old, return to the same breeding site year after year, presumably until death (Bendell 1955c, Boag 1966, Schladweiler 1968, McNicholl 1978, Hoffman 1981). Most yearling males range over a small number of territories of adult males, one of which they may occupy the following year if vacant; some settle near an unoccupied territory, others wander widely (Jamieson and Zwickel 1983). Each year most adult females return to the same general areas chosen as yearlings (Bendell and Elliott 1967, Schladweiler 1968, Jamieson and Zwickel 1983). In Colorado, 9 of 10 marked grouse used same wintering areas in 2 consecutive years (Cade 1985). In coastal British Columbia, 7 of 7 marked adults and yearlings were on winter range within 200 m of previous winter sites; 10 of 13 juveniles wintered at same sites in postjuvenile years as in first winters (Hines 1986a).

Home range. In spring/summer, average size and range in size of territories of adult males: se. Alberta = 0.6 ha, range = 0.2–0.9 ha, $n = 11$ (Boag 1966); Montana = 0.8 ha, 0.4–1.5 ha, $n = 14$ (Martinka 1972); Colorado = 1.5 ha, 1.2–1.9 ha, $n = 16$ (Hoffman 1981); coastal British Columbia = 2.1 ± 0.3 ha, 0.4–5.2 ha, $n = 34$ (McNicholl 1978). Mean area used by radio-marked territorial males in peak breeding period, Hardwicke Island, 0.6 ± 0.1 ha, 0.3–0.9 ha, $n = 10$; in entire territorial season, 1.9 ± 0.2 ha, 0.9–2.8 ha, $n = 8$ (Lewis 1985b).

Home range size varies widely among females (Bendell and Elliott 1967), and seasonally. Preincubation ranges for yearlings on Vancouver Is. = 20.7 ± 5.08 ha, $n = 12$; for adults, 6.4 ± 2.19 ha, $n = 8$; for laying period only, yearlings = 2.3 ± 0.33 ha, $n = 12$; adults = 2.3 ± 0.50 ha, $n = 8$ (Hannon et al. 1982). Generally similar results, with some overlap of ranges, on Hardwicke Island (Hines

1986a). Mean brood ranges from hatch to 6 wk posthatch on Vancouver Is. = 12.9 ± 2.3 ha, range = 3.2–39.2 ha, $n = 18$; 61% were less than 10 ha (Armleder 1980). No difference between yearling and adult females. Some brood ranges 12–16 ha in Idaho (Caswell 1954); maximum diameters of most brood ranges in Montana less than 800 m, up to 1200 m (Mussehl 1960). Broodless females may make moves of 1–3.2 km, $n = 11$, after loss of clutch or brood, then localize on home ranges of 3–31 ha (Sopuck 1979). Home ranges of 15 breeding females throughout summer in se. Alberta averaged 14.6 ha; non-breeders here may wander and not localize (Boag 1966).

Winter information limited; two radio-tracking studies only. In Colorado, most grouse moved up to 200 m between consecutive locations: juveniles' median home range = 18.7 ha, range = 9.2–42.2 ha, $n = 3$; yearling/adult median = 3.0 ha, 1.6–7.1 ha, $n = 10$; all but three birds moved among different stands of trees (Cade 1985). In coastal BC, winter home ranges (mostly juveniles) averaged 16.8 ha, 3.0–42.5 ha, $n = 20$ (Hines 1986b).

POPULATION STATUS

Densities vary greatly (Table 4). Interior subspecies tend to be sparser than coastal, where most studies have been in lowland forest after clear-cut logging or fire. In coastal old-growth forest, densities usually lower than in early serres (Niederleitner 1987), but this is reversed in se. Alaska (Doerr et al. 1984). Subalpine densities low but few data available.

Density of interior populations usually fluctuates within fairly narrow limits (Table 4; Hoffman 1981, Schladweiler 1968), but not always (Boag 1964). Populations in early coastal forest serres suggest wider ranges in density, within and among populations (Table 4). Frandsen (1980) reported 2–33 territorial males/km² among 17 coastal serres that ranged from 5–25 yr post-logging, with a positive correlation between density and age of dominant trees up to about 10 yr post-logging, a negative correlation after that. Specific causes of variations among and within early coastal serres prior to tree canopy closure are still poorly understood (Zwickel and Bendell 1985; Zwickel et al. 1988).

POPULATION REGULATION

A controversial concept that depends partly on definitions. That used here follows Zwickel and Bendell (1972: p. 150), "...we view regulation as the mechanism involved with maintaining relative homeostasis at the population level." Some have proposed that size of breeding populations may

Table 4. Population densities (Blue Grouse per km²) of adult male (AM) and yearling plus adult female (Y+AF) in selected parts of their range. Number of years of data are in parentheses.

AREA	DENSITY	SOURCES ¹
<i>INTERIOR POPULATIONS</i>		
Green Mt., CO (AM)	9–10 (6)	1
(Y+AF)	9–12 (6)	1
Montana (AM) ²	7–9 (6)	2
Washington (AM) ³	13 (1)	3
Alberta (AM)	2–19 (9)	4
Interior, BC (AM) ⁴	3 (1)	5
<i>COASTAL POPULATIONS</i>		
Lower Quinsam, BC (AM)	89–103 (3)	6
Comox Burn, BC (AM)	12–20 (13)	7
(Y+AF)	21–29 (10)	5
Mt. Washington, BC (AM) ⁴	4 (1)	8
Hardwicke Island, BC (AM)	17–33 (5)	9
(Y+AF)	26–83 (6)	9
Prevost Island, BC (AM)	6–10 (2)	10

¹1, Hoffman (1981); 2, Schladweiler (1968); 3, Lewis (1985a); 4, Boag (1964); 5, FCZ; 6, Bendell (1955c); 7, Zwickel et al. (1983); 8, King (1971); 9, Zwickel et al. (1988); 10, Donaldson and Bergerud (1974).

²Calculated from Schladweiler (1968) on basis of a revised study area size of 477 ha.

³Calculated from Lewis's Fig. 1 and data in his text.

⁴Subalpine population.

be self-regulated, perhaps through some kind of spacing behavior (Bendell et al. 1972, Zwickel 1972a, 1980, Hannon et al. 1982); others, that extrinsic factors may be more important (Fowle 1960, Bergerud 1988), or that regulation may be effected by multifactorial influences (Hines 1986a). Despite extensive study with Blue Grouse this remains a complex, contentious issue and more work is needed.

CONSERVATION AND MANAGEMENT

EFFECTS OF HUMAN ACTIVITY

Blue Grouse still occupy most of their original range, though historical accounts suggest densities in some areas were greater than now. Local extirpation in areas taken over by agriculture and cities, e.g., the Puget Sound trough between Seattle, WA and Portland, OR. *D. o. howardii* likely gone from southern parts of its range, from Mt. Pinos to the Tehachapi Mts., CA; reasons unknown.

South coastal populations (BC to n. CA) often increase, at times spectacularly, after clear-cut logging (Zwickel and Bendell 1972). Higher densities short-lived, about 15–20 yr, with rapid declines to low levels as tree canopy closes, especially in plantations; likely to remain low until canopy reopened (Zwickel and Bendell 1985). Study needed of alternative logging and forestry practices that might maintain continuous, rather than boom-and-bust, populations in coastal forest. North coast populations may respond negatively to clear-cut logging (Doerr et al. 1984). Logging at higher elevations, now commonplace, may impact winter ranges (Cade and Hoffman 1990, Zwickel and Bendell 1985), but effects little known. In general, effects of forest management practices on interior grouse ranges are poorly understood. Grazing by domestic livestock of shrub/steppe and forested breeding ranges may be a problem (Mussehl 1963, Zwickel 1972b, Harju 1974), but evidence equivocal and more work needed.

A popular game bird, hunted virtually everywhere found, except parks and municipalities. Rates of band recovery by hunters suggest a light population impact in most areas: on Vancouver Is., 1% of 435 males (Bendell 1955c) and 5% of 1160 hens and chicks (Bendell 1955c, Bendell and Elliott 1967); in Montana, 10% of 226 birds of all sexes/ages (Mussehl 1960); in Washington, 4% of 750, all sexes and ages (data from Bauer 1962); in Colorado, 4% of 600, all sexes and ages (Hoffman 1985). Under present management regimes in most areas, autumn migration into rugged terrain reduces hunting impacts.

Despite intensive study of Blue Grouse over the past 40 years, ability to predict population levels and trends remain poor. A first priority should be long-term, basic research, with mission-oriented studies applied to immediate problems. Rugged mountainous habitat has helped protect Blue Grouse, so the long-term outlook for many populations is good. Nevertheless, logging, grazing of domestic livestock, and urbanization remain threats.

APPEARANCE

MOLTS AND PLUMAGES

Natal plumage. At hatch, covered with down. Interior subspecies: gray dorsally, whitish ventrally; coastal: reddish brown dorsally, yellowish ventrally. Head and back mottled with black, blackish brown, and/or reddish brown. Mottled patterns most like those of Sage Grouse and Capercaillie (*Tetrao urogallus*). See Moffitt

(1938) and Ridgway and Friedmann (1946) for detail. No differences noted between sexes.

Juvenal plumage. Brownish in hue, superficially similar to adult female but with light shaft streaks on many contour feathers. Crown with varying amounts of reddish brown. Outer webs of p1–8 mottled with buff and reddish brown. Rectrices narrow and pointed, with light shaft streaks distally. No differences noted between sexes or interior/coastal groups.

Basic I and definitive basic plumage MALES. Basic I (postjuvenile or yearling) plumage, completed at 4–5 months of age, generally similar to Definitive Basic (adult) but with more brownish cast on back and wings. P9 and 10 are pointed rather than rounded as in adult (Braun 1971). Rectrices narrower and shorter than in adult; little or no overlap between age-classes (Bendell 1955b, Boag 1965). Narrow, transverse, whitish gray bars on upper tail coverts (Nietfeld and Zwickel 1983) absent in adults. Definitive Basic plumage completed at about 16 months of age; medium plumbeus (#87) to blackish neutral gray (#82) in general hue. Interior subspecies paler than coastal; within each group, southern subspecies paler than northern. Contour feathers darkest on head, neck, and upper back; those of mid and lower back, upper wing, and upper tail coverts with light gray vermiculations, blended with soft shades of brown. Darkish gray upper breast blends into lighter gray, or bluish gray, at mid breast; continuous to vent where feathers are narrowly tipped with whitish gray. Flanks are gray of the abdomen, some feathers with white shaft streaks and white tips. Lower legs brownish gray. Under wing coverts mostly white; under tail coverts blackish, often mottled with gray, broadly tipped with white. Chin and upper throat feathers flecked with white. Cervical apteria ringed with white feathers, tipped with gray of surrounding neck feathers; white not visible when feathers are fully sleeked, but creates spectacular rosettes around apteria during display. White lesser wing coverts at underside of proximal end of humerus may be exposed dorso-anteriorly as a "shoulder spot" (Jamieson 1983). Proximal two-thirds of rectrices blackish neutral gray, blending toward jet black (#89) more distally; distinct tail band of medium neutral gray (#84) to dark neutral gray (#83) in all subspecies except *pallidus* and *richardsonii*, in which band is indistinct or absent; band tends to decrease in width from south to north.

FEMALES. Basic I (postjuvenile or yearling) plumage completed at 4–5 mo of age, generally indistinguishable from Definitive Basic (adult). P9 and 10 pointed rather than rounded as in adult (Braun 1971); rectrices average shorter and

narrower than in adult, but with much overlap (Bendell 1955b, Boag 1965). Definitive Basic plumage completed at about 16 mo of age; much mottled with various shades of black, gray, brown, and small amounts of white. Overall hue of coast females is brown, a mix of dark colors such as blackish neutral gray or dusky brown (#19) with lighter browns such as russet (#34) or army brown (#219B). Overall hue of interior females is gray, a mix of dark colors such as blackish neutral gray tempered with soft browns like drab (#27) and/or light grays like glaucous (#79). Contour feathers generally darkest on back, shoulders, and upper surfaces of wings; may be banded with lighter shades of gray, brown, or grayish brown. Head, neck, and upper breast similar to back but a lighter hue, more brown and less black. Ventrally, upper breast feathers blend into nearly solid gray in lower breast region; continuous to vent where feathers are narrowly tipped with white. Feathers at shoulder may have triangular white tips extending proximally partway down rachis. Flanks of mottled browns or grays; some feathers with white tips and shaft streaks. Lower legs brownish gray. Chin brown or gray, flecked with white. Brown mottling of interior subspecies more subdued than in coastal birds. Under wing coverts mostly white but with mottled grays and browns toward leading edges of wings. Females, too, can expose a white "shoulder spot." Two central rectrices transversely banded with alternating black, or blackish, and light brown bars. Distinct gray tail band in all subspecies except *pallidus* and *richardsonii*, in which it is indistinct or absent; may be obscured on central rectrices in all subspecies. Upper tail coverts transversely banded with alternating black, or blackish, and light brown bars.

Molt. Usually complete (but see Bendell 1955b). Begins with loss of p1 shortly after peak breeding. Initiation varies with time of breeding in males and broodless females, with time of hatch in brood females. On lowland Vancouver Is., p1 is shed: 13–29 May in yearling males, $n = 45$; 22 May–12 Jun in adult males, $n = 63$; 31 May–4 Jul in yearling females without brood, $n = 39$, 14 Jun–16 Jul with brood, $n = 94$; 5–24 Jun in adult females without brood, $n = 16$, 9 Jun–22 Jul with brood, $n = 111$; brood females molt p1 at 1–15 d posthatch (Zwickel and Dake 1977). Rate of p molt faster in yearling than adult males, but neither differs from females without brood, all are linear with time; rate increases temporally and is curvilinear in females with brood (Zwickel and Dake 1977). P molt progressive, proximal to distal; ends mid to late Oct; spans entire postnuptial molt (FCZ). Initiation of p molt followed shortly by that of head and

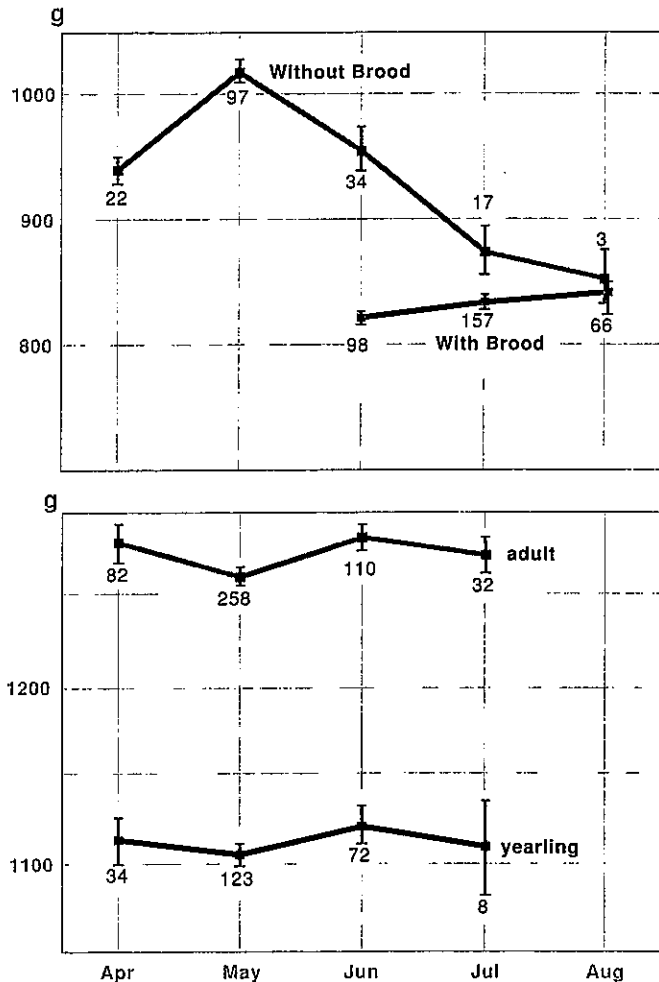
neck. On lowland Vancouver Is. all feather tracts except rectrices are in active molt in yearling/adult males by about 20 Jun; in yearling/adult females by about 20 Jul. Secondary molt complex; probably starts with s3, proceeding inward to about s9, at which time a second molt center at s2 is activated; continues inward from s9 and outward from s2. Rectrix molt more truncate than other tracts, laterad to mediad; begins late Jul to mid-Aug, ends late Sep to Oct (FCZ). Molts of *pallidus* (Standing 1960) and *richardsonii* (Boag 1965) similar to birds on Vancouver Is. (Fig. 4); differ mainly in timing.

BARE PARTS

Cervical apteria sexually dimorphic, highly specialized in males, homologous to those of Sage Grouse, Sharp-tailed Grouse, and Prairie Chicken (*Tympanuchus cupido*); unmodified in females. They are thick, tuberculate, and near buff yellow (#53) in coastal males; yellow presumably due to heavy fat deposits in dermis (Degner 1983). Thinner, less tuberculate, much less fat (M. Degner pers. comm.), and vinaceous (#3) to deep vinaceous (#4) in interior males. Tubercles and color in interior males somewhat transitory as they attain maximum amplification due to flushing with blood at peak display (Blackford 1958). Supraorbital apteria of males hypertrophy in breeding season, are erectile during display; almost meet on top of crown and change rapidly from yellow to orange to bright red at peak courtship (Hjorth 1970); may be concealed by feathers of crown at other times. Those of female not erectile and often covered by feathers of crown; dull orange-yellow (Ridgway and Friedmann 1946). Beak blackish in mature males, blackish to dark brown in females. Iris brown to hazel brown (Ridgway and Friedmann 1946). Ventral surfaces of tarsometatarsi and plantar surfaces of feet and toes reticulate; dull yellowish. Dorsal and lateral surfaces of toes scutellate. Toes of male light brownish gray, claws blackish brown; toes of female brownish gray to pale greenish gray, claws pale horn gray (Ridgway and Friedmann 1946).

MEASUREMENTS

External linear measurements and mass may differ between sexes and yearling/adult age-classes: on Vancouver Is.; within age-classes, all measurements (Appendix 1) differed significantly between sexes. Within sexes, all but lengths of tibiotarsi and middle toes differed between age-classes. Linear measurements and mass may differ among populations, even within subspecies, e.g., mean mass and mean length of foot of adult males in a population of *pallidus* in ne. Washington were



1171 ± 13 g, n = 41, and 94 ± 0.8 mm, n = 16; both significantly smaller than for a population of *pallidus* in w. Montana, 1271 ± 10 g, n = 29, and 99 ± 0.5 mm, n = 27, respectively (FCZ).

Adult female mass increases in early spring, declines during incubation, slowly recovers over summer (Fig. 8); mass of non- or unsuccessful breeders changes less than in females that complete incubation; yearlings similar to adults, but at lower levels (Redfield 1973). Late summer mass of females, compared to early spring, suggests an increase in winter (FCZ), but few winter weights are available. Males show little change between spring and mid to late summer (Fig. 8). In spring and summer in coastal BC, mean masses of the two major breast muscles, heart, and liver, tend to vary with body mass. That of ventriculus varies with diet; heaviest in early spring when birds are shifting from a fibrous conifer diet to more succulent foods (FCZ).

Figure 8. Mean monthly masses (g ± SE) of adult female Blue Grouse with and without brood (top) and of yearling and adult males (bottom) on lowland breeding range, Vancouver Is. (FCZ).

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ABOUT THE AUTHOR

Fred C. Zwickel was born in Seattle, WA in 1926. He completed B.Sc. (1950) and M.Sc. (1958) programs in Wildlife Biology at Washington State University and launched his studies of Blue Grouse in 1953 while he was employed as a wildlife biologist with the State of Washington, Department of Game (1950-1961). A return to school in 1961 brought him a Ph.D. in Zoology at the University of British Columbia (1965), followed by a postdoctoral fellowship at the Nature Conservancy (Unit of Grouse and Moorland Ecology in Scotland) one year in the Department of Fisheries and Wildlife at Oregon State University, and 18 years in the Department of Zoology at the University of Alberta. Population studies of Blue Grouse have been the main focus of his research since 1953, principally in coastal British Columbia. A monograph on Blue Grouse, in collaboration with J. F. Bendell, is in preparation. Since retirement in 1985, Fred and his wife, Ruth, have occupied 6 ha of an old homestead on the shores of Manson's Lagoon, Cortes Island, British Columbia. Current address: Box 81, Manson's Landing, BC, Canada V0P 1K0.

Appendix 1. External body measurements of yearling and adult male and female Blue Grouse, Vancouver and Hardwicke Islands, B.C. (FCZ). Lengths = mm \pm SE; mass = g \pm SE.¹

	Sex	Yearling	Adult
Body	M	475 \pm 2.1 (39)	501 \pm 2.1 (109)
	F	442 \pm 2.1 (79)	448 \pm 1.5 (117)
Wing (flat)	M	222 \pm 0.6 (121)	229 \pm 0.4 (263)
	F	204 \pm 0.3 (350)	208 \pm 0.3 (358)
Tail	M	151 \pm 1.7 (41)	169 \pm 1.1 (119)
	F	131 \pm 1.0 (75)	138 \pm 0.7 (114)
Culmen	M	21 \pm 0.4 (42)	20 \pm 0.2 (115)
	F	19 \pm 0.2 (75)	18 \pm 0.2 (108)
Foot length	M	98 \pm 0.2 (336)	99 \pm 0.2 (333)
	F	90 \pm 0.1 (670)	91 \pm 0.2 (413)
Tibiotarsus	M	95 \pm 1.3 (34)	96 \pm 0.8 (87)
	F	87 \pm 0.9 (61)	88 \pm 0.7 (99)
Middle toe	M	58 \pm 0.8 (47)	59 \pm 0.3 (124)
	F	54 \pm 0.4 (81)	54 \pm 0.3 (120)
Mass ²	M	1112 \pm 5 (237)	1273 \pm 4 (482)
	F	790 \pm 5 (154)	839 \pm 4 (223)

¹Body, wing, tail and culmen measured as in Anderson (1965); foot from back of bent heel to end of middle toe; tibiotarsus from proximal to distal ends, anterior surface; middle toe from proximal to distal ends, upper surface; foot and middle toe measured without claw.

²Male yearlings Apr–Jul, male adults Mar–Jul; all females Jul/Aug.

