



Spruce Grouse

Falci pennis canadensis
Order GALLIFORMES - Family PHASIANIDAE

BNA No. 5
Authors: D. A. BOAG, M. A. SCHROEDE
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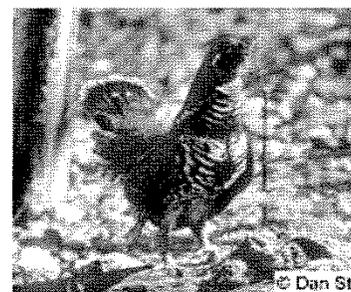
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INTRODUCTION

The Spruce Grouse is a species of the northern coniferous forests, with a closely related form in the eastern Palearctic. In North America it is a bird typical of the taiga and northern montane coniferous forests. Its generally remote habitat and inconspicuous behavior have, until recently, made it a rare subject of study. Most of what is known of this species is the result of research undertaken in the past 30 years.

The Spruce Grouse shows little morphological variation over its range, particularly among females. Males, however, fall into two distinct plumage and behavioral types: the southwestern subspecies (*D. c. franklinii*) has retrices that differ in form and color from those of the northeastern subspecies (*D. c. canadensis*). Aspects of courtship behavior are also distinct in these two forms.

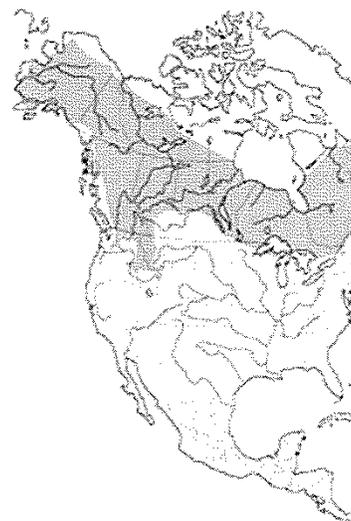
This grouse is a conifer specialist, feeding on pine (*Pinus* spp.) or spruce (*Picea* spp.) needles for much of the year. Populations appear to fluctuate over time, primarily in response to the degree of maturation of postfire regrowth and secondarily to predation pressure. Modern industrial forest exploitation, with its creation of open clear-cuts and subsequent single species plantations, reduces populations locally and often eliminates them entirely.



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Spruce Grouse, male
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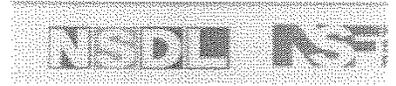
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Figure 1. Year-round range of Spruce Grouse in North America.

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Spruce Grouse

Falcapennis canadensis
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DISTINGUISHING CHARACTERISTICS

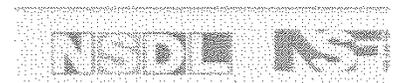
Small, compact, woodland grouse confined mainly to conifer forests. Sexes dimorphic; subspecies distinctive. Resembles Willow Ptarmigan (*Lagopus lagopus*) in shape and lacks the white winter plumage and feathering on the distal elements of the toes present in ptarmigan. Much smaller than Blue Grouse (*Dendragapus obscurus*) with which it shares conifer habitat, especially in winter, and from which it differs structurally in having few rectrices (16 vs. 18 or 20) and in lacking an inflatable cervical vocal sac in males. Females similar in appearance, but differ in size and in pattern of underparts (center of breast and belly heavily barred black and white in Spruce Grouse, plain gray in Blue Grouse). Females of Spruce Grouse might be confused with Ruffed Grouse (*Bonasa umbellus*), but easily distinguished by color of rectrices (pale with a subterminal dark band in Ruffed Grouse, dark with a paler terminal band in Spruce Grouse) and by the fact that Spruce Grouse does not erect the crown feathers as do Ruffed Grouse when alarmed.

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DISTRIBUTION

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AOU CHECK-LIST REGION

Breeding range

Resident across much of northern North America, closely associated with conifers that characterize the taiga and its southern equivalent, the montane forests of the cordillera. Range extends from Alaska to Labrador southward into New England, and into the north states in western U.S. (Fig. 1). The two well-differentiated subspecies (see Systematics) a long zone of contact that runs diagonally across southern Alaska, British Columbia, a southwestern Alberta, with *D. c. canadensis* typically occupying the northern taiga and *D. c. franklinii* occupying the montane coniferous forests of the cordilleras. Southern edge range characterized by islands of coniferous habitat of varying size in the broad ecotone where northern coniferous softwoods give way to deciduous hardwoods in the east and grasslands in the west. A similar situation exists along the northern edge of the range where fingers of taiga extend onto the tundra, usually along water courses. Within such insular and peninsular habitats, populations of this grouse appear to obey the laws of island biogeography (Fritz 1979), showing periodic local extinction followed by reinvasion. It probably during recolonization of such islands (usually initially by females because of differences in dispersal of the sexes—see Migration) that hybridization with other spruce grouse occurs, for example, Ruffed Grouse (Quellet 1974, Tufts 1975) and Blue Grouse (Quellet 1955) along the southern edge, and Willow Ptarmigan (Lumsden 1969) along the northern edge.

Winter range

Similar to breeding range, although individuals make short migratory movements (see Migration).

RANGE OUTSIDE AOU CHECK-LIST REGION

Not applicable.

HISTORICAL CHANGES IN DISTRIBUTION

Introduced onto the island of Newfoundland (134 birds from the Northwest River area central Labrador) in 1964 (Tuck 1968), and Anticosti Island in 1985–86 (343 birds from north shore of the St. Lawrence River between Port Cartier and Romaine River; Lemay 1986). Both populations are expanding and the former is now harvested.

FOSSIL HISTORY

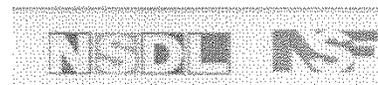
Fossil materials attributed to this species were recovered from supposed ancient owl pellets found in the fissures of a cave at Natural Chimneys, near Mount Solon in Virginia (Wetmore, 1962). These remains date from the end of the Wisconsin glaciation in the Pleistocene. Accompanying fossils of other typically boreal species suggest that this fauna existed much farther south at that time.

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SYSTEMATICS

GEOGRAPHIC VARIATION | SUBSPECIES; RELATED SPECIES

GEOGRAPHIC VARIATION

See Appearance.

SUBSPECIES; RELATED SPECIES

American Spruce Grouse were classified as two separate species in the genus *Canachites* during the first half of this century (Ridgway and Friedmann 1941): Spruce Grouse (*C. canadensis*) and Franklin's Grouse (*C. franklinii*). Subspecies were described only for the Spruce Grouse: *C. c. canadensis* in the northern taiga from Labrador to the base of the Mountains, *C. c. osgoodi* from the MacKenzie drainage through northern British Columbia and Yukon, into central Alaska, *C. c. canace* around the Great Lakes east into the Maritime Provinces and New England, and *C. c. atratus* along coastal south-western Alaska. More recently, *C. franklinii* was relegated to subspecific status (*C. c. franklinii*) on the basis of hybridization and apparent introgression (Short 1967) between *canadensis* and *franklinii* groups along their line of contact in British Columbia and Alberta, and *C. c. osgoodi* was merged into *C. c. canadensis* on the basis of similarity throughout the entire taiga (J. V. Aldrich in Jewett et al. 1953).

Taxonomic status presently a subject of debate. Short (1967) recognized only one species, American Spruce Grouse, which he classified under the genus *Dendragapus* (*D. canadensis*) along with the Blue Grouse (*D. obscurus*), in the belief that monotypic genera should be avoided and that the criteria for separating *Canachites* from *Dendragapus* (difference in number of rectrices and the absence of inflatable cervical vocal sacs in Spruce Grouse) were invalid. He recognized the Siberian Spruce Grouse as a third and separate species (*D. falcapennis*) under this genus. The *franklinii* group he considered a race of *D. canadensis*.

Potapov (1986) did not accept the congeneric status of Blue and Spruce grouse. He placed American and Siberian Spruce grouse in the genus *Falcapennis* because this generic name had precedence over *Canachites*. He recognized three species: Siberian Spruce Grouse (*F. falcapennis*), Canada Spruce Grouse (*F. canadensis*), and Mountain Spruce Grouse (*F. franklinii*).

Unlike Short (1967), we believe that Spruce Grouse should not be classified as congeneric with Blue Grouse. We find no evidence of inflatable cervical sacs in adult male Spruce Grouse, nor any good evidence that they produce sounds that would require such structures for amplification. Thus, one of the criteria used to unite Spruce and Blue grouse in the same genus (presence of inflatable cervical sacs in both) would seem unjustified. Moreover, Short (1967) noted, the natal plumage of these two forms is not alike; downy chicks of Spruce Grouse resemble most closely those of ptarmigan (*Lagopus* spp.), whereas Blue Grouse chicks are most similar to those of Sage Grouse (*Centrocercus urophasianus*). We believe Potapov's (1986) classification to be the more realistic, although the species

of the two American forms needs further study. This account follows the American Ornithologists' Union (1983) but recognizes only two subspecies of the American Spruce Grouse (*D. c. canadensis* and *D. c. franklinii*).

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MIGRATION

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NATURE OF MIGRATION IN THE SPECIES

Movement between separate breeding and wintering ranges recorded by Herzog and Ke (1980), Schroeder (1985b), Schroeder and Boag (1987). In a population of *D. c. frank* south-western Alberta, 25% of adults ($n = 93$ radio-marked birds) undertake annual migrations of up to 11 km between wintering and breeding ranges; females more likely migrate (32%, $n = 65$) than males (7%, $n = 28$; Schroeder 1985b) and generally migrate farther (median = 0.8 km) than males (median = 0.4 km). Grouse that do not migrate of the population) apparently breed in or near habitat where they spend their first winter remaining sedentary throughout life; most migrants (at least 82%), however, return from breeding sites to the location where they first wintered. Thus, the general habitat used by some migrants in winter is used by other grouse in summer. The specific habitats occupied in winter, when birds are largely arboreal (Keppie 1977b), probably differ from those occupied in summer, when they are largely terrestrial (DeFranceschi and Boag 1991).

Individuals in populations of *D. c. canadensis* also somewhat migratory. Among 27 bar adults in Alaska, average distance moved in autumn was 0.9 km (0.2–8.0 km), with the longest movement by a female (Ellison 1973). Some individuals also migratory in New Brunswick and Ontario (Herzog and Keppie 1980, D. Keppie pers. comm.), but the extent of which migration occurs remains unknown.

MIGRATORY MOVEMENTS

Timing

For *D. c. franklinii* in southwestern Alberta, not highly synchronized (Fig. 2). Departure from winter range between mid-February and mid-May, with males ($n = 11$) moving earlier than females ($n = 40$; Herzog and Keppie 1980). Autumn migration even less synchronous; on the winter range varies from mid-August to late December, with females (median = 14 Oct, $n = 53$) preceding males (median = 24 Oct, $n = 14$). However, females undertaking long migrations (> 2 km) are relatively synchronous, departing from winter range between 16 April and 11 May ($n = 8$) and from breeding range between 30 August and 13 October (Schroeder 1985b). These migratory movements generally last less than several days (Herzog and Keppie 1980, Schroeder 1985b).

Routes

In southwestern Alberta, migratory movements of individuals highly unidirectional, even on rugged terrain. Two females, followed by radiotelemetry during both their autumn and spring migrations, chose the same route for each movement (Herzog and Keppie 1980). Radiotelemetered grouse showed no significant directional orientation to migratory movements (Schroeder 1985b). Most birds (61%, $n = 13$), however, had a westerly component in their migratory movement, possibly because this took them into contiguous pine forests without havin

pass over or through potential habitat barriers (river gorges or deciduous forest). In Ontario a similar tendency to move west has been recorded, but in this case they were moving in stands of young pine (J. Bendell pers. comm.). Much remains to be learned about the particulars of these migratory movements.

Routes taken during migration appear to retrace spring dispersal movements of yearlings between their first wintering and first breeding ranges (Herzog and Keppie 1980, Schroeder 1985b). In at least certain areas, migratory individuals are highly philopatric, returning year to year to their respective breeding and wintering ranges (Herzog and Keppie 1980, Schroeder 1985b). Hence, individuals categorized as migratory are also those that undertake spring dispersal movements (Schroeder and Boag 1987).

MIGRATORY BEHAVIOR

Males poorly known, but migrant and non-migrant females differ in several ways. Migratory females more likely to flock in winter, perhaps because nonmigrants may retain territories (Schroeder 1985b). Furthermore, during the week preceding migration, migrants move significantly less each day (mean = 50 m, $n = 14$) than do nonmigrants (mean = 100 m, $n = 86$; Herzog and Keppie 1980). The extent to which this difference is reflected in time spent on other activities (e.g., feeding) remains unknown, as does the nature of the cue(s) that stimulate(s) migration in Spruce Grouse.

Most movements apparently undertaken during periods of low light at dawn and dusk. Most of the day is spent feeding and resting with a mean distance moved between midmorning and early evening of only 0.1 km ($n = 4$), in contrast to 1.3 km ($n = 18$) between mid-morning and mid-afternoon locations on subsequent days (Herzog and Keppie 1980). Most individuals migrate alone although some females initiate autumn migration with their broods, break-up occurring en route to or after arrival on winter range (Schroeder 1986a). Weather conditions seem to influence either timing or duration of migration.

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HABITAT

Spruce Grouse, as the name implies, are always closely associated with conifer-dominated forests, albeit not always spruce (*Picea* spp.). Over most of its boreal and cordilleran range, fire serotinous forests dominated by pine (jack: *Pinus banksiana*, and lodgepole: *P. contorta*) are the typical habitat of this grouse, with limited use being made of islands of unburned forest generally wet lowland spruce. Where these pines do not exist, Spruce Grouse occupy forests dominated by spruce in Alaska (Ellison 1966), redspruce (*P. rubens*) and balsam fir (*Abies balsamiae*) in Maine (Allan 1985), black spruce (*P. mariana*) in Minnesota (Anderson 1991), open subalpine forests dominated by Subalpine Fir (*Abies lasiocarpa*) in the Cascade Mountains of Washington (F. Zwickel pers. comm.), or coastal forests of hemlock (*Tsuga*) and cedar (*Thuja* spp.) on the islands in the Alexander Archipelago of southeast Alaska (Weeden and Ellison 1968).

Where studied within these forests, Spruce Grouse apparently prefer relatively young successional stands. Despite differences in species composition of conifers, these birds do use similarly structured forests: stands that are relatively dense (2,500 to 3,500 stems/ha), 7–14 m in height, with a relatively well-developed middle story (McCourt 1969, Hill 1974, Hedberg 1980, Szuba and Bendell 1983, Boag and Schroeder 1987, Boag 1991, Schroeder and Boag 1991). Within jack pine forests in Ontario, grouse density is predicted (explaining 76% of the variation) by an index of foliar area, a measure of total canopy and middle story cover (Szuba and Bendell 1983). Thus, density is high where pine is 4–6 m tall and the shrub layer is dense. Density in lodgepole pine forests can be predicted from a regression equation that is based on canopy height alone (Schroeder and Boag 1991).

Within specific forests Spruce Grouse seem to choose microhabitats. This selection is more marked between seasons than among sex and age groups. With snow, for example, they move from more open stands to denser stands, returning to open stands as the snow melts (Robinson and Maxwell 1969, Anderson 1973, Hedberg 1980, Herman 1980, Allan 1988). Whether this movement is related to availability of snow of sufficient depth for snow cover is unknown. Density of breeding females increases where food is more available in the shrub and herb layer (Naylor and Bendell 1989), suggesting a selection of specific areas within the forests for their territories.

Males choose territorial sites with greater canopy coverage and stem density overall, but less shrub cover, than non-territorial sites (McLachlin 1970, Hedberg 1980). Nevertheless, within each territory the actual display site (see Behavior) is relatively open. Among females, brooding females choose a more open forest canopy than broodless females (McCourt 1969, Hedberg 1980). The selection of such microhabitats appears to be a compromise between food acquisition and predator avoidance.

The close association of Spruce Grouse with conifer forests is sometimes violated during periods of dispersal and migratory movements. At these times the birds may traverse areas of deciduous growth, apparently avoiding nonforested areas except for rivers and streams which they fly across rapidly. In autumn, however, they have been found in deciduous

many kilometers from the nearest conifer habitat.

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FOOD HABITS

FEEDING BEHAVIOR | DIET | NUTRITION AND ENERGETICS

FEEDING BEHAVIOR

Largely herbivorous, taking small amounts of animal matter only during the snow-free of the year (Ellison 1966, Pendergast and Boag 1970, Lattner 1982). Over most of the range, rely heavily on needles of pine (*Pinus banksiana* or *P. contorta*) as the main, an some months in winter, the sole food items in the diet (Crichton 1963, Pendergast and 1970, Naylor and Bendell 1989). Where pines not readily available, needles of other cc such as spruce (*Picea glauca* or *P. mariana*) are taken (Ellison 1966, 1976). Foraging in conifers occurs mainly at midcrown level, perhaps because needles there are nutritious better, branches provide sturdy support, and the grouse can see approaching avian prey but still remain partially concealed. Characteristically, this foraging involves clipping of swallowing the distal half to five-sixths of the needle, usually leaving its basal portion attached to the branch. When not browsing on conifers, the birds feed mainly from the clipping off the growing tips of small shrubs and forbs, their flowers and fruits, the fruit parts of forest fungi, as well as small arthropods, terrestrial snails and grit (Pendergast Boag 1970, Lattner 1982, Naylor and Bendell 1989, DeFranceschi and Boag 1991).

During the snow-free part of the year, typically forage alone on the ground (except for with chicks), but in winter often in loose flocks of 2 to approximately 30 birds. In Alaska flock size varied from 3.6 birds in October to 2.8 in March (Ellison 1972). Brood female their chicks from one foraging site to another (Schroeder and Boag 1985), usually small openings in the forest where insects, flowers, and fruits of small plants are denser and microclimate warmer than in surrounding forest (McCourt 1969, DeFranceschi and Boag 1991).

Forage throughout the day, with peaks in early morning and late afternoon (after and in the nightly fast). Peaks most marked in incubating females, with 79% of feeding done 05:30 and after 19:00 (Herzog 1978). Foraging rate slow, about 7 pecks/min for females calculated over the whole day in spring ($n = 21,262$ min; Naylor and Bendell 1989), an 5 pecks/min in summer ($n = 810$ min; DeFranceschi and Boag 1991), but rate varies with food items taken and time of day; e.g. up to 50 pecks/min when pine needles are being consumed at dusk.

Beak well adapted for browsing. Forage can be gripped between tips of the mandibles and broken off with a flick of the head. Such action wears off the tip of the upper mandible end of winter, contributing to variance in culmen length measured over the year. Much consumed during peak foraging late in the day is stored in the crop, the rest of the gut having been filled during earlier feeding. Crop can hold up to 45 cc of spruce needles (Ellison 1966; about 10% of body mass, D. Keppie pers. comm.), which move into the lower gut digested over the duration of the night fast (Pendergast and Boag 1971b).

DIET

Spruce Grouse select among conifer species when foraging. Prefer pine over spruce (C 1963, Pendergast and Boag 1970, Hohf et al. 1987), white spruce over black spruce if unavailable (Ellison 1976), and, within species, for example, yellowing over green larch needles in autumn (Crichton 1963, Jonkel and Greer 1963, Allan 1985). Preferences are linked to nutrient content, such as protein and/or carbohydrate (Boag and Kiceniuk 1971), presence of plant secondary compounds (Bryant and Kuropat 1980), or ease of browsing the case of the two species of spruce (longer and more widely spaced needles of white being preferred). Same criteria seem to be used to select among individual trees of the species (Gurchinoff and Robinson 1972, Ellison 1976, Hohf et al. 1987). Why some trees selected and heavily browsed yet adjacent ones ignored needs further study, as does the difference among individuals in their degree of selectivity.

During incubation, female *D. c. franklinii* appear to forage in a highly selective manner. For example, 74% of their foraging time ($n = 1,514$ min) was spent consuming the growing leaders of white spruce, a species that occupied only 4% of habitat (Herzog 1978). This selection may have been linked to a relatively high calcium content of spruce and/or that with which a large volume could be consumed within a short time (Pendergast and Boag 1971b).

Major items in diet vary with age of bird, season of year, and geographic location (Table 2). Despite seasonal and spatial variation, conifer needles (*Pinus* spp., *Picea* spp.) form the major component in diet of adults, being consumed year-round, exclusively so in winter. Needles of larch taken mainly in autumn (Allan 1985) after they have become yellow and probably contain relatively high levels of carbohydrates (Boag and Kiceniuk 1968). Growing tips, leaves, flowers, and fruits of *Vaccinium* spp. form a second major component, being consumed in spring, summer, and autumn. Other foods are taken in much lower quantities on an annual basis and possibly opportunistically as, for example, the flowers of trailing arbutus (*Epigaea repens*) and sporecapsules of moss (*Polytrichum* spp.) by prelaying hens (Naylor and Bendell 1989) and the summer use of fungi (see below).

Among juveniles, diet changes from mostly animal matter in the first months of life to progressively more vegetation at the end of summer (Pendergast and Boag 1970, Lattin 1982). By November, young birds feed on the same items and in the same proportions as adults. Fungi are important in diet of chicks. In the wild, 16% of 2,604 observed foraging pecks directed at the lamellae of large sporocarps of basidiomycetes (DeFranceschi and Robinson 1991), 16% at arthropods (mainly ants), 25% at fruit of *Vaccinium*, and by late August on needles of *Pinus contorta*.

Juveniles and adults apparently take advantage of unusual foraging opportunities. Jon Greer (1963) commented on large volumes of rarely taken items, e.g. a crop containing a grasshopper (Acrididae). Likewise, in an instance of contagious foraging on mushrooms by one young bird, having discovered a sporocarp, began uttering the *purr* call (Table 2), apparently attracted its siblings to the fungus upon which all fed voraciously (DeFranceschi and Boag 1991). The extent to which fungi contribute to the diet in parts of the range outside Alberta remains unknown.

NUTRITION AND ENERGETICS

Nutritional studies have concentrated on the ability of Spruce Grouse to subsist on a diet consisting largely of conifer needles (Ellison 1966, Pendergast and Boag 1971b, Ellison 1976) and on the role of spring food in female reproductive success (Naylor and Bendell 1989). Heavy reliance on conifer browse in all populations studied (Ontario, Crichton 1963; Montana, Jonkel and Greer 1963; Alaska, Ellison 1966, 1976; Michigan, Gurchinoff and Robinson 1972; Washington, Hohf et al. 1987) raises questions about how these grouse adapted to a diet of such low nutritive value (Boag and Kiceniuk 1968). Individuals held in captivity during January in Alberta consumed on average 40.4 g (dry weight) of pine (*P. contorta*) needles per day, from which their total fecal output was 29.5 g (dry weight; Pendergast and Boag 1971b), thus assimilating ca 27% of the dry weight. About 30% of gross energy available was assimilated, a level that gave an average daily intake of 63 kJ. This was apparently insufficient to keep most grouse tested in energy balance under the environmental conditions experienced (low ambient temperatures but a sedentary existence) because they were losing ca. 1 g body protein per day (Pendergast 1969). The large volume of conifer browse consumed to meet energy demands seemed to assure an appropriate

of amino acid uptake, despite the low protein content (6%–8% dry weight) of conifer browse (Pendergast and Boag 1971b, Ellison 1972). Low digestibility of the main energy component (cellulose) of conifer browse (Fenna and Boag 1974a) thus obliges these grouse to consume sufficiently large quantities that they meet not only their energy demands but also other nutrient requirements (protein and mineral, the latter with the help of grit). As such, winter presents no food problems for this grouse (Ellison 1972). This seems not to be the case for breeding females in spring when access to high quality foods may be a requisite for successful breeding (Naylor and Bendell 1989).

Seasonal changes in diet are accompanied by seasonal changes in the gastrointestinal tract. The mass of the ventriculus increases by ca 75% and the lengths of some gut components such as the caeca, increase by ca 40% in winter relative to summer (Pendergast and Boag 1973). The stimulus for this change is the volume of food that must be processed per unit time in order to maintain the birds in energy balance (Fenna and Boag 1974a).

Observations of birds during winter indicate that one dropping is produced ca every 6 h, about 30% more often than in summer (M. Schroeder unpubl. data). The caeca, however, retain their contents, which undergo digestion and absorption over extended periods, and are evacuated about once every 24 h, usually in the early morning (Fenna and Boag 1974a). Caecal feces are distinct, formless pasty masses, dark greenish olive. The physiology of the caeca needs further investigation, particularly their potential role in endogenous heat production and in nitrogen cycling through counterflow of uric acid from the cloaca to the caeca.

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Xerox WorkCentre Pro SMTP Transfer Report

XEROX

Job Status: **FAILED** Scan image transfer failure.

Job Information

Device Name: XRX_0000AA6B6EAB
Submission Date: 07/10/06
Submission Time: 03:56 PM
Images Scanned: 0
Size: 0

SMTP Server

Address: 10.30.100.23:25

Message Settings:

Subject: Scan from a Xerox WorkCentre Pro
From: WCP90@ttec.com
To:

1. brita.woeck@ttec.com



Spruce Grouse

Falcipectes canadensis

Order GALLIFORMES - Family PHASIANIDAE

BNA No. 5

Authors: D. A. BOAG, M. A. SCHROEDER

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SOUNDS

VOCALIZATIONS | NONVOCAL SOUNDS

Despite producing an array of sounds, both vocal (Table 2) and nonvocal (Lumsden 1968, MacDonald 1968, Harju 1969, Hjorth 1970), Spruce Grouse are among the most silent tetraonids. Most sounds are apparently produced by both subspecies, except *wing-clap*, only from territorial males of *D. c. franklinii*. Whether this subspecific difference reflect adaptation to a specific environment and/or to its evolutionary history is not known.

VOCALIZATIONS

Vocalizations include 11 distinct sounds (Table 2; Figs. 3-5), all but one of which are considered calls, usually given under specific circumstances.

Only one vocalization has been classed as a song, the *cantus* (Fig. 5a, b), recorded from females of *D. c. franklinii* on their spring territories. In southwestern Alberta, during the prelaying and laying periods, females sing from specific pinetrees usually well spaced within their territories (Nugent and Boag 1982). These trees, used as song perches, are also used as feeding trees at dawn and dusk, and as roost trees, where birds pass the night. This song is apparently sung spontaneously when light intensities are low (< 33 lx) at dawn and dusk and can be stimulated at any time of day during this period by playing a recording of it inside the territories. The *cantus* has never been heard in a courtship context (Nugent and Boag 1982). Apparently female *D. c. canadensis* utter a similar "long cackling call with several inflections" (J. Bendell pers. comm.), but its significance remains poorly understood. Spruce Grouse are reported to produce a hoot similar to that of Blue Grouse (Greenewalt 1968: 22), but this call has not been recorded by any student of Spruce Grouse. We concur with Hjorth (1970) that the recording upon which Greenewalt's description is based is probably from a Spruce Grouse but rather an interior Blue Grouse.

NONVOCAL SOUNDS

Nonvocal sounds recorded only from territorial males. The loudest such produced by territorial male *D. c. franklinii* during the *wing-clap* display (Table 3), two sharp claps (about 0.5 s apart), usually in a small opening after a short flight (< 25 m) through the trees (MacDonald 1968: Fig. 7, Hjorth 1970, Nugent 1979). These *wing-claps* can be heard by the human ear to 150 m under most field conditions and consequently can provide an index of species abundance (Schroeder and Boag 1989). It is not known whether they are produced by displacement of air or actual physical contact of the wings.

Descent from perch to ground does not include a *wing-clap* display in *D. c. canadensis*. In the latter subspecies the descent also produces a whirring sound, although of different tonal frequency than that typical of the ascent (D. Keppie pers. comm.). The descent is also accomplished almost vertically and on rapidly beating wings (Lumsden 1961).

Five other nonvocal sounds are produced during various courtship displays. *Drumming* Spruce Grouse produces soft thumps, audible to the human ear only over a very short distance. Pecking sounds are scarcely audible, being produced by males when they strike beaks against some solid substrate, usually a branch or some object on the ground. This activity is usually seen when males threaten an intruder on their territory. During various displays, the faint dull sound of stamping is produced when the feet are raised and lowered rapidly without displacing the bird.

The *tail-swish* and *whoosh* (MacDonald 1968: Fig. 15) are produced by the rectrices. The former occurs when rectrices on one side of the midline are spread laterally (with a step forward of the foot on the opposite side) and then closed medially when the rectrices on the opposite side are spread (and the other foot is brought forward) as the male struts in the *swish* display (Table 3), giving the oncoming bird an apparent swaying motion. The soft rasping sound is produced as the dorsal surface of a rectrix is drawn beneath the ventral surface of the adjacent more medial rectrix. The ventral ridges on the rami of the barbs form a projecting keel that rubs against the dorsal surface of the more lateral rectrix moving past it. The *whoosh* produced during the *tail-flick* display (Table 3) is a louder rendition of the *swish*, being produced by a rapid simultaneous lateral displacement of all the rectrices with exaggerated fanning of the tail (Lumsden 1961: Fig. 2).

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Spruce Grouse

Falcapennis canadensis

Order GALLIFORMES - Family PHASIANIDAE

BNA No. 5

Authors: D. A. BOAG, M. A. SCHROEDE

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BEHAVIOR

LOCOMOTION | SELF-MAINTENANCE | AGONISTIC BEHAVIOR | SEXUAL BEHAVIOR | SOUND AND INTERSPECIFIC BEHAVIOR

LOCOMOTION

Largely terrestrial, apparently preferring to walk when moving from place to place. Exc is shift to arboreal foraging on conifer needles during autumn and winter; the stimulus remains unknown, but it occurs irrespective of snow cover (Keppie 1977b). In conifers, generally move about by walking along limbs and hopping from branch to branch, prot aided by the pectinations on the lateral edges of the toes, which regrow annually in ea autumn, creating an additional surface area for contact with the substrate. Pectinations help sustain the weight of the bird while walking on snow (Höhn 1977). They are shed spring.

Spruce Grouse seem reluctant to fly other than to enter conifers for foraging, roosting, during spring display by males when flights are mainly between the ground and the bra of trees a few meters above the ground (Lumsden 1961, MacDonald 1968). Apart from almost-vertical flights, the birds use two major flight modes: rapid but almost silent ar dextrous flight among the trees of the relatively dense forests they inhabit, usually ove short distance (< 50 m), or, more rarely, rising noisily in near vertical flight until clear canopy to level off and fly rapidly a considerable distance (> 100 m) before plunging b coniferous cover. The first flight mode occurs most often in response to either vocal or vocal (usually flight) sounds of an intruder in the bird's territory, whereas the second is response to an unsuccessful attack by an avian predator. Their wings are well adapted such flight, having an elliptical form with a low aspect ratio (ca 2:1), deep camber, and slotted primaries; the broad tail acts as an effective rudder and possibly an airfoil.

SELF-MAINTENANCE

Many self-maintenance behaviors described (Table 3), but little known of their frequen sex, age, time of day, or season. Maintenance activities examined only in broods (Harj Ellison 1973, Alway 1977, Alway and Boag 1979, Schroeder 1985a, Schroeder and Boag 1985). The simultaneous stretching of wing and leg on one side, as well as standing at maximum height and flapping the wings a few times, may include stretching the neck and opening the mouth.

Appear to seek microhabitats safe from predators and energetically optimal for roostin on the ground under the shelter of overhanging shrubs or conifer boughs or in conifers the stem and at midcrown position. When temperatures fall below ca -10°C and suitab conditions prevail, they may roost in snow burrows (Robinson 1980, DAB unpubl.), inv located in small openings in relatively dense forest where snow has not been intercept vegetation or blown by wind and has accumulated to a depth of at least 30 cm. In sno density, such burrows provide a microclimate in which the ambient temperature rises t C (Andreev 1980), probably within the thermoneutral zone for this species.

AGONISTIC BEHAVIOR

Intrasexually territorial, so most agonistic interactions occur between members of the sex. Males typically respond to the presence of other males by partially erecting their breast feathers, and often by pecking aggressively at inanimate objects. The territory occupant may perform any or all of the following displays: the *tail-swish*, *flutter-flight* and *D. c. franklinii*, the *wing-clap* in response to an intruder (Table 3). Interactions usually end with the intruder retreating, either with or without the territory occupant in pursuit. In the former case, the occupant runs toward the intruder with plumage sleeked. If the intruder fails to fly off, it is attacked. When fights occur between males or when a territorial male is presented with a mirror image of itself, it attacks the head, neck, and back of the intruder with feet, bill, and wings (Lumsden 1961, Stoneberg 1967, MacDonald 1970, McLachlin 1970, Robinson 1980). Physical contact between females may occur during the laying period (Nugent and Boag 1982); interactions typically include singing, threatened raised plumage and hisses, chasing, as in males, and buffeting with the wings (MacDonald 1968, Harju 1969, McCourt 1969, Robinson 1980, Nugent and Boag 1982).

Territorial tendencies peak in spring, when both sexes defend minimal areas within or larger home ranges (see Table 5). Male territoriality is shown maximally at the display with the level of defense declining as a male moves away from this site (Nugent 1979). Acquisition of territorial status seems to differ between the sexes. Most females attempt to hold territories and breed as yearlings: at least 95% of *D. c. canadensis* and 71% of *D. c. franklinii* (Keppie 1987b). Those successful in acquiring territories respond defensively to playbacks of the *cantus*, whereas yearling females not yet established on territories (birds that were probably still undertaking spring dispersal) do not respond to this female sound; in fact usually move away from the source of the sound (Herzog and Boag 1977). Among males, about half the yearlings show territorial behavior: 44% ($n = 9$) of *D. c. canadensis* from south-central Alaska (Ellison 1971), 51% ($n = 122$) in New Brunswick and Ontario (Keppie pers. comm.), and 48% ($n = 42$) *D. c. franklinii* in southwestern Alberta (McKinnon 1983a). Yearling males make up 29% of all territorial males of *D. c. canadensis* in Ontario (Szuba and Bendell 1988) and 15% of *D. c. franklinii* in Alberta (McKinnon 1983b). Nonterritorial yearling males appear to display no courtship behavior, to have lower levels of circulating androgens, lower body weights, larger home ranges, and longer dispersal distances than territorial yearlings (McKinnon, 1983b). Yearlings of both sexes occupy larger home ranges and territories than adults in both winter and spring (see Table 5).

Despite a peak in advertising displays during the breeding season, territories may be maintained all year (McLachlin 1970, Robinson 1980). Territorial activity increases slightly in both sexes in autumn (Herzog and Boag 1977, 1978), and a lack of winter flocking in adult males may indicate the occupancy of winter territories (Ellison 1973). Resident adult females flock less than migratory adult females in winter (Schroeder 1985b), suggesting that they may retain territorial tendencies at this time. Further more, a stable and apparently linear dominance hierarchy is established in captive winterflocks (Alway 1977).

SEXUAL BEHAVIOR

Females are assumed to be monogamous, males polygynous; individual radio-marked females were recorded consorting with only one male, but not always on contiguous territories, individual males were recorded consorting with more than one female (D. Nugent pers. comm.).

Upon locating a female during the breeding season, a territorial male exhibits a series of characteristic behaviors: erects much of the plumage (particularly the breast and tail feathers), droops wings slightly, erects the superciliary combs, bobs the head vertically and often pecks the substrate (ground or branch) while presenting the side of the head, thus showing off the combs. The *tail-swish*, *tail-flick*, and *head-jerk* displays (Table 3) are the primary male courtship displays. The *tail-swish* involves moving slowly forward with the tail erect and under tail coverts spread widely (Robinson 1980: Fig. facing p.118), and with an alternate spreading of lateral rectrices that is synchronized with the movement of the legs. This gives an exaggerated swaying motion that is accompanied by a swishing sound produced by the movement of the rectrices. The *tail-flick* is the climax of the *tail-swish* and follows a short rush. The male stops suddenly near the female with wings drooped and snaps the rectrices laterally where they are held briefly before being closed (MacDonald

Fig.15). The *head-jerk* occurs when the male squats near the female and stamps his feet rapidly. The wings are spread slightly away from the flanks, rectrices are repeatedly fanned and the head is turned rapidly from side to side in a jerky manner. Males may remain in this position, often motionless, for short periods of time.

Copulation is preceded by the female squatting with wings slightly extended (Harju 1979). The male approaches and steps onto the female's scapulo-humeral tract, balancing by grasping her nape feathers with his beak and extending his wings laterally. Then he lowers his tail to rest on the rump beneath the female's upturned tail to establish vent contact, which lasts less than 10 seconds. Postcopulatory behavior involves immediate vigorous shaking and preening by the male. No male postcopulatory display has been recorded.

SOCIAL AND INTERSPECIFIC BEHAVIOR

Sociality

Largely solitary birds, females with broods in summer being an exception. Loose flocks of 2-5 birds, however, may form in late August and September, and can number up to ca 30 birds as broods combine (Ellison 1973). In south-central Alaska, mean flock size (excluding solitary birds) declined from 3.6 ($n = 58$) in October to 2.8 ($n = 16$) in March (Ellison 1972). Small flock sizes in October may result from the departure of adult females from groups during brood break-up and dispersal in autumn (Alway and Boag 1979). At this time juveniles and migratory females are most likely to form foraging flocks (Schroeder 1985a), with resident adults of both sexes joining such flocks only when the flock enters their home ranges (Ellison 1973, Herzog and Boag 1978). The decline over winter seems to reflect a tendency for adults to become increasingly solitary as well as the loss of birds to predation. Flock composition rarely remains stable for more than 2-3 days in Alaska (Ellison 1973), 3-5 days in southwestern Alberta (Schroeder 1985a).

In spring, both sexes become solitary, ultimately defending all or part of their home range (McLachlin 1970, Herzog and Boag 1977). Females become more aggressive, uttering *cantus* more frequently, a behavior that peaks after becoming established on territories (Herzog and Boag 1977). The probability of an aggressive response between females is greatest during the early prelaying period (Nugent and Boag 1982); by late incubation females tend to ignore each other.

Play

The *flap-run*, interpreted as a form of play, has been described for juveniles in broods of 3. Each bird, with raised and flapping wings, runs and leaps about over short distances. On occasion, brood hens may also join in this behavior (Schroeder and Boag 1985).

Predation

A major egg predator appears to be the red squirrel (*Tamiasciurus hudsonicus*; Robins 1980, Boag et al. 1984, Naylor and Bendell, 1987), although corvids also are suspected (Boag et al. 1984). Most mammalian predators (canids and mustelids) take eggs and birds while hawks and owls tend to take only birds. Red squirrels, coyote (*Canis latrans*), red fox (*Vulpes*), weasels (*Mustela* spp.), Northern Goshawk (*Accipiter gentilis*), and Barred Owl (*Bubo varia*) have been identified as predators in northern Michigan (Robinson 1980); Northern Goshawk, Northern Hawk Owl (*Surnia ulula*), and Great Horned Owl (*Bubo virginianus*) in south-central Alaska (Ellison 1974); red squirrel, coyote, mustelids, and raptors in southwestern Alberta (Keppie and Herzog 1978, Boag et al. 1984, Schroeder 1985a, Schreiner and Boag 1985); and Sharp-shinned Hawk (*Accipiter striatus*), Northern Harrier (*Circus cyaneus*), and lynx (*Lynx canadensis*) in Ontario (D. Keppie and J. Bendell pers. comm.).

Predation is assumed to be the major cause of mortality in Spruce Grouse. At the egg stage, the average rate of nest loss ranges from 19% ($n = 36$) in *D. c. canadensis* to 70% ($n = 6$) in *D. c. franklinii* (Redmond et al. 1982). The loss of entire clutches is most common, usually the result of mammalian predation. In most instances, the incubating female escapes, albeit sometimes at the last possible moment, as attested by feathers (often all the rectrices missing) and potential victims (individuals banded) later seen alive (D. Boag and M. Schreiner unpubl. data). Partial loss of clutches usually attributed to red squirrels (Robinson 1980).

et al. 1984, Naylor and Bendell 1987). Most chick mortality, 76% in a population of *D. c. franklinii* (Smyth and Boag 1984), occurs during the first two weeks of life, with a second period of lesser loss during the first autumn or winter (Ellison 1974, Keppie 1975). Overall mortality in all age and sex classes is low (mean = 12%) in *D. c. franklinii* in southwest Alberta (Keppie 1979) but greater (mean = 23%) in *D. c. canadensis* in south-central Alberta (Ellison 1974). Among territorial females of *D. c. franklinii*, annual mortality is greatest May through August (63%), particularly when they are gravid (Keppie 1975). In contrast territorial males in this area suffer only 35% of their annual mortality during this period (Keppie 1975). Most predation on yearlings and adults appears to be by raptors, especially Northern Goshawks (Ellison 1974, Robinson 1980).

Little is known about the response of Spruce Grouse to predation. The cryptic nature of plumage, particularly of females, coupled with the tendency to remain immobile until approached by a potential predator, suggest that predation pressure by visual predators has been, and probably continues to be, an effective selective force in the evolution of the semorphological and behavioral attributes. The combination of camouflage and immobility may provide the grouse with the best means of avoiding such predators.

Females with newly hatched chicks threaten small mammalian predators such as red squirrels and weasels by rushing at them with raised plumage, particularly on the neck and breast while uttering the *hiss* call. Their response to larger mammalian predators is to show threat or distraction displays in an attempt to draw the predator away from the immediate location of the brood, which has usually scattered and hidden in response to the female's *hum* call (Harju 1969, Schroeder and Boag 1985). These responses of the female are most intense at the outset of the post-hatch period, diminishing in intensity as the chicks grow older (Harju 1969).

Brood movements appear to be a trade-off between predator avoidance and food acquisition (Schroeder and Boag 1985). Average distance between hen and chicks, maintained through *heep* calls of the female and *sreep* calls of the chicks, is relatively short, averaging less than 1 m in the first 21 days but increasing to over 4 m at 100 days (Schroeder and Boag 1985). Proximity of the brood to the female enables them to act as a coordinated group, which, in the face of a predator attack, may avoid mortality more effectively. It also enables the female to control the direction taken by the brood, directing it to places where the combination of microclimate, food resources, and opportunity for early detection of predators appears most favorable (Schroeder and Boag 1985). The route traveled between these places, usually small clearings or trails in the forest, is typically direct; yet the route within the latter is typically meandering and apparently random, lacking pattern (Schroeder 1985a), possibly a defense against the "win-stay search strategy" of predators such as certain raptors (Sonerud 1985).

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BREEDING

CHRONOLOGY | NEST SITE | NEST | EGGS | INCUBATION | HATCHING | YOUNG BIRD: PARENTAL CARE | FLEDGLING STAGE

CHRONOLOGY

Egg laying begins about 17 days after ground becomes 50% snow-free (Keppie and Towers 1990). In southwestern Alberta (Fig. 2) this is usually about 30 May (McCourt 1969, McLachlin 1970). Here, however, the onset of laying can vary annually by as much as ($n = 16$ years) depending upon ambient conditions (Smyth and Boag 1984). Low temperatures with precipitation can delay the onset whereas moderate temperatures and an early snowmelt can accelerate it. Within a given year, most (67%) clutches hatch within a ten-day period (Smyth and Boag 1984, Keppie and Towers 1990). The early loss of a clutch of eggs, generally through predation, can be mitigated by replacement, usually with a clutch of smaller size (Keppie 1982). In most years, the first chicks hatched are those of adult females (McCourt 1969, Smyth and Boag 1984). The chicks hatch relatively synchronously, usually leaving the nest within their first 24 hours of life (McCourt et al. 1973). Broods begin to disperse when the chicks are ca 9–12 weeks old (Alway and Boag 1979), juvenile males leave the brood earlier (median ~ 4 Sep) than juvenile females (median ~ 15 Sep, Schroeder 1990).

NEST SITE

Spruce Grouse always nest on the ground, usually in a natural or created depression. Nest locations, selected by the female, appear to have one feature in common: overhead cover usually at the base of coniferous growth. In Minnesota, *D. c. canadensis* generally nest in depressions in sphagnum moss at the base of a black spruce (*Picea mariana*; Haas 1977) whereas in New Brunswick 95% of nests ($n = 37$) are at the base of trees in spruce-pine-jackpine forests but only 5% are in spruce-balsam fir (Redmond et al. 1982), the dominant forest type. In forests of southwestern Alberta, dominated by lodgepole pine (*Pinus contorta*) 55% of nests ($n = 67$) of *D. c. franklinii* are at the base of a pine, 27% close to the base of white spruce (*Picea glauca*), and 18% under a clump of willow (*Salix* spp.), a mat of juniper (*Juniperus communis*), or a horizontal log (Keppie and Herzog 1978). Nests are located within the female's territory, usually at a point maximally dispersed from other nests and the sites of territorial males (Herzog and Boag 1978).

A comparison of cover at nest sites of *D. c. canadensis* (New Brunswick) and *D. c. franklinii* (Alberta) suggests that the former nest in heavier cover (overhead and lateral) than the latter (Redmond et al. 1982). Nest success was significantly lower in *D. c. franklinii* (30%) than in *D. c. canadensis* (81%). The two age categories of females of *D. c. franklinii* choose different amounts of cover: 91% of yearlings ($n = 22$) and 50% of adults ($n = 36$) nest in poorly concealed microhabitats (Keppie and Herzog 1978). Nests near trails are less successful than those farther away (37%), possibly because the assumed principal nest predators of *D. c. franklinii*, coyotes, regularly travel on trails from which they can smell nesting birds (Herzog and Herzog 1978). Where the principal predator was the red squirrel, predation was highest away from trails and where nest densities were highest (Boag et al. 1984).

NEST

Little more than a simple bowl-like depression in the substrate, lined with whatever dead needles or leaves are present in and around the nest bowl, plus some ventral tract fecal (Redmond et al. 1982). Nests of *D. c. canadensis* in New Brunswick and Michigan are somewhat smaller than those of *D. c. franklinii* in southwestern Alberta (Robinson 1981; Redmond et al. 1982). The nest bowl may become deeper as incubation proceeds (McCourt et al. 1973, Robinson 1980), partly because the female pulls bits of dead vegetation toward nest perimeter while incubating, often partially covering the eggs before leaving to forage, particularly in late incubation (McCourt et al. 1973). Nests have not been recorded used the same or subsequent years, either by the same or different females.

EGGS

Egg shape is between oval and short oval. Color varies within each subspecies from taupe to olive (Smithe 1975-81: #223D) to pale tawny olive background with markings (spots or irregular blotches) of burnt umber (#22) to tawny brown (#223A). Eggs of *D. c. franklinii* in southwestern Alberta measured on average ($n = 17$) 42.43 mm in greatest length by 30.3 mm in greatest breadth (D. Keppie, D. Boag, and M. Schroeder unpubl. data). This gives an average egg volume (based on Hoyt 1979 formula) of 20.4 cc, similar to the eggs of *D. c. canadensis* in New Brunswick, which averaged 19.7 cc (range 16.2-22.3; Keppie 1981). Average mass of a fresh, unincubated egg of *D. c. canadensis* is 22.0 g ($n = 53$) in New Brunswick (Keppie 1985) and 21.9 g ($n = 32$) in northern Ontario (Naylor and Bendell 1989). Using proportional data on egg volume, the fresh egg mass of *D. c. franklinii* would be

These values for the mass of individual eggs represent 4.1% of mean body weight in a female *D. c. canadensis* (Naylor and Bendell 1989), and 4.3% in *D. c. franklinii* (Fig. 7). The percentage of female body weight represented by the average clutch is 23.0% in *D. c. canadensis* and 20.6% in *D. c. franklinii*.

Clutch size of *D. c. canadensis* (mean = 5.6 ± 1.3 , $n = 24$) is greater than that of *D. c. franklinii* (mean = 4.8 ± 1.1 , $n = 40$; Keppie 1982). Yearling females lay smaller clutches than adults in both subspecies (*D. c. canadensis*: 6.6 ± 1.1 , $n = 8$ vs. 5.0 ± 1.1 , $n = 14$; *D. c. franklinii*: 4.9 ± 1.2 , $n = 25$ vs. 4.5 ± 1.0 , $n = 14$ (Keppie 1982). The first egg is laid in a simple depression in the ground, sometimes initially scraped out by the female with no preparation other than the pressing down of dead plant material that forms the lining of the nest (McCourt et al. 1973). Oviposition appears to occur in the afternoon at the rate of one egg every 1.4 days (McCourt et al. 1973, Alway 1977). As the clutch approaches completion the female spends more time on the nest (McCourt et al. 1973). Intraspecific egg parasitism has not been recorded in this species and would seem unlikely because intraspecific aggression peaks at this time (Herzog and Boag 1977, Nugent and Boag 1982).

INCUBATION

Only the female incubates. Incubation begins with the last egg laid, by which time the female has begun to develop a central brood patch in the ventral pterygia. Only well into incubation, however, does the brood patch become fully developed (Keppie 1987b). Incubation lasts approximately 21 days, recorded in captivity for *D. c. canadensis* (Pendergast and Boag 1971a), but 23.5 days recorded in the field for *D. c. franklinii* (McCourt et al. 1973), a difference that could reflect only relative attentiveness of the female. During incubation, hens lose 0.175-0.18 g/day for the first 20 days of incubation (Keppie 1985, Naylor and Bendell 1989). Incubating hens leave their nests to defecate and forage one to six times daily (Naylor et al. 1973, Haas 1974, Herzog 1978, Alway 1977), with three being most common (Naylor et al. 1988). Reccess length averages 26.4 minutes in *D. c. canadensis* in Ontario, and is inversely correlated with cooling rate of the eggs; temperatures decline an average of 5.5 degrees during a recess (Naylor et al. 1988). The distance traveled from the nest to foraging sites by a radio-marked female *D. c. franklinii* ($n = 9$) in southwestern Alberta is relatively short, averaging 83 m (Herzog 1978). The large fecal masses that accumulate in the cloaca while incubating (clocker droppings) are usually deposited at distances of more than 10 m from the nest (Keppie and Herzog 1978) often while foraging in conifers (Herzog 1978). Only late in incubation, when foraging trips are fewer and often briefer, are clocker droppings deposited nearer the nest (Keppie and Herzog 1978). In late incubation, females often partially c

their eggs with litter when leaving the nest (McCourt et al. 1973). Most (74%, $n = 114$) feeding trips by incubating females occur in early morning (before 05:30) or late in the afternoon (after 19:00; Herzog 1978).

HATCHING

Precise onset of communication between hen and chicks in the egg is unknown. Hens respond to playbacks of chick calls about the time eggs begin pipping (Harju 1969, Alway 1977). Time from pipping to hatching is about 24 hours (J. Bendell and D. Keppie pers. comm.). Chick departure from the nest occurs as soon as all chicks are dry and mobile (ca 8 hours later). The initial distance traveled from the nest seems to depend upon ambient conditions and the rate of cooling of the chicks. It can vary from less than 10 m under cold, wet conditions to over 100 m if ambient conditions are dry and warm (Schroeder and Boag 1985).

YOUNG BIRDS

Average mass of chicks at hatching is ca 15 g (McCourt 1969, D.M. Keppie pers. comm.). Chick growth in mass and linear measurements is rapid (Fig. 6). For the first 14 days, male and female chicks show similar average growth rates (1.96 g/d), but thereafter males grow faster than females (days 15–62: males, 5.96 g/d; females, 4.95 g/d; Quinn and Keppie 1981). Differences in chick growth rates between years are not related to body condition of the hen but seem to be influenced most by environmental conditions posthatch (Quinn and Keppie 1981). Adult body mass and some measurements are not achieved until the birds are 12 months of age (Fig. 7).

Initially, the only mode of locomotion possible for chicks is walking. Weak flight recorded in the field at 6–8 days of age (Stoneberg 1967, Robinson 1980, Schroeder and Boag 1985). Early flights are of short duration and distance, usually taking the young birds onto the branches of trees; only later are they better able to fly horizontally (D. Boag unpubl. data).

Behaviors, including *loafing* (generally in the sun), *preening*, *dust bathing*, and the *flap run* (Table 3), and calls, including the *sreep*, *sury*, *seer*, and *purr* (Table 2), have been observed throughout the brood period (Alway 1977, Alway and Boag 1979, Schroeder and Boag 1985). Other behaviors appear later in the brood period. The *jerky-crouch*, similar to the *heep* display of adult males (except that the tail is held close to the ground in the former but raised and alternately spread laterally in the latter), has been observed in both sexes of chicks after ca 6 weeks of age, apparently stimulated by the approach of a more dominant bird (Alway 1977, Alway and Boag 1979, Schroeder and Boag 1985). The *tail-swish* and *tail* have been observed only in young males more than 45 days of age, when they figure in male and even male-female interactions (Hjorth 1970, Alway 1977, Alway and Boag 1985, Schroeder and Boag 1985).

PARENTAL CARE

Hens brood their chicks all night and frequently during the day until they are about 3 weeks of age (Alway 1977, Schroeder and Boag 1985). Chicks appear to initiate a female's brooding behavior by uttering *sury* calls and to terminate brooding by either uttering *sreep* calls or moving out from beneath the female. The stimulus for selecting an appropriate location for assuming the brooding posture seems to be the *sury* calls of the chicks, uttered when they are cold (Alway 1977, Schroeder and Boag 1985). The percentage of time spent brooding decreases from ca 80% when chicks are less than 10 days of age, to 0 when more than 30 days of age (Schroeder and Boag 1985). The frequency of brooding during the day is affected by both age, which is related to the development of thermoregulation, and by ambient conditions, cool and wet conditions increasing the frequency (Robinson 1980, Schroeder and Boag 1985). By contrast, the duration of a brooding bout during daylight hours is relatively constant (median of 11 min), showing little variation with either age of chicks or weather conditions (Schroeder and Boag 1985).

Young birds are apparently not shown what to eat by their female parent (Schroeder and Boag 1985). In normal feeding situations, chicks utter *sreep* calls and the female replies with *heep* calls (Table 2) (Schroeder and Boag 1985). Chicks may recognize the *heep* calls of their own female parent, thus minimizing the possibility of brood mixing (Alway 1977, Keppie

1977a). Visual or vocal isolation from the female parent prompts the young to utter *see* to which the hen responds with louder *heep* calls (Table 2). Typically, young range farther from their female parent as they grow older; this is also true for the distances at which calls are uttered by young (Schroeder and Boag 1985).

Young birds also spend more of the daylight period feeding as they grow older (Schroeder and Boag 1985), compensated for by a reduction in time spent being brooded. Broods, in moving from one feeding site to another (Robinson 1980, Schroeder 1985a), travel faster as they grow older (Schroeder and Boag 1985). Young birds may control the rate of movement: the *purr* call, travel being slowed when this call is uttered (Schroeder 1985a).

FLEDGLING STAGE

Young generally remain in broods for 70–100 days (Fig. 2); in *D. c. franklinii* males sooner (median of 4 Sep, $n = 46$) than females (median of 15 Sep, $n = 33$; Schroeder and Boag 1985, Schroeder 1986a). Although no overt agonistic interactions between the chicks have been observed during brood break-up (Alway and Boag 1985), distances between them increase throughout the brood period (Schroeder and Boag 1985). Evidence from (Schroeder and Boag 1985) and captive studies (Alway and Boag 1979) indicates that break-up may occur when brood cohesiveness diminishes to the point that *sweep* and *see* calls no longer elicit *heep* calls from the female parent.

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Spruce Grouse

Falci pennis canadensis

Order GALLIFORMES - Family PHASIANIDAE

BNA No. 5

Authors: D. A. BOAG, M. A. SCHROEDE

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MEASURES OF BREEDING ACTIVITY

Age at first breeding

Most males and females seem to be physiologically capable of breeding during their first year following hatching. Among populations of *D. c. canadensis*, most females apparently nest within 100% in Minnesota (Haas 1974), at least 95% ($n = 230$) in New Brunswick, and 94% of females ($n = 162$) in Ontario whereas among *D. c. franklinii* in Alberta the minimum is significantly less, 71% of females ($n = 233$; Keppie 1987). Population density does not appear to influence the propensity to breed among females; all 50 females on an area with 19 females/100 ha, and all 19 females on an area with 3 females/100 ha nested in Ontario (Keppie 1987b). Among males, evidence of first-year breeding is more difficult to detect. In *D. c. franklinii*, many (ca 50%) males apparently do not defend territories (they are seen repeatedly at a given display site) during their first potential breeding season (McKinnon 1970, McKinnon 1983b). In *D. c. canadensis* this percentage is somewhat less (39%; ♀ and Bendell 1988). A comparison of several attributes of yearling males considered territorial and nonterritorial shows a number of differences (Table 5). Territorial yearling males on smaller areas in spring, disperse over shorter distances between winter and spring, have larger body mass with more interstitial tissue in the testes, and show less displacement between the first and second year than do nonterritorial yearling males (McKinnon 1983b). There is no difference, however, in survival rates of the two groups. Whether territoriality represents subordination, physiological immaturity, or a trade-off between territory quality and survival has not been determined.

Clutch

Clutch size of *D. c. canadensis* (mean = 5.6 ± 1.3 , $n = 24$) is greater than that of *D. c. franklinii* (mean = 4.8 ± 1.1 , $n = 40$; Keppie 1982). Yearling females lay smaller clutches than adults in both subspecies (*D. c. canadensis*: 6.6 ± 1.1 , $n = 8$ vs. 5.0 ± 1.1 , $n = 14$; *D. c. franklinii*: 4.9 ± 1.2 , $n = 25$ vs. 4.5 ± 1.0 , $n = 14$; Keppie 1982).

Annual and lifetime reproductive output

Lifetime reproductive output not yet determined. Annual reproductive success differs among individuals, between subspecies, and among years. Hatching success (percentage of eggs hatching one or more chicks) in a population of *D. c. franklinii* ranges between 29% (Keppie 1982) and 37% (Boag et al. 1979) in southwestern Alberta. Among populations of *D. c. canadensis*, reported values are 40% in northern Minnesota (Haas 1974), 81% in southern central Alaska (Ellison 1974), 72% in northern Michigan (Robinson 1980), 81% in New Brunswick (Keppie 1982), and 67%–81% in Ontario (Szuba 1989). The average number of chicks produced (alive in August) per brood from clutches that hatched also differ: 3.2 in *D. c. franklinii* in southwestern Alberta (Boag et al. 1979), and 5.5 in *D. c. canadensis* in

southcentral Alaska (Ellison 1974), 3.7 in northern Michigan (Robinson 1980), and 3.3 Brunswick (Keppie 1982).

The number of chicks produced per female in the population is perhaps the best index overall production. In populations of *D. c. franklinii*, reported values are 1.9 in Washington based on hunter-killed birds (Zwickel and Brigham 1970), and 0.8 in Alberta, based on counts of females (Smyth and Boag 1984). In *D. c. canadensis* by contrast, these values (based on shot birds) are 4.1 in Ontario (Lumsden and Weeden 1963) and 5.4 in southcentral Alaska (Ellison 1974), but only 1.4–2.0 in New Brunswick and Ontario, based on counts of females (Szuba 1989). Some of the year-to-year difference in reproduction was related to spring weather. Nesting success (or chick survival) in a given year has been found to correlate positively with early-summer (warm) weather in the same year in northern Michigan (Robinson 1980) and in southwestern Alberta (Smyth and Boag 1984).

LIFE SPAN AND SURVIVORSHIP

Survival rates vary widely, especially between subspecies. Annual survival rates for the sex and age classes in a population of *D. c. canadensis* ($n = 196$) in south-central Alaska were 22% for yearling males, 24% for yearling females, 32% for adult males, and 43% for adult females (Ellison 1974). In Michigan, the same subspecies had an estimated annual survival rate of 37.5% for males and 22.7% for females (Robinson 1980), whereas in New Brunswick these values were 44% ($n = 99$) for males and 49% ($n = 106$) for females (Keppie 1979). For *D. c. franklinii*, estimated survival rates were much higher: 75% for males and 63% for females (Keppie 1979). The overall annual survival rate of this population in southwestern Alberta was 67.5% (Boag et al. 1979), more than double that (30.1%) in two populations of *D. c. canadensis*. Most of the mortality in *D. c. franklinii* occurred during the breeding season and summer; survival rates in winter (31 Aug–31 Mar) were 86.8% for adult males, 88.4% for yearling males, 90.6% for adult females, and 84.4% for yearling females (Keppie 1979). See also Behavior: social and interspecific behavior.

Most mortality among the young occurs either while in broods (Smyth and Boag 1984) during the young birds' first autumn and winter (Ellison 1974). The annual reduction in size of *D. c. franklinii* in southwestern Alberta averages 55% (Smyth and Boag 1984) versus 12% in *D. c. canadensis* it ranges from 8% in northern Michigan (Robinson 1980) to 48% in Brunswick (Keppie 1982). In addition, more than twice as many broods of *D. c. franklinii* (12%) as *D. c. canadensis* (5%) disappeared after hatching (Keppie 1982).

Determination of longevity is influenced by both sample size and duration of the study. In a population of banded *D. c. canadensis* in Michigan, the three oldest were males (Robinson 1980): the oldest male was at least 7.5 years old and the oldest female was 5.5. Of more than 2,500 *D. c. franklinii* banded over 21 years in southwestern Alberta, two males and one female lived at least 13 years of age (DB and MS).

MORTALITY AND DISEASE

Diseases and body parasites

Many parasites have been reported (Table 4), but none has been implicated as a serious mortality agent. Survival rates of parasitized and non-parasitized Spruce Grouse do not differ (Robinson 1980). Certain diseases and conditions, however, may be important under some circumstances. For example, *Aspergillus fumigatus*, a fungus that usually infects lung tissue, may cause death, particularly in winter (Ellison 1974), and renal gout was diagnosed as a cause of death in four radio-marked birds during periods of prolonged heavy precipitation (Herzog 1979).

POPULATION RANGE

The range of Spruce Grouse broadly overlaps that of several other grouse: Ruffed Grouse across North America, Blue Grouse in the west, and ptarmigan in the north and at high elevations (Aldrich 1963). Despite the apparent overlap, the actual distribution of these species tends to be parapatric rather than sympatric. They are separated from each other largely by vegetation and topography. For example, in southwestern Alberta, Spruce Grouse rarely occupy mixed deciduous-coniferous forests along the valley floors, a habitat

occupied by Ruffed Grouse year-round and Blue Grouse in summer. They are also absent from the ecotonal areas between forest and grassland on south- and west-facing slopes, a habitat occupied by breeding Blue Grouse at low elevations and by White-tailed Ptarmigan (*Lagopus leucurus*) year-round at high elevations.

Individual home ranges average less than 24 ha, but yearling males may range widely in summer in Alaska (up to 346 ha). Home range size estimates, including breakdowns by sex, and season, are provided for males in Alaska by Ellison (1971), males in Michigan by Robinson (1980), females in Ontario by Lattner (1982), and both sexes in Alberta by Herzog (1977).

Female territory size is negatively correlated with the amount of preferred food used by females during the period of weight gain before laying (Naylor and Bendell 1989). In Ontario and Alberta, home ranges of females with brood expand several-fold in summer. Home ranges occupied by females in autumn are also large, but smaller than those occupied in summer. Data from radio-marked birds indicate that home ranges of males are larger in winter than in spring, when only a core area is defended. Among females, however, the winter home range expands somewhat into a defended territory in spring.

Dispersal, the movement of an individual from its brood range to its place of breeding or attempted breeding, involves two phases: autumn and spring, separated by winter, during which little movement occurs (Schroeder 1985b). The autumn phase is undertaken only by young birds. In a population of *D. c. franklinii* in southwestern Alberta, more females (61%, $n = 67$) moved off the study area than males (41%, $n = 73$) during autumn (Keppie 1977). Similarly, in a population of *D. c. canadensis* in New Brunswick, more females (95%) than males (77%) dispersed off the study area (Keppie 1982). These observations were supported by data from radio-marked females (median distance moved = 5.0 km, $n = 9$) and males (median distance moved = 0.7 km, $n = 22$) in southwestern Alberta (Schroeder 1986a). In south-central Alaska, the average autumn dispersal distance of *D. c. canadensis*, based on hunter-shot birds, was 3.2 km (Ellison 1973).

Autumn dispersal of the brood does not appear to be initiated by aggressive interactions; it is essentially spontaneous (Alway and Boag 1979, Schroeder and Boag 1985). In *D. c. franklinii*, distances moved by each sex are apparently influenced by the location of wintering areas relative to the direction taken after brood break-up, by differences between the sexes in the timing of brood break-up (males leave earlier than females), and by the overlap in time between brood break-up and migration (young females are more likely than young males to accompany the migrating parent; Schroeder 1986a).

Dispersal movements during a bird's first spring are probably made in response to the behavior of resident grouse; they appear to be retraced as subsequent migratory movements between the original wintering site and the first breeding range (Schroeder 1985b). Such individuals are highly philopatric, returning annually to their breeding and wintering ranges (Herzog and Keppie 1980, Schroeder 1985b). The tendency for young grouse to disperse in spring and become the migratory portion of the population appears to have a heritable component: male offspring of migratory females are more likely than those of nonmigratory females to become migratory (Keppie 1980, Schroeder 1987).

The relationship between the number of yearlings recruited into the spring population, as a percentage of those available, is negatively correlated with the density of resident territorial birds in the spring when that density is stable (Boag et al. 1979, McKinnon 1983b, Szuba 1989). Moreover, yearling males that become territorial disperse over shorter distances than nonterritorial yearling males (McKinnon 1983b). The role of agonism in spring dispersal is implicated by an increase in aggressive interactions among captive yearlings (Alway et al. 1979), and by an increase in the frequency of uttering the *cantus* by territorial females in the time of spring dispersal (Herzog and Boag 1977). Thus, it is possible that both inherited and aggressive interactions influence dispersal movements in spring.

The combined autumn and spring phases of dispersal in *D. c. canadensis* resulted in 10% of males ($n = 31$) and 9% of females ($n = 43$) returning to breed on a south-central Alaska study area where they originated (Ellison 1973), and in Ontario this value fell to less than 1% (Szuba 1989). By contrast, in *D. c. franklinii* these two phases of dispersal left 36% of

($n = 73$) and 6% of females ($n = 67$) on the study area (Keppie 1979), with average distances of 0.65 and 4.97 km, respectively (Schroeder 1985). In northern Michigan average dispersal distances were 2.3 km for 16 males and 3.2 km for 14 females (Robinson 1980).

POPULATION STATUS

Population density of Spruce Grouse is estimated in various ways. *Wing-clap* indices using playbacks of the female *cantus* (Table 2) are effective in estimating population size of territorial males in southwestern Alberta (Schroeder and Boag 1989). Other census techniques include line transects with or without dogs to give absolute numbers of both sexes (Boag and McKinnon 1982), and line transects with dogs to give an index of abundance of both sexes (grouse per hour; Szuba and Bendell 1983). Population samples indicate that sex ratio is approximately 1:1 in southwestern Alberta (Schroeder and Boag 1989), in north-central Washington (Zwickel and Brigham 1970), in northern Michigan (Robinson 1980), and in Ontario and New Brunswick (D. Keppie pers. comm.).

To document the behavior of individuals and the demography of populations, birds must be captured, usually with a noosing pole (Zwickel and Bendell 1967, Schroeder 1986b), and marked, usually with unique combinations of colored bands—the young chicks with pat tags and/or flags (Schroeder and Boag 1985). To measure rate and direction of movement, size of home range, and use of habitat, radiotelemetry has been used (Herzog 1979, Robinson 1980). All these techniques are possible because these groups allow close approach without flight.

Estimated densities of grouse per 100 ha in spring range from 0 to 50 for *D. c. franklinii* in southwestern Alberta (Boag and Schroeder 1987), 8 to 12 for *D. c. canadensis* in south-central Alaska (Ellison 1974) and 0–83 in Ontario (Szuba and Bendell 1983).

POPULATION REGULATION

Over a period of 21 years (1965–85), the density of *D. c. franklinii* in the spring fluctuated almost six-fold in southwestern Alberta, ranging from 5 to 29 birds per 100 ha over a study area; two lows (1965 and 1985) were recorded (Boag and Schroeder 1987). The between 1979 and 1985 was correlated with habitat change (succession). Tree density and shrub cover declined, as did productivity (chicks/hen) and recruitment (proportion of yearlings in population; Boag and Schroeder 1987). Similarly, tree height (an estimate of forest structure) in 31 smaller areas in southwestern Alberta was negatively correlated with territorial male density (Boag and Schroeder 1987, Boag 1991, Schroeder and Boag 1991). Szuba (1989) reported a comparable decrease in the recruitment of yearlings into a declining population in Ontario. A similar negative relationship was found between spring density of Spruce Grouse and age of jack pine habitats in Ontario (Szuba and Bendell 1983). Burning affected density in south-central Alaska: density (birds/100 ha) fell from 5.8 to 2.5 for males and 6.5 to 2.5 for females on a burned area while density on an adjacent unburned area was 3.1 and 5.1 for males and 5.8 and 5.8 for females in the same two years (Ellison 1975).

A comparison of years with high and low spring densities in southwestern Alberta suggests that changes in population densities are influenced by conditions in the environment (extrinsic factors) as well as by the resident birds in the population (intrinsic factors). Changes in years with increasing densities are closely correlated with the previous year's productivity (a function of environmental conditions) whereas changes among years of stable density show no such relationship (Boag and Schroeder 1987, Szuba 1989). In years of increasing productivity appears to be correlated with the number of birds subsequently recruited (McKinnon 1983b, Boag and Schroeder 1987). In years of stable density the number recruited into the spring population is negatively correlated with the number of resident adults and consequently may be regulated directly by spacing behavior of the territorial cohort (Boag and Schroeder 1987, Szuba 1989), as suggested by Herzog and Boag (1978) and Boag et al. (1979). Thus, density of territorial adults and yearlings may determine the proportion of available recruits that enters the population (McKinnon 1983b). Individuals that cannot defend a territory either remain nonterritorial (some yearling males) or are apparently forced to disperse (Szuba 1989), with nonterritorial yearling males dispersing farther than territorial yearlings (McKinnon 1983b). The impact of autumn dispersal on the density of winter populations remains equivocal; in a population of *D. c. canadensis* in New Brunswick, emigration exceeded immigration, causing the number of young birds in the winter population to decline.

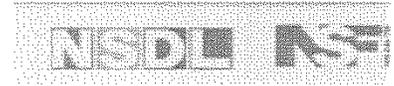
to fall from 18.8 to 8.3 per 100 ha, but in a population of *D. c. franklinii* in Alberta the was true (8.9–9.7 per 100 ha; [Keppie 1982](#)). The difference may reflect the relative attractiveness of the habitat for the dispersing birds.

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Spruce Grouse

Falci pennis canadensis

Order GALLIFORMES - Family PHASIANIDAE

BNA No. 5

Authors: D. A. BOAG, M. A. SCHROEDER

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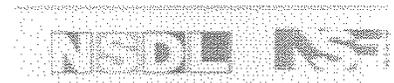
CONSERVATION AND MANAGEMENT

Spruce Grouse rely on conifer forests, particularly those species (pine) that are fire-adapted. Loss of such forests, particularly along the southern edge of the range, leads either to extermination of Spruce Grouse or to their confinement to islands of habitat (Fritz 1977, Robinson 1980). Fires, which typically leave islands of habitat as they burn through for provide renewed patches of habitat in a mosaic across the landscape (Ellison 1975). These islands are reoccupied after regrowth, appearing to support grouse at maximum density periods of only 10 to 15 years (Szuba and Bendell 1983, Boag and Schroeder 1987, Boag 1991, Schroeder and Boag 1991). Modern forest exploitation can mimic fire only if clear areas are kept small and interspersed with optimal habitat (Szuba and Bendell 1983).

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FEATHERING

Natal plumage

Downy chicks of both subspecies generally kingfisher rufous (Smithe 1975–81: #240) and straw yellow (#56) beneath (Johnsgard 1973: Plate 61, Robinson 1980: Plate 3). Similar. Crown, like that of ptarmigan (*Lagopus* spp.) chicks, solid kingfisher rufous, bordered laterally by a narrow sepia (#119) stripe. Sides of face straw yellow with generally a small sepia spot in the midloral position. Behind the eyes a sepia stripe extends to the nape, interrupted by the straw yellow ear coverts. A narrow sepia stripe or a series of spots runs either side of the posterior culmen. Spinal tract composed of dense down anteriorly straw yellow, darkening posteriorly into kingfisher rufous. Sepia spots of down arranged longitudinally and laterally to the midline. The caudal tract is a continuation of the dors ventral down with their respective colors. Ventrally, down is straw yellow, with the color intense on the lower neck and breast. Prejuvinal molt essentially complete within four days, proceeding from posterior to anterior and finishing on the throat.

Juvenal plumage

Chicks begin the Prejuvinal molt before hatching: juvenal remiges (primaries 1–7, secondaries and tertiaries) have erupted as have the juvenal feathers of the scapulo-humeral tract. Juvenal primary 7 at hatching has already grown, on average, 8 mm above the secondary (McCourt and Keppie 1975, Towers 1988). These remiges are Vandyke brown (#121), drab gray (#119D) leading edges to the primaries and chamois (#123D) leading edges to the secondaries. Tertiaries are striped with mottled bands of sepia, kingfisher rufous, and buff (#124) with a central longitudinal stripe, adjacent to the white rachis, of pale pinkish buff (#125) which broadens terminally. Dorsally, chicks appear mottled as the feathers of the capitulum, spinal, caudal (upper tail coverts), scapulo-humeral, and alar tracts are sepia colored with transverse bars of kingfisher rufous and buff (#124), with a drab gray distal rachis from an inverted triangle of the same color expands terminally. Sides of the face and throat pale neutral gray (#86) feathers with glaucous (#79) subterminal spots. Ear coverts a neutral gray (#83). In the ventral tract, the pale neutral gray grades to cinnamon (#87) reaching maximum intensity on the breast and extending onto the flank feathers. The cinnamon grades back to pale neutral gray on the belly and under tail coverts. The glaucous barring also diminishes posteriorly and ventrally. Rectrices short (4–5 cm), barred in green and cinnamon with the distal third of the rachis white, broadening into an inverted triangle of pale neutral gray at the tip of the vane. Feathers on tarsi cinnamon, mottled with dark gray (#83). Sexes similar.

First Prebasic molt begins with the shedding of juvenal primary 1 at ca 19 days of age (Robinson 1980), and progresses laterally through juvenal primary 8. Juvenal primary 9 which first erupts when the chicks are 10–14 days of age, completes its growth by ca 16 days (McCourt and Keppie 1975, Robinson 1980). Juvenal primaries 9 and 10 are retained until early September of their second year (McKinnon 1983a). Rectrices are molted centripetally.

and body molt from posterior to anterior. Prebasic molt involves all body feathers, except primaries 9 and 10, and is completed by late September.

Basic 1 plumage

Carried between late September (ca 3 mo of age) of the first year until late August to early September (ca 14 mo of age) of the second year when the last feathers of this plumage are lost (juv. primary 10). Males can be separated from females on the basis of distinctive feathers that begin to appear in the anterior ventral and upper caudal tracts at ca five to six weeks. This plumage resembles the Definitive (Basic 2) plumage of the adults (described below) except that: (1) white tips on feathers in the ventral tract, particularly of the breast and flanks, are generally larger in yearling than adult grouse, giving the younger birds a more conspicuous appearance, and (2) the lengths and diameters of the rachis at the superior umbilical primary, the central rectrices, and the central upper tail coverts are shorter and narrower in yearlings than adults (Table 6). Further more, the pale tips of the central upper tail coverts of yearling males are shorter than those of adult males (*D. c. franklinii*: yearling (white) tips ≤ 4 mm, adult (white) tips ≥ 6 mm; *D. c. canadensis*: yearling smoke gray (#45) tips ≤ 4 mm, adult smoke gray (#44) ≥ 4 mm). The central rectrices of males of both subspecies are white tipped (2–7 mm) in yearlings but have little (< 2 mm) or no white tip in adults.

Definitive (Basic) plumage

This plumage is acquired during the second summer. Adult males of both subspecies are dark brown with conspicuous scarlet (#14) superciliary combs. Dorsal feathers generally are dark brown with neutral gray (#84) barred with blackish neutral gray (#82). Wings similarly marked but barring tends to be drab (#27) to olive brown (#28). Scapulo-humeral feathers streaked centrally with white that broadens terminally. Upper tail coverts narrowly tipped with gray (#79) in *D. c. canadensis* but with bold white tips in *D. c. franklinii*. Underparts jet black (#89) with the posterior border of the throat patch mottled with white; ventral feathers of the anterior and lateral parts of the breast are variously white tipped as are those of the flank feathers more mottled with dark drab (#119B), having a central white streak that broadens terminally. Under tail coverts are sepia (#119) with large terminal white tips. Rectrices, usually 16 in number (range 15–17), relatively short, narrow, and rounded in *canadensis* but long, broad, and truncated in *D. c. franklinii* (Table 6). They are sepia colored with a broad (robin rufous, #340) terminal band in *D. c. canadensis* (Robinson 1980: Plate 2) but jet black with or without a narrow white tip in *D. c. franklinii* (MacDonald 1968: Plate 2).

Adult females of both subspecies are paler than males and superbly camouflaged against a forest litter of dry conifer needles. Dorsal feathers predominantly grayish horn color (#123A) and sepia. Scapulo-humeral feathers similar but with a white streak that broadens terminally. Upper tail coverts mottled with raw sienna (#136) barred with sepia and tipped narrowly with glaucous (#80) or white. Underparts more cinnamon than the spinal tract, particularly anteriorly. Lower neck and breast variously with sepia and cinnamon, tipped with white, which on the flank feathers becomes a central white streak that broadens terminally, giving the ventral region a pale color (Robinson Plate 2). Under tail coverts sepia, barred with cinnamon and tipped with large white spots. Rectrices relatively short (shorter and narrower in *D. c. canadensis* than *D. c. franklinii* (Table 6), dusky brown (#19), variously barred with robin rufous, and narrowly tipped with white.

Subtle intrasexual differences exist between individuals within populations as well as among populations, largely a function of the relative intensity of the background colors (particulating the gray to cinnamon spectrum) and the extent of white tipping on the feathers; females more varied than males. Remiges are shed sequentially from proximal to distal with primary 10 being lost in males in early June (Fig. 2) and completely regrown by mid-August (McLellan 1970, Robinson 1980). By early September all primaries have been molted (Robinson & McKinnon 1983a). Among females, the timing of this molt depends upon the presence or absence of a brood. Broodless females lose primary 1 about the end of June (Fig. 2) and females with broods shed primary 1 during the second week of July. This difference is increased as the molt progresses, with primary 10 being lost in broodless females during the second week of September but not until the second week of October in females accompanied by a brood (McCourt 1969). Molt of the rectrices (and upper tail coverts) proceeds centripetally, with shedding usually over a brief period, particularly in males (often all

synchronously, usually less than a week) beginning when primary 3 is shed. In males it occurs in late June (Fig. 2), with complete regrowth by early September (McLachlin 1999). In females, timing depends upon their breeding status. Those without broods lose the rect and upper tail coverts during the second week of July and those with broods during the week of July (McCourt 1969). Among populations of *D. c. canadensis* in eastern Canada, the chronology of the molt is about two weeks advanced over that described above for *D. c. franklinii* (D. Keppie pers. comm.). It progresses generally from posterior to anterior with feathers on the crest being the last replaced.

BARE PARTS

Distal phalanges of the toes and superciliary combs permanently nonfeathered. Spruce Grouse, like ptarmigan, lack inflatable colored vocal sacs in the cervical apertures. The upper mandible in all age classes is sepia, lower mandible in the downy chick beige (#219D), becoming cinnamon (#39) ventrally but dark brownish olive (#129) laterally in Juvenile plumage. In adults, the lower mandible like the upper is sepia. Scales and claws on the surface of the toes are beige in chicks, becoming smoke gray (#44) in young birds in Juvenile plumage, and russet (#34) in adults. The superciliary combs, which in both sexes reach maximum development in adults, can be retracted beneath the feathers of the capital crest. They are papillose in structure, and scarlet (#14) in color, becoming geranium (#12) in adults when fully charged with blood (ca 15 mm high). The iris of the eye is amber (#36) in adults.

MEASUREMENTS

Linear

Yearlings of both sexes are smaller than adults, males have longer and wider rectrices than females, and *D. c. franklinii* has longer and wider rectrices than *D. c. canadensis* (Table 7). Nevertheless, the skeletal measurements of *D. c. canadensis* show it to be significantly larger than *D. c. franklinii*. Females of the former subspecies are similar in size to males of the latter. In contrast to the general pattern of males being larger than females, the humerus appears to be shorter in males than females, possibly associated with differences in the use of the wings during display.

Mass

Total body mass varies with sex, age, time of year, and geographic location (Fig. 7). The sexes are size dimorphic with males beginning to exceed females in total mass by August of their first year (mean = 345 vs. 330), when about eight weeks of age (McCourt 1969, Robinson 1980). Males continue to weigh more than females, both as yearlings and adults throughout the year (Fig. 7), except during the prelaying and laying periods (April and May) when the converse is true (Pendergast and Boag 1973, Ellison and Weeden 1979, Roberson 1980, Szuba and Bendell 1984). Neither sex achieves adult mass until September of their second year (Fig. 7).

In general, body mass is greater in winter than summer (Szuba and Bendell 1984), the exception being adult females in spring, which weigh as much or more during the prelaying period than in winter (Fig. 7). These changes in body mass are related in part to recrudescence and regression of the reproductive organs and tract but also to changes in mass of skeletal (flight) and cardiac muscle and the gut (ventriculus, caeca; Pendergast and Boag 1973).

D. c. canadensis is heavier than *D. c. franklinii* in each month for both sex and age class (Fig. 7). Within subspecies, northern and inland populations tend to be heavier than southern and coastal populations.

The reproductive status of a female appears to have an impact on its mass. Robinson (1980) recorded a mean mass in summer of 424 g ($n = 31$) for female *D. c. canadensis* with broods and 436 g ($n = 17$) for those without broods in Michigan, and Szuba and Bendell (1984) recorded 436 g (405–525 g) ($n = 74$) and 453 g (410–505 g; $n = 31$), respectively, in Ontario. During this same period, yearling and adult female *D. c. franklinii* with a brood weighed significantly less than those without a brood (Fig. 8, DB and MS, unpubl. data). These data suggest that there is a relatively high energetic cost of raising a brood in the

species. Most of this cost would seem to be associated with incubation since the rate of body mass after hatching was similar in the two groups.

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Spruce Grouse

Falci pennis canadensis

Order GALLIFORMES - Family PHASIANIDAE

BNA No. 5

Authors: D. A. BOAG, M. A. SCHROEDE

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Spruce Grouse

Falcapennis canadensis

Order GALLIFORMES - Family PHASIANIDAE

BNA No. 5

Authors: D. A. BOAG, M. A. SCHROEDE

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ABOUT THE AUTHORS

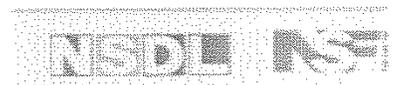
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Spruce Grouse

Falcipectes canadensis

Order GALLIFORMES - Family PHASIANIDAE

BNA No. 5

Authors: D. A. BOAG, M. A. SCHROEDER

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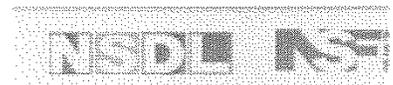
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Spruce Grouse

Falcipectes canadensis

Order GALLIFORMES - Family PHASIANIDAE

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