

May 2008

13 Willow Ptarmigan

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Willow Ptarmigan

Lagopus lagopus (Linnaeus) 1758

OTHER VERNACULAR NAMES

*A*LASKA ptarmigan, Alexander ptarmigan, Allen ptarmigan, Arctic grouse, red grouse (Scotland form), Scottish grouse, white grouse, white-shafted ptarmigan, willow grouse, willow partridge.

RANGE

Circumpolar. In North America from northern Alaska, Banks Island, Melville Island, Victoria Island, Boothia Peninsula, Southampton Island, Baffin Island, and central Greenland south to the Alaska Peninsula, southeastern Alaska, central British Columbia, Alberta, Saskatchewan, Manitoba, central Ontario, central Quebec, and Newfoundland (*ex A.O.U. Check-list*).

NORTH AMERICAN SUBSPECIES (*ex A.O.U. Check-list*)

L. l. albus (Gmelin): Keewatin willow ptarmigan. Breeds from northern Yukon, northwestern and central Mackenzie, northeastern Manitoba,

northern Ontario, and south central Quebec south to central British Columbia, northern Alberta and northern Saskatchewan, and the Gulf of St. Lawrence in Quebec. Wanders farther south in winter.

L. l. alascensis Swarth: Alaska willow ptarmigan. Breeds from northern Alaska south through most of Alaska. Winters in southern part of breeding range.

L. l. alexandrae Grinnell: Alexander willow ptarmigan. Resident on the Alaska Peninsula south to northwestern British Columbia.

L. l. ungavus Riley: Ungava willow ptarmigan. Resident in northern Quebec and northern Labrador south to central Ungava.

L. l. leucopterus Taverner: Baffin Island willow ptarmigan. Resident from southern Banks Island and adjacent mainland to Southampton and southern Baffin islands; wanders farther south in winter.

L. l. alleni Stejneger: Newfoundland willow ptarmigan. Resident in Newfoundland.

L. l. muriei Gabrielson and Lincoln: Aleutian willow ptarmigan. Resident in the Aleutian Islands from Atka to Unimak, the Shumagin Islands, and Kodiak.

MEASUREMENTS

Folded wing: Adult males, 182–216 mm; adult females, 168–214 mm (males average 190 mm or more; females [except Baffin Island race] average less than 190 mm).

Tail: Adult males, 108–35 mm; adult females, 94–139 mm (males average 118 mm or more, females 116 mm or less).

IDENTIFICATION

Adults, 14–17 inches long. All ptarmigan differ from other grouse in that (except during molt) their feet are feathered to the tips of their toes (winter) or base of their toes (midsummer) and their upper tail coverts extend to the tips of their tails. The primaries and secondaries of all the North American populations of this species are white in adults throughout the year, while in winter all the feathers are white except for the dark tail feathers, which may be concealed by the long coverts. Males have a scarlet “comb” above the eyes (most conspicuous in spring) and during spring and summer are extensively rusty hazel to chestnut with darker barring above except for the wings and tail. The tail feathers are dark brown tipped with white except for the central pair, which resemble the upper tail coverts. In summer females lack this chestnut color and are heavily barred with

dark brown and ochre. In autumn the male is considerably lighter, and the upperparts are heavily barred with dark brown and ochraceous markings, lacking the fine vermiculated pattern found in males of the other ptarmigans at this season. The female in autumn is similar to the male but is more grayish above and more extensively white below. In winter both sexes are entirely white except for the tail feathers, of which all but the central pair are dark brownish black. In addition, the shafts of the primaries are typically dusky and the crown feathers of males are blackish at their bases. In first-winter males and females the bases of these feathers are grayish.

FIELD MARKS

The dark tail of both sexes at all seasons separates the willow ptarmigan from the white-tailed ptarmigan but not from the rock ptarmigan. In spring and summer the male willow ptarmigan is much more reddish than the rock ptarmigan, and although the females are very similar, the willow ptarmigan's bill is distinctly larger and higher and is grayish at the base. In fall males are more heavily barred than are male rock ptarmigan, and females likewise have stronger markings than do female rock ptarmigan. In winter males lack the black eye markings that occur in male rock ptarmigan, but since this mark may be lacking in females, the heavier bill should be relied upon to distinguish willow ptarmigan.

AGE AND SEX CRITERIA

Females lack the conspicuous bright reddish "eyebrows" of adult males, are more grayish brown and more heavily barred on the breast and flanks than are males, and lack the distinctive rusty brown color of males in summer. In fall, females are somewhat grayer above and more heavily barred on the breast and flanks than are males. In winter they are like males but the concealed bases of the crown feathers are more grayish (Ridgway and Friedmann, 1946). They can be fairly accurately identified at this time by their brown rather than black tail feathers and central upper tail coverts and by certain wing and tail measurements (Bergerud, Peters, and McGrath, 1963).

Immatures in first-winter plumage tend to have the tip of the tenth primary more pointed than the inner ones, but this is not so reliable as the fact that (1) there is little or no difference in the amount of gloss on the three outer primaries of adults, whereas immatures have less gloss on the outer two primaries than on the eighth, and (2) there is about the same amount of black pigment on primaries eight and nine (sometimes more on eight

than on nine) of adults whereas juveniles have more on the ninth than on the eighth (Bergerud, Peters, and McGrath, 1963).

Juveniles may be identified by the fact that their secondaries and inner eight primaries are grayish brown with pale pinkish buff margins or barring. However, the late-growing outer two primaries are white, often speckled with black, like the first-winter flight feathers that soon replace the secondaries and inner primaries.

Downy young are illustrated in color plate 61. Willow ptarmigan downies are reported (in the Scottish population) to be darker on both the dark and lighter areas, and have less clear-cut margins between these areas than downy rock ptarmigan (Watson, Parr, and Lumsden, 1969). These authors mention other differences that may also serve to separate downy young of these two species, although these may not apply equally well to North American populations. For example, in the Labrador populations, birds under three weeks are almost impossible to identify as to species, although young willow ptarmigan are slightly darker and somewhat greenish instead of yellowish on the underparts (Bendire, 1892). After three weeks they may be distinguished by differences in the bill.

DISTRIBUTION AND HABITAT

The North American breeding range of the willow ptarmigan is primarily arctic tundra, although it extends southward somewhat in alpine mountain ranges and in tundra-like openings of boreal forest (Aldrich, 1963). The basic habitat consists of low shrub, particularly willow or birch, in lower or moister portions of tundra. Weeden (1965b) has characterized the general breeding habitat of willow ptarmigan as follows: Typical terrain is generally level or varies to gentle or moderate slopes but frequently is at the bottom of valleys. Vegetation is relatively luxuriant, with shrubs usually three to eight feet high, and scattered through areas dominated by grasses, hedges, mosses, dwarf shrubs, and low herbs. The birds usually occur at the upper edge of timberline, among widely scattered trees, or may occur somewhat below timberline where local treeless areas occur.

Because of the relatively minor effect man has had on tundra to date, there have been few if any major evident changes in the total range of the species.

POPULATION DENSITY

Ptarmigans are among the arctic-dwelling species that exhibit major fluctuations in yearly abundance and are believed by some to exhibit cyclic

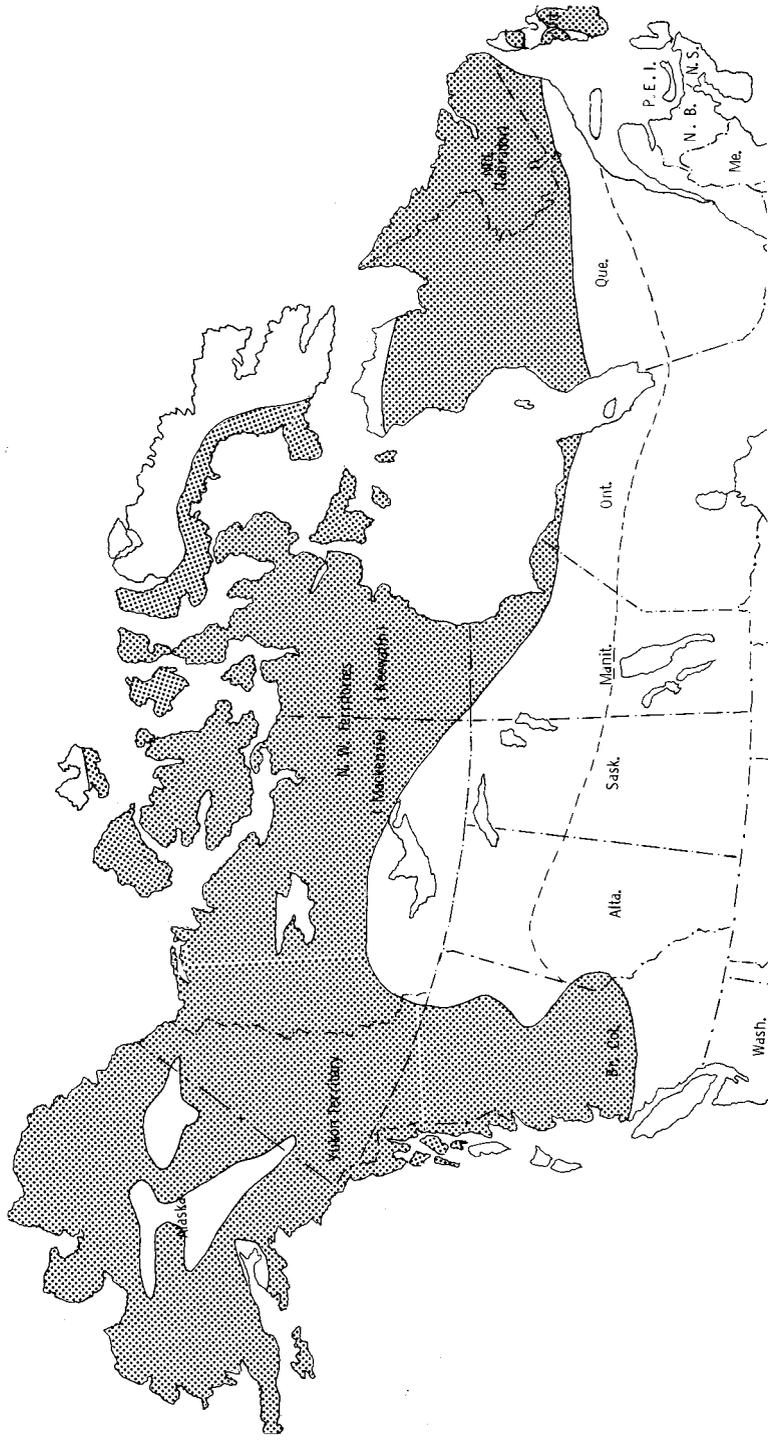


FIGURE 26. Current North American distribution of the willow ptarmigan. Dashed line indicates normal southern wintering limits.

population changes (Buckley, 1954). In any case, major changes in population density do occur, thus estimates of density may vary greatly by year as well as by locality. Weeden (1963) summarized estimates of population density for various areas in Canada. These estimates ranged from less than 1 adult per square mile (2.5 square miles per adult) to as many as 8 adults per square mile, with the sparser densities generally based on large areas that include much unfavorable habitat. He also reported (1965b) that a study area of 0.75 square miles had spring populations of males ranging from 38 to 150 males during seven years of study, which represents from 3.2 to 12.3 acres per male. Somewhat comparable density figures have been reported from Newfoundland (Mercer and McGrath, 1963), who estimated spring 1962 populations on Brunette Island of from 147 to 207 birds per square mile, depending on technique used. Considerable population work has been done on the Scottish red grouse (now generally considered conspecific with the willow ptarmigan) by Jenkins, Watson, and Miller (1963), who estimated spring densities of from 4.5 to 9 acres per pair.

HABITAT REQUIREMENTS

Wintering Requirements

Weeden (1965b) reported that winter habitat of willow ptarmigan consists of willow thickets along streams, areas of tall shrubs, and scattered trees around timberline and burns, muskegs, and river banks below timberline. Bent (1932) noted that in winter willow ptarmigan move to interior valleys, river bottoms, and creek beds, where there is available food in the form of tree buds and twigs of willows (primarily), alders and spruces, and such berries and fruits as can be found above the snow. Godfrey (1966) indicates that during winter the birds may be found well south of treeline, in muskegs, lake and river margins, and forest openings.

Spring Habitat Requirements

Weeden (1965b) stated that male habitat preferences for territorial establishment include shrubby and "open" vegetation, with the plants lower than eye-level for ptarmigan. Elevated sites such as rocks, trees, or hummocks are used by males during display. Resting areas are provided by small clumps of shrubs at the edges of open areas.

At least in Scotland, territorial establishment occurs during fall, although territories may be abandoned temporarily during winter if snow conditions require it. In Alaska some full display and calling also occurs (Weeden,

1965b). Continued residence, however, is not typical in Alaska or probably in any part of the North American breeding range, since considerable seasonal movement is typical. Thus, local topography, as it affects snow deposit and rate of snow thaw exposing territorial sites, may have considerable effect on territorial distribution of birds in arctic North America.

Nesting and Brooding Requirements

Requirements for willow ptarmigan nest sites are apparently fairly generalized. Brandt (in Bent, 1932) reported that nesting may occur anywhere from coastal beaches to mountainous areas, and nests may be placed beside drift logs, in grass clumps, under bushes, in mossy hummocks, or similar sources of screening protection. Weeden (1965b) indicates that the nest is usually protected from above and the side by shrubby vegetation, while one side borders an open area. The nest is located within the periphery of the male's territory.

Brooding habitat is similar to nesting habitat, according to Weeden (1965b), with chicks using areas of very low vegetation, while older broods use shrub thickets for escape cover. Maher (1959) noted that broods used a variety of habitats with good cover and were common on upland dwarf-shrub and hedge tundra, as well as being sometimes found in riparian shrub and willow shrub at the bases of hills.

FOOD AND FORAGING BEHAVIOR

At least in Alaska, the most important single food source for willow ptarmigan is provided by willow buds and twigs. Weeden (1965b) noted that this source provided almost 80 percent of winter foods found in 160 crops from interior Alaska, and Irving et al. (1967) also indicated that winter foods consisted almost entirely of the buds and twig tips of willow. Weeden noted that dwarf birch buds and catkins were second in importance, and Irving et al. similarly found that in wooded areas some birch catkins and poplar buds are taken. West and Meng (1966) found that 94 percent of the winter diet of willow ptarmigan from northern Alaska consisted of various willow species, and 80 percent was from a single species (*Salix alaxensis*). They also noted that some birch may be used, but although alder is often available and has a higher caloric content than willow, it is seldom used.

One exception to the general winter diet of willow for North American willow ptarmigan has been noted, in Peters's study (1958) of the Newfoundland population. He found that the winter diet consists almost entirely of

the buds and twigs of *Vaccinium* species, the buds and catkins of birch and alder, and the buds of sweet gale (*Myrica*).

With spring, the willow ptarmigan's dependence on willow declines in Alaska, and in addition to the leaves of willow, the birds begin to eat a larger variety of leafy materials (Weeden, 1965b). Peters (1958) also noted a spring return to fruit and leafy materials and the berry seeds of crowberry (*Empetrum*) and *Vaccinium*.

Summer foods in Alaska consist of various berries, especially blueberries, willow and blueberry leaves, and the tips of horsetail (*Equisetum*), which grows in willow thickets near streams (Weeden, 1965b). Peters noted that crowberries, blueberries, and the leaves of *Vaccinium* species, especially *V. angustifolium*, provided major sources of summer foods in Newfoundland.

In the fall, as the berry supplies are exhausted and leaves fall from *Vaccinium* bushes, the ptarmigan in Newfoundland return to a diet of buds and twigs again (Peters, 1958). The same situation applies to Alaska, although it is willow rather than *Vaccinium* buds and twigs that are resorted to (Weeden, 1965b). Irving et al. (1967) found a gradual increase in total crop contents of Alaskan ptarmigan from October to January, followed by reduced contents until April. This population migrates southward in October and November and northward from January until May. Evidently feeding is related to changing patterns of daylight, rather than to temperature cycles or to the cycle of migratory activities.

MOBILITY AND MOVEMENTS

The willow ptarmigan and its relative the rock ptarmigan are perhaps the most migratory of all North American upland game. Snyder (1957) reports that the willow ptarmigan is migratory to a considerable extent, occasionally wandering as far as the southern parts of the prairie provinces, northern Minnesota, the north shore of Lake Superior, southern Ontario, and southern Quebec. To some degree these southern movements may be related to unusually dense populations in the northern areas (Buckley, 1954). Evidently considerable differential movement according to sex occurs in Alaska (Weeden, 1964). At Anaktuvuk Pass, for example, most wintering willow ptarmigan are males, while many of the wintering birds in timbered areas to the south are females. Likewise, alpine-fringe areas of the Alaska Range and the Tanana Hills are utilized mostly by males during winter, while females are to be found abundantly in the Tanana Valley (Weeden, 1965b). Weeden (1964) suggested that this differential movement may represent a dispersal mechanism or serve as a means of reducing food competition

or perhaps indicate that females may survive better in forested areas under winter conditions.

Irving et al. (1967) have documented the migration of willow ptarmigan through Anaktuvuk Pass in the Brooks Range. Although few ptarmigan nest there, some 50,000 birds pass through this point each year. The fall migration reaches a peak in October and is over by December, while the spring migration starts in January and early February, subsides in March, and is renewed in April. The early fall migrants are mostly juvenile males and females, whereas the number of adult males gradually increases to a maximum in March, or two months later than the maximum movement of juvenile males. The authors reported no clear indication of cyclic changes in population numbers annually. A spruce forest area occurring thirty-five miles south of the pass is one of the areas used for wintering, and breeding occurs on the north slope of the Brooks Range and beyond to the Arctic coast. Some of these breeding areas may not be occupied until late in May.

So far, virtually nothing is known of daily movements of willow ptarmigan, and such information will require detailed studies of individually marked birds. Jenkins, Watson, and Miller (1963), studying red grouse, found the birds to be remarkably sedentary in this nonmigratory population. Of 739 birds banded as chicks, only 5 were recovered more than 5 kilometers away that season, and some of this movement may have been caused by the birds' being driven for hunting purposes. Of 290 birds banded as chicks but recovered as adults, 230 were recovered within 1.5 kilometers of the point of banding. It would thus appear that willow ptarmigan move only as far as is necessary to maintain a source of food and cover during the coldest parts of the year. Weeden (1965b) reported that a male and its mate were both found a year after they were banded as adults, defending a brood about 100 yards away from the original point of banding a year previously, which would attest to considerable site fidelity in this species. Bergerud (1970b) reported that females are more mobile than males, with one banded female moving 61 kilometers in about three months.

REPRODUCTIVE BEHAVIOR

Territorial Establishment

Most observations of territorial behavior in this species derive from studies of the red grouse in Scotland by A. Watson, D. Jenkins, and their associates. Likewise, display descriptions are also based on this population, unless otherwise indicated.

Territorial behavior and the success of territorial establishment appears

to be a crucial factor in the biology of red grouse populations, judging from the work of Jenkins and Watson. Territories in red grouse are established in early fall, and the numbers of such territorial males that can be accommodated on a habitat apparently limits the density of the breeding population. Nonterritorial males are forced out of the preferred areas into marginal habitats, where they are more heavily exposed to predation, starvation, and disease. However, such losses play little if any role in the success of the population. Since juvenile birds are rarely able to attain territorial status their first fall, early territorial establishment would favor reproduction by mature males.

Territorial establishment in the North American willow ptarmigan is presumably in spring, although some fall display and calling by males may occur (Weeden, 1965b). However, it is not until late April or May that the willow ptarmigan have acquired their striking nuptial plumage, which presumably provides important visual signals for territorial proclamation and attraction of females. Weeden (1965b) has made the interesting point that whereas the male willow ptarmigan undergoes courtship in this bright brown and white plumage, the rock ptarmigan is still in completely white plumage during courtship, which perhaps provides important visual distinction for species recognition between the two species.

Territorial size has been studied intensively by Jenkins, Watson, and Miller (1963) for red grouse. They found that in each year, some individual territories were larger than others, but in years of high grouse populations the territories in general averaged smaller than in years when grouse were few. Territories selected by previous residents were usually larger than could later be defended against newly colonizing juvenile birds. Sketched maps presented by these authors indicate that territorial size rarely exceeded a maximum diameter of three hundred yards, and most were much smaller. One study area of 56 hectares (138 acres) supported twenty-four territorial males (two of which were unmated) in 1961, thus territorial sizes averaged 5.7 acres in the area during that year. In 1960, sixteen males (two unmated) occupied the same area, and in 1958 there were over forty territorial males (ten unmated) on it. For the study areas as a whole, the breeding density over the years varied from one pair to about 5 acres, in 1957 and 1958, to about one pair per 15 acres in 1960.

Agonistic and Sexual Behavior

In contrast to the species considered previously, it is almost impossible to differentiate completely between male and female behavior patterns in the ptarmigan. This is primarily a reflection of their monogamous or

nearly monogamous pair bond and a subsequent reduction of sexual selection pressures for dimorphic behavior patterns. Watson and Jenkins (1964) have provided a detailed account of behavior patterns in the red grouse which will be summarized here in the belief that their findings should apply to the North American willow ptarmigan with little or no modification. Although they also discuss displacement activities, distraction behavior, comfort and maintenance activities, and other aspects of behavior, only those patterns directly concerned with reproduction will be mentioned here.

Agonistic behavior patterns of males associated with establishment and defense of territories include sitting on an exposed lookout, such as a hillock or stone, where most of the territory can be seen. Intruders are approached in an attack-intention posture characterized by erect combs, the head and neck stretched forwards, the body near the ground, the wings held in the flanks, and the bill open. Prior to such an approach the bird may fan its tail and droop its wings in a manner resembling the waltzing display. A lesser type of threat consists of standing in one place and uttering *kohway* and *kohwayo* calls. Still weaker threat consists of standing and uttering a *krrow* call, which in turn grades into watchful behavior, flight intention, and finally fleeing by running or flying away.

Several kinds of aggressive encounters may occur. Brief encounters may last only a few seconds and involve birds of either sex, which may or may not occur on a territory. "Jumping" is a communal encounter that also is not limited as to sex and not related to territory. In this, two or more aggressive birds will begin to jump about with wing-flapping, causing them to become more fully separated. Prolonged chases may occur when a dominant male follows a subordinate bird for great distances, often beyond its territory, and may in fact kill or wound it. "Facing" occurs when two equally dominant birds face each other with combs erect, heads forward, and wings flicking, with neither one showing signs of retreat. When actual fighting occurs the birds usually do not face each other, but rather face in the same direction and strike each other from the side with their bills, wings, and feet. "Walking-in-line" consists of two birds' walking side by side some twenty inches apart. While so walking they utter *kohway* and *ko-ko-ko* calls that indicate attack intention, and they may also utter the *krrow* threat call. Such a display by two males often occurs at the edges of territories, while hens may perform the same display anywhere in the territory. Occasionally the display occurs outside breeding territories, where up to five or six birds may participate.

Sexual patterns involve pair formation behavior and copulatory behavior. Pair formation is achieved by the males' advertising their territories, and

the females' being attracted to the more vigorous males. On arriving on a territory, the female may utter a *krrow* call and look for a displaying male to approach. If there is none, she may fly to another territory, until a resident male makes a song-flight landing near her and begins to strut towards her. The female then flees but may be driven back to the territory by the male. Sexual activity occurs in Scotland every month but is most common from February to April, and many pair bonds that had been established earlier are only temporary and may be easily disrupted. When in breeding condition, the male has a highly conspicuous red eye-comb that can be erected to about one centimeter. Although the hen's combs are much smaller and paler, they can also be erected.

The male's approach to another bird of either sex is essentially a threatening one, and in the case of a receptive hen the response is one of submissive gestures. Thus the sexual differences in display are not so much qualitative as they are quantitative, in terms of relative dominance and submission. Sex recognition is probably also achieved by the different voice, plumage, and comb development of the hen.

The postures performed by a male in the presence of a female but not elicited in the presence of other males may be considered "courtship" displays. Watson and Jenkins (1964) list five such displays: tail-fanning, waltzing, rapid-stamping, bowing, and head-wagging.

Tail-fanning is performed by a male when approaching a hen. While cocking his tail, he may fan it with a rapid flick, at the same time lowering his wings and scraping the primaries on the ground as he moves forward. In this stage, the wings are drooped equally and the tail is not tilted. Often the male moves in a slight curve in front of the female, or he may pass in front of her alternately from both sides. Sometimes the undertail coverts are exposed by his turning away from the hen. Such movements grade into "waltzing," during which the male circles the female closely, pivoting around her with short, high steps and drooping the wing nearer her, at the same time tilting the tail to expose its upper surface more fully to her view. The body may be tilted toward the hen as well. During "rapid-stamping" the male runs toward the hen with his tail slightly fanned, his neck thickened and arched, and his head held low with the bill wide open. In this posture he might pass close beside the other bird and appear to be attacking her, but the differences in wing and neck positions make it possible to distinguish these two types of behavior easily. If the hen does not flee and mounting does not occur at that time, the male will often raise and lower his head, with his body still held low, the tail partly fanned and the nape feathers raised, in a display called "bowing."

The last of the courtship displays is head-wagging, which both sexes

perform. The bird crouches near its mate, extends its neck forward, and quickly wags its head in lateral fashion, exposing its eye combs and twisting its head slightly with each wag. When a hen approaches a cock, the male may also crouch low, erect his combs, and lower his head, producing a posture strongly suggestive of the precopulatory "nuptial bow" of prairie grouse. Although both sexes perform head-wagging, it is not a mutual display, and instead the birds often perform it alternately. When the female performs it, the male may attempt to mount her. However, during actual solicitation, the female crouches without head-wagging, opens her wings, and holds her head up. The male immediately mounts, drooping his wings around the hen during copulation. Afterwards, the male utters several threat calls, displays strongly for a few minutes, and often moves to a lookout post.

Vocal Signals

Watson and Jenkins (1964) describe fifteen different vocal signals of adults which are uttered by both sexes, although the hen's calls may be recognized by their higher pitch. Song flight, or "becking" is uttered as the bird takes off, flies steeply upwards for thirty feet or more, sails, and then descends gradually while fanning its tail and beating its wings rapidly. On landing the bird may stand erect, droop its wings, fan its tail, and bob its head. During the ascent phase the call is a loud, barking *aa*, while a *ka-ka-ka-ka* is uttered some eight to twelve times with gradually slower cadence. After landing a gruffer and slower call *kohwa-kohwa-kohwa* (also interpreted as *go-back*, *kowhayo*, and *tobacco*), is uttered for a varying length of time. Hens and nonterritorial males do not fly as high or call as loudly as territorial males, and no doubt this call is important in territorial proclamation.

In calling on the ground, a similar signal is uttered, often from a song post such as a stone. The bird stretches his neck diagonally upwards and utters a vibrating *ko-ko-ko-ko-krrrrr*, up to about twenty syllables, increasingly faster toward the end. Such calls may be used to threaten approaching animals or birds flying overhead and are largely but not entirely territorial advertisement.

During attack, the birds utter a *kowha* sound, like the last part of the flight song but without preliminary notes. It may be given during attack, when trying to mount hens, or immediately after copulation. A similar call, *koway*, is an attack-intention, or threat, call and is rapidly repeated as a series of hurried notes. A variant is *kowwayo*, also repeated, but indicating less aggressiveness than the last call. Still less aggressive notes are

krrow and *ko-ko-ko*, the latter representing a flight-intention call. This call is given by a bird about to fly or one being handled by a human and may stimulate other birds to take flight.

When a grouse is charging another bird, a single note, *kok*, may be uttered, especially by the chased bird. The same call may be used as an in-flight alarm note. A similar *kok* note serves as a mammalian predator alarm note, while a *chorrow* note serves for an aerial raptor warning signal. A sexual note, *koah*, the emphasis on the first syllable, is used between members of a pair when crouching and head-wagging, when examining nest sites, or when bathing. Hens may also utter it when a nest is approached, but hissing is more often elicited under these conditions. Hissing may also occur when a bird is being handled. A *krow* note is used during distraction display by parents, causing the young to crouch, while a *korrr* or *koo-ee-oo* serves as a call to chicks, especially those uttering distress calls. Finally, a harsh, chattering *krrr* note is used as a defense against avian predators that are attacking the bird or its family.

Watson and Jenkins report that the distress *cheep* of chicks is uttered until the young are nearly full-grown, but that it gradually changes to a *kyow* note and finally to the adult *krrow* and probably then serves as a contact call. Even newly hatched chicks will utter a chattering call which evidently is aggressive in nature and apparently develops into the adult "ground song." By the age of ten to twelve weeks, the male begins to acquire a voice that differs from that of females, resembling more the voice of an adult cock.

Nesting and Brooding Behavior

The only available analysis of nest-site selection behavior is that of Jenkins, Watson, and Miller (1963) for Scottish red grouse. They studied 163 nests, nearly all of which were in heather cover (*Calluna*). The average height of the heather cover was twenty-seven centimeters, compared with a mean cover height of seventeen centimeters. Most nests were partly overhung with vegetation, but 17 percent were completely uncovered and 12 percent were completely covered. Most were on hard, well-drained ground, and 67 percent were on flat ground. Most were shallow scrapes, sparsely lined with various plants, including grasses and heather. Usually the nests were within five hundred feet of grit sources, water, and mossy or grassy areas where the chicks could feed. The clutch size of this population varied in different years and in different study areas from 6.1 to 8.1 eggs (average of 395 nests was 7.1 eggs) and the estimated incubation period was twenty-two days.

Some comparable information is available for North American willow ptarmigan. Kessel and Schaller (1960) reported that 5 nests in Alaska had 6 to 7 eggs, averaging 6.8. Eight clutches from northern Alaska in the Denver Museum average 7.8 eggs. Bergerud (1970b) reported an average clutch of 10.2 eggs in 106 Newfoundland nests. Nests containing up to 17 eggs would appear to be the work of at least two females. The incubation period of the North American birds is likewise twenty-one to twenty-two days, and the egg-laying interval is somewhat greater than twenty-four hours (Westerskov, 1956). Bergerud (1970b) judged that in Newfoundland reneating probably accounted for between 12 and 18 percent of the young produced.

Unlike the other species of ptarmigan, the male typically remains with the female through the incubation period and assists in brood defense. Jenkins, Watson, and Miller (1963) reported that the percentage of broods observed with both parents in attendance ranged from 61 percent to 90 percent in various years and areas. In good breeding years, most broods were attended by both parents until they were at least two months old, while in poor breeding years 30 to 40 percent were not attended by parents at any stage. The percentage of parents observed performing distraction display ranged from 4 to 72 percent. Individual brood sizes ranged to as many as 12, and averages varied greatly in different years. Roberts (1963) reported an average brood size of 6.3 chicks for Alaskan willow ptarmigan. This figure is higher than any yearly average reported by Jenkins, Watson, and Miller, whose highest reported brood size was 5.2 for one study area in 1960.

EVOLUTIONARY RELATIONSHIPS

Evolutionary relationships of the genus *Lagopus* as a whole would seem to be very close to both *Dendragapus* and *Tetrao*, as Short (1967) has already suggested. It is perhaps impossible to judge which of these two genera *Lagopus* most closely approaches, and presumably all three genera differentiated from common stock at about the same time.

Relationships within the genus *Lagopus* represent another problem. The white-tailed ptarmigan differs from the rock and willow ptarmigans in several respects, which have been enumerated by Short (1967), and it is clearly the most isolated of the three species. Höhn (1969) suggested such an early offshoot of ancestral white-tailed ptarmigan stock in North America, with which I am in agreement. Höhn judged that the willow and rock ptarmigan ancestral stock also diverged in North America, with the rock ptarmigan moving east to Greenland and both species moving west across the Bering Strait into Eurasia. This kind of speciation model seems

unlikely to me, as I can visualize no major barriers that might have allowed for separation of ancestral willow and rock ptarmigan stock in northern North America. It seems more likely to me that one of these types developed in Eurasia and the other in North America after a splitting of common gene pools and after secondary contact the rather marked ecological differences between them allowed the development of the extensive geographic contact between them that now exists. In contrast, Johansen (1956) suggested that the genus *Lagopus* originated in Asia and reached North America at an early date, during which the ancestral white-tailed ptarmigan separated from *pre-mutus* stock.

In a strictly behavioral sense, I would regard the willow ptarmigan as more primitive than the other two ptarmigan, in both of which a breakdown on strong pair bonds and a tendency toward polygamy may be seen. It seems probable to me that the evolution of mating patterns in the grouse was from an originally monogamous situation to a polygamous or promiscuous one, rather than to believe that the monogamous situation of the willow ptarmigan is derived from a non-monogamous mating type. The retention of monogamy or near monogamy in the ptarmigans seems to me to be an ecological artifact, resulting from the greater needs for intensive parental care in an arctic situation than in a subarctic or temperate one, in which the duties of incubation and brood-rearing can be more effectively undertaken by the female alone. This latter arrangement thus frees the male to fertilize a potentially larger number of females, and these resulting reproductive advantages have led to reduced pair bonds or to promiscuous matings. It is curious, however, that the willow ptarmigan, rather than the rock ptarmigan, has more strongly retained a monogamous and prolonged pair bond, since the rock ptarmigan has an even more northerly breeding distribution and must nest under equally severe breeding conditions. Arnthor Gardnarsson* has found that in Iceland the males suffer a much higher rate of predation by gyrfalcons than do females, apparently as a result of the male's more conspicuous plumage during the breeding season. The mating system there is an essentially promiscuous one, since the females do not closely associate with males or their territories. Such differential sexual predation pressures might account for the rock ptarmigan's less strongly monogamous mating system and the reduced period of contact between the sexes.

*Arnthor Gardnarsson, 1970: personal communication.