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## 31 Gray Partridge

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# Gray Partridge

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*Perdix perdix* (Linnaeus) 1758

## OTHER VERNACULAR NAMES

*B*OHEMIAN partridge, English partridge, European partridge, Hungarian partridge, Hun, Hunkie.

## RANGE

Native to Europe and Asia but introduced into North America and now widely established in southern Canada and the northern United States (see distribution map). The North American population was probably derived from stock representing several different geographic races.

## MEASUREMENTS

Folded wing: Adult males, 144–57 mm; adult females, 146–54 mm (males average 152 mm; females, 150 mm).

Tail: Adult males, 78–84 mm; adult females, 76–80 mm (males average 80 mm, females, 78 mm).

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## IDENTIFICATION

Adults, 12–13 inches long. Sexes similar in appearance. The head color of adults is tawny cinnamon except for an uncrested buffy brown crown and ear-patch. The breast and upper abdomen is a finely vermiculated gray which is interrupted by a chestnut brown horseshoe marking in males (smaller or absent in females), and the gray flanks are similarly interrupted by vertical chestnut barring. The upperparts are grayish to brownish, with darker mottling in the wing region and with conspicuous white shaft-streaks on the scapulars. The upper tail coverts and two central pairs of tail feathers are heavily vermiculated and barred, while the other tail feathers are rusty brown.

## FIELD MARKS

In flight, the rusty tail feathers are spread and are usually conspicuous; otherwise the impression is one of a grayish brown bird without bright markings. Chukar partridge also exhibit rusty outer tail feathers in flight but in addition have conspicuous white throats. The bobwhite occurs in some of the same regions as the gray partridge but is smaller and shows a grayish tail when flushed. In spring a raspy *tur-ip* call may be heard (Godfrey, 1966), which has also been described as a "rusty-gate" or *keee-uck!* call (McCabe and Hawkins, 1946).

## AGE AND SEX CRITERIA

*Females* may sometimes but not always be identified by the scapulars and median wing coverts, which have a wide buff stripe along the shaft and two to four buff crossbars; in males the feathers are darker and have only a narrow buff stripe along the shaft (McCabe and Hawkins, 1946). Furthermore, the scapulars of males are yellowish brown with very fine wavy black lines running across each feather and with a chestnut patch near the outside edge. Females have scapulars that are blackish at the base with about two light yellow crossbars, and only the outer parts of the feather are vermiculated (Lodge, quoted in Bannerman, 1963).

*Immatures* have the usual condition of pointed outer primaries and, at least for a time, have yellow rather than blue gray feet (Edminster, 1954). In immatures the outer two primary coverts from the juvenal plumage are also retained; the ninth covert is typically pointed rather than rounded and, although it is like that of adults in being brown with white barring, is only rarely edged with white at the tip (Petrides, 1942).

*Juveniles* have yellow feet and tail feathers that are much like the adult's, but the rectrices are tipped with buff and have subterminal dark bars and spots, while the central feathers are speckled and barred with dusky (Ridgway and Friedmann, 1946). White shaft-streaks are conspicuous on the breast, neck, and interscapular regions (McCabe and Hawkins, 1946).

*Downy young* (illustrated in color plate 61) of this species are highly distinctive; the head is buffy yellow, with a slightly darker and more rufous crown, while scattered over the sides and top of the head are a large number of dark brown spots which tend to be arranged into anterior-posterior stripes. The largest of these black markings is on the nape, and another large stripe extends from below the eye back toward the "shoulder" region and forward almost to the beak. The throat and underparts are a pale yellow, and patches of rufous occur at the rear edges of the wings and in the rump region, but the dorsal part of the body is only faintly patterned with fuscous and buff streaks.

#### DISTRIBUTION AND HABITAT

The present distribution of this introduced species is a highly disjunctive one, a reflection in part of the patterns of introduction. However, four fairly discrete populations can presently be recognized. The earliest established populations were those of the Pacific northwest, with birds being first released before 1900 in California and Washington. In the early decades of the 1900s there were additional and successful releases in Washington and successful introductions in Oregon, Idaho, and Montana (Yocom, 1943). The species was also introduced during 1911 in Utah (Porter, 1955) and during 1923 in Nevada (Gullion and Christensen, 1957). This population currently is largely restricted to the high, relatively arid intermountain region between the Cascade and Sierra ranges and the Rocky Mountains between forty degrees and fifty degrees north latitude. Low to moderate populations also occur in western Washington on the western slope of the Cascade ranges (Yocom, 1943) north to extreme southern British Columbia (Guiguet, 1955) and south to the Willamette Valley (Masson and Mace, 1962). Except for these most westerly populations, the birds are generally associated with grassland and semidesert vegetational types. In Oregon they are most abundant on bunch grass and sagebrush areas adjacent to wheat and other farmlands (Masson and Mace, 1962), and in eastern Washington they commonly occur in arid areas dominated by bunch grass and sagebrush where farms also occur (Yocom, 1943). In northern Nevada they are limited largely to habitats along stream bottoms and near pastures and hayfields where willows, berry-bearing bushes, and grasses are abundant

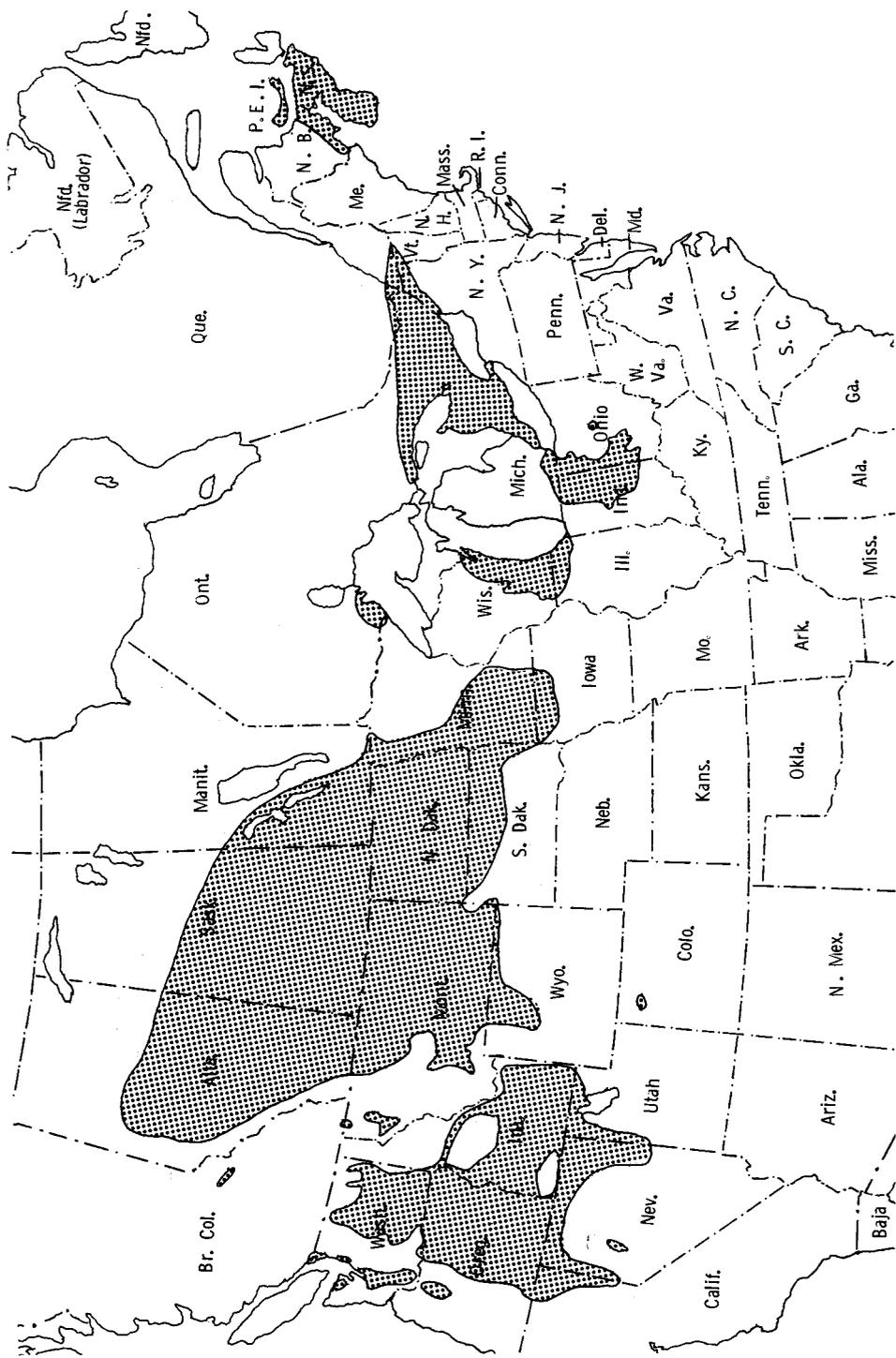


FIGURE 44. Current North American distribution of the gray partridge.

(Gullion and Christensen, 1957). In Utah they are generally found where alfalfa, wild hay, and grain grow near streams, with sagebrush nearby (Porter, 1955). In Idaho they are widely distributed throughout agricultural areas, but broods have been seen as far as fifty miles from agricultural lands in the aspen zone (Upland game birds of Idaho, 1951). This Pacific northwest population has undergone considerable retraction of range; it is now gone from the southern part of interior British Columbia, and it is probably a good deal less common throughout the intermountain region than it once was. The current yearly hunter harvest is probably under two hundred thousand, with most of this kill occurring in Oregon and Idaho.

The second major population segment is the Great Plains population, which extends from the "prairie provinces" of Alberta, Saskatchewan, and Manitoba (Rowan, 1952), southward across eastern Montana, northwestern Wyoming, the Dakotas, western Minnesota, and northwestern Iowa. This population has its origin in limited but highly successful releases that began in Alberta in 1908, supplemented by releases in Montana, North Dakota, and Manitoba during the next few decades. The Alberta releases were so successful (the first season being held in 1913) that Saskatchewan was colonized by birds of this source, and a season there was established in 1927, followed by one in Manitoba in 1931. Both Montana and North Dakota also benefited from the Alberta releases, and open seasons were established in 1929 and 1934, respectively (Johnson, 1964). A limited season was initiated by South Dakota in 1937, and in 1939 by Minnesota. Iowa first introduced the bird in 1910, but it has never extended its range beyond the north central part of the state (Green and Hendrickson, 1938). Although Nebraska began to release partridges as early as 1907, the bird has never become established and at present is only rarely encountered in the state. Throughout this extensive area, by far the largest contiguous portion of the gray partridge's range in North America, the bird is associated with small grain cultivation (wheat, oats, and barley) on high quality soils, moderate spring precipitation, severe winters, and adequate amounts of available nesting cover in the form of native grasslands or hayfield pasturelands. The average yearly hunter kill is in excess of four hundred thousand birds, with the largest current harvests in Alberta and Saskatchewan and somewhat smaller harvests in Montana and North Dakota. The population and hunter kill in Minnesota has declined considerably since the late 1950s, and the same is probably true of South Dakota.

The third population segment is the Great Lakes area, including eastern Wisconsin, southern Michigan, eastern Indiana, western Ohio, southern Ontario, and northern New York. This population was extensively studied by Yeatter (1935) in Michigan, where the birds were first released in 1911.

Releases at about the same time in Wisconsin, Indiana, and Ohio were also relatively successful. In spite of considerable efforts by the Michigan Department of Conservation in releasing birds between 1930 and 1940, nearly all these releases were failures, with the best successes occurring on light-textured soils along the southern border of the state. In contrast, Wisconsin's introductions were much more successful. After first being introduced in 1908, the birds gradually extended their range northward at a rate of about 4 miles per year, until they had moved 102 miles north in twenty-nine years. Between 1944 and 1954 the birds further extended their northern range at a rate of about 8 miles a year and also moved southwesterly at a rate of about 1 mile a year (Resadny, 1965). Apparently the Wisconsin population is now fairly stabilized, with limitations of soil and land use restricting further range extension. The birds are most abundant on red clay soils, particularly on flat lands that have few woodlands and are about 65 percent cultivated. They thrive where about half the land is planted to hay and small grains and do no better on large farm acreages than on smaller farming units (Resadny, 1965).

In Ohio a fairly extensive release program was carried out between 1909 and 1940, and by the late 1920s the birds were well established in lacustrine limestone and glacial limestone soils of western Ohio. The population probably peaked in the mid-1930s, and by 1965 had apparently all but disappeared from the state. However, surveys in the late 1960s indicate that the birds have been seen in twenty counties and may not be quite so rare as had been thought (Bachant, 1969). In Indiana the status of the gray partridge is still moderately favorable, with the birds being hunted to some extent over much of the northeastern part of the state. Wright (1966) has recently reviewed the status of this species in Indiana. The Illinois population is a southern extension of the large Wisconsin population and is limited to the northeastern corner of the state where moderate numbers are harvested each year. Early attempted introductions in New York were failures, but nearly thirty thousand birds were released between 1927 and 1932. Of these releases, only those birds in the St. Lawrence Valley prospered to the point that a limited season was possible in 1952 (Brown, 1954). The New York population is limited largely to areas with soils of limestone origin, and the best densities occur in areas of 30 to 45 percent croplands, with large areas of pasture and hay present. Major factors favoring the species there include dry weather during the hatching and brooding seasons, large areas planted to grain crops, ample nesting and brooding cover, and the presence of few pheasants and fairly light hunting (Brown, 1954). Little information is available as to the density and geographic range of the

southern Ontario and adjacent Quebec population, but it is of interest that Yocom (1943) indicates no eastern Canada population, whereas Aldrich and Duvall (1955) report an extensive one extending all the way to the mouth of the St. Lawrence River. I have accepted Godfrey's estimation (1966) of the eastern Canada distribution, which indicates that most of the area south of forty-nine degrees north latitude is occupied range. No information is available as to the size of the Canadian yearly hunter kill, but probably about fifty thousand birds are currently harvested annually in the Lake States, with the majority of these taken in Wisconsin.

There are also established gray partridge populations on Prince Edward Island, southern New Brunswick, and Nova Scotia, but they are probably fairly small and no details as to habitats utilized are available to me. These populations apparently date from introductions made in the late 1920s.

### POPULATION DENSITY

Most density figures for United States populations of gray partridge come from the Lake States area. Yeatter (1935) reported spring populations of 4.4, 11 and 13.3 acres per bird on three 160-acre study areas in southern Michigan. During nine years of study on a Faville Grove study area in Wisconsin, fall populations varied from an estimate of 7.5 to 26 acres per bird, averaging 15 acres per bird over the entire period. Since winter losses averaged 40 percent, expected spring densities would be nearly 30 acres per bird. Such breeding densities are far below those reported for England, where estimates of a pair per 8 or 10 acres are not uncommon (McCabe and Hawkins, 1946). The nearest comparable figures I have found are for North Dakota, where estimates of from 3.5 to 5.3 acres per bird during February have been reported on study plots of a game refuge (Hammond, 1941). It would seem probable that densities in the prairie provinces of Canada may exceed these, at least during favorable years. In England, May densities vary from 1.9 to 10.7 acres per pair, with densities of less than 5 acres per pair considered high (Jenkins, 1961).

### HABITAT REQUIREMENTS

In spite of numerous attempts to introduce the gray partridge in virtually all parts of North America, no clear agreement on what constitutes ideal partridge habitat is yet available. Correlations with soil types have not proven highly successful, but the birds are typically associated with highly fertile soils associated with natural grassland and avoid both extremely

sandy and heavy clay soils. Topographic conditions associated with high populations are usually flat or gently rolling lands, with the birds sometimes occurring at elevations of up to about five thousand feet in the bunch grass hills of Washington (Yocom, 1943). Favored climates are those with fairly short growing seasons and limited precipitation during the incubation and brooding periods. Severe winters are normally no serious limitation as long as snowfall is not so great that it makes grain or other seeds unavailable (Westerskov, 1965).

Perhaps the most important aspects of habitat needs of the gray partridge are those related to vegetation. Combinations of croplands, particularly small grain crops, and herbaceous cover in the form of native grasses, hayfields, or weedy herbaceous growth provides necessary nesting and escape cover. Woody cover is little utilized, and the birds seemingly avoid extensively wooded areas. Brushy areas may be used for winter shelter, and nests may sometimes be located in brushy edges, but the birds are surprisingly independent of such cover sources during most parts of the year.

The preferred nesting cover of gray partridges is clearly native grasslands or hayfields, where an abundance of dead herbaceous plant growth is to be found. Yeatter's study (1935) of 143 nest sites indicated that hayfields and grainfields accounted for more than half of the nest locations. Yocom (1943) noted that about 60 percent of 68 nests were located in hayfields, with alfalfa providing preferred nesting cover. McCabe and Hawkins (1946) also noted that hayfields provided cover for more than half of 427 nests and that alfalfa was the plant species immediately surrounding nearly 50 percent of 403 nest sites located. Most birds selected locations fairly near the edges of hayfields for nesting and were rarely more than one hundred feet from the edge, as had been earlier noted by Yeatter.

Brooding cover is essentially like nesting cover: hayfields, grainfields, or natural grasslands are all utilized. Evidently the young birds do not require a nearby source of water (Yocom, 1943), provided that succulent vegetation and insect foods are available. However, during hot weather they may move to brushy or woody cover for shade during the middle of the day.

During winter the birds may roost in the manner of bobwhites or may plunge into a snowdrift to spend the night. They are also able to tunnel under the snow, at least to a depth of a foot, to obtain food (McCabe and Hawkins, 1946; Westerskov, 1965).

Although free water is probably not essential to partridges, a supply of grit is definitely needed, particularly at times when the diet is composed primarily of grain and seeds (Trippensee, 1948).

## FOOD AND FORAGING BEHAVIOR

The food intake of gray partridges comes from three primary sources, cultivated grains, seeds of various weedy herbs, and green leafy materials. Only during summer are insects taken in any appreciable amount, and rarely do they comprise more than 10 percent of the summer diet.

The grain sources utilized vary with locality, but in the Canadian Great Plains population they consist primarily of oats, barley, and wheat, which during the winter represent about 70 percent of the food consumed. Yocom (1943) also reported that these three grains, especially wheat, are major winter food sources in Washington, while in Michigan corn is perhaps the most important grain crop for partridges (Yeatter, 1943). Other cultivated crops, such as buckwheat, soybeans, and peas, may be of secondary or local significance.

The kinds of weed seeds used no doubt vary greatly in different regions but include a wide range of forbs and a few grasses. These are used mainly from late spring until grain crops become available in late summer. Green leafy materials are probably taken as soon as they become available; Yocom (1943) reported their major use during the winter season in the Palouse region of Washington, where moist, mild winters are typical. In the Canadian prairies green foliage is of minor importance in winter but rather is used heavily in spring, when it may represent about 50 percent of the food volume, and is used again in diminishing amounts during the fall (Wester-skov, 1966).

## MOBILITY AND MOVEMENTS

Under normal conditions relatively short movements are typical of gray partridges. There is no major habitat shift between seasons that requires any great mobility, although flights of from half to three-quarters of a mile have sometimes been noted. Usually, flights are less than a quarter mile in length, and Yocom (1943) noted that during the winter, coveys usually moved less than a quarter mile, rarely as much as half a mile. In Michigan, Yeatter (1935) noted a similar winter mobility that averaged about a fifth of a mile, and 20 percent of the coveys had a cruising radius of no more than one-eighth of a mile. Over the course of a year, Yocom found that a single female had a cruising radius of seven-eighths of a mile.

In spite of their sedentary nature, the gray partridges in Canada exhibited a remarkable rate of range expansion during the early years after their introduction. Leopold (1933) calculated that during the first fourteen years after their introduction in Alberta, a maximum average range extension

of twenty-eight miles a year occurred, which is little short of astonishing. Comparable estimates of range extension in Michigan and Wisconsin were only from two to four miles a year during the period shortly after successful introduction.

## SOCIAL AND REPRODUCTIVE BEHAVIOR

To a degree surprisingly similar to that of the bobwhites, the basic social unit of the gray partridge is a moderate-sized covey that infrequently exceeds 15 birds, with maximum covey sizes of about 30 birds. Probably the nucleus of each fall covey is a pair and their well-grown young, which usually number about 10 by the time the chicks are two months old (Yocom, 1943). Johnson (1964) has tabulated the average covey sizes of gray partridges by month from midsummer until March as reported from 1938 to 1963 in North Dakota. These figures and those of Hammond (1941) indicate that from the time the broods emerge in July and August, when the covey size is from 12 to 13 birds, there is a monthly decline that averages about a 9 or 10 percent reduction per month, so that by February the average covey size is approximately 7.5 birds. An average covey size of 4.7 birds in March suggests that during that month considerable covey breakup occurs as the birds prepare for nesting.

Pair formation probably begins well before the breakup of coveys, since McCabe and Hawkins (1946) noted that fighting may be seen as early as January, and Yocom (1943) reports the same activity for late January and early February. This fighting behavior is at least in part ritualized into a display during which the birds maintain a distance of about six to eight yards from one another, each alternately chasing and being chased. Once two birds were seen by one observer to run toward one another at full speed, only to stop at the last possible moment and rear up with their beaks and breast almost touching in a nearly vertical stance (Cooke, 1958). The call uttered during such threats, and especially during early morning and evening, is a "rusty-gate" call sounding like *keee-uck!*, with a very metallic tone to the first note and an accent on the second one (McCabe and Hawkins, 1946).

The social displays of the gray partridge have been studied by Jenkins (1961). He noted that coveys remain intact until pairing starts in January or February. Since the aggression that he observed did not appear to be related to defense of a nesting site or the defense of any other specific area, he did not feel that the term territoriality should be used for partridge behavior. Likewise, Blank and Ash (1956) indicated that true territorial behavior is lacking in this species (as well as *Alectoris*), and that the nearest

thing to territorial behavior is the stability exhibited in covey structure. Watson found that pairing was achieved by two different methods. Pairing within coveys occurred when a pair of the previous season was re-formed or when a female actively solicited a mate from her own covey, which in no case was found to be her father or one of her brothers. Most of the chasing Jenkins observed was between yearling hens, but sometimes older females would also participate. Since most young males were not chosen by females of their own covey for mates, they left the covey and moved about singly or in groups, displaying to or attacking birds in other coveys. When an unmated cock met a covey it might display before females, which usually resulted in attacks by males within the covey, and sometimes it was able to lure a female away from the covey. Pair formation was apparently a gradual process, and many of the birds pairing for the first time changed their mates several times before a permanent pair bond was established. Often an unmated male would attach itself to a mated pair, remaining fifteen to twenty yards away and frequently displaying or crowing.

Displays mentioned or illustrated by Jenkins included an upright threat posture that resembles an upright alert posture, in which the breast was protruded, exposing the chestnut markings, and the bird stood erect, jerked its tail, and crowed. This posture is virtually identical to that assumed before copulation. Females were not observed to perform this display. Display by the male toward the female apparently emphasized his barred flanks, and the female directed her displays toward this area of the male. She often ran toward the male with her neck stretched and head held low, and directed her bill toward the male's flanks or brown breast markings while making sinuous neck movements. The lateral display of the male consists of a slight tilting of the dorsal surface of the male toward the female, but evidently there is little or no wing-lowering present (see figure 21). Sometimes the female was observed to raise her head and pass it over the flanks and back of the male as she circled him. Eventually she might stand breast-to-breast with him, rubbing her neck along his, pointing her beak upwards, and the two birds might finally rub their beaks together.

According both to Jenkins and to Blank and Ash, copulation is not preceded by elaborate displays and is begun by the female's crouching before the male. The male then approaches her in an erect posture (see figure 21) and grasps her nape, and copulation occurs.

It is not known whether a tidbitting display occurs as a courtship display in the gray partridge, but Jenkins noted that feeding behavior included courtship feeding, suggesting that such a display is present.

Nest-building, according to Yocom (1943), is performed by the female, with the male standing guard. A scrape is dug first, usually about two and

a half inches deep and six or eight inches wide. Dead herbaceous vegetation is used to line the scrape, but few if any feathers are used. The first egg is probably laid shortly after the nest is finished, and after the first egg is deposited the clutch is usually covered with leafy materials between visits of the female. The egg-laying rate is probably 1.1 days per egg (McCabe and Hawkins, 1946), and the average clutch size of first nestings is probably between fifteen and seventeen eggs, with somewhat lower figures being reported for England. Lack (1947) concluded that minor annual variations in clutch sizes do occur, that the clutch size is not limited by potential egg production by females, and that hatching success is no less in clutches of twenty than in much smaller ones. He judged that the limits of clutch size in this species are probably those imposed by limits of food available to the young.

The incubation period has been established to be from 24½ to 25 days, and the female is believed to perform all of the incubation. However, in two instances the male has been observed sitting beside the female on the nest, and it is thought that this might occur only at the time of pipping (McCabe and Hawkins, 1946). The rate of nesting failure may be fairly high; three different United States studies have indicated nesting failures of 68 percent, often with mowing of hayfields being a major source of nesting losses. However, partridges are known to attempt to renest regularly, with only a slight average reduction in clutch size.

Following hatching, both parents closely attend the chicks, but, perhaps because of their large number and small size, brood losses are often substantial. Yocom (1943) estimated that almost 50 percent of the brood may be lost during the first two weeks, with chilling apparently being an important mortality factor. Recent extensive studies in England (Blank, Southwood, and Cross, 1967) have clearly indicated that at least there the key mortality factor affecting fall partridge populations is chick mortality. Further, the primary factor associated with variations in chick mortality is the relative degree of insect abundance, whereas unfavorable summer weather was believed to have only a secondary effect on breeding success (Southwood and Cross, 1969). Thus, apparently fall densities in England are related to breeding success in terms of chick survival, whereas spring breeding densities are determined by the habitat, particularly the amount of spring ground cover and the extent to which cultivated fields are broken up by hedge rows or grassy tracts, with a greater degree of habitat interspersion associated with higher breeding densities.

By the hunting season, the juvenile-to-adult ratio may vary from as little as 1.44:1 to as much as 4.35:1, depending on breeding success and chick survival, with a ratio of 3.9:1 perhaps being an average age ratio, judging

from data on more than fourteen thousand birds sampled in North Dakota between 1950 and 1963 (Johnson, 1964). This would represent about eight young per pair surviving to the start of the hunting season, which agrees well with the average covey sizes of ten to twelve birds typical for that time of year.

### *Vocal Signals*

One of the few attempts to summarize the calls of the gray partridge is that of McCabe and Hawkins (1946), who recognized six different calls. One of these is the distress *peep* of chicks. A second "rattle" *peep*, first given by birds when they are about a month old, is transitional between the chick call and the call of adult birds. An excited *kuta-kut-kut-kut* is uttered when the birds are frightened and is accompanied by tail-flicking. Adults of both sexes hiss during the breeding season, especially when the coop of a captive pair is approached or sometimes when birds are being handled. The feeding call is uttered both by older chicks and by adults and sounds like *güp, güp*. When a brooding adult calls toward its young, it utters a low, purring *burruck-burruck*, which when imitated causes the birds to take cover and "freeze." The last of the calls that McCabe and Hawkins recognized was the "rusty gate" crowing call which, judging from Jenkins's observations, is characteristic of unmated males rather than mated ones and is associated with a threatening posture. He also noted that threatening males sometimes uttered a harsh *tit-tik-tik*.

According to Yocom (1943), birds in a covey often utter soft conversational or contact *chrrr* notes when settling down for the night, and when flushed with his mate during the prenesting season, the male nearly always "cackles." Coveys sometimes also utter a series of cackling notes when flushed, or they may remain silent.

## EVOLUTIONARY RELATIONSHIPS

Inasmuch as the other probable relatives of *Perdix* that are found in southeastern Asia, Borneo, and Madagascar are not included in the current work, a discussion of the evolutionary relationships of *Perdix* is not appropriate here. It is, however, interesting to compare the similarities of evolutionary adaptation in the behavior and ecology of *Perdix* to those of such New World quail as *Colinus*. Strong similarities of covey behavior, with greatly reduced social aggression during the nonbreeding season, are found in both groups. In addition, in both groups territoriality is poorly or not at all developed during the breeding season, and male hostile behavior is

associated primarily with protection of the female from unmated males. Unlike *Colinus* females, female partridges also become aggressive during the spring and may compete actively with other hens for mates, sometimes even stealing them. In both males, and especially young males, are forced to leave their coveys in spring and attempt to seek out mates from other coveys and may make themselves conspicuous by crowing behavior. This behavior probably brings about a certain degree of population mixing and may facilitate range extension. In both groups, strong monogamy is characteristic, probably as a result of a need for both sexes to care for the typically large brood of developing young. In both also, the throat, lower breast, and flank areas are important sources of visual signals in males and are associated with frontal (primarily threat) and lateral (primarily sexual) displays.